Interpersonal Reactivity and the Attribution of Emotional Reactions

Brian W. Haas, Ian W. Anderson, and Megan M. Filkowski University of Georgia

The ability to identify the cause of another person's emotional reaction is an important component associated with improved success of social relationships and survival. Although many studies have investigated the mechanisms involved in emotion recognition, very little is currently known regarding the processes involved during emotion attribution decisions. Research on complementary "emotion understanding" mechanisms, including empathy and theory of mind, has demonstrated that emotion understanding decisions are often made through relatively emotion- or cognitive-based processing streams. The current study was designed to investigate the behavioral and brain mechanisms involved in emotion attribution decisions. We predicted that dual processes, emotional and cognitive, are engaged during emotion attribution decisions. Sixteen healthy adults completed the Interpersonal Reactivity Index to characterize individual differences in tendency to make emotion- versus cognitive-based interpersonal decisions. Participants then underwent functional MRI while making emotion attribution decisions. We found neuroimaging evidence that emotion attribution decisions engage a similar brain network as other forms of emotion understanding. Further, we found evidence in support of a dual processes model involved during emotion attribution decisions. Higher scores of personal distress were associated with quicker emotion attribution decisions and increased anterior insula activity. Conversely, higher scores in perspective taking were associated with delayed emotion attribution decisions and increased prefrontal cortex and premotor activity. These findings indicate that the making of emotion attribution decisions relies on dissociable emotional and cognitive processing streams within the brain.

Keywords: social cognition, attribution, personal distress, perspective taking, emotion understanding

People are extremely skilled at recognizing the emotional states of others. Further, people are well skilled at determining the cause of another person's emotional reaction. By doing so, people improve their ability to help other people in need or to flee from a potential source of danger. Although many of the mechanisms involved during the recognition of other people's emotional reactions have been thoroughly investigated, the mechanisms involved when deciding the cause of another person's emotional reaction are currently not well understood. This study was designed to investigate the behavioral and neural mechanisms involved when deciding the cause of another person's emotional reaction.

Understanding of the cause of someone else's emotional reaction is contingent on the ability to accurately recognize emotions but also likely requires additional cognitive resources. Adolphs (2002, 2006) has outlined several systems involved in emotion recognition that include perceptual processes (e.g., seeing the geometric configuration of an emotional face) and knowledge-based processes (e.g., recognizing and categorizing the emotional meaning of a face). Accordingly, these processes rely on brain systems that include visual cortices to rapidly detect the presence of an emotional stimuli and emotional and cognitive areas (e.g.,

This article was published Online First February 23, 2015.

Brian W. Haas, Department of Psychology and Interdisciplinary Neuroscience Graduate Program, University of Georgia; Ian W. Anderson and Megan M. Filkowski, Department of Psychology, University of Georgia.

Correspondence concerning this article should be addressed to Brian W. Haas, Department of Psychology, University of Georgia, Athens, GA

30602. E-mail: bhaas@uga.edu

amygdala, hippocampus, orbitofrontal cortices) to categorize stimuli according to existing knowledge sets. However, the processes involved in determining the cause of another person's emotional reaction likely involve additional mental and neural resources. Behavioral research shows that emotion attribution decisions require a longer duration of time than does recognizing or labeling an emotion (Krull & Dil, 1998). Emotion attribution decisions also rely on overlapping and distinct brain regions with respect to those involved in basic emotion recognition. Spunt and Lieberman (2012) showed that thinking about why someone else is emotionally reacting is associated with activity in brain regions within mentalizing and mirror systems, comprising the medial prefrontal cortex, precuneus, temporoparietal junction, posterior superior temporal sulcus, and inferior frontal gyrus.

Many social- and emotion-based decisions are carried out through multiple processing streams (Stanovich, 2012). Dual process theory states that social decisions occur as a result of two different processes. Often, processes are characterized as relatively rapid/automatic/emotional versus controlled/cognitive. Dual processing streams are engaged during reasoning, judgment, and social cognition (Evans, 2008). In addition, there is evidence that the attribution of traits is carried out through both automatic and controlled processing (Wells, Skowronski, Crawford, Scherer, & Carlston, 2011). Dual process theory has been applied to models of emotion understanding that include empathy and theory of mind. Emotional empathy and theory of mind are thought to involve automatically feeling what others feel (i.e., emotion contagion), whereas cognitive empathy and theory of mind are thought to involve understanding another person's perspective or mental state

(Preston & De Waal, 2002; Preston & Hofelich, 2012; Shamay-Tsoory, 2011).

Within the brain, emotional empathy and theory of mind rely on limbic structures, including the cingulate cortex, insula, and amygdala (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Singer, Critchley, & Preuschoff, 2009), whereas cognitive empathy and theory of mind rely on a cognitive network that includes the prefrontal cortex (PFC) and premotor area (Kalbe et al., 2010; Sebastian et al., 2012). Both emotional empathy and theory of mind and cognitive empathy and theory of mind are thought to rely on a common brain network that includes the medial PFC and temporoparietal junction (Spengler, von Cramon, & Brass, 2009; Van Overwalle, 2009). On the basis of existing models of dual processing streams engaged during emotion understanding, we predicted that emotion attribution decisions may also be carried out through multiple processing systems: a relatively rapid, emotion-based process and a relatively controlled, planned, cognitive-based process.

