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Modulations of Neural Circuits in Response to Own and Others' Social Predicaments

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THE SOCIAL EMOTION OF EMBARRASSMENT

MODULATIONS OF NEURAL CIRCUITS IN RESPONSE TO OWN AND OTHERS' SOCIAL PREDICAMENTS

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The Social Emotion of Embarrassment
Modulations of Neural Circuits in Response to Own and Others’ Social Predicaments

Embarrassment is a so called social emotion arising during the interaction with our surrounding social world. It is present in various situations in our daily lives and holds a regulative function telling us how to perform according to prevalent norms and moral values. Due to the human ability to infer and share others' emotions, thoughts or intentions embarrassment is often also experienced vicariously for others.

This thesis is focused on the neural and physiological correlates of embarrassment and its vicarious form. The main focus thereby lies on treating both as social phenomena and the implementation and development of social paradigms. The results show that during embarrassment and its vicarious form two neural networks are involved, the mentalizing network, potentially mapping the component of thinking about the others’ evaluations, and a network comprised of anterior insula and anterior cingulate cortex, potentially mapping the component of affective arousal. Both networks interacted with ventral aspects of the anterior insula and the amygdala, areas closely related to emotion processing, during the first-hand experience of embarrassment. Further, the studies could show that social closeness affected processing of vicarious embarrassment and increased interoceptive sharing of another’s embarrassment, while individuals with a diagnosis of autism spectrum disorder show deficient processing of vicarious embarrassment. Increased levels of trait social anxiety were associated with increased activations of the mentalizing network, potentially corroborating the assumption of heightened attention to social cues and negative thoughts about others’ evaluations in social anxiety disorder.

De sociale emotie van schaamte
Modulatie van neurale circuits in reactie tot iemands eigen en andermans sociaal benarde situaties

Schaamte is een zogenaamde sociale emotie die ontstaat tijdens interacties met onze sociale omgeving. Het is aanwezig in verschillende situaties in ons dagelijks leven en vervult een regulerende functie die ons informeert over hoe we presteren ten opzichte van de geldende normen en waarden. Door het menselijk vermogen om emoties, gedachten en intenties van anderen af te leiden en te delen, wordt schaamte vaak ook plaatsvervangend ervaren.

Deze thesis richt zich op de neurale en fysiologische correlaten van schaamte en diens plaatsvervangende vorm. De focus ligt hierbij voornamelijk op het behandelen van beide vormen van schaamte als een sociaal fenomeen en de implementatie en ontwikkeling van sociale paradigma’s hiervoor. De gepresenteerde resultaten laten zien dat zowel bij zelf ervaren schaamte als bij plaatsvervangende schaamte twee neurale netwerken betrokken zijn: het mentalisatie netwerk, dat verantwoordelijk is voor het begrip van andermans evaluaties en oordelen, alsook een netwerk bestaande uit de anterieure insula en de anterieure cingulate cortex, dat verantwoordelijk is voor de affectieve opwinding. Beide netwerken interacteren met het ventrale deel van de anterieure insula en de amygdala, gebieden die nauw betrokken zijn bij het verwerken van emoties wanneer zelf schaamte ervaren wordt. De resultaten laten ook zien dat sociale verbondenheid tussen personen invloed heeft op het verwerken van plaatsvervangende schaamte en resulteert in het verhoogd mee-ervaren van iemand anders’ schaamte, terwijl individuen met autisme spectrum stoornis een gebrekkige verwerking van plaatsvervangende schaamte vertonen. Verhoogde sociale angst als karaktereigenschap wordt geassocieerd met verhoogde activatie van het mentalisatie netwerk. Dit bevestigt de aanname dat verhoogde aandacht voor sociale cues en voor negatieve gedachtes over andermans oordeel een rol speelt bij sociale angst stoornissen.

