Mentalizing and the Role of the Posterior Superior Temporal Sulcus in Sharing Others’ Embarrassment

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The experience of embarrassment provides a highly salient cue for the human moral apparatus. Interestingly, people also experience embarrassment on behalf of others’ inappropriate conditions. The perceiver’s embarrassment often lacks an equivalent expression of embarrassment in the social counterpart. The present study examines this phenomenon and distinguishes neural circuits involved in embarrassment with and embarrassment for another person’s mishaps. Using functional magnetic resonance imaging, we show that the embarrassment on behalf of others engages the temporal pole and the medial prefrontal cortex, central structures of the mentalizing network, together with the anterior insula and anterior cingulate cortex. In contrast, sharing others’ embarrassment additionally stimulated the posterior superior temporal sulcus (STS), which exhibited increased functional integration with inferior parietal and insular cortex areas. These findings characterize common neural circuits involved in the embodied representation of embarrassment and further unravel the unique role of the posterior STS in sharing others’ affective state.

Keywords: embodiment, empathy/mentalizing, mirroring, superior posterior temporal sulcus, vicarious embarrassment

Introduction

“The age of privacy is over” (Mark Zuckerberg, CEO of Facebook Inc.). Over the last decade, the advent of the internet has dramatically changed the transparency within our social networks. What were previously private flaws and predicaments now easily reach the public, with social consequences for the compromised individuals—but also for witnesses in the audience. The corresponding vicarious reaction of embarrassment on behalf of others’ behaviors has a conceptual and neurobiological overlap with the empathic experience of physical pain (Macdonald and Leary 2005; Krach et al. 2011). As the negative affect of physical pain provides strong signals for injuries of the body, the experience of social pain—and particularly embarrassment—is thought to serve a similar function, but signaling threats to the social integrity (Eisenberger et al. 2003; Macdonald and Leary 2005; Masten et al. 2011; Eisenberger 2012). Notably, the shared etymological background of the terms embarrassment and pain might also provide intriguing evidence for the common nature of embarrassing and physically painful experiences. The High-German term for embarrassment “peinlich” [pain,lic] and the English “pain” both stem from Latin “poena”, for penalty or punishment. In old German, the meaning of “peinlich” originally referred to the experience of physical pain. This is illustrated with the term “peinliche Strafen” [pain,lic ʃraːfən], which in fact referred to death or maiming penalties of German blood courts during the Middle Ages. Over time, the meaning of the term “peinlich” changed to its current usage for describing shameful, mortifying, or embarrassing incidents. Although “observing negative social experiences [as compared to observing others’ physically painful situations] is likely to be a more frequent occurrence” (Masten et al. 2011) in everyday life, so far, surprisingly few studies have investigated the neural mechanisms of vicarious social pain experiences, such as compassion (Immordino-Yang et al. 2009) or social rejection (Beeney et al. 2011; Masten et al. 2011).

In a series of studies, we recently established embarrassment at others’ mishaps as a form of social pain. A good example of this is what we feel when observing a waiter in a fully occupied restaurant stumbling and dropping dishes to the floor (Krach et al. 2011; Müller-Pinzler et al. 2012; Paulus, Kamp-Becker, et al. 2013). In this example, the waiter attracts the attention of the audience under circumstances which are perceived as severely unfavorable for his social image. Here, bystanders experience embarrassment with the waiter (i.e., the waiter is embarrassed and we share this embarrassment). However, a bystander can also experience embarrassment for another, without the other actually experiencing embarrassment. For example, a person walking around with their fly open might not be embarrassed, because he or she does not realize that their zip is open. A perceiver, however, notes the open zip and is well aware of others’ negative evaluations in that very moment, and thus may experience embarrassment for the social target. We have previously argued how both the embarrassment with and for another provide salient and highly relevant emotional cues for threats to another’s social integrity (Paulus, Müller-Pinzler, et al. 2013).