One way that emotion attribution decisions may be made is by taking on the emotions of the target person on whom the attribution decision is based. For example, if one automatically feels what another person is feeling, one may be positioned to assess whether his or her current emotional feeling state matches the feeling state generated from a potential cause. This emotion-based process would therefor depend on a person's tendency to take on the emotions of others, as with emotion contagion. Emotion contagion is the tendency to automatically experience the emotions of other people (Hatfield, Cacioppo, & Rapson, 1993). One way that individual differences in emotion contagion can be measured is with the personal distress (PD) subscale (Sturm et al., 2013) of the Interpersonal Reactivity Index (IRI; Davis, 1983). People who score high on PD tend to automatically feel the emotional states of others (Jabbi, Swart, & Keysers, 2007; Saarela et al., 2007), be less inhibited (Eisenberg et al., 1994), and exhibit an orientation bias toward the self (i.e., be egocentric; Batson, Fultz, & Schoenrade, 1987). On the basis of prior research on emotion contagion, we predicted that higher scores on the PD subscale would be associated with more rapid (less inhibited) attribution decisions and greater engagement of brain regions involved in interoceptive awareness and subjective experience of emotions—namely, the anterior insula and the rostral anterior cingulate (rAC; Craig, 2011; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004).

Another way that emotion attribution decisions may be made is by looking through the perspective of the target. For example, if one adopts the perspective of the target, one may be positioned to evaluate how likely the target is to respond to potential causes. This cognitive-based process would therefor depend on a person's tendency to adopt the perspective of another person and to evaluate and compare target-cause associations. One way that individual differences in cognitive perspective taking can be measured is with the perspective-taking (PT) subscale of the IRI. People who score higher on PT tend to be less emotionally reactive (Mohr, Howells, Gerace, Day, & Wharton, 2007), less prone to stereotyping (Ku, Wang, & Galinsky, 2010), and less inhibited (Spinella, 2005) and to exhibit an orientation bias toward others (i.e., be allocentric; Batson, Early, & Salvarani, 1997). On the basis of prior research on cognitive PT, we predicted that higher scores on the PT subscale would be associated with longer attribution decisions and greater engagement of brain regions involved in cognitive theory

of mind and planning—namely, the PFC and premotor area (Kalbe et al., 2010; Sebastian et al., 2012).

We tested these predictions using a multilevel approach. First, we characterized individual differences in PD and PT using the IRI. We used the PD subscale to characterize the tendency toward emotion-based decision making and the PT subscale to characterize the tendency toward cognitive-based decision making during emotion attribution. Next, we acquired behavioral and functional MRI (fMRI) data while participants made emotion attribution decisions. We predicted that across participants, emotion attribution decision making would be associated with greater neural activity within brain regions that comprise the mirror and mentalizing systems (Spunt & Lieberman, 2012). Further, we predicted that higher PD scores would be associated with quicker emotion attribution decisions and with greater anterior insula and rAC activity and that higher PT scores would be associated with longer emotion attribution decisions and greater PFC and premotor activity.

Method

Participants

Sixteen healthy, fluent, English-speaking adults (nine female, seven male; mean age = 21.80 years, SD = 2.11 years) adults were recruited from the University of Georgia and surrounding community. Prior power analyses for fMRI data have shown that a sample size of 16 participants achieves 80% power at the single-voxel level for typical activations (Desmond & Glover, 2002). All participants were screened for neurological conditions and MRI counter indications. All participants provided written informed consent as detailed in the Declaration of Helsinki, and the University of Georgia Institutional Review Board approved all procedures within this study.

Interpersonal Reactivity Measure

Prior to fMRI scanning, each participant completed the IRI (Davis, 1983), a 28-item self-report measure of interpersonal emotional and cognitive functioning. We used the PD subscale to characterize individual differences in emotion contagion (emotion-based decision making; Preston & Hofelich, 2012; Sturm et al., 2013) and the PT subscale to measure individual differences in cognitive PT (cognitive-based decision making). PD measures self-oriented feelings of distress and arousal when other people are involved in emotionally salient experiences (Davis, 1983). PT measures the tendency to adopt the viewpoint of another person (Davis, 1983). Scores were also obtained for the empathic-concern (EC) and fantasy (F) subscales and were retained to examine the discriminant validity of associations with each dependent variable (reaction time [RT] and neural activity).

Target and Cause Stimuli

For the emotion attribution task, two types of stimuli were created and used in each single trial. Happy and sad emotional facial expressions, with varying intensity levels, were used as targets, and images of social-emotional scenes were used as potential causes (see Figure 1). The target emotional faces were

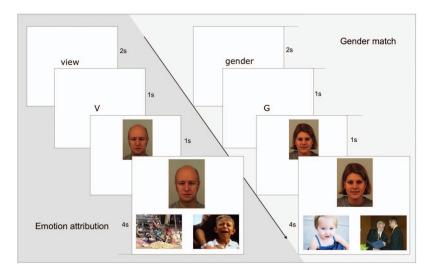


Figure 1. Schematic diagram of emotion attribution task. Participants underwent functional MRI while being presented a target face and two emotionally provocative social scenes as potential causes. Participants were informed that photographs were taken of people while they were reacting to images of social scenes. During the emotional attribution condition, participants were instructed to decide which of the two social scenes they believed the person was reacting to. During the gender match condition, participants were instructed to select the social scene that contained the largest proportion of the gender of the target face on the top of the screen. See the online article for the color version of this figure.

selected from a standardized database (Lundqvist, Flykt, & Öhman, 1998) and were modified to produce variability in emotion intensity across targets. The decision to vary the emotional intensity of target faces was made to improve the ecological validity of the task. Specifically, we wanted each participant to believe that each target face was a photograph of a person naturally reacting to an emotionally provocative image of a social scene. Empirical research has demonstrated that the intensity of emotional expressions is highly variable within and across people (Larsen, Diener, & Emmons, 1986). Variation of emotional intensity was carried out using morphing software (FantaMorph 5 http://www.fantamorph .com). Each happy or sad face was morphed with an image of a neutral expression of the same identity. Half of the target faces were created to be of mild intensity, using a gradient of 30%-40% emotional-neutral, and half of the target faces were created to be of high intensity, using a gradient of 70%-80% emotional-neutral.