TABLE OF CONTENTS

CHAPTER 1

INTRODUCTION

CHAPTER 1

As human beings we have the capacity for introspection and self-knowledge and are able to evaluate ourselves and our behavior in the context of our surrounding social world. From the moment we are able to comprehend what others think of us, we often care about their opinions. This is a useful trait considering that the way others treat us typically depends on what they think of us. Caring about others' thoughts can therefore help us to control the impressions we make and how we are perceived (Leary & Kowalski, 1990). At the same time these complex capacities make us susceptible to the "possibly uniquely human emotion of embarrassment" with its "uncomfortable aroused state of mortification, abashment, and chagrin" (Miller, 1996).

1.1. EMBARRASSMENT

Embarrassment is an unpleasant feeling that arises when one behaves in a clumsy and unflattering way and fails to uphold one's public image in a social situation (Leary & Kowalski, 1995; Miller, 1996). Embarrassment, among guilt, pride or shame is a so called social emotion and is present in various situations in our daily lives. It functions as an emotional moral barometer, which tells us how we perform according to prevalent norms and moral values (Tangney, Stuewig, & Mashek, 2007) being it at school or work (Pekrun, 2006) or during leisure time. Social emotions require individuals to perceive and evaluate themselves in the context of others and by this require self-referential thoughts. Therefore, previous research has framed embarrassment, shame, guilt, and pride also as self-conscious emotions (Tracy & Robins, 2004). These emotions often arise in context of other human beings and gain a particular relevance during direct social encounters because they regulate social interactions (Keltner & Buswell, 1997; Keltner & Haidt, 1999; Tracy & Robins, 2004). The experience of embarrassment for example has a two-fold function for regulating interpersonal behaviors. On the one hand, it enforces people to behave in compliance with current social norms and etiquettes and, on the other hand, it motivates people to engage in reparative actions to restore one's social image after a deviation from a normative standard has been recognized and triggered embarrassment (Keltner & Buswell, 1997). The latter is supported by bodily and facial expressions, so called appeasement gestures that are clearly linked to embarrassment. These are controlled smiles, lowering of the head, and orienting the gaze downwards (Keltner & Buswell, 1997). Individuals who express their embarrassment through these appeasement gestures in response to an unwanted mishap are judged later on as more likeable and social, accordingly (Feinberg, Willer, & Keltner, 2012; Semin & Manstead, 1982). However, besides these positive effects for behavioral adaptations to the social world, embarrassment is also related to maladaptive consequences under certain circumstances: Excessive and persistent concerns about the evaluations of others are a hallmark of social anxiety disorders and individuals suffering from social anxiety disorder fear embarrassment to the point they feel discomfort in almost every social encounter (Morrison & Heimberg, 2013). In affected individuals the fear of the embarrassment experience can even lead to social withdrawal and depression (Schneier, 1992) with the result that social anxiety disorders are a major burden for individuals and society (Kessler et al., 2005).

The aim of this work (see specifically **chapter 2**) was to characterize the physiological and neural processes of embarrassment. To this end we decomposed the emotion of embarrassment into a physiological, affective component and a cognitive component and will describe the conditions, under which embarrassment emerges in everyday live. According to current models of embarrassment, two factors need to converge to evoke embarrassment. The first one is the deviation from personal standards and failing to show appropriate behavior such as physical pratfalls, loss of control over the body, or cognitive shortcomings. The second is the publicity of the observed behavior, which motivates individuals to think about others' evaluations (Miller, 1996).

At its core the cognitive aspects of embarrassment comprise thoughts about the expected negative evaluation in-the-eyes-of-others (Tangney et al., 2007) during 'public deficiencies' (Miller, 1996). Mental-state attribution is therefore the lynchpin of the social emotion of embarrassment (Tangney et al., 2007). While thinking about another person's state of mind and putting oneself in the mental world of the other the medial prefrontal cortex (mPFC) and the precuneus, both areas of the so-called "mentalizing network", are involved (Frith & Frith, 1999; Frith & Frith, 2003). The few studies examining the neural underpinnings of embarrassment could show that these brain areas in the mentalizing network were active while processing embarrassment (Finger, Marsh, Kamel, Mitchell, & Blair, 2006; Takahashi et al., 2004).