In general, the threat to the social integrity in the context of embarrassment results from the assumed negative evaluations in the eyes of bystanders and hence requires an understanding of the beliefs of these other individuals (Miller 1996; Keltnner and Buswell 1997; Takahashi et al. 2004; Tangney et al. 2007). Accordingly, the earliest conceptualization of embarrassment on behalf of others’ mishaps considered reflections about one’s own and other’s perspective as one of the core mediating mechanisms for the emotional experience in the perceiver (Miller 1987). Neuroscience studies have related such processes to brain structures in the “mentalizing” system. Mentalizing involves adopting the perspective and knowledge of a social target and allows perceivers to build an internal model and to reflect on how the other thinks and behaves in a specific...
situation (Hein and Singer 2008; Keysers and Gazzola 2009; Waytz and Mitchell 2011). Such processes are typically associated with activation of the medial prefrontal cortex (mPFC), the temporo-parietal junction, and the temporal poles (TP; Saxe and Kanwisher 2003; Grèzes et al. 2004; Saxe and Wexler 2005; Frith and Frith 2006). In this respect, the mPFC has been linked to various aspects of social cognition (Frith and Frith 2006; Schilbach et al. 2012), but more specifically to reflective processes about the self and others and their beliefs and values (Mitchell et al. 2005). In this line, first-hand experiences of embarrassment were associated with mPFC engagement (Takahashi et al. 2004), and patients with mPFC damage were found to experience less embarrassment after engaging in inappropriate behaviors (Beer et al. 2006), suggesting a central role of the mPFC in modeling the embarrassment-related negative evaluations in the eyes of others.

The emotional content of social pain experiences while witnessing threats to another’s social integrity engages neural systems comparable with pain empathy (Immundino-Yang et al. 2009; Krach et al. 2011; Masten et al. 2011). Studies confronting participants with physically painful situations of others consistently reported activations of regions involved in the first-hand experience of pain, including the anterior insula (AI), and the anterior cingulate cortex (ACC; Lamm et al. 2011), and when the somatic cause of the pain is explicit, the somatosensory cortices (SI/ II) (Keysers et al. 2010). This neural activation, specifically within the AI, is thought to provide an embodied measure of the aversive quality of another’s physical pain that is consciously accessible (Singer et al. 2004; Saarelta et al. 2007; Akitsu and Decety 2009). Several neuroscience studies have now shown a similar neural network to be engaged in various forms of vicarious social pain, providing the perceiver with an embodied representation of the aversive feeling triggered by threats to others’ social integrity (Immundino-Yang et al. 2009; Beeney et al. 2011; Krach et al. 2011; Masten et al. 2011). This has been conceptually supported by correlates of this network activity with behavioral outcomes, such as helping behavior (Masten et al. 2011), individual differences in trait empathy (Krach et al. 2011), or the status of the relationship between the perceiver and social target (Beeney et al. 2011).

Both components, the representation of the negative affect in the AI and the ACC as well as mentalizing in the mPFC, are important in the context of embarrassment for and with another. However, the two-fold phenomenon affords the opportunity to distinguish neural processes specific to sharing another person’s social pain from those that depend on the appraisals of the perceiver. To exemplify this using the previously described situations, one can imagine the waiter expressing his embarrassment in the first example through appeasement gestures, such as blushing, averted gaze, or covering his face with his hands after dropping the dishes (Keltner and Buswell 1997). Besides the ongoing mentalizing, which allows perceivers to represent the threat to the social target’s integrity in the eyes of others, they can also share the emotional experience during the depicted action, including the sensation, for example, of the social target’s blushing. In the second example, the perceiver’s embarrassment is exclusively triggered by an appraisal of the threat to the image of the social target while walking around with the fly open. In these kinds of situations, there is no possibility for perceivers to share the social target’s embarrassment and related actions and sensations.

The sharing of another’s behavior, emotions, and sensations in this way occurs through a comparatively automatic and reflexive neural route called “mirroring” or “shared circuits.” This route operates through a direct mapping of another’s behavior onto matching motor states in the perceiver’s brain (Gallese et al. 2004; Gallese and Sinigaglia 2011). Mirroring of another’s actions involves premotor, primary, and higher-order somatosensory cortex areas (Grèzes et al. 2003; Dinstein et al. 2007; Filimon et al. 2007; Keysers and Gazzola 2009; Ricciardi et al. 2009; Turella et al. 2009; Caspers et al. 2010; Keysers et al. 2010), and the neural representation of this behavior is thought to trigger emotional states that are normally congruent with this behavior in the perceiver (Carr et al. 2003; Jabbi and Keysers 2008; Jabbi et al. 2008). Within the mirroring system, the superior temporal sulcus (STS), a multimodal region known for its sensitivity to social stimuli like facial expressions, bodily movements, and eye gazes (Puce and Perrett 2003), is thought to be an important source of information in sharing another’s emotions (Keysers and Perrett 2004). The STS has anatomical connections with limbic regions (Freese and Amaral 2009; Ethofer et al. 2011) as well as premotor and parietal cortex areas, which suggest a role of the STS circuits “in the elaboration of affective aspects of social behavior” (Rizzolatti et al. 2001). Accordingly, the posterior portion of the STS, in particular, shows greater activity during abstract and modality-independent representations of others’ emotional states (Peelen et al. 2010; Zaki et al. 2010) and when people share another’s emotional state based on nonverbal information (Zaki et al. 2009).