Images of social–emotional scenes (positive and negative emotional valence) were used as potential causes within the emotion attribution task. Each image of an emotionally provocative social scene was selected from either the Geneva Affective Picture Database (Dan-Glauser & Scherer, 2011) or the International Affective Picture System (Lang & Greenwald, 1993). Many of these social scenes have previously been used to investigate emotional reactivity (Vrtička, Sander, & Vuilleumier, 2012). The mean valence (V) and arousal (A) ratings (based on Geneva Affective Picture Database or the International Affective Picture System scores) for the positive social–emotional scenes were as follows: $V = 75.48 \ (SD = 11.17)$, and $A = 39.38 \ (SD = 12.31)$. The mean valence and arousal ratings for the negative social–emotional scenes were as follows: $V = 30.52 \ (SD = 16.01)$, and $V = 56.09 \ (SD = 14.41)$.

Emotion Attribution Task

Immediately prior to fMRI scanning, each participant completed a practice version of the emotion attribution task (see Figure 1). The practice version of the task was identical to the fMRI version of the task except for the use of different stimuli (target and cause) within the paradigm. Prior to the task, each participant was read the following statement:

We are interested in your ability to identify the cause of someone else's emotional response. In this experiment you will be presented photographs taken of people while they were presented images of social scenes.

Next, each participant was instructed to make two types of decisions, either emotion attribution or gender matching. During the emotion attribution condition, each participant was instructed to decide which of the two social scenes (cause) they believed the person (target) at the top of the screen was reacting to. As a comparison/baseline condition (gender matching), each participant was instructed to match the gender of the person in the photograph (target) with the social scene that contained the highest proportion of that gender.

Stimuli within each trial were matched according to valence (positive: happy target face—two positive social scene causes; negative: sad target face—two negative social scene causes). Each condition (emotion attribution and gender match) contained an equal number of positive- and negative-valence trials. The primary behavioral metric for this task was RT (i.e., how quickly each participant made an emotion attribution decision as compared with a gender matching decision). This task was not designed to characterize how accurate each participant was at determining the cause (see the Discussion for further details).

Participants were presented with a total of 64 trials (32 emotion attribution and 32 gender matching). All of the trials and stimuli within each trial were novel (i.e., there were no repeats). Trials were presented in 18 blocks of three- or four-trial lengths with alternating conditions (emotion attribution and gender match). Prior to each emotion attribution block, participants were presented with the word view ("which scene did the person/target view?"), and prior to each emotion attribution trial, participants were presented with the letter V. Prior to each gender match block, participants were presented with the word gender, and prior to each gender match trial, participants were presented with the letter G. The trials included in each condition (attribution vs. gender match) were counterbalanced across participants. Participants indicated their response via a button box, and RT for each response was recorded. Following the fMRI scan, each participant was fully debriefed and informed of the details within the study. No participant reported any knowledge that the target face stimuli were modified and not photographs taken of people actually reacting to social scenes.

Image Acquisition

Whole-brain imaging data were acquired on a GE-Signa 3 T scanner (General Electric, Milwaukee, WI). A total of 195 functional images were acquired using a gradient echo T2*-weighted echoplanar imaging scan (flip angle = 90° , repetition time = 2.0 s, echo time = 25.0 ms, 40 slices, field of view = 220 mm \times 64 matrix). For structural whole-brain images, a three-dimensional high-resolution spoiled gradient scan (flip angle = 20° , repetition time = 24 ms, echo time, 4.5 ms, 164 contiguous slices, slice thickness = 1.0 mm; field of view = 25.6 cm, matrix size = 256×256) was conducted.

Neuroimaging Analysis

Functional data were preprocessed and statistically analyzed using SPM8 software (Wellcome Department of Imaging Neuroscience, London, United Kingdom) and implimeted through Matlab R2012a (http://www.mathworks.com). The images were temporally realigned to the middle slice, spatially realigned to the first in the time series. The images were then coregistered and spatially normalized into standard stereotactic space (Montreal Neurological Institute [MNI] template) and spatially smoothed with an 8-mm full width at half maximum isotropic Gaussian filter.

Statistical analyses of fMRI data were performed to compare the blood-oxygen-level-dependent (BOLD) signals acquired during the emotion attribution condition with those acquired during the gender matching condition (emotion attribution > gender match). Each block within each condition was modeled on the basis of a convolution to the hemodynamic response function and represented BOLD signals acquired throughout each block (boxcar), including cues. Data within each model were high-pass filtered using default settings (128 s). On a group level, *t*-contrast maps were entered into a random effects model. Correlation analyses were used to identify neural activity exhibiting associations with individual differences in PD or PT. Lastly, a conjunction analysis was used to identify neural activity that exhibited both an association with the individual differences measures (PD and PT) and response latencies (emotion attribution > gender match). For

whole-brain analysis, we report clusters that survived a p < .05 (false discovery rate-corrected) threshold. For correlation analysis within regions of interest, we used a combined statistical and extent threshold of p < .005 (uncorrected [20-voxel extent]; Lieberman & Cunningham, 2009). Lastly, for conjunction analysis within regions of interest, we used a combined threshold of p < .01 (for PD or PT) $\times p < .01$ (RT).

We examined the discriminant validity for each association by performing correlation analysis between the EC and F subscales of the IRI and for each dependent variable (BOLD signal and RT) by using a combined statistical and extent threshold of p < .005 (uncorrected [20-voxel extent]; Lieberman & Cunningham, 2009).

Results

Behavioral Results

Means and standard deviations were determined for each subscale of the IRI: PT (M=27.81, SD=3.40), F (M=27.13, SD=5.34), EC (M=23.69, SD=4.30), and PD (M=17.57, SD=4.32). We used a Shapiro–Wilk test to verify that the data acquired using the IRI were normally distributed within our sample. The results of this analysis demonstrated that the IRI data were normally distributed (all ps>.15). A paired-sample t test was used to compare RT between conditions, and a series of linear regression analyses were conducted to investigate the association between individual difference measures and RT differences (emotion attribution – gender matching). The results of this analysis demonstrated that, on average, emotion attribution decisions (M=2,291.93 ms, SD=253.89) required a longer duration of time than did gender matching decisions (M=1,762.16 ms, SD=260.16), t(15)=9.81, p<.001, Cohen's d (effect size) = 2.06, r=.72.