The failure to show behavior in correspondence with one's own expectations and in compliance with the prevalent social etiquettes and norms elicits the component of affective physiological arousal of embarrassment (Edelmann, 1987; Miller, 1996). On the somatovisceral level embarrassment is associated with increased heartrate (Gerlach, Wilhelm, & Roth, 2003; Harris, 2001), increased skin conductance levels (Hofmann, Moscovitch, & Kim, 2006; Mulkens, De Jong, & Bögels, 1997; Shearn, Bergman, Hill, Abel, & Hinds, 1990), and blushing (Drummond, 1997; Shearn et al., 1990), altogether supposedly a general pattern of broad sympathetic activation and vagal withdrawal (Kreibig, 2010). On the neural systems level the conscious representation of affective physiological arousal is associated with increased activation of the anterior insula and anterior cingulate cortex (ACC) (Craig, 2009). Previous studies could show that the insula receives input from sensory cortical areas as well as the thalamus (Kelly et al., 2012). Information is then re-represented along the posterior to anterior axis of the insula and it was suggested that the anterior end, the AI, helps to generate a consciously accessible representation of one’s own bodily and affective states (Craig, 2009; Critchley, 2005; Harrison, Gray, Gianaros, & Critchley, 2010; Lamm & Singer, 2010). Recent neuroimaging studies and meta-analytic evidence point to a functional and anatomical subdivision of the AI into a dorsal aspect and a ventral aspect (Cerliani et al., 2012; Kelly et al., 2012; Kurth, Zilles, Fox, Laird, & Eickhoff, 2010). The dorsal anterior insula (dAI) seems to be involved during attention tasks and cognitive functions but also during social-emotional and interoceptive functioning (Kurth et al., 2010; Touroutoglou, Hollenbeck, Dickerson, & Feldman Barrett, 2012) not responding in a task-specific manner but rather to cognitively, interoceptively, or emotional salient events that require somatovisceral changes (Craig, 2009; Seeley et al., 2007). Therefore the dAI can also be referred to as a part of the arousal network. The arousal network should therefore be active whenever the current behavior deviates from the own expectations, namely during perceived failures eliciting the affective physiological arousal of embarrassment.

Meta-analyses of imaging data consistently show that specifically ventral aspects of the AI (vAI), which are densely connected to the amygdala (Cerliani et al., 2012; Mesulam & Mufson, 1982), are involved in emotional processing (Chang, Yarkoni, Khaw, & Sanfey, 2013; Kelly et al., 2012). There is also substantial evidence showing the amygdala’s involvement in processing many different positive and negative emotions (Adolphs, Tranel, Damasio, & Damasio, 1995; Morris et al., 1998; Phan, Wager, Taylor, & Liberzon, 2002) as well as to exhibit increased firing in contexts, in which participants are potentially evaluated by others (Guyer et al., 2008; Lorberbaum et al., 2004). Hence, these (para-)limbic areas (vAI and amygdala) should play a critical role in the specific integration of both components, the cognitive evaluation of others’ thoughts and the affective arousal during one’s ‘public failures’.

Several studies could demonstrate that the AI and amygdala were associated with the experience of anger (Damasio et al., 2000), disgust (Wicker et al., 2003), and fear (Adolphs, 2008). However, previous studies on embarrassment were not able to find any evidence for an involvement of these brain areas (Finger et al., 2006; Takahashi et al., 2004). One explanation for this non-finding could be that these studies made use of the traditional ‘spectator approach' of social neuroscience. With this spectator approach the participants' brain activity is measured in social isolation while they are viewing pictures, movies, or vignettes of social situations. Embarrassment, in particular, requires one to fail in front of a judging audience and is therefore also defined by the social context and real-life interactions. The spectator approach might thus fail to induce the genuine embarrassment experience and lacks the emotional significance (Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012; Schilbach et al., 2013). Previous studies therefore might have captured some of the cognitive aspects of embarrassment but failed to induce the full blown unpleasant experience of physiological arousal and strong affectivity, which usually accompanies embarrassment. One goal of this work therefore was to overcome this hindrance by implementing a socially interactive fMRI paradigm in **chapter 2** (Krach, Müller-Pinzler, Westermann, & Paulus, 2013).