Based on the above considerations, the conceptual differentiation of embarrassment on behalf of others into embarrassment with and embarrassment for allows two aspects of the neural foundation of social cognition to be studied. Within the interacting routes of the reflective “mentalizing” and reflexive “mirroring” systems (Keysers and Gazzola 2007), on the one hand, we hypothesize mentalizing to be involved in signaling threats to the integrity of the social target. This is independent of the emotional state of the target and is a common requirement for embarrassment with and for another that results in the embodied representation of social pain in both the AI and the ACC. On the other hand, we suggest that the integration of the affective quality occurring while mirroring the social target’s actions and sensations would specifically relate to the embarrassment with condition. This should result in a general enhancement of the shared circuits and of the STS region in particular.

We tested these hypotheses in a sample of 32 adults who processed a previously described embarrassment task during functional MRI (fMRI). Briefly, using a validated set of graphical stimuli showing complex social settings, we manipulated whether a depicted social target experienced embarrassment him- or herself [embarrassment with] another or not [embarrassment for another]. Regardless of the emotional condition of the social target, participants were instructed to rate the intensity of their experience of embarrassment while observing the scene.

Materials and Methods

Participants and Data Acquisition

Thirty-two naive right-handed subjects (undergraduates from the Philipps-University Marburg, 17 females, aged 20–28 years, mean age = 22.81 ± 2.19 years) participated in the fMRI study. Other aspects of
Stimulus Material
Fifty stimuli were selected from a validated set of drawn sketches displaying a social target in a public scenario (Krach et al. 2011). All drawings were based on written vignettes describing the social context of the situation (e.g., “You are at a theatre:”) and the condition of the social target (e.g., “You observe an actor forgetting his words on stage …”). All sketches used in this study were designed in a standardized way such that they fulfilled the following criteria: (1) They display a public scenario, so that other perceivers are present in close vicinity; (2) the observation has an incidental character, so that no association between perceiver and social target could be assumed; (3) they have counterbalanced sex of the social target; (4) the actors were single persons, with two exceptions in which a couple was used instead; and (5) no emotional facial expressions such as smiles or appeasement gestures were present in the sketches. We decided not to display embarrassment-related facial expressions or appeasement gestures, since this behavior typically evolves over the course of a social interaction and is not immediately present in the embarrassing moment.

Ten of the 50 stimuli showed an emotionally engaged embarrassed other. These situations are characterized by high awareness of the social target regarding the threat to his or her social image and the accidental character of the norm transgression [embarrassment with another; EMB WITH]. To elicit embarrassment for another in the absence of embarrassment in the social target [EMB FOR], three different classes of scenarios showed social targets who also accidentally violated a social norm, but were unaware of the ongoing norm transgression or intentionally violated social norms in public either being aware of the transgression or not. Previous studies have shown that perceivers do not attribute embarrassment to the social target in such situations, but nevertheless experience strong states of embarrassment for the target (Krach et al. 2011). The three types of EMB FOR stimulus classes were represented with 10 situations each. For control purposes, 10 neutral scenarios [NEUT] depicting comparable public contexts in the absence of threats to another’s social integrity complemented the stimulus set. For detailed descriptions of the stimulus material, validation procedures, and the embarrassment framework, see Krach et al. (2011) and Supplementary Table 1; for purposes of illustration, one situation of the EMB WITH, EMB FOR, and NEUT condition is displayed in Figure 1A.

fMRI Paradigm
All sketches were presented for 12 s together with the two sentence description of the semantic context of the situation. The text was presented below the drawings in a black nonserif font on a white background. The stimulus presentation was followed by a blank screen for 1 s and a subsequent rating period lasting for 3 s. During the rating period, subjects were asked to evaluate the intensity of their preceding embarrassment experiences (“How strong was your embarrassment from the perceiver’s perspective?” “[Wie stark hast Du Dich fremdgeschämt?”]). In the German language, embarrassment on behalf of others is referred to with the term “Fremdscham”. According to the official German dictionary, “Fremdscham” [ˈfʁɛmtʃaːm] means “To be vicariously ashamed for another, whose manner is perceived as embarrassing” [“Sich stellvertretend für andere, für deren als peinlich empfundenes Auftreten schämen”]. This umbrella term “Fremdschämen” [ˈfʁɛntʃaːmən] thus refers to various social encounters in which another’s social integrity is threatened, and it equally accounts for the EMB WITH and EMB FOR conditions.). Responses were made on a scale ranging from 1 (“not at all”) to 5 (“very strongly”) using a button press of the right hand. A jittered low-level baseline showing a fixation cross for an average of 8 s was interleaved between the rating period and the following trial. Jittering was achieved by an overall TR-asynchronous trial structure and pseudorandomization of the intertrial interval between ±150 ms with SD = 100 ms. Stimuli were presented in a pseudorandomized order, ensuring that no class of situation was immediately repeated and different situations had equal frequency throughout the entire fMRI time series. The total experiment lasted for 22:28 min. Stimuli were presented on an LCD screen with the

