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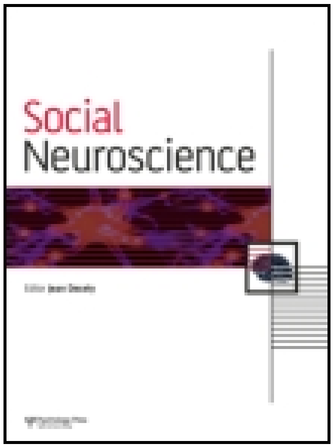

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Distinct neural circuits subserve interpersonal and non-interpersonal emotions

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Emotions elicited by interpersonal versus non-interpersonal experiences have different effects on neurobiological functioning in both animals and humans. However, the extent to which the brain circuits underlying interpersonal and non-interpersonal emotions are distinct still remains unclear. The goal of our study was to assess whether different neural circuits are implicated in the processing of arousal and valence of interpersonal versus non-interpersonal emotions. During functional magnetic resonance imaging, participants imagined themselves in emotion-eliciting interpersonal or non-interpersonal situations and then rated the arousal and valence of emotions they experienced. We identified (1) separate neural circuits that are implicated in the arousal and valence dimensions of interpersonal versus non-interpersonal emotions, (2) circuits that are implicated in arousal and valence for both types of emotion, and (3) circuits that are responsive to the type of emotion, regardless of the valence or arousal level of the emotion. We found extensive recruitment of limbic (for arousal) and temporal–parietal (for valence) systems associated with processing of specifically interpersonal emotions compared to non-interpersonal ones. The neural bases of interpersonal and non-interpersonal emotions may, therefore, be largely distinct.

Keywords: Emotion; Interpersonal; Social; Circumplex model of affect; fMRI.

Interpersonal interactions play a crucial role in functioning and development. Disruptions in specifically interpersonal versus non-interpersonal aspects of experience have substantial psychophysiological effects in animals and humans as well as important long-lasting consequences for physical and mental health (Britton, Taylor, Berridge, Mikels, & Liberzon, 2006; Chiang, Eisenberger, Seeman, & Taylor, 2012; Eisenberger & Cole, 2012; Hofer, 2009; Landa, Peterson, & Fallon, 2012; Slavich, Way, Eisenberger, & Taylor, 2010; Taylor, Eisenberger, Saxbe, Lehman, & Lieberman, 2006). Prior brain imaging studies identified neural circuits that support social cognition (Van Overwalle, 2009). The study of neural bases of emotions has, however, rarely addressed the interaction of interpersonal experience with emotions and whether interpersonal versus non-interpersonal emotional experiences are distinguishable on a neural level. The aim of our study was, therefore, to use functional magnetic resonance imaging (fMRI) to assess whether differing neural circuits are implicated in interpersonal and non-interpersonal emotions.

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Psychologists have conceptually distinguished interpersonal from non-interpersonal emotions for more than a century (Calkins, 1914), often using the terms "social" and "non-social" emotions interchangeably with "interpersonal" and "non-interpersonal" emotions. In our study, we use the term "interpersonal," as we believe that "social" may refer to a wider range of experiences than we intend. The Merriam Webster dictionary, for example, defines "social" as "of or relating to human society, the interaction of the individual and the group," and "interpersonal" as referring specifically to "being, relating to, or involving relations between persons." Our study aims to focus on the latter. Several prior studies that we cite refer to their stimuli as "social," however, and for accuracy of reference, we retain their original terminology.

Recent studies have begun investigating the distinction between neural circuits that subserve interpersonal and non-interpersonal emotions. One study of healthy participants viewing a short video and photographs, for example, reported that brain areas subserving the non-social emotions of appetite and disgust (the posterior insula and visual cortex) differed from those subserving the interpersonal emotions of joy and sadness (amygdala, superior temporal gyrus, hippocampus, and posterior cingulate) (Britton, Phan, et al., 2006). Another study reported that adolescents and adults thinking about scenarios emphasizing social emotions (guilt and embarrassment) compared with scenarios emphasizing non-social emotions (disgust and fear) selectively recruited medial prefrontal cortex (Burnett, Bird, Moll, Frith, & Blakemore, 2009), which was in turn more strongly functionally connected with the posterior superior temporal sulcus and anterior temporal cortex (Burnett & Blakemore, 2009). Another study of healthy women using script-driven emotional imagery reported that social compared with non-social emotions differentially activated dorsomedial prefrontal cortex, posterior cingulate, precuneus, bilateral temporal poles, bilateral temporoparietal junction, and right amygdala (Frewen et al., 2011). One possible explanation for inconsistencies in the specific findings for interpersonal emotions is that these studies differed in the emotional states they elicited (e.g., guilt or disgust). The designs of these studies, therefore, did not permit the study of neural systems involved across the full range of emotional experiences.

In contrast to the "categorical" theory of emotions, the affective circumplex theory postulates that emotional experience involves activity in two distinct, independent neurophysiological systems that subserve the experience of valence and arousal, that activity in each of these circuits varies progressively and linearly along a continuum, and that the combined activity of these two systems accounts for the entire range of human emotional experience (Posner, Russell, & Peterson, 2005; Russell, 1980). This neurophysiological activity is then interpreted and labeled according to experiential context and past history. A specific emotional state, therefore, consists of a combination of neural activity in arousal and valence circuits as well as neural activity supporting the interpretation, attribution, and meaning making during that particular emotional state (Posner et al., 2005). Several prior fMRI studies, all using different emotional stimuli (e.g., emotional words, faces), demonstrated the validity of the affective circumplex model by reporting significant correlations of self-ratings of the arousal and valence of emotions with neural activity in distinct neural networks (Colibazzi et al., 2010; Gerber et al., 2008; Lewis, Critchley, Rotshtein, & Dolan, 2007; Posner et al., 2009). To our knowledge, the question whether separate neural circuits support the underlying arousal and valence components of interpersonal and non-interpersonal emotions has not yet been studied.

The goal of our study was to investigate whether the neural circuits associated with valence and arousal differ for interpersonal compared with non-interpersonal emotions. We identified brain regions in which blood-oxygen-level-dependent (BOLD) signal, as an index of neural activity, systematically covaried with ratings of arousal or valence for interpersonal and non-interpersonal emotions. We determined the areas in which these correlations were statistically different across emotion types, indicating the differential association of these regions with processing arousal or valence for interpersonal compared with non-interpersonal emotions. We also identified regions that were differentially associated with processing of interpersonal versus non-interpersonal stimuli, regardless of the emotional arousal or valence of those stimuli, as well as regions associated with processing of both types of emotions.