Next, we investigated the association between individual difference measures and RT difference latencies. Correlation coefficients are presented in Table 1. We found that higher PD scores were associated with reduced RTs required to make emotion attribution decisions, t(15) = 2.41, p = .015. Conversely, we found that higher PT scores were associated with a longer RTs required to make emotion attribution decisions, t(15) = 1.93, p = .04. We used a Fisher r-to-z transformation to test the significance of the difference between each r value (PD \times RT vs. PT \times RT). The r value for the association between PD and RT (-.54) was significantly different from the r value for the association between PT and RT (.46; p = .005).

Table 1
Associations Between Interpersonal Reactivity and Reaction
Time Latencies

Variable	ΔRT	PD	PT	EC	F
Δ RT	_				
PD	54^{*}				
PT	.46*	42	_		
EC	.10	.35	.35	_	
F	.13	42	.16	.59*	_

Note. RT = reaction time; PD = personal distress; PT = perspective taking; EC = empathic concern; F = fantasy. $^*p < .05$.

Table 2

All Regions Observed in the Main Effect of Condition: Emotion Attribution > Gender Matching

	MNI					
Anatomical region	L/R	x	у	Z	t(15)	k
Inferior frontal gryus	L	-56	14	20	9.91	
Extending into insula	L	-24	14	2	6.56	1,644
Inferior frontal gryus	R	56	32	0	8.06	970
Medial prefrontal cortex	L	-4	48	38	6.81	3,642
Premotor	R	48	2	52	4.73	197
Cuneus	L	-10	-92	38	9.13	
Extending into cuneus	R	18	-100	22	8.06	
Extending into temporoparietal junction	R	48	-66	12	7.79	7,176
Temporoparietal junction	L	-54	-52	12	6.88	885
Anterior temporal cortex	R	54	6	-30	6.73	311
Amygdala/hippocampus	L	-12	-2	24	5.30	115
Fusiform	L	-40	-52	-24	4.64	191
Cerebellum	L	-18	-76	-40	5.82	653
Cerebellum	R	28	-83	-38	4.73	301

Note. MNI = Montreal Neurological Institute template of standard stereotactic space; L = left; R = right.

Neuroimaging Results

Across participants, BOLD signals were compared between the emotional attribution condition and the gender matching condition. Emotion attribution was associated with greater neural activity within a network of brain regions comprising the mentalizing and mirror systems (see Table 2). Specifically, we observed greater activation within the medial prefrontal cortex (left [MNI: -4, 48, 38]: t[15] = 6.81, p < .0001, k = 514 voxels, Cohen's d = 3.52; bilateral [MNI: -4, 30, 44]: t[15] = 6.62, p < .0001, k = 320 voxels, Cohen's d = 3.42), inferior frontal gyrus (left [MNI: -56, 14, 20]: t[15] = 9.91, p < .0001, k = 1,644 voxels, Cohen's d = 5.12), and temporoparietal junction (left [MNI: -54, -52, 12]: t[15] = 6.88, p < .0001, k = 885, Cohen's d = 3.55; right [MNI: 48, -64, 12]: t[15] = 7.79, p < .0001, k = 1,062 voxels, Cohen's d = 4.02) during

emotion attribution as compared with gender matching (see Figure 2). These findings are consistent with prior evidence that these brain systems are involved in the causal attribution of emotions (Spunt & Lieberman, 2012).

We next tested for associations between individual difference measures and brain activity during emotion attribution. For the emotion-based process, we found that higher PD scores were associated with greater bilateral anterior insula activity during emotion attribution versus gender matching (left [MNI: -46, 0, 14]: t[15]=4.17, p<.001, k=73 voxels, Cohen's d=2.15; left [MNI: -42, 0, -10]: t[15]=3.99; p=.001, k=33 voxels, Cohen's d=2.06; right [MNI: 26, 0, 12]: t[15]=4.10, p=.001, k=46 voxels, Cohen's d=2.12 [see Figure 3A]). There were no significant clusters of activity associated with PD scores within the rAC. There were no statistically signifi-

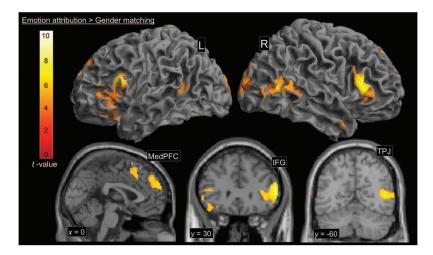


Figure 2. Results of whole-brain comparison between emotion attribution and gender matching. Areas of significant activation (false discovery rate corrected) are overlaid on a standardized template of the brain. L = left; R = right; MedPFC = Medial prefrontal cortex; IFG = inferior frontal gyrus; TPJ = temporoparietal junction. See the online article for the color version of this figure.

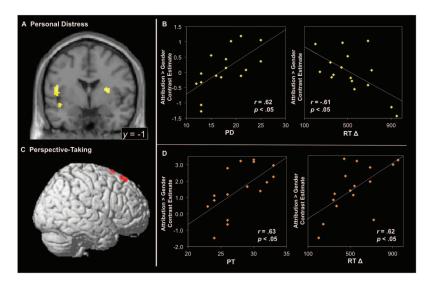


Figure 3. Results of individual differences analysis. A: Areas exhibiting activation significantly associated with personal distress (PD) during emotion attribution compared with gender matching within the anterior insula. B: Plots show the results of the conjunction analysis for PD and reaction time (RT). Within plots, contrast estimates for emotion attribution > gender matching are plotted against individual differences in PD (left panel) and mean RT differences between the emotion attribution and gender match conditions (right panel). C: Areas exhibiting activation significantly associated with perspective taking (PT) during emotion attribution compared with gender matching within the prefrontal cortex and premotor area. D: Plots show the results of the conjunction analysis for PT and RT. Within plots, contrast estimates for emotion attribution > gender matching are plotted against individual differences in perspective taking (left panel) and mean RT differences between the emotion attribution and gender match conditions (right panel). See the online article for the color version of this figure.

cant associations between any other IRI subscale (EC, F, or PT) and anterior insula or rAC activity during emotion attribution versus gender matching.