Figure 1. Stimulus material and experimental paradigm. (A1) Examples of displayed situations. Subjects see social targets in different scenarios, being embarrassed (embarrassment with, EMB WITH) or not (embarrassment for, EMB FOR), as well as in neutral scenarios (NEUT). The sketches were displayed together with a short description of the situation. For the given examples, these are “You are at the grocery store: a person at the cashier realizes that she cannot pay for her purchase …” (EMB WITH), “You are at the library: the person in front of you is wearing her pants so low that you can see her underwear …” (EMB FOR), and “You are at the library: a person returns some books to the service desk …” (NEUT). (A2) Sequences of the experimental paradigm exemplifying the parametric weighting procedure. The hemodynamic response for each of the situations was weighted with the intensity of the self-report of the embarrassment.
Participants received careful instructions about the experimental procedure outside the scanner using two example situations that were not displayed again during the fMRI session. While observing the social setting, participants were asked to imagine the scenarios as if they were observing the situations in everyday life with the following instruction: “Imagine you are observing the person in the situation. Do you feel vicarious embarrassment in that moment? If yes, how intense is this feeling?” The perspective the participants were asked to take was highlighted in bold (“you”).

fMRI Analyses
fMRI data were analyzed using SPM8 (www.fil.ion.ucl.ac.uk/spm). The first four volumes of the session were discarded from further analyses. The remaining 549 EPI volumes were corrected for timing differences of the slice acquisitions, motion-corrected, and co-registered with the T1 image. The EPI volumes were spatially normalized into MNI space based on the unified segmentation of the co-registered anatomical image (Ashburner and Friston 2005). Normalized volumes were resliced with a voxel size of 3 x 3 x 3 mm, smoothed with an 8-mm full-width half-maximum isotropic Gaussian kernel, and high-pass-filtered at 1/256 Hz.

Statistical analysis was performed using a two-level, mixed-effects procedure. The fixed-effects generalized linear model (GLM) on the individual subject level included six epoch regressors. The regressors modeled the hemodynamic responses to EMB WITH situations, EMB FOR situations, and NEUT situations, as well as the rating period and stimulus presentation with the above-described stimulus durations. The ratings after each situation were entered as parametric modulators of the corresponding preceding situation in order to explain variance in neural activation due to differences in emotional responses on the within-subject level (see Fig. 1B). Six regressors modeling head movement parameters were introduced to account for noise. Individually weighted β-maps of activation differences between the embarrassing and neutral situations, as well as β-maps of the parametric modulators, were analyzed on the second level.

The second-level analyses of activation differences on the group level were conducted with GLMs containing one repeated factor coding the four classes of embarrassment situations. First, in order to identify the network of brain regions involved in EMB WITH and EMB FOR, subjects’ averaged ratings within each class of situation were entered as covariates in the GLM. The four covariates were centered on the mean of each type of situation to explain additional variance induced by individual differences in self-reported embarrassment experiences within each class of situation. Thus, a conjunction analysis of the contrasts of EMB FOR and EMB WITH compared with NEUT was able to identify activated brain regions irrespective of the emotional state of the social target. Secondly, to identify brain regions specifically involved in EMB WITH, a conjunction analysis of EMB WITH contrasted to EMB FOR, and EMB WITH contrasted to NEUT, was conducted. This GLM was controlled for potential mean level differences of the intensity of the perceivers showing a positive effect ($P < 0.05$) in a sphere of 6 mm radius. Time series were high-pass-filtered at 1/256 Hz, mean-adjusted, and variance explained by the movement regressors; moreover, the hemodynamic response function of the rating period was removed with an effect of interest correction. For each time series, the PPI regressor was computed contrasting EMB WITH to EMB FOR (see procedure described in Gitelman et al. (2003)). For each subject, the fixed-effects connectivity GLMs each contained: (1) The original pSTS time series, (2) the PPI time series coding the dynamics in the connectivity of pSTS, (3) the corresponding difference in the hemodynamic response between EMB WITH and EMB FOR, (4) the task-induced hemodynamic responses, and (5) the six head movement parameters. Resulting β-maps of the PPI regressors were analyzed on the group level with a one-sample t-test. Positive effects were examined in order to identify brain regions with a stronger functional integration with the pSTS during EMB WITH compared with EMB FOR. All results of the fMRI activation analyses were corrected for multiple comparisons on the individual voxel level using Gaussian random field theory (family-wise error correction; FWE) as implemented in SPM8. Since we considered the one-factorial design as not optimally powered for the PPI analysis due to increased dependencies between regressors in the design matrix (see O’Reilly et al. 2012), we expected less strong effects for the connectivity analyses. Therefore, we adjusted the correction procedure for the PPI analyses to be less conservative for the magnitude of the effect and instead applied FWE correction on the cluster-extent threshold at $P < 0.005$. All anatomical coordinates are reported in MNI standard space.