METHODS

Participants

Ten healthy volunteers were recruited from the community. They were 19–34 years old ($M = 25$, $SD = 4.5$), five men and five women, right-handed, Caucasian, English native speakers, and of middle to high socioeconomic status, as assessed by Hollingshead Index of Social Status. They were of average to high-average intelligence, as measured by Wechsler Abbreviated Scale of

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Intelligence (Full-Scale IQ $M = 112.4$, SD $= 13.7$). Exclusion criteria consisted of current major Axis I psychopathology (as assessed by the structured diagnostic interview for Diagnostic and Statistical Manual of Mental Disorders (DSM-IV; First, Spitzer, Miriam, & Williams, 2002)), any current medications, and a history of psychosis, substance abuse disorder, head trauma, or a neurological disorder.

Procedure

All participants participated in a diagnostic assessment to confirm that they met inclusion and exclusion criteria. On a separate day participants came in for the fMRI scan. Prior to the scan participants heard explanations of the behavioral task and practiced five trials of stimuli presentation outside of the scanner to assure their understanding of the instructions. During the fMRI scan, participants viewed the stimuli using LCD goggles (Resonance Technology Inc., Northridge, CA). We used E-Prime software (v. 1.0; Psychology Software Tools Inc., Pittsburgh, PA) and an MRI-compatible mouse for the stimuli presentation and recording of participants' responses.

fMRI paradigm

In the mood induction task, participants were asked to imagine themselves in a situation described in a sentence on the screen and to experience how they would feel in that situation (Velten, 1968). The following instructions were used: "Try to think about how the emotion feels. Some people think about situations, and others draw on memories of situations that have made them feel the emotion in the past." Following a 30-second presentation of a sentence, participants rated the valence and arousal of emotion they experienced on a Likert scale consisting of a 9×9 affect circumplex grid, wherein valence was rated on the *x*-axis and arousal on the *y*-axis with one click of the mouse. (Behavioral studies show that simultaneous and separate ratings of valence and arousal provide similar results (Russell, Weiss, & Mendelsohn, 1989)). Participants had 20 seconds to provide the rating, and if they rated arousal and valence sooner, a fixation point appeared on the screen for the remaining time until the next stimulus was presented. Thirty stimuli (presented in two runs, 15 stimuli per run) ranged in valence (positive or negative) and in levels of arousal. They were presented in a semi-random order, with the same order of sentences for all the participants. The stimuli were then categorized as interpersonal or non-interpersonal, with "interpersonal emotion" defined as "emotion elicited by real, imagined, or perceived interaction or relationship with another person(s)." For example, "Your beloved must leave you and may never return" was categorized as eliciting interpersonal emotion, whereas "You are drinking a glass of sour milk" was categorized as eliciting non-interpersonal emotion. This classification yielded 12 interpersonal stimuli and 17 non-interpersonal stimuli (one stimulus was excluded due to ambiguity).

fMRI acquisition

Images were obtained with a 3T GE Signa whole body scanner (Milwaukee, WI) using single channel quadrature head coil. T1-weighted images were used for positioning of the axial functional images along an anterior commissure–posterior commissure (AC–PC) line. A three-dimensional (3D)-spoiled gradient recall (SPGR) was acquired for coregistration with the functional images and with the standard reference image using the template of the Montreal Neurological Institute, Canada. The parameters for the functional images were as follows: repetition time (TR) $= 2800$; echo time (TE) $= 25$ ms; flip angle $= 90°$; field of view $= 24 \times 24$ cm^2; acquisition matrix $= 64 \times 64$; slice thickness $= 3$ mm; gap $= 0.5$ mm; resolution $= 3.75 \times 3.75 \times 3.5$ mm^3; whole brain coverage; 43 slices per volume; and 273 volumes per run.

Image preprocessing

Image preprocessing was performed using an integrated GUI-based batch platform implemented from Statistical Parametric Mapping-8 (SPM8), run on a MATLAB 2008b (The MathWorks, Natick, MA, USA). First, images were visually inspected to ensure the absence of artifacts such as ghosting and head movements of more than 2.5 mm in any direction. Preprocessing included: (1) slice-timing correction using the middle slice of each run as the reference image; (2) motion-correction for three translational directions and rotations (Friston et al., 1995); (3) spatial normalization to the standard MNI template using a hybrid algorithm of affine transform and nonlinear warping; each participant's SPGR images were normalized to the template, and then these participant-specific warping parameters were used to normalize the functional images to the same template; (4) image reformatting to 2 mm^3 voxels; and (5) spatial filtering to remove spatial noise with a Gaussian filter having a full width, half-maximum of 8 mm. A discrete cosine

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transform-based high-pass filter with a basis function length of 128 s was used to remove low-frequency noise such as scanner drift from the baseline image intensity.

fMRI statistical analysis

The goal of this study was to investigate whether different neural circuits are associated with arousal and valence of interpersonal versus non-interpersonal emotions. Therefore, we assessed: (1) whether the interaction of stimulus type (interpersonal versus non-interpersonal) and arousal or valence ratings affected the strength of the BOLD signal (an index of neural activity)—i.e., we identified regions in which the stimulus type significantly modified activity in the valence and arousal circuits, (2) the main effects of arousal and valence on BOLD signal, regardless of stimulus type, and (3) the main effect of stimulus type on BOLD signal, controlling for arousal and valence. In addition, we plotted the association of BOLD signal with ratings of arousal and valence in the areas of significant interaction to determine whether the source of the interaction was (a) the difference in the strength or direction of the association, or (b) the presence of the association for one stimulus type only.

We concluded that a region was differentially associated with the processing of arousal or valence of interpersonal versus non-interpersonal emotions if the interaction was present in that brain region (i.e., if the correlation between arousal or valence ratings with BOLD signal differed significantly between the two stimulus types), and if this interaction was driven by a significant linear association of arousal or valence ratings with BOLD signal for one stimulus type only.

We concluded that a region was associated with the processing of emotions elicited by both interpersonal and non-interpersonal stimuli if we detected a significant main effect of arousal or valence in that brain region (i.e., if BOLD signal correlated linearly with ratings of arousal or valence, independent of stimulus type) and we did not detect a significant arousal- or valence-by-stimulus-type interaction in that region.

1. Interaction: Differential association of arousal and valence ratings with BOLD signal for interpersonal and non-interpersonal stimuli

First level analysis. We used the general linear model (GLM) in SPM8 for the analyses of data at an individual subject level. We modeled a linear relationship at each voxel between the on-line ratings of arousal and valence, interpersonal versus non-interpersonal stimulus type, and the BOLD signal for each participant using eight independent functions and a constant:

1. the canonical hemodynamic response function (HRF) convolved with a boxcar function (BCF) derived from the onsets and durations of presentation of the interpersonal emotion-induction stimuli;
2. function (1) modulated by the arousal rating for each corresponding stimulus;
3. function (1) modulated by the valence rating for each corresponding stimulus;
4. the canonical HRF convolved with a BCF derived from the onsets and durations of presentation of the non-interpersonal emotion-induction stimuli;
5. function (4) modulated by the arousal rating for each corresponding stimulus;
6. function (4) modulated by the valence rating for each corresponding stimulus;
7. the canonical HRF convolved with a BCF indexing the presentation of the 9×9 response grid; and
8. the canonical HRF convolved with a BCF indexing gaze fixation.