1.2. VICARIOUS EMBARRASSMENT

Surprisingly, during the last decade it was not the embarrassment from the first person perspective but the *vicarious* experience of embarrassment from the third person perspective that has gained increased scientific and media attention. Famous TV shows like "American Idol" or social networks like "Facebook" show that observing others' mishaps or following another person presenting him- or herself in an inappropriate manner can elicit embarrassment on behalf of another without being in an awkward situation oneself. Notably, a bystander thereby can experience emotions vicariously for another, without the other actually experiencing the same emotion. For example, a person walking around with his/her flies open might not be embarrassed, because he/she doesn't realize that his/her zip is open. Although such vicariously embarrassing situations are not a new phenomenon, as recently as 2009, this vicarious emotion was included in German dictionaries and referred to as "Fremdscham" (Bibliographisches Institut GmbH, 2011) due to its increasing usage in colloquial language. After embarrassment from the first-person perspective has been examined using a novel socially immersive experimental paradigm (**chapter 2**), the last chapters of this work (**chapter 3**, **chapter 4**, **chapter 5**, and **chapter 6**) concentrate on the phenomenon of *vicarious* embarrassment.

It was argued that the experience of embarrassment as a form of social pain has similarities with bodily pain (Krach et al., 2011; Macdonald & Leary, 2005). From a conceptual point of view this is not surprising since social pain signals a threat to one's social integrity similar to how physical pain has the function to alarm one's bodily injuries (Macdonald & Leary, 2005). Therefore the scientific examinations of vicarious embarrassment can now draw on a large body of literature on empathy for others' feelings, especially empathy for bodily pain (Singer et al., 2004). However, more recent studies also examined the neural underpinnings of empathy for social pain (Beeney, Franklin, Levy, & Adams, 2011; Eisenberger, Lieberman, & Williams, 2003; Immordino-Yang, McColl, Damasio, & Damasio, 2009; Masten, Morelli, & Eisenberger, 2011).

Most studies rely on empathy as a core process, by which individuals infer others' affective states through generating an isomorphic affective state themselves (Engen & Singer, 2012). This happens while being fully aware that the cause of this affective state lies not in oneself but in the other. Mainly two separate but interacting processes enable us to share others' affective states (Engen & Singer, 2012; Paulus, Müller-Pinzler, Westermann, & Krach, 2013). Both processes are different ways of simulating another's affective state using one's own body (Waytz & Mitchell, 2011). First, so-called "mirroring" processes are a direct mapping of another person's observed actions or affective states onto one's own neural system using "shared circuits". This allows sharing the other's states in an embodied manner (Engen & Singer, 2012; Keysers & Gazzola, 2009). The AI and ACC for example exhibit characteristics of "shared circuits" and show increased activations while experiencing an affective state oneself and empathically sharing the same state with another person (Singer et al., 2004; Wicker et al., 2003). Second, another person's affective state can be inferred by generating a cognitive representation of the other's supposed mental state engaging "mentalizing" processes (Engen & Singer, 2012; Keysers & Gazzola, 2007; Waytz & Mitchell, 2011). This is particularly the case when there is a lack of direct perceptual evidence that could provoke mirroring. Cognitively inferring or theorizing about another's mental state is associated with activations of the mentalizing network and projecting oneself in the other's positions helps intuitively grasping the other's emotions as if they were one's own (Waytz & Mitchell, 2011). Following this, mentalizing can result in mapping another's affective state in the own "shared circuits" in the AI and ACC.