Results
The results for the behavioral data indicate strong embarrassment from the perceivers’ perspective in response to all modeled situations (Krach et al. 2011). Notably, participants reported greater embarrassment intensity in the EMB WITH condition (3.50 ± 0.70 SD) compared with EMB FOR (2.84 ± 0.78 SD, repeated-measures ANOVA, post hoc contrast comparing EMB WITH with EMB FOR, $F_{1,31} = 53.35, P < 0.001$). Individual differences in the intensities of the corresponding embarrassment reactions from the perceivers’ perspective were thus controlled for in the fMRI data analyses. Reaction times did not differ between the two experimental conditions (EMB WITH 1039 ± 312 ms SD and EMB FOR 1003 ± 325 ms SD, repeated-measures ANOVA, post hoc contrast comparing EMB WITH with EMB FOR, $F_{1,31} = 1.18, P = 0.286$), but were significantly slower compared with NEUT (716 ± 158 ms SD, post hoc contrast comparing EMB WITH and EMB FOR with NEUT, $F_{1,31} = 28.15, P < 0.001$).

Neural Systems Embarrassment with and Embarrassment for Another
The first hypothesis was that the observation of threats to another’s social integrity activates neural systems involved in mentalizing processes and the embodied representation of the aversive feeling triggered by the mishaps of others. To test this hypothesis, we implemented a conjunction analysis contrasting EMB WITH and EMB FOR to NEUT. Even though we had prior anatomical hypotheses, we chose a conservative threshold and corrected all of the subsequent analyses for multiple comparisons in the whole brain. The results indicated...
consistent activation of those brain systems coding for the negative affect of social pain in the left ACC and the left AI, but also the left thalamus, brainstem, and bilateral cerebellum (repeated-measures GLM, post hoc contrast [EMB WITH – NEUT] ∩ [EMB FOR – NEUT], t(120) > 4.62, P < 0.05, corrected, see Fig. 2 and Table 1). These activations were consistently high and independent of the emotional state of the social target. The activations within the AI (x = −36, y = 26, z = −2

Figure 2. Common activation of embarrassment on behalf of others’ mishaps. (A) Activation of the medial prefrontal cortex (mPFC), ACC, left AI, and sub-cortical structures during observation of threats to the social integrity of target person. Render images display the results of a GLM random-effects analysis of the differences of the neutral (NEUT) situations to embarrassment with (EMB WITH) and embarrassment for another (EMB FOR) in a conjunction analysis ([EMB WITH – NEUT] ∩ [EMB FOR – NEUT]). Results have a threshold at t(120) > 4.62, P < 0.05, FWE corrected. (B) Parameter estimates at the peak of significant effects for the EMB WITH and EMB FOR conditions. Parameter estimates show mean ± SEM.

Table 1

<table>
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<tr>
<th>Anatomical region</th>
<th>Cyto area</th>
<th>Side</th>
<th>Cluster size</th>
<th>MNI coordinates</th>
<th>T-value</th>
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Note: All P-values are family-wise error-corrected and displayed for the peak voxels within each cluster. Statistics for the common activation were obtained with a conjunction analysis contrasting embarrassment with and embarrassment for another to the neutral condition for clusters k > 21. The statistics of the parametric modulations are derived from the average effect of the parametric weights for both conditions. The Cyto area column indicates the assigned cytoarchitectonical area as indicated by the SPM ANATOMY toolbox v1.8 if available (Eickhoff et al. 2005). Anatomical labels were derived respectively.
mm) and the ACC ($x = -3, y = 14, z = 55$ mm) were in good accordance with previous meta-analytic findings on empathy for bodily pain [Lamm et al. (2011) found $x = -40, y = 22, z = 0$ mm as the peak coordinate for the AI and $x = -2, y = 23, z = 40$ mm for the ACC]. Furthermore, social target state-independent activation was found in the left mPFC ($x = -6, y = 56, z = -22$ mm) and TP ($x = 45, y = 17, z = -29$ mm). To verify that the above effects were not due to deactivations during the neutral condition, we also explored the responses to the neutral condition within all significant clusters. Within the activated network, we also found robust positive responses to the neutral condition, indicating that the above effects were, in fact, due to increased hemodynamic responses during the EMB WITH and EMB FOR conditions (see Supplementary Table 2 and Supplementary Fig. 1).