Voxel-based correlation estimates for each participant were determined by a weighted least squares fit based on a Restricted Maximum Likelihood (ReML) algorithm. Statistical parametric maps were thresholded using the conjoint requirement of $p < .01$ and a cluster of 25 contiguous voxels. Based on Monte Carlo simulations across the entire imaging volume, this conjoint requirement yielded an effective p-value $< .05$ when corrected for multiple comparisons (Forman et al., 1995; McAvoy, Ollinger, & Buckner, 2001).

Second level analysis. We conducted a second level analysis by applying a one-sample t-test design to the contrast images corresponding to the interaction effects generated in the first level analysis. We represented this interaction visually (Figures 1d and 3d) as the contrast map comparing the group average maps for the main effects of interpersonal (Figures 1b and 3b) and non-interpersonal (Figures 1c and 3c) stimuli separately. In addition, we plotted the correlations of BOLD signal change with arousal and valence ratings for the interpersonal and non-interpersonal stimuli in representative regions where we detected interaction effects, averaged over all the voxels located within a significant cluster.

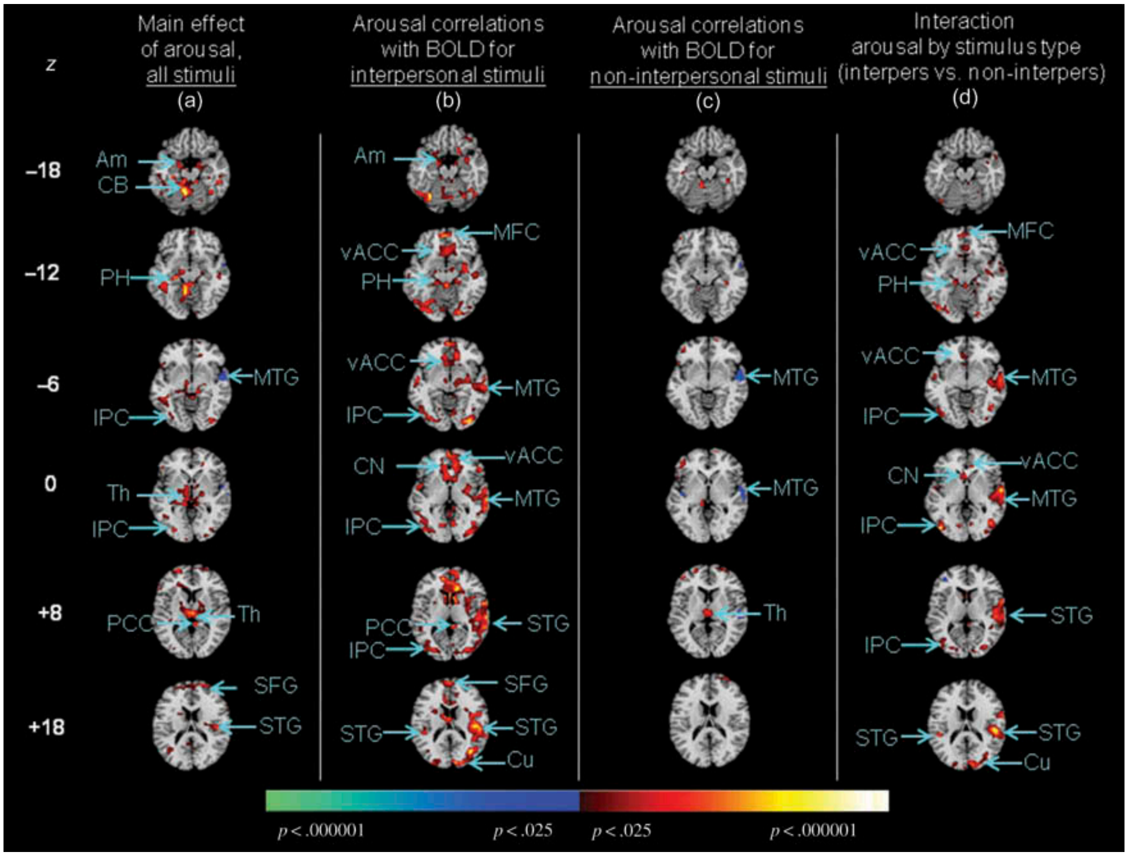

Figure 1. Regions of significant correlations of BOLD signal with ratings of arousal for (a) all stimuli (i.e., main effect of arousal), (b) interpersonal stimuli only, and (c) non-interpersonal stimuli only. (d) The regions where the correlation of arousal ratings with BOLD for interpersonal emotions differs significantly from the correlation of arousal ratings with BOLD for non-interpersonal emotions (i.e., arousal-by-stimulus-type interaction). (Positive correlations are coded in red to yellow, and inverse correlations are coded in green to purple.) Am = amygdala, CB = cerebellum, CN = caudate nucleus, Cu = cuneus, IPC = inferior parietal cortex, MTG = middle temporal gyrus, PH = parahippocampus, PCC = posterior cingulate cortex, SFG = superior frontal gyrus, STG = superior temporal gyrus, Th = thalamus, vACC = ventral anterior cingulate cortex.

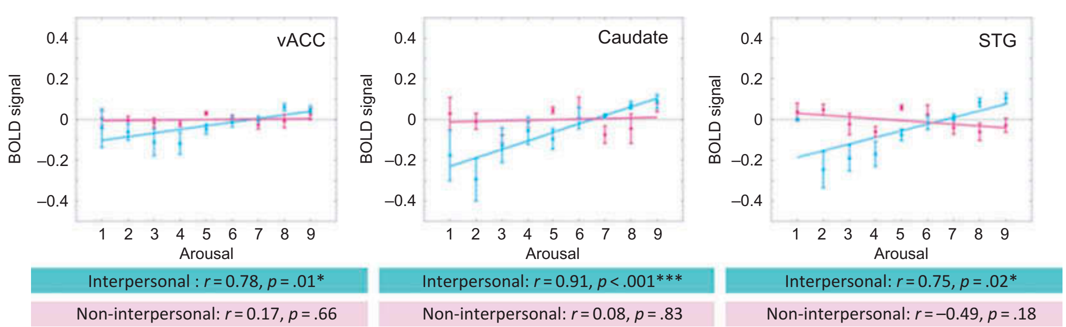

Figure 2. Examples of correlation between BOLD signal change and ratings of arousal for interpersonal and non-interpersonal emotions in several regions: ventral anterior cingulate cortex (vACC), caudate, and superior temporal gyrus (STG). Arousal ratings correlated positively with BOLD signal in these regions for interpersonal emotions, and did not significantly correlate with BOLD signal during non-interpersonal emotions. Correlation coefficients for interpersonal and non-interpersonal emotions and their significance levels are presented below the graphs. $^{*}p < .05$, $^{***}p < .001$.