An earlier study could show that vicarious embarrassment was associated with increased activations of the AI and ACC similar to other empathic affective states (Krach et al., 2011). Additionally areas of the mentalizing network were involved during vicarious embarrassment. As described above, this might be due to the fact that the observed person's affective state was inferred relying on mentalizing processes since there has been few perceptual evidence for embarrassment like facial expressions or gestures in the stimulus material (Krach et al., 2011). On the other hand mentalizing should be involved during embarrassment in any case and activations could be due to thoughts about the surmised negative evaluations in-the-eyes-of-observers during one's mishaps (Miller, 1992; Tangney et al., 2007).

Somatovisceral responses of vicarious embarrassment might be broad sympathetic activations similar to those of embarrassment in the first person. But there are only few studies directly investigating the somatovisceral correlates of vicarious embarrassment. Two studies could report elevated skin conductance levels or response numbers during vicarious embarrassment, elicited when participants watched previously recorded videos of another person singing (Miller, 1987; Shearn, Spellman, Straley, Meirick, & Stryker, 1999). In general, emotion specific physiological response patterns are supposed to be functional in preparing the individual for adaptive actions and shape the execution of particular behaviors (Critchley, 2009), in case of embarrassment reparative actions (Keltner & Buswell, 1997). Since somatovisceral responses are specifically patterned and depend on the exact situation and emotion (Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000; Stemmler, Aue, & Wacker, 2007; Stemmler, Heldmann, Pauls, & Scherer, 2001), in **chapter 3** we examined how differential appraisals of situations affect physiological response patterns of vicarious embarrassment.

1.2.1. Perspective taking in vicarious embarrassment

Although the terms "empathic emotions" (e.g. Hein & Singer, 2008; Lamm, Batson, & Decety, 2007) and "vicarious emotions" (e.g. Keysers & Gazzola, 2009; Meyer et al., 2012; Niedenthal & Brauer, 2012) have been used with the almost identical meaning, empathy, i.e. sharing another's affective state, only refers to a small amount of vicarious emotions people may experience while interacting with their social environment (Paulus et al., 2013; Singer & Lamm, 2009). In many social situations observers might feel vicarious emotions in the absence of this specific emotional state or even any emotions in the social target. In case of vicarious embarrassment the social target would be unaware of the ongoing etiquette violation or not be sharing the same normative frame of reference with the observer and therefore is not embarrassed by the own behavior. Observing a person unconsciously walking around with their flies open might induce a strong experience of vicarious embarrassment in the observer without the other experiencing any emotion (Krach et al., 2011). A similar effect could be demonstrated when participants observed needle stitches in an anesthetized hand and vicariously felt pain for someone who is not feeling anything at all (Lamm, Nusbaum, Meltzoff, & Decety, 2007). Mentalizing as well as mirroring processes are a simulation of others' affective states using one's own body, therefore having a strong subjective component

(Bastiaansen, Thioux, & Keysers, 2009). Taking this into account makes it easier to understand why egocentrically biased vicarious emotions can arise in the observer. Using one's own subjective experiences and frame of reference as a starting point is also called subjective "anchoring". Exactly similar situations should elicit cognitive representations and affective experiences that substantially deviate across different observers because observers have idiosyncratic learning experiences and subjective views of the situation. Depending on the appropriateness of the initial simulation (anchoring) observers can serially "adjust" their internal representation to a certain degree to account for differences between themselves and others and eventually generate a shared experience (Epley, Keysar, Van Boven, & Gilovich, 2004; Paulus et al., 2013).