To further substantiate the above findings, we analyzed whether the intensity of the embarrassment at threats to another’s social integrity was associated with neural activation of areas involved in embodied representations of the negative affective quality of social pain (see Fig. 1B). As expected, the average effect of parametric weights showed a consistent positive association with hemodynamic responses of the right and left AI as well as a large cluster in the ACC [repeated-measures GLM, average effect of the parametric modulators within EMB WITH and EMB FOR, $t_{(123)} > 4.64, P < 0.05$, corrected]. Furthermore, positive associations were found in the bilateral inferior parietal lobe (IPL) extending to the left parietal operculum at $x = -51, y = -31, z = 25$ mm and the right dorsolateral prefrontal cortex (DLPFC, see Fig. 3 and Table 1). No statistically significant negative associations were found.

**Specific Responses to Embarrassment With and Embarrassment For Another**

The second hypothesis was that the observation of another’s social pain experience activates neural systems that are specifically involved in mirroring the emotional state of the social target. To test this hypothesis, we compared EMB WITH with EMB FOR and NEUT. The results showed a specific reactivity of the bilateral pSTS (repeated-measures GLM, post hoc contrast [EMB WITH − EMB FOR] $\cap$ [EMB WITH − NEUT], $t_{(123)} > 4.61, P < 0.05$, corrected, see Fig. 4, Table 2, and Supplementary Fig. 2). We also explored the reverse contrast and found stronger activation of the left amygdala in EMB FOR compared with EMB WITH and NEUT (repeated-measures GLM, post hoc contrast [EMB FOR − EMB WITH] $\cap$ [EMB FOR − NEUT], $t_{(123)} > 4.61, P < 0.05$, corrected). Notably, these specific activations were controlled for effects of differences in the intensity of the perceivers’ embarrassment experience during the EMB WITH and the EMB FOR conditions (see Methods).

Based on these findings, we further examined the dynamics of the functional interactions of the activated pSTS clusters. To this aim, we conducted PPI analyses contrasting the functional connectivity of the bilateral pSTS in the context of EMB WITH and EMB FOR. The results show the right pSTS to have significantly greater signal correspondence, specifically with the bilateral IPL, and the left posterior and middle insular cortex in the EMB WITH condition (see Fig. 5 and Table 2). These clusters were sufficiently large to survive the corrected cluster-extent threshold [one-sample $t$-test, $t_{(31)} > 2.74, P < 0.005$ uncorrected, $k \geq 415$]. A region of interest (ROI) analysis within the brain regions activated by the conjunction ([EMB WITH − NEUT] $\cap$ [EMB FOR − NEUT]) also revealed stronger correlations of the BOLD response with the left AI [one-sample $t$-test, $t_{(31)} = 3.28, P = 0.025$, corrected within ROI]. For the left pSTS, a similar pattern was observed; however, this was significant only at the uncorrected threshold. There were no significant effects for the PPI contrasting EMB FOR with EMB WITH, either for the left or the right pSTS. Finally, we conducted an exploratory PPI analysis for the left amygdala (see Supplementary Methods), but did not find any positive or negative effects at corrected thresholds.

**Figure 3.** Variability in the hemodynamic responses positively related to the intensity of the self-reported embarrassment participants felt while watching the situation. (A) Render images display the average effect of a GLM random-effects analysis of the parametric weights with a threshold at $t_{(123)} > 4.64, P < 0.05$, FWE corrected. Significant associations were found in the ACC, bilateral AI, bilateral IPL, and the right DLPFC. (B) Parameter estimates at the peak of the effects for the embarrassment for and the embarrassment with condition. Parameter estimates show mean ± SEM.
The ability to extract subtle behavioral cues from complex social environments in order to evaluate the appropriateness of one’s own and others’ behaviors forms a foundation for sociability and contingent behavior. People’s display of embarrassment provides such a cue. However, in everyday life, there is a broad range of situations in which people exhibit flaws, blunders, or norm violations without displaying any signs of embarrassment about their actions. Nevertheless, perceivers experience embarrassment on behalf of another. With the current study, we provide new insights into common and dissociated neural processes of these forms of social pain.