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2. Main effects of arousal and valence for all emotion-eliciting stimuli

We conducted an analysis of arousal and valence main effects on BOLD signal, regardless of stimulus type.

First level analysis. This model of the data was the same as the model presented above, the only difference being the absence of the term representing stimulus type (interpersonal or non-interpersonal), yielding 5 independent functions and a constant. The analysis of main effects using all stimuli was previously published with slightly different statistical thresholds (Colibazzi et al., 2010).

Second level analysis. We then conducted a group level analysis by applying the SPM8 factorial module, a one-sample t-test design, to the contrast images each corresponding to the presentation stimulus for each participant that were generated in the first level analysis, to detect the random effects of the association of BOLD signal with valence and arousal ratings for all stimuli without differentiation into interpersonal and non-interpersonal stimulus types (Figures 1a and 3a).

3. Main effect of stimulus type

We then conducted an analysis of the main effects of stimulus type on BOLD signal while controlling for arousal and valence ratings.

First level analysis. This model of the data was the same as the model presented in the interaction section, yielding eight independent functions and a constant.

Second level analysis. We conducted a group level analysis by applying the SPM8 factorial module, a one-sample t-test design, to the contrast images each corresponding to the difference in BOLD signal between the presentation of the interpersonal and non-interpersonal stimuli, while covarying for arousal and valence ratings (Figure 5).

RESULTS

Behavioral ratings

Interpersonal and non-interpersonal stimuli did not differ significantly in the variance of the arousal and valence ratings, allowing us to compare the association of BOLD activity with ratings for these two stimuli types in a parametric analysis (interpersonal-arousal: SD = 1.8, range 3.4–8.7 versus non-interpersonal-arousal: SD = 2.4, range 1.7–8.6, Levene's statistic = 2.1, p = .16; and interpersonal-valence: SD = 2.9, range 1.0 to 8.6, versus non-interpersonal valence: SD = 3.0, range 1.2 to 8.9, Levene's statistic = .85, p = .37). In addition, the mean of arousal ratings in response to interpersonal stimuli did not differ significantly from the mean of arousal ratings in response to non-interpersonal stimuli (M = 6.6, SD = 1.8 versus M = 5.07, SD = 2.4, t = −1.9, p = .06). The mean of the valence ratings in response to interpersonal stimuli also did not differ significantly from the mean of the valence ratings in response to the non-interpersonal stimuli (M = 3.6, SD = 2.9 versus M = 5.7, SD = 3.0, t = 1.8, p = .07).

Stimulus type-by-arousal and stimulus type-by-valence interactions affecting BOLD signal

Stimulus type-by-arousal interaction

To assess the differential effects of the interpersonal or non-interpersonal types of mood-inducing stimuli on the relationship between arousal ratings and BOLD signal, we identified locations of significant interactions of arousal with stimulus type. These were located primarily in limbic regions, including the ventral anterior cingulate cortex (vACC), caudate, and parahippocampus, as well as medial temporal gyrus (MTG), superior temporal gyrus (STG), medial frontal cortex (MFC) and inferior parietal cortex (IPC), and cuneus (Figure 1d, Table 1). To examine the source of these significant differences (i.e., to determine whether the interactions were driven primarily by interpersonal or non-interpersonal stimuli, or by the differences in their effects), we assessed as statistical main effects of the correlations of BOLD signal with arousal ratings separately for interpersonal and non-interpersonal stimuli. These analyses indicated that in all regions except the MTG, the significant stimulus type-by-arousal interactions derived from statistically significant positive correlations of BOLD signal with arousal ratings for interpersonal emotions and the absence of statistically significant correlations of BOLD signal with arousal ratings for non-interpersonal emotions (Figures 1b, c, and 2). The differences between the stimulus types in the strength of correlations between BOLD signal and arousal ratings are shown in scatterplots in Figure 2. (MTG was the only region in which the BOLD signal significantly correlated with arousal ratings for both stimulus types, with the sign

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TABLE 1
Centers of activation in regions where BOLD signal intensity significantly correlated with arousal ratings (Figure 1a–c) or where this association was significantly different between interpersonal and non-interpersonal emotions (Figure 1d)

	Location		*MNI coordinates*			
Anatomical regions	*Side*	*BA*	*x*	*y*	*z*	*t*
Figure 1a. ***Main effect of arousal***						
Amygdala	L	28	−16	−9	−18	3.21
	R	34	16	−3	−21	3.28
Cerebellum	L		−16	−48	−24	9.78
Parahippocampus	L	27	−24	−27	−12	4.76
Middle temporal gyrus	R	22	52	−4	−4	−4.39
Inferior parietal cortex	L	39	−38	−69	20	2.60
Thalamus	L		−3	−19	7	4.15
	R		8	−19	5	3.28
Posterior cingulate cortex	R	29	5	−41	5	6.00
Superior frontal gyrus	R	10	20	62	20	4.06
Superior temporal gyrus	R	13	45	−20	18	3.73
Figure 1b. ***Correlations of arousal ratings and BOLD for interpersonal stimuli***						
Amygdala	L		−18	−8	−20	3.94
Middle frontal cortex	R	11	−5	55	−12	3.77
	L	11	5	55	−12	3.71
Ventral anterior cingulate cortex	L	33	0	16	6	9.17
Parahippocampus	L	36	−34	−18	−32	3.65
Middle temporal gyrus	R	22	66	−42	4	7.26
Inferior parietal cortex	L	39	−38	−74	12	3.11
Caudate nucleus	L		−6	18	6	7.83
	R		7	14	6	5.27
Posterior cingulate cortex	R	29	6	−40	8	4.44
Superior temporal gyrus	R	42	66	−22	4	6.03
Superior frontal gyrus	L	10	−1	61	20	3.75
Cuneus	R	18	10	−92	18	4.96
Figure 1c. ***Correlations of arousal ratings and BOLD for non-interpersonal stimuli***						
Middle temporal gyrus	R	22	54	−10	−4	−4.27
Thalamus	L		−4	−18	6	3.77
	R		2	−20	6	3.71
Figure 1d. ***Arousal-by-stimulus-type interaction (interpersonal versus non-interpersonal)***						
Middle frontal cortex	L	11	−4	52	−10	4.80
Ventral anterior cingulate cortex	R	24	10	38	0	3.54
	L	24	−6	32	−4	2.95
Parahippocampus	L	30	−14	−32	−12	4.02
Middle temporal gyrus	R	22	62	−8	0	5.01
	L	22	−56	−6	−4	3.50
Inferior parietal cortex	L	10	−46	−80	0	6.03
Caudate nucleus	L		−6	18	4	3.95
Superior temporal gyrus	R	41	52	−26	12	6.57
Cuneus	R	18	6	−88	24	5.26

of the correlation varying depending on stimulus type (Figure 1b–d).