For the cognitive-based process, we found that higher PT scores were associated with greater right PFC and premotor area activity during emotion attribution versus gender matching (right PFC [MNI: 2, 34, 62]: t[15] = 3.99, p = .001, k = 93 voxels, Cohen's d = 2.06; right premotor area [MNI: 0, 20, 70]: t[15] = 2.92; p = .002, k = 31 voxels, Cohen's d = 1.51 [see Figure 3C]). There were no statistically significant associations between any other IRI subscale (EC, F or PD) and PFC or premotor activity during emotion attribution versus gender matching.

We performed a conjunction analysis designed to identify brain loci exhibiting significant associations with both individual difference measures (PD or PT) and behavior (RT difference: emotion attribution – gender matching). The results of this analysis revealed a cluster within the right anterior insula significantly associated with both individual differences in PD and reduced RT (five voxels; MNI: 30, 0, 12 [see Figure 3B]). Activity within this cluster was significantly positively correlated with PD (r = 62), t(15) = 2.95, p < .05,and reduced RT (r = -.61), t(15) = 2.88,p < .05. This finding shows that people scoring higher in PD exhibited greater anterior insula activation and that greater anterior insula activation is associated with quicker emotion attribution decisions. For the cognitive-based process, we found a cluster within the PFC significantly associated with both individual differences in PT and longer RTs (15 voxels; MNI: -4, 34, 46 [see Figure 3D]). Activity within this cluster was significantly positively correlated with PT (r = 63), t(15) = 3.03, p < .01, and

longer RTs (r = .62, t(15) = 2.97, p < .05. This finding shows that people scoring higher in PT exhibited greater PFC activation and that greater PFC activation is associated with delayed emotion attribution decisions. The results of the conjunction analysis using the EC and F subscales with RT did not reveal any statistically significant clusters within the anterior insula, rAC, PFC, or premotor area.

Lastly, we performed a multiple regression analysis with individual differences (PD and PT) and neural activity (insula and PFC) entered as independent variables and RT entered as the dependent variable. The results of this analysis demonstrated that the combined regression model was statistically significant, F(4, 15) = 3.60, p < .05, and explained a total of 57% ($R^2 = .57$) of variance in RT. In addition, we performed multiple regression analyses for each process independently. The results of these analyses indicated that individual differences (PD or PT) and neural activity (insula or PFC) significantly predicted RT for the emotion-based process, F(2, 15) = 4.63, $R^2 = .42$, p = .03, and the cognitive-based process, F(2, 15) = 4.22, $R^2 = .39$, p = .03.

Discussion

This study was designed to investigate the behavioral and neural mechanisms involved when deciding the cause of another person's emotional reaction. Not surprisingly, we found that making emotion attribution decisions required a longer duration of time than did gender matching. In addition, we found that making attribution decisions was associated with greater activity within several brain

regions within the mirror and mentalizing systems. Further, we found evidence of dissociable processing streams involved in emotion attribution decisions. The emotion-based process was represented by a tendency to experience emotion contagion, increased anterior insula activity, and relatively rapid attribution decisions. Conversely, the cognitive-based process was represented by a tendency to take on the perspective of others, increased PFC and premotor activity, and relatively delayed attribution decisions.

The observation that emotion attribution decisions are associated with activity within the medial PFC, inferior frontal gyrus, and temporoparietal junction is consistent with prior neuroimaging studies on emotion understanding and attribution (Bastiaansen, Thioux, & Keysers, 2009; Ochsner et al., 2004; Shamay-Tsoory, 2011; Spunt & Lieberman, 2012). Activation within this network was found consistently across all participants during emotion attribution in this study. The observation that across all participants, emotion attribution was associated with increased medial PFC, inferior frontal gyrus, and temporoparietal junction activity indicates that this may be a core brain network involved in the interpretation of mental states of others. This finding complements the results of a recent meta-analysis demonstrating the consistency of medial PFC and temporoparietal activation across many types of tasks that involve mental state attribution (Van Overwalle, 2009).

The primary behavioral metric in this study was the speed with which emotion attribution decisions were made (as compared with gender matching). Longer durations required to make attribution decisions may represent several psychological phenomena. One parsimonious interpretation is that increased RT represents a greater amount (or greater level of complexity) of cognitive recourses required to complete the task. There is evidence that RT is longer during cognitive-based decision making than during emotional-based decision making (Quartz, 2009). Many dual process theories, as related to social decision making, draw a distinction between processing streams on the basis of the speed required to complete the task. For example, Eisenberg and Eggum (2009) described the contagious form of empathy as being processed through the subcortical route and being quick and reflexive, whereas the cognitive form of empathy is processed through the cortical route and is likely slower. There are, however, other interpretations of the RT differences in this study. For example, reduced RT may represent not caring about the task or caring considerably about the task but "knowing" the "correct" answer. Future research is necessary to elucidate how RT during emotion attribution decisions may lead to other psychological functions (e.g., empathy) or overt behaviors (e.g., helping).