On the broadest level, the present results highlight that areas involved in empathizing with others’ physical pain, the AI and the ACC (Lamm and Singer 2010), as well as those associated with the inference about another person’s mental state, the mPFC and TP (Lieberman 2007; Hein and Singer 2008), consistently respond to threats to another’s social integrity. These results confirm previous neuroscience studies using social rejection to induce social pain from the first-person perspective.
brain systems linked to processes of mentalizing. The latter areas that code the affective quality of the social suffering and general role related to re-

From the expected negative evaluations in-the-eyes-of-others the perceiver (Immordino-Yang et al. 2009; Beeney et al. 2011; Masten et al. 2011). This shared evidence corroborates that social pain from the perceiver’s perspective involves activation both within areas that code the affective quality of the social suffering and brain systems linked to processes of mentalizing. The latter particularly gains relevance in the context of embarrassment at others’ flaws, because threats to one’s social integrity result from the expected negative evaluations in-the-eyes-of-others (Miller 1996; Keltner and Buswell 1997; Takahashi et al. 2004; Tangney et al. 2007). Here, the mPFC and the TP have a general role related to reflecting about oneself in the context of a complex social scenario (Finger et al. 2006), which is the dominant feature of the embarrassment experience from the perceiver’s perspective (Krach et al. 2011). The mPFC, specifically, has been associated with the processing of social event knowledge (Krueger et al. 2009), a fundamental component in generating assumptions about the do’s and don’ts of social situations. Accordingly, patients with extensive damage to mPFC have been reported to experience less embarrassment after engaging in inappropriate behavior compared with controls (Beer et al. 2006). Neuroimaging evidence further suggests that the mPFC is consistently engaged in recalling experiences from the past (Schacter et al. 2007), as well as reflecting about one’s own and others’ future events (Buckner and Carroll 2007). Intriguingly, this mPFC engagement is in line with the earliest conceptualization of embarrassment on behalf of others’ mishaps, which already considered reflections about one’s own past experiences (Miller 1987).

With the present results, we extend previous evidence by showing that the neural signaling of the AI and the ACC does not exclusively represent the empathic component of sharing others’ social pain experiences. The consistent response, regardless of the emotional state of the social target, clearly indicates that perceivers also generate their representation of threats to another’s social integrity based on their own evaluation of the social setting (i.e., embarrassment for another). This notion has already been discussed in recent conceptualizations of mentalizing processes (Waytz and Mitchell 2011; Paulus, Müller-Pinzler, et al. 2013). In this line, previous studies demonstrated that the AI and ACC activation is not specific to perceived threats to another’s physical or social integrity, but is similarly involved in observing others’ happiness (Jabbi and Keysers 2008; Mobbs et al. 2009) or sharing of others’ disgust experiences (Wicker et al. 2003; Jabbi and Keysers 2008). We therefore interpret the activity in the AI and the ACC rather as an embodied representation of affect (Craig 2003, 2009), which, as we show, may not necessarily map the social target’s affective state in an isomorphic fashion. This dissociation is supported by previous studies on vicarious physical pain, which demonstrated that the affective responses within the AI and ACC are modulated by perceivers’ evaluations of the social setting (Singer et al. 2006; Cheng et al. 2007; Lamm et al. 2007).

The correspondence between the subjectively experienced embarrassment on behalf of others’ mishaps and the neural signaling of the AI, ACC, and the IPL exactly reproduces the results previously found for empathy for physical pain (Saarela et al. 2007) and extends these findings to the domain of social pain. This evidence supports the notion that neural activation of these regions—and specifically the AI—forms an embodied measure of affective states that are consciously accessible (Craig 2009) and hence can be articulated in the context of the present experiment. Moreover, the correlations at the within-subject level primarily emerged in limbic structures rather than in the mPFC and the TP. This dissociation corresponds with the assumption that the affective resonance to another person’s state and reflections on others’ mental states are processed in distinct neural networks (Zaki and Ochsner 2012). Notably, our findings suggest that intense embarrassment experiences at others’ mishaps are necessary to reveal IPL activation extending to the parietal operculum. This finding is in line with recent evidence, indicating that the first-person experience of social pain shares somatosensory cortex activation with physical pain if it is sufficiently strong (Kross et al. 2011).