Stimulus type-by-valence interactions

To assess the differential effects of the interpersonal or non-interpersonal types of mood-inducing stimuli on the correlations of valence ratings with BOLD signal, we identified locations of significant interactions of stimulus type with valence. These were identified in the STG, IPC, posterior cingulate cortex (PCC), middle cingulate cortex (MCC), and precuneus (Figure 3d, Table 2). To examine the source of these significant differences (i.e., whether the interactions were driven primarily by interpersonal or non-interpersonal stimuli), we assessed the correlations of BOLD signal with valence ratings separately for interpersonal and non-interpersonal

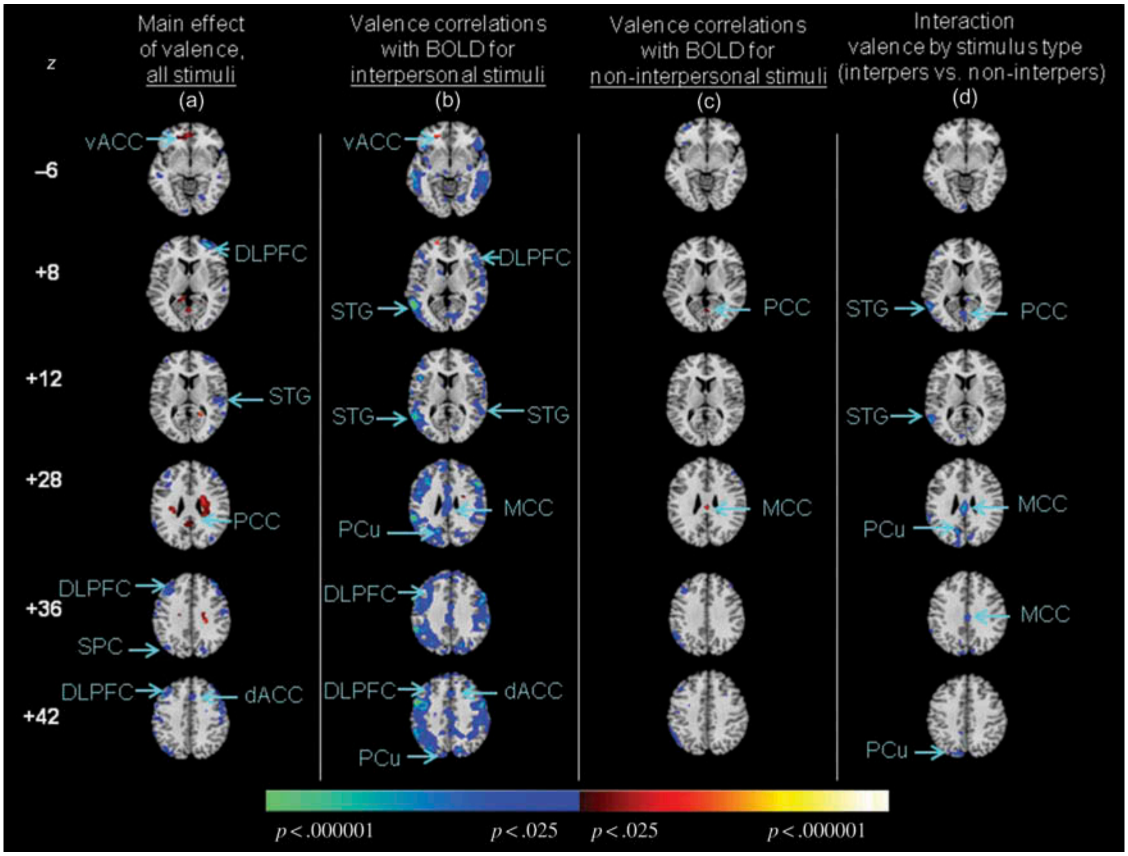

Figure 3. Regions of significant correlations of BOLD signal with ratings of valence for (a) all stimuli (i.e., main effect of valence), (b) interpersonal stimuli only, and (c) non-interpersonal stimuli only. (d) The regions where the correlation of valence ratings with BOLD for interpersonal emotions differ significantly from the correlation of valence ratings with BOLD for non-interpersonal emotions (i.e., valence-by-stimulus-type interaction). (Positive correlations are coded in red to yellow, and inverse correlations are coded in green to purple.). dACC = dorsal anterior cingulate cortex, DLPFC = dorsolateral prefrontal cortex, MCC = middle cingulate cortex, PCC = posterior cingulate cortex, PCu = precuneus, SPC = superior parietal cortex, STG = superior temporal gyrus, vACC = ventral anterior cingulate cortex.

stimuli (Figure 3b and c). These analyses indicated that in nearly all instances, the significant interactions derived from much stronger inverse correlations of BOLD signal with valence ratings for emotions elicited by interpersonal stimuli than for emotions elicited by non-interpersonal stimuli. In fact, correlations of valence ratings with BOLD signal for non-interpersonal stimuli (Figure 3c) rarely reached the levels of statistical threshold. The differences between the stimulus types in the strength of correlation between BOLD signal and valence ratings are shown in scatter plots in Figure 4.

Main effects

Main effect of arousal

We assessed the statistical significance of the main effect of arousal on BOLD signal during emotion induction for all stimuli combined, regardless of the stimulus type. This analysis revealed significant positive associations of BOLD signal with arousal ratings in the cerebellar, amygdala, parahippocampal gyrus, superior frontal cortex, thalamus, PCC, IPC, and dorsal part of the STG, as well as an inverse association in the ventral part of STG (Figure 1a). Of these regions, activity only in the amygdala, cerebellum, and thalamus did not differ significantly between stimulus types—i.e., they were not implicated in producing the interaction (Figure 1d).