Empathy enables us to predict and understand others' behavior and react in an appropriate way constituting an important contribution to successful social interaction (Engen & Singer, 2012). But even non-shared, vicarious emotions can provide useful information for observers, enable helping behavior, and facilitate social interactions. While the social target might not adapt his/her behavior appropriately, observers are able to learn from the other's behavior by suffering vicariously. In case of embarrassment the observer can experience a threat to the other's social integrity and this may even help to motivate observers to intervene in order to re-establish the other's social integrity (e.g. making someone aware about the open flies; Paulus et al., 2013). Not only empathic but also vicarious embarrassment can thereby regulate social behavior and help maintaining social structures. In **chapter 4** we directly compared empathic embarrassment experienced *with* another person and vicarious embarrassment *for* another person. In line with the above considerations, we expected involvement of the mentalizing network during both vicarious and shared embarrassment independent of the emotional state of the target, which results in an embodied representation in both the AI and ACC. During shared embarrassment, however, we expected enhanced mirroring of the social target's actions and sensations, because in contrast to a non-emotional target's actions they should provide information about the emotional state the social target experiences. This should result in increased activations of the "shared circuits" of AI and ACC and the STS region, due to its role in processing of multimodal social stimuli and bodily and facial emotion expressions (Puce & Perrett, 2003; Zaki, Hennigan, Weber, & Ochsner, 2010).

1.2.2. Vicarious embarrassment for close others

In our daily lives we share emotional states with people ranging in closeness from strangers on the street to our best friends and family. The social relation with the target can be an important modulator of empathic responses, with increased closeness often leading to increased empathic response (Beeney et al., 2011; Cheng, Chen, Lin, Chou, & Decety, 2010; Meyer et al., 2012; Singer et al., 2006). For example, empathic responses on the neural systems level were increased when participants observed their friend outside the scanner while he/she was excluded in a ball-toss game (Beeney et al., 2011). The ACC and AI showed increased activations when participants watched stimuli of hands and feet in painful situations assuming that their loved-one is hurt (Cheng et al., 2010). Increased empathic responses could be due to a strengthened affective link to a socially close person and a more positive attitude, which then results in more intense caring for the other's affect (Cheng et al., 2010). Another argument states that the mental representation of close others is more vivid and rich and shared representations are greater, accordingly enhancing empathy (Cheng et al., 2010; Meyer et al., 2012). In the context of embarrassment the expected negative evaluation in-the-eyes-of-others is an important factor (Tangney et al., 2007). Lickel and colleagues argued that social closeness causes a shared social identity with the social target (Lickel, Schmader, Curtis, Scarnier, & Ames, 2005). Another person's behavior and its consequences therefore are relevant for the shared social identity and could negatively reflect on one's own social image (Lickel et al., 2005). Due to this, not only cognitions about the negative evaluation of the social target, but also about the evaluation of oneself in-the-eyes-of-others, might be increased. This notion is supported by behavioral studies on vicarious embarrassment, which indicated that social closeness increases vicarious embarrassment and the observers' concerns about their own images while they observe inappropriate behaviors of e.g. friends (Chekroun & Nugier, 2011; Fortune & Newby-Clark, 2008). In **chapter 5** we investigated if social closeness increases the neural activations of vicarious embarrassment within the "shared circuits" of the AI and ACC, mapping a conscious representation of affect and physiological arousal. In addition, enhanced self-related thoughts about the own social image should increase activations of the precuneus, a brain area that has been associated with self-referential cognition in earlier studies (Northoff et al., 2006).

1.2.3. Interoceptive representations of vicarious embarrassment in autism spectrum disorder

Individuals with autism spectrum disorder (ASD) are impaired in their ability to intuitively represent other persons’ mental states (Levy, Mandell, & Schultz, 2009). This impacts their behavior in various situations of everyday life but specifically during complex social situations like the situations that can elicit vicarious embarrassment in the observer. This could be explained with the patients’ often described deficits in embodying others’ affective states with bodily arousal and interoceptive representations on their own body (Hill, Berthoz, & Frith, 2004), which is associated with activations of the AI and ACC (Craig, 2009). Interoceptive representations of another person’s affect are assumed to contribute in generating empathy via embodied simulations and the conscious experience of these inner states (Keysers & Gazzola, 2009). Empathy then enables individuals to show appropriate behavior in social situations (Eisenberg & Miller, 1987). **Chapter 6** therefore investigated if individuals with ASD are impaired in their ability to experience vicarious embarrassment for another person. In particular, we assessed if difficulties in embodying vicarious embarrassment manifest on the neural systems level within the AI and ACC.