In contrast to the context-independent response of areas within the mentalizing system to threats of another’s social integrity, our results show a specific activation of the pSTS region during the embarrassment with condition. While this activation could, on the one hand, support our hypothesis of an enhancement of the mirror system in the embarrassment with condition, one need to consider that the STS region is not only part of the mirror system, but also involved in other socially relevant tasks. In support of the mirror enhancement hypothesis, the pSTS—as a multimodal integration site—has been ascribed a specific role for the evaluation of the affective quality of another’s actions and sensation within the mirroring circuits (Rizzolatti et al. 2001). In our stimuli, the amount of mirroring processing devoted to an embodiment of the actions and sensations of the target as well of bystanders is comparable for the embarrassment for and with condition. The main difference between the embarrassment with and for condition is the evaluation of the affective state of the target in the embarrassment with condition. This would explain why we did not observe an overall change in the strength of the activation of the shared circuit but a specific involvement of the pSTS region. This interpretation fits with previous studies suggesting a role of STS in representations of others’ emotions as presented by Peelen et al. (2010) as well as Zaki et al. (2010). On the other hand, imaging and lesion studies have also associated pSTS functioning with the observation of biological motion, such as facial expressions and bodies (Pelphrey et al. 2003, 2005) or detection of eye gaze (Bonda et al. 1996;
Allison et al. 2000; Hoffman and Haxby 2000). In the context of these studies, one explanation for the present findings might be that perceivers predict what the social target would do next out of the embarrassed state, that is, averting the gaze or displaying appeasement gestures. However, representations about possible upcoming actions within the social target are inherent to all of the social scenarios presented here, including the neutral, embarrassment with, or embarrassment for condition. This should render the alternate explanation for the pSTS response as exclusively resulting from inferred biological motion in the stimuli rather unlikely. Instead, we suggest that evidence on the movement of bodies and faces, as well as eye-gaze behavior, might contain an emotional connotation, and the pSTS activity within the mirroring circuits could at least partly be modulated by “the emotional content of an action” (Blake and Shiffrar 2007). In fact, facial expressions, body postures, and eye-gaze behavior are fundamental sources for the expressions of internal affective states in the social target (Keltner 1995), which should prompt inferences about the affective content of the action in the perceiver.

This notion finds support from the dynamics of the functional connectivity of the pSTS. While sharing the embarrassment of the social target, the right pSTS has greater functional integration with the bilateral IPL, left posterior and middle insula, and the left AI. This context-dependent increase of the functional coupling within the anatomical network of the pSTS corresponds to previous findings on the dynamics in the functional connectivity while processing social aspects of eye gaze (Ethofer et al. 2011). The role of the pSTS in representing others’ emotional states (Peelen et al. 2010; Zaki et al. 2010) and the observed increase in functional coupling with the IPL and the AI suggests that these shared representations drive the emotional experience in perceivers. Previous studies have interpreted AI activation as indicative of sharing another’s emotion in an isomorphic fashion (Wicker et al. 2003; de Vignemont and Singer 2006). However, the AI has a very broad connectivity (Cerlani et al. 2012), and activity there can be elicited through a variety of routes, including mirroring circuits, but also more cognitive routes, when emotions are triggered by verbal information about another’s situation (Jabbi et al. 2008). As we have shown, the AI activation does not necessarily depend on perceiving and thus mirroring an emotion in the social target, which refines our understanding of these activations in the context of social emotions. Our data confirm that different routes, including mirroring another’s emotion and/or generating an emotion based on one’s own appraisals, might result in similar outcomes with regard to measures of neural activity in the interoceptive cortex.

In this line, we conclude that the amygdala may also play an important role in triggering emotions during embarrassment for another. The amygdala is strongly anatomically interconnected with the AI, and a large body of evidence from lesion and neuroimaging studies has already demonstrated the role of the amygdala in the generation and self-initiation of emotions (Ochsner et al. 2009). This is compatible with the specificity of the amygdala’s activation in the present study, but it remains unclear whether the amygdala activity triggered the insula activity or vice versa.

Taken together, the present study provides new insights on the neural foundations of embarrassment with and embarrassment for another person’s mishaps. Paralleling previous work on social pain, our results indicate that the embarrassment at threats to another’s social integrity yielded cortical activation in networks that represent an embodied measure of affective states. Thereby, the social pain experience basically depends on the perceiver’s perspective. The possibility to induce embarrassment for another, with the other not experiencing embarrassment him- or herself, allowed insight to be gained into the unique role of the pSTS in representing another’s affective state and distributing information across the parietal and insular system.

Author’s Contributions
F.M.P. and S.K. designed the experiment. F.M.P., L.M.P., A.J., and S.K. prepared and conducted the experiment. F.M.P., L.M., P., and S.K. analyzed the data and wrote the paper with V.G. All authors discussed the results.

Supplementary material
Supplementary material can be found at http://www.cercor.oxfordjournals.org/online.

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Notes
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References