We did not quantify the accuracy of emotion attribution decisions in this study. The emotion attribution condition was designed to engage mental processes involved when trying to identify a cause of someone else's reaction. One way that accuracy could have been modeled within this paradigm would have been to pair each target face with a valenced (positive or negative) social scene and a neutrally valenced social scene. Therefore, the "correct" attribution decision for a sad target face would be the negatively valenced social scene, and the "incorrect" attribution decision would be the neutrally valenced social scene. This paradigm, however, would be comparably much less difficult and more obvious and would likely rely on brain networks involved in

valence matching (Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001). To address the issue of speed–accuracy trade-offs in this study, we calculated the accuracy for each participant during the gender matching condition. We found that accuracy during the gender matching condition was high (90%) and that there were no significant associations between RT (during gender matching or difference in RT between conditions) and accuracy (p = .55).

The absence of accuracy as a factor for the emotion attribution condition may have influenced contrasts (behavioral and neuroimaging) between each condition. Specifically, participants may have experienced the gender matching condition with greater valence relative to the emotion attribution condition as a result of being more confident in their responses.

We found that individual differences in PD were associated with greater anterior insula activity during emotion attribution decisions. The insula is broadly involved in the subjective experience of emotions (Craig, 2011), with the anterior portion of the insula playing a key role in emotional forms of empathy (Fan, Duncan, de Greck, & Northoff, 2011). Prior neuroimaging research has shown that higher PD scores are associated with greater gray matter volume of the anterior insula (Banissy, Kanai, Walsh, & Rees, 2012). Together, these findings indicate that the structure and function of anterior insula may affect the tendency for individuals scoring high in PD to experience high emotionality and exhibit low emotional regulation (Eisenberg et al., 1994).

Contrary to our predictions, we did not find an association between higher PD scores and greater rAC activation during emotion attribution. To examine this further, we performed an exploratory analysis to investigate the association between PD and rAC using a reduced statistical threshold of p = .05 (10-voxel extent). The results of this exploratory analysis demonstrated that higher scores of PD were associated with greater rAC activation during emotion attribution versus gender matching (MNI: 6, 26, -2; t[15] = 2.21, p = .022, 11 voxels). There was no significant association between PT and rAC activation during emotion attribution using the same statistical threshold. The reason we did not observe an association using a more conservative statistical threshold is not clear, but it may have been influenced by factors such as sample size or paradigm length. In addition, this pattern of results may represent differences between the anterior insula and the rAC in terms of how each region is involved in empathic processing. There is empirical evidence that lesions within the anterior insula affect empathic processing to a greater extent than do lesions within the rAC (Gu et al., 2012). Together, the anterior insula may be particularly involved in emotion contagion in general, whereas the rAC may be more involved in other components of empathic processing.

We observed that individual differences in PT were associated with greater PFC and premotor area activity. This finding may represent the fact that individuals who score higher in PT tend to think through and plan their answers to a greater extent than do individuals who score lower in PT. The location of the PFC cluster observed in this study was in close proximity (though slightly medial) to the location reported by Kalbe et al. (2010), who used transcranial magnetic stimulation to show that temporary lesions of the PFC result in disrupted cognitive theory of mind but spared emotional theory of mind. Behavioral research shows that higher PT is associated improved emotion regulation (Webb, Miles, & Sheeran, 2012) and a reduced tendency to make rash and

stereotype-based decisions (Todd, Bodenhausen, Richeson, & Galinsky, 2011; Todd, Galinsky, & Bodenhausen, 2012). Together, this research indicates that increased PFC activity may be a neural construct underlying the tendency of high PT scorers to be more thorough and conscientious when making social decisions.

Although this study advances current models of social decision making, it is also limited in several important ways. We used a multilevel approach, including self-report, neuroimaging, and behavior. In terms of attribution, it would be valuable to examine how emotion- and cognitive-based processes lead to different decisions and how these decisions are affected by specific factors. For example, one might predict that the emotion-based process would be more affected by egocentric factors (e.g., through mood induction), whereas the cognitive-based process would be more affected by allocentric factors (e.g., perceptual cues in the environment). This study is also limited in terms of having a relatively small sample size. Although a sample size of 16 is suitable for fMRI studies (Desmond & Glover, 2002), an increased sample size would improve the power to demonstrate individual differences in behavioral responses. In addition, future emotion attribution studies would be improved by using videos of people reacting to specific, real-life emotional events (Zaki & Ochsner, 2009, 2011) and the inclusion of other relevant empathy measures, such as the Empathy Quotient (Baron-Cohen & Wheelwright, 2004).

In conclusion, identifying the cause of another person's emotional reaction is an important factor in human social life. Although humans tend to be well skilled in identifying other people's emotions and determining the cause of other people's emotional reactions, individual differences exist in the way emotion attribution decisions are made. As with many social phenomena, some people tend to be more contemplative and thorough, whereas others tend to be more emotional and rash.

References

- Adolphs, R. (2002). Neural systems for recognizing emotion. Current Opinion in Neurobiology, 12, 169–177. http://dx.doi.org/10.1016/ S0959-4388(02)00301-X
- Adolphs, R. (2006). Perception and emotion: How we recognize facial expressions. *Current Directions in Psychological Science*, *15*, 222–226. http://dx.doi.org/10.1111/j.1467-8721.2006.00440.x
- Banissy, M. J., Kanai, R., Walsh, V., & Rees, G. (2012). Inter-individual differences in empathy are reflected in human brain structure. *Neuro-Image*, 62, 2034–2039. http://dx.doi.org/10.1016/j.neuroimage.2012.05 081
- Baron-Cohen, S., & Wheelwright, S. (2004). The empathy quotient: An investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *Journal of Autism and Developmental Disorders*, 34, 163–175. http://dx.doi.org/10.1023/B:JADD .0000022607.19833.00
- Bastiaansen, J. A., Thioux, M., & Keysers, C. (2009). Evidence for mirror systems in emotions. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 364, 2391–2404. http://dx.doi.org/10.1098/rstb.2009.0058
- Batson, C. D., Early, S., & Salvarani, G. (1997). Perspective taking: Imagining how another feels versus imaging how you would feel. Personality and Social Psychology Bulletin, 23, 751–758. http://dx.doi.org/10.1177/0146167297237008
- Batson, C. D., Fultz, J., & Schoenrade, P. A. (1987). Distress and empathy: Two qualitatively distinct vicarious emotions with different motivational consequences. *Journal of Personality*, 55, 19–39. http://dx.doi.org/ 10.1111/j.1467-6494.1987.tb00426.x