There are complex contextual demands when we generate vicarious responses for others’ vicarious embarrassment. Current norms and values need to be represented and the social target’s thoughts as well as other observers’ expectations need to be considered. Theories in autism research suggest that individuals with ASD learn to compensate their lack of social intuition in making sense of other people’s minds by relying on learned social rules and conventions from their childhood on (Baron-Cohen, Richler, Bisarya, Gurunathan, & Wheelwright, 2003; Klin, Jones, Schultz, & Volkmar, 2003). Especially when trying to make sense of complex vicariously embarrassing situations such compensation strategies can be used. This might recruit brain regions like the hippocampus, which previously has been associated with memory formation (Squire & Zola-Morgan, 1991; Squire, 1992). Similarly to experiencing vicarious embarrassment, sharing another person’s bodily pain involves interoceptive processing, but contextual demands are less complex when observing others’ bodily pain. Comparing both, vicarious embarrassment and empathy for pain, across groups (**chapter 6**), thus allows testing for a domain-general impairment of interoceptive processing in ASD in contrast to specific deficiencies depending on the complexity of contextual demands.

1.3. PARADIGMS

1.3.1. A socially immersive paradigm to induce embarrassment

The neural correlates of embarrassment were investigated in a few studies that made use of the spectator approach. As these studies neglected the social aspect of embarrassment they might have failed to trigger a full-fledged emotional experience of embarrassment and failed to activate the corresponding arousal network (Finger et al., 2006; Takahashi et al., 2004). Contemporary emotion research tried to address this issue. Using staged interactions instead of hypothetic or remembered scenes, these studies attempt to increase the internal validity of the paradigms (Fourie, Kilchenmann, Malcolm-Smith, & Thomas, 2012; Herrald & Tomaka, 2002; Williams & DeSteno, 2008). Williams and DeSteno (2008) for example made participants estimate the number of dots presented on a screen. In the following the experimenter gave positive feedback on their performance (structured interaction) to elicit pride in the participants. In social neuroscience similar concepts and methods addressing direct interactions between subjects gained recent attention under the term “second-person neuroscience” (Schilbach et al., 2013). Due to spatial restrictions, the implementation of social paradigms that allow direct social interactions between two or more participants in the MRI is challenging. One approach to solve this problem is to immerse participants into a “social” situation and uphold this state of social immersion for the time of fMRI scanning (Krach et al., 2013). To immerse participants and to create a situation, in which interaction partners are perceived as salient and significant for the participant, cover stories and structured interactions can be used. This technique is supposed to instantiate a stable mental representation of the social situation that maintains even when the interaction partners are physically not present anymore. Until now, only a few neuroimaging studies induced social stress or rejection using social or performance feedback in an immersive environment (e.g. Cooper, Dunne, Furey, & O’Doherty, 2014; Muscatell et al., 2014; Somerville, Heatherton, & Kelley, 2006; Wager et al., 2009).

In **chapter 2** we implemented a socially immersive paradigm to elicit genuine experiences of embarrassment. In this paradigm participants were made to fail in front of a judging audience by selectively revealing their failures and achievements to the public. We used a cover story to create a socially immersive environment and together with three confederates, the participant was invited to take part in a study on the neural basis of cognitive estimation (for the study set-up see Figure 1). This enabled us to investigate the effect of the presence of an audience (publicity) on the experience of one’s own failures or achievements.

We combined fMRI with measures of pupillometry to capture the neural and physiological correlates of embarrassment. We further obtained behavioral data, measures of trait social anxiety as well as eye-tracking data to gain a full picture of the involved processes.