Main effect of valence

We assessed the statistical significance of the main effect of valence on BOLD signal during mood induction for all stimuli combined, regardless of stimulus type. This analysis revealed significant positive associations of BOLD signal with valence

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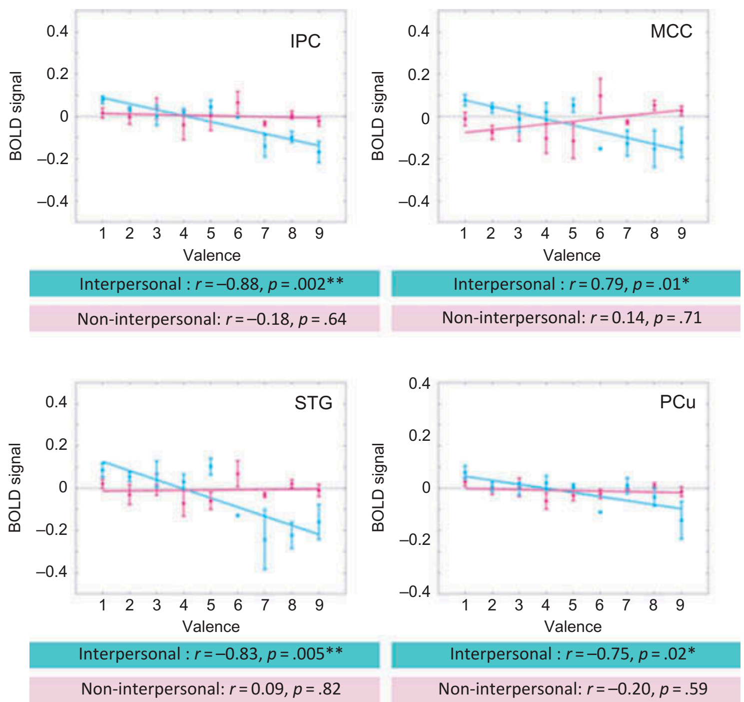

Figure 4. Examples of correlation between BOLD signal change and ratings of valence for interpersonal and non-interpersonal emotions in several regions: inferior parietal cortex (IPC), middle cingulate cortex (MCC), superior temporal gyrus (STG), and precuneus (PCu). Valence ratings correlated inversely with BOLD signal in these regions for interpersonal emotions (i.e., stronger BOLD signal was associated with increasing unpleasantness of emotion), and did not significantly correlate with BOLD signal during non-interpersonal emotions. Correlation coefficients for interpersonal and non-interpersonal emotions and their significance levels are presented below the graphs. $^{*}p < .05$, $^{**}p < .01$.

ratings in the vACC, and PCC, and inverse associations in the dorsolateral prefrontal cortex (DLPFC), STG, dACC, and superior parietal cortex (Figure 3a). Activity in all of these regions, except the PCC, did not differ significantly between stimulus types—i.e., they were not implicated in producing the interaction (Figure 3d).

Main effect of stimulus type

While covarying for arousal and valence ratings, we detected significant reductions in BOLD signal elicited by interpersonal compared with non-interpersonal stimuli in the vACC, STG, insula, medial frontal gyrus, thalamus, IPC, MCC, and PCC, as well as significant increases in BOLD signal in MFG and STG (Figure 5, Table 3).

DISCUSSION

The goal of our study was to assess whether activity in distinct neural circuits is associated with processing of arousal and valence of interpersonal and non-interpersonal emotions. We detected several regions where the correlation of BOLD signal with ratings of arousal or valence depended strongly on stimulus type (Figures 1 and 3), indicating that these regions are differentially recruited by the processing of arousal or valence according to whether the emotion-inducing stimulus was primarily interpersonal or non-interpersonal.

In almost all instances in which stimulus type interacted significantly with arousal or valence ratings, significant interactions were driven by strong correlations of BOLD signal with arousal or valence ratings of emotions elicited by the interpersonal but not non-interpersonal stimuli (Figures 1d, 2, 3d, and 4), suggesting that those brain regions are primarily implicated in processing of interpersonal emotions. Specifically, for emotions elicited by interpersonal stimuli, activity in several regions of the limbic and paralimbic systems correlated significantly with arousal ratings, whereas activity in the temporal–parietal circuits correlated significantly with valence ratings.

In addition, we also identified regions that were associated with processing of arousal and valence of both interpersonal and non-interpersonal stimuli

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TABLE 2
Centers of activation in regions where BOLD signal intensity significantly correlated with valence ratings (Figure 3a–c) or where this association was significantly different between interpersonal and non-interpersonal emotions (Figure 3d)

	Location		MNI coordinates			
Anatomical regions	*Side*	*BA*	*x*	*y*	*z*	*t*
Figure 3a. ***Main effect of valence***						
Ventral anterior cingulate cortex	L	32	−3	40	−6	3.58
Dorsolateral prefrontal cortex	R	9	42	41	35	−7.08
	L	9	−46	22	40	−5.55
Superior temporal gyrus	R	42	56	−34	12	−4.70
Posterior cingulate cortex	R	23	4	−48	22	3.65
Superior parietal cortex	L	7	−41	−70	46	−2.97
Dorsal anterior cingulate cortex	R	32	5	19	42	−2.78
Figure 3b. ***Correlations of valence ratings and BOLD for interpersonal stimuli***						
Dorsolateral prefrontal cortex	L	9	−35	32	36	−3.57
	R	9	51	19	35	−3.42
Superior temporal gyrus	L	40	−60	−44	32	−8.31
	R	42	55	−36	12	−3.43
Middle cingulate cortex	R	24	1	−8	28	−3.86
Precuneus	L	31	−14	−66	28	−4.07
Dorsal anterior cingulate cortex	R	32	3	19	42	−3.37
Figure 3c. ***Correlations of valence ratings and BOLD for non-interpersonal stimuli***						
Posterior cingulate cortex	R	30	0	−68	4	3.06
Middle cingulate cortex	L	23	0	−26	28	3.32
Figure 3d. ***Valence-by-stimulus-type interaction (interpersonal versus non-interpersonal)***						
Superior temporal gyrus	L	22	−60	−60	12	−5.24
Posterior cingulate cortex	R	32	10	−46	8	−3.25
Middle cingulate cortex	L	23	−4	−26	30	−4.94
Precuneus	L	31	−12	−70	26	−5.38
	R	31	18	−64	22	−3.92

(Figures 1 and 3), where the type of emotional stimulus significantly interacted with and modulated activity in the valence and arousal systems. In these regions (MCC for valence and MTG for arousal), BOLD signal correlated with valence and arousal ratings, with the direction of the correlation varying between the stimulus types.

In some brain regions, BOLD signal correlated with arousal and valence ratings regardless of stimulus type (Figures 1a and 3a), indicating that those regions are recruited by the processing of valence or arousal across different types of emotions. Consistent with previous studies, these regions included portions of the limbic and paralimbic systems (i.e., amygdala, thalamus, and cerebellum) for arousal, and vACC, DLPFC, dACC, and right STG for valence.