- Carr, L., Iacoboni, M., Dubeau, M.-C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 5497–5502. http://dx.doi.org/10.1073/pnas.0935845100
- Craig, A. D.(B.). (2011). Significance of the insula for the evolution of human awareness of feelings from the body. *Annals of the New York Academy of Sciences*, 1225, 72–82. http://dx.doi.org/10.1111/j.1749-6632.2011.05990 x
- Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, 7, 189–195. http://dx.doi.org/10.1038/nn1176
- Dan-Glauser, E. S., & Scherer, K. R. (2011). The Geneva Affective Picture Database (GAPED): A new 730-picture database focusing on valence and normative significance. *Behavior Research Methods*, 43, 468–477. http://dx.doi.org/10.3758/s13428-011-0064-1
- Davis, M. H. (1983). Measuring individual differences in empathy: Evidence for a multidimensional approach. *Journal of Personality and Social Psychology*, 44, 113–126. http://dx.doi.org/10.1037/0022-3514.44.1.113
- Desmond, J. E., & Glover, G. H. (2002). Estimating sample size in functional MRI (fMRI) neuroimaging studies: Statistical power analyses. *Journal of Neuroscience Methods*, 118, 115–128. http://dx.doi.org/ 10.1016/S0165-0270(02)00121-8
- Eisenberg, N., & Eggum, N. D. (2009). Empathic responding: Sympathy and personal distress. In J. Decety & W. Ickes (Eds.), *The social neuroscience of empathy* (pp. 71–83). Cambridge, MA: MIT Press.
- Eisenberg, N., Fabes, R. A., Murphy, B., Karbon, M., Maszk, P., Smith, M., . . . Suh, K. (1994). The relations of emotionality and regulation to dispositional and situational empathy-related responding. *Journal of Personality and Social Psychology*, 66, 776–797. http://dx.doi.org/10.1037/0022-3514.66.4.776
- Evans, J. St. B. T. (2008). Dual-processing accounts of reasoning, judgment, and social cognition. *Annual Review of Psychology*, 59, 255–278. http://dx.doi.org/10.1146/annurev.psych.59.103006.093629
- Fan, Y., Duncan, N. W., de Greck, M., & Northoff, G. (2011). Is there a core neural network in empathy? An fMRI based quantitative metaanalysis. *Neuroscience and Biobehavioral Reviews*, 35, 903–911. http:// dx.doi.org/10.1016/j.neubiorev.2010.10.009
- Gu, X., Gao, Z., Wang, X., Liu, X., Knight, R. T., Hof, P. R., & Fan, J. (2012). Anterior insular cortex is necessary for empathetic pain perception. *Brain*, 135, 2726–2735. http://dx.doi.org/10.1093/brain/aws199
- Hatfield, E., Cacioppo, J. T., & Rapson, R. L. (1993). Emotional contagion. Current Directions in Psychological Science, 2, 96–99. http://dx.doi.org/10.1111/1467-8721.ep10770953
- Jabbi, M., Swart, M., & Keysers, C. (2007). Empathy for positive and negative emotions in the gustatory cortex. *NeuroImage*, 34, 1744–1753. http://dx.doi.org/10.1016/j.neuroimage.2006.10.032
- Kalbe, E., Schlegel, M., Sack, A. T., Nowak, D. A., Dafotakis, M., Bangard, C., . . . Kessler, J. (2010). Dissociating cognitive from affective theory of mind: A TMS study. *Cortex*, 46, 769–780. http://dx.doi.org/ 10.1016/j.cortex.2009.07.010
- Krull, D. S., & Dil, J. C. (1998). Do smiles elicit more inferences than do frowns? The effect of emotional valence on the production of spontaneous inferences. *Personality and Social Psychology Bulletin*, 24, 289– 300. http://dx.doi.org/10.1177/0146167298243006
- Ku, G., Wang, C. S., & Galinsky, A. D. (2010). Perception through a perspective-taking lens: Differential effects on judgment and behavior. *Journal of Experimental Social Psychology*, 46, 792–798. http://dx.doi.org/10.1016/j.jesp.2010.04.001
- Lang, P. J., & Greenwald, M. K. (1993). International Affective Picture System standardization procedure and results for affective judgments (Technical Reports 1A–1C). Gainesville: Center for Research in Psychophysiology, University of Florida.