Analysis of the main effect of stimulus type also revealed several regions (thalamus, anterior and posterior insula, and MFG) that were differentially recruited by the two types of emotions, regardless of arousal and valence ratings, and that were not identified in the interaction analysis. This finding suggests that imagining oneself in an interpersonal emotion-inducing situation activates different neural systems than does imagining oneself in a non-interpersonal one, independent of the valence and arousal level of the experienced emotion. In our study, the thalamus was implicated in both the main effect of stimulus type, and main effect of arousal, suggesting perhaps that some portions of the thalamus are processing the arousal of any emotion, while others process the interpersonal nature of the stimulus. Alternatively, the thalamus could be differentially involved in processing of arousal of interpersonal and non-interpersonal emotions, and this finding did not reach the level of statistical significance in interaction analyses. The posterior insula has been implicated in the processing of sensory information in prior studies, consistent with the greater activation of this region for non-interpersonal stimuli in our study. The anterior insula has been implicated in processing of the social emotions specifically, such as emotional autobiographical recall (Damasio, 1999;

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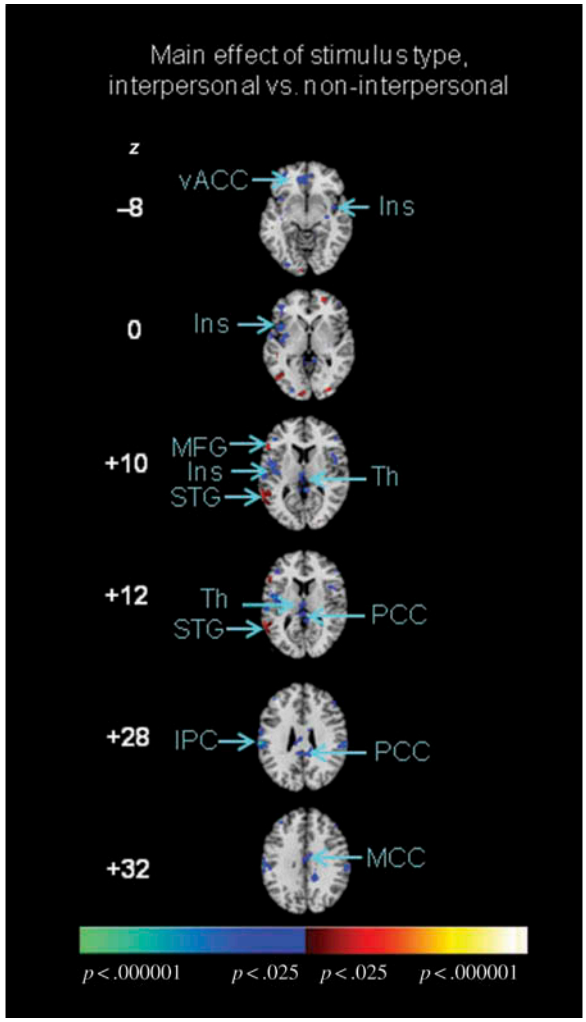

Figure 5. Difference in BOLD signal elicited by interpersonal emotion-inducing stimuli versus non-interpersonal emotion-inducing stimuli, with arousal and valence ratings controlled for (i.e., main effect of stimulus type). Red to yellow indicates greater BOLD signal during the presentation of the interpersonal versus non-interpersonal stimuli; green to purple indicates greater BOLD signal during the presentation of the non-interpersonal versus interpersonal stimuli. Ins = insula, IPC = inferior parietal cortex, MFG = middle frontal gyrus, MCC = middle cingulate cortex, PCC = posterior cingulate cortex, STG = superior temporal gyrus, Th = thalamus, vACC = ventral anterior cingulate cortex.

TABLE 3
Centers of regions with significantly different BOLD signal between the interpersonal and non-interpersonal emotions (controlling for arousal and valence)

	Location		*MNI coordinates*			
Anatomical regions	*Side*	*BA*	*x*	*y*	*z*	*t*
Ventral anterior cingulate cortex	L	32	−2	37	−7	−2.32
Insula	L	13	−42	14	0	−3.52
Middle frontal gyrus	L	45	−54	30	12	3.32
Superior temporal gyrus	L	22	−64	−50	10	3.63
Thalamus	L		−1	−16	12	−3.01
Posterior cingulate cortex	R	29	4	−40	10	−4.60
Inferior parietal cortex	L	40	−63	−25	28	−9.39
Middle cingulate cortex	L	23	0	−14	32	−2.54

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Phan, Wager, Taylor, & Liberzon, 2002), as well as in awareness of bodily states (Zaki, Davis, & Ochsner, 2012). The direction of the difference of BOLD signal change during the presentation of interpersonal versus non-interpersonal stimuli presented in Figure 5 is difficult to interpret, however, as the neural activity underlying the BOLD response can result from either inhibitory or excitatory synapses. Although the interaction analyses and analyses of the main effect of arousal and valence were based on the correlations of BOLD signal and behavioral ratings, the analysis of the main effect of stimulus type was not parametric. Therefore, it is possible that other differences between the stimulus types contributed to those findings. Mood induction is a complex task that requires attention, cognitively directed imagination, and integration of cognitive and emotional processes. It is possible that interpersonal and non-interpersonal stimuli differed on these dimensions and that the findings for stimulus type could derive from these differences.

Neural circuits associated with the arousal components of interpersonal and non-interpersonal emotions

Correlations of BOLD signal with arousal ratings differed significantly between stimulus types in limbic and paralimbic regions, including the vACC, caudate, parahippocampus, occipital, superior and medial temporal cortices, and MFC. This difference was primarily driven by the stronger association of BOLD and arousal ratings for interpersonal stimuli than non-interpersonal stimuli. Activity in most of these regions was associated with arousal ratings exclusively during the presentation of interpersonal stimuli, as evidenced by significant arousal-by-stimulus-type interactions (Figure 1d), significant findings for interpersonal emotional stimuli only (Figure 1b), and lack of significant correlations of BOLD and arousal ratings for non-interpersonal stimuli in these areas (Figure 2). These findings taken together suggest that these areas are involved in the processing of arousal for specifically interpersonal emotional experience.

The vACC has been consistently implicated in the experience of emotion (Kross, Davidson, Weber, & Ochsner, 2009; Phillips, Drevets, Rauch, & Lane, 2003). It is densely connected with other portions of the limbic system, such as the amygdala, nucleus accumbens, orbitofrontal cortex, and periaqueductal gray (Devinsky, Morrell, & Vogt, 1995; Etkin, Egner, & Kalisch, 2011). In our study, BOLD signal in vACC correlated strongly with the degree to which interpersonal emotional experiences were arousing, suggesting that arousing interpersonal emotions selectively recruit emotion regions compared to non-interpersonal emotions.

Correlations of BOLD signal with arousal were also much stronger for interpersonal than non-interpersonal stimuli in regions thought to be implicated in social cognition (STG, and precuneus) (Schilbach et al., 2012; Van Overwalle, 2009). Numerous studies have shown that imagining (Lotze et al., 1999; Oosterhof, Tipper, & Downing, 2012) or explicitly recalling (Nyberg et al., 2001) an action or experience activates nearly the same brain regions as the action or experience itself. Therefore, imagining oneself in an interpersonal situation could trigger the same neural activity as being in that interpersonal situation. Additionally, BOLD signal in the auditory and visual areas strongly correlated with ratings of arousal for interpersonal but not for non-interpersonal stimuli. This difference between stimulus types may reflect the greater vividness of visual and auditory imagery elicited by interpersonal than non-interpersonal scenarios. This may reflect the tendency of participants to remember their own prior experiences when imagining the interpersonal scenarios. Activation in the caudate nuclei and parahippocampus—areas involved in memory formation and retrieval—was more strongly associated with arousal ratings in the interpersonal versus non-interpersonal situations, again supporting the possibility that participants were likely drawing on memory of their interpersonal experiences when imagining the scripted scenarios.

Neural circuits associated with the valence components of interpersonal and non-interpersonal emotions

Activity in STG, IPC, PCC, MCC, and precuneus correlated strongly and inversely with the valence of interpersonal emotions but not with the valence of non-interpersonal emotions. The inverse correlation indicates that neural activity increases monotonically as the valence of emotional experiences becomes increasingly unpleasant or aversive. Recruitment of large expanses of parietal and temporal cortices—networks paradigmatically associated with attentional and higher order cognitive regulation functions—as emotional experiences become more negatively valenced suggest that the brain recruits these cortical regions to enable increased awareness, attention, and cognitive control in preparation for action that an aversive emotion presumably requires.

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Specifically, IPC, especially in the right hemisphere, has been implicated in processing salient environmental events, maintaining attention on task, and responding to new important information in the environment (Singh-Curry & Husain, 2009). PCC and precuneus have been implicated in maintaining self-awareness and retrieving autobiographical memories (Maddock, Garrett, & Buonocore, 2001), which could be particularly relevant for our study as our participants were likely to draw on their prior interpersonal experiences when imagining the scripted scenarios. The greater activations in these brain regions associated with valence during the experience of interpersonal emotions furthermore indicate that these cortically based cognitive mechanisms are triggered particularly within interpersonal contexts. We speculate that the brain allocates more attention and regulatory resources to interpersonal experiences, given that interpersonal stimuli, particularly aversive ones, are highly salient to human beings and therefore require the allocation of considerable attentional resources.

Relation of our findings to prior studies of interpersonal and non-interpersonal emotions

Our findings contribute to the emerging literature suggesting that distinct neural circuits are recruited by interpersonal and non-interpersonal emotions. Several previous imaging studies have reported substantial differences between the neural activations during “social” versus “non-social” emotions (Britton, Phan, et al., 2006; Burnett & Blakemore, 2009; Burnett et al., 2009; Frewen et al., 2011; Kross, Egner, Ochsner, Hirsch, & Downey, 2007; Vrticka, Bondolfi, Sander, & Vuilleumier, 2012), yet differing in the specific brain regions identified.

The methods of our study differed from these prior investigations in that (1) our study was designed to identify the activity in neural circuits that is associated with parametrically varying levels of arousal and valence of interpersonal and non-interpersonal emotions, (2) we accounted for varying valence and arousal levels of stimuli simultaneously, and (3) our participants were instructed to imagine themselves—rather than to observe others—in emotion-eliciting situations. The findings of these studies are therefore not contradictory, but rather address somewhat different research questions. Nevertheless, several regions (superior temporal gyrus, insula, and posterior cingulate) have been consistently reported across the studies regardless of stimulus type and study design, and all the studies point to substantial differences in the ways that the brain processes interpersonal and non-interpersonal emotions.

The extensive neural activity we identified as subserving emotions experienced in specifically interpersonal situations is also consistent with numerous studies showing a crucial role of interpersonal emotions in health and disease among humans and animals alike. For example, lesions to the orbitofrontal cortex in rats influenced emotional responses to non-social fear-inducing stimuli, whereas lesions to the ACC specifically disrupted behavioral responses to social interaction and memory for social stimuli (Rudebeck et al., 2007). Social stressors induced more changes in behavioral and physiologic markers of emotions in quails than did non-social stressors (Valance et al., 2008). In addition, several human studies have reported that exposure to interpersonal negative emotions and interpersonal traumatic events (e.g., a betrayal or an assault) is much more strongly associated with the development of psychiatric symptoms and poor functioning than is exposure to non-interpersonal negative emotions and non-interpersonal trauma (e.g., an earthquake or a fire) (Briggs-Gowan et al., 2010; Conner et al., 2012; Flynn & Rudolph, 2011; Gunthert, Cohen, Butler, & Beck, 2007; Gustafsson, Larsson, Nelson, & Gustafsson, 2009; Gustafsson, Nilsson, & Svedin, 2009; Nilsson, Gustafsson, & Svedin, 2010; Parrish, Cohen, & Laurenceau, 2011).

Limitations

We used self-report ratings of arousal and valence as indicators of these aspects of emotional experience. Because we cannot isolate the emotional experience itself from a cognitive appraisal of the experience, some of the neural systems identified in our study may be involved in forming judgments about the emotional experience. Additionally, the mood induction task itself involved a complex integration of cognitions and emotions. Nevertheless, a parametric design with varying levels of arousal and valence presumably controlled for the “judging” and integration of cognitions with emotions, as they were present during all stimulus presentations and were unlikely to have varied monotonically with arousal or valence ratings. Only if the neural systems involved in the cognitive appraisal of emotion also varied systematically with valence or arousal would cognitive appraisal be a likely confound. Our emotion-eliciting situations presented to participants had strong ecological validity and enhanced the likelihood that participants could

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"feel" the emotion while in the scanner. Due to the small number of participants, our findings should be considered preliminary. The small sample size also precluded exploration of gender and age effects on our findings.

CONCLUSIONS

Our study highlights the importance of the interpersonal nature of emotions by showing that neural circuits implicated in processing the arousal and valence components of emotions experienced in interpersonal situations differ markedly from circuits implicated in processing those components of emotions experienced in non-interpersonal situations. The remarkable difference in the extent to which the brain activates during interpersonal and non-interpersonal emotions at the same level of valence or arousal raises a question whether much of the brain activity reported during emotion tasks is, in fact, driven by interpersonal emotions specifically. Re-examining the stimuli used in previous studies on the neural bases of emotion could yield an improved understanding of the many inconsistencies in findings across studies of emotion. Future emotion research should take into account the distinction between interpersonal and non-interpersonal emotions.

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