- Larsen, R. J., Diener, E., & Emmons, R. A. (1986). Affect intensity and reactions to daily life events. *Journal of Personality and Social Psychol*ogy, 51, 803–814. http://dx.doi.org/10.1037/0022-3514.51.4.803
- Lieberman, M. D., & Cunningham, W. A. (2009). Type I and Type II error concerns in fMRI research: Re-balancing the scale. Social Cognitive and Affective Neuroscience, 4, 423–428. http://dx.doi.org/10.1093/scan/ nsp052
- Lundqvist, D., Flykt, A., & Öhman, A. (1998). The Karolinska directed emotional faces. Stockholm, Sweden: Karolinska Institute.
- Mohr, P., Howells, K., Gerace, A., Day, A., & Wharton, M. (2007). The role of perspective taking in anger arousal. *Personality and Individual Differences*, 43, 507–517. http://dx.doi.org/10.1016/j.paid.2006.12.019
- Narumoto, J., Okada, T., Sadato, N., Fukui, K., & Yonekura, Y. (2001).
 Attention to emotion modulates fMRI activity in human right superior temporal sulcus. *Cognitive Brain Research*, 12, 225–231. http://dx.doi.org/10.1016/S0926-6410(01)00053-2
- Ochsner, K. N., Knierim, K., Ludlow, D. H., Hanelin, J., Ramachandran, T., Glover, G., & Mackey, S. C. (2004). Reflecting upon feelings: An fMRI study of neural systems supporting the attribution of emotion to self and other. *Journal of Cognitive Neuroscience*, *16*, 1746–1772. http://dx.doi.org/10.1162/0898929042947829
- Preston, S. D., & de Waal, F. B. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences*, 25, 1–20.
- Preston, S. D., & Hofelich, A. J. (2012). The many faces of empathy: Parsing empathic phenomena through a proximate, dynamic-systems view of representing the other in the self. *Emotion Review*, *4*, 24–33. http://dx.doi.org/10.1177/1754073911421378
- Quartz, S. R. (2009). Reason, emotion and decision-making: Risk and reward computation with feeling. *Trends in Cognitive Sciences*, 13, 209–215. http://dx.doi.org/10.1016/j.tics.2009.02.003
- Saarela, M. V., Hlushchuk, Y., Williams, A. C. C., Schürmann, M., Kalso, E., & Hari, R. (2007). The compassionate brain: Humans detect intensity of pain from another's face. *Cerebral Cortex*, 17, 230–237. http://dx.doi.org/10.1093/cercor/bhj141
- Sebastian, C. L., Fontaine, N. M. G., Bird, G., Blakemore, S.-J., De Brito, S. A., McCrory, E. J. P., & Viding, E. (2012). Neural processing associated with cognitive and affective Theory of Mind in adolescents and adults. *Social Cognitive and Affective Neuroscience*, 7, 53–63. http://dx.doi.org/10.1093/scan/nsr023
- Shamay-Tsoory, S. G. (2011). The neural bases for empathy. *The Neuroscientist*, 17, 18–24. http://dx.doi.org/10.1177/1073858410379268
- Singer, T., Critchley, H. D., & Preuschoff, K. (2009). A common role of insula in feelings, empathy and uncertainty. *Trends in Cognitive Sciences*, 13, 334–340. http://dx.doi.org/10.1016/j.tics.2009.05.001
- Spengler, S., von Cramon, D. Y., & Brass, M. (2009). Control of shared representations relies on key processes involved in mental state attribution. *Human Brain Mapping*, 30, 3704–3718. http://dx.doi.org/10.1002/ hbm.20800
- Spinella, M. (2005). Prefrontal substrates of empathy: Psychometric evidence in a community sample. *Biological Psychology*, 70, 175–181. http://dx.doi.org/10.1016/j.biopsycho.2004.01.005

- Spunt, R. P., & Lieberman, M. D. (2012). An integrative model of the neural systems supporting the comprehension of observed emotional behavior. *NeuroImage*, 59, 3050–3059. http://dx.doi.org/10.1016/j .neuroimage.2011.10.005
- Stanovich, K. E. (2012). Cumulative progress in understanding our multiple minds [Review of the book *Thinking twice: Two minds in one brain*]. *American Journal of Psychology, 125*, 116–121. http://dx.doi.org/10.5406/amerjpsyc.125.1.0116
- Sturm, V. E., Yokoyama, J. S., Seeley, W. W., Kramer, J. H., Miller, B. L., & Rankin, K. P. (2013). Heightened emotional contagion in mild cognitive impairment and Alzheimer's disease is associated with temporal lobe degeneration. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 9944–9949. http://dx.doi.org/10.1073/pnas.1301119110
- Todd, A. R., Bodenhausen, G. V., Richeson, J. A., & Galinsky, A. D. (2011). Perspective taking combats automatic expressions of racial bias. *Journal of Personality and Social Psychology*, 100, 1027–1042. http://dx.doi.org/10.1037/a0022308
- Todd, A. R., Galinsky, A. D., & Bodenhausen, G. V. (2012). Perspective taking undermines stereotype maintenance processes: Evidence from social memory, behavior explanation, and information solicitation. Social Cognition, 30, 94–108. http://dx.doi.org/10.1521/soco.2012.30.1.94
- Van Overwalle, F. (2009). Social cognition and the brain: A meta-analysis. Human Brain Mapping, 30, 829–858. http://dx.doi.org/10.1002/hbm .20547
- Vrtička, P., Sander, D., & Vuilleumier, P. (2012). Influence of adult attachment style on the perception of social and non-social emotional scenes. *Journal of Social and Personal Relationships*, 29, 530–544. http://dx.doi.org/10.1177/0265407512443451
- Webb, T. L., Miles, E., & Sheeran, P. (2012). Dealing with feeling: A meta-analysis of the effectiveness of strategies derived from the process model of emotion regulation. *Psychological Bulletin*, 138, 775–808. http://dx.doi.org/10.1037/a0027600
- Wells, B. M., Skowronski, J. J., Crawford, M. T., Scherer, C. R., & Carlston, D. E. (2011). Inference making and linking both require thinking: Spontaneous trait inference and spontaneous trait transference both rely on working memory capacity. *Journal of Experimental Social Psychology*, 47, 1116–1126. http://dx.doi.org/10.1016/j.jesp.2011.05 013
- Zaki, J., & Ochsner, K. (2009). The need for a cognitive neuroscience of naturalistic social cognition. *Annals of the New York Academy of Sciences*, 1167, 16–30. http://dx.doi.org/10.1111/j.1749-6632.2009.04601.x
- Zaki, J., & Ochsner, K. (2011). Reintegrating the study of accuracy into social cognition research. *Psychological Inquiry*, 22, 159–182. http://dx .doi.org/10.1080/1047840X.2011.551743

Received February 28, 2014
Revision received June 12, 2014
Accepted December 4, 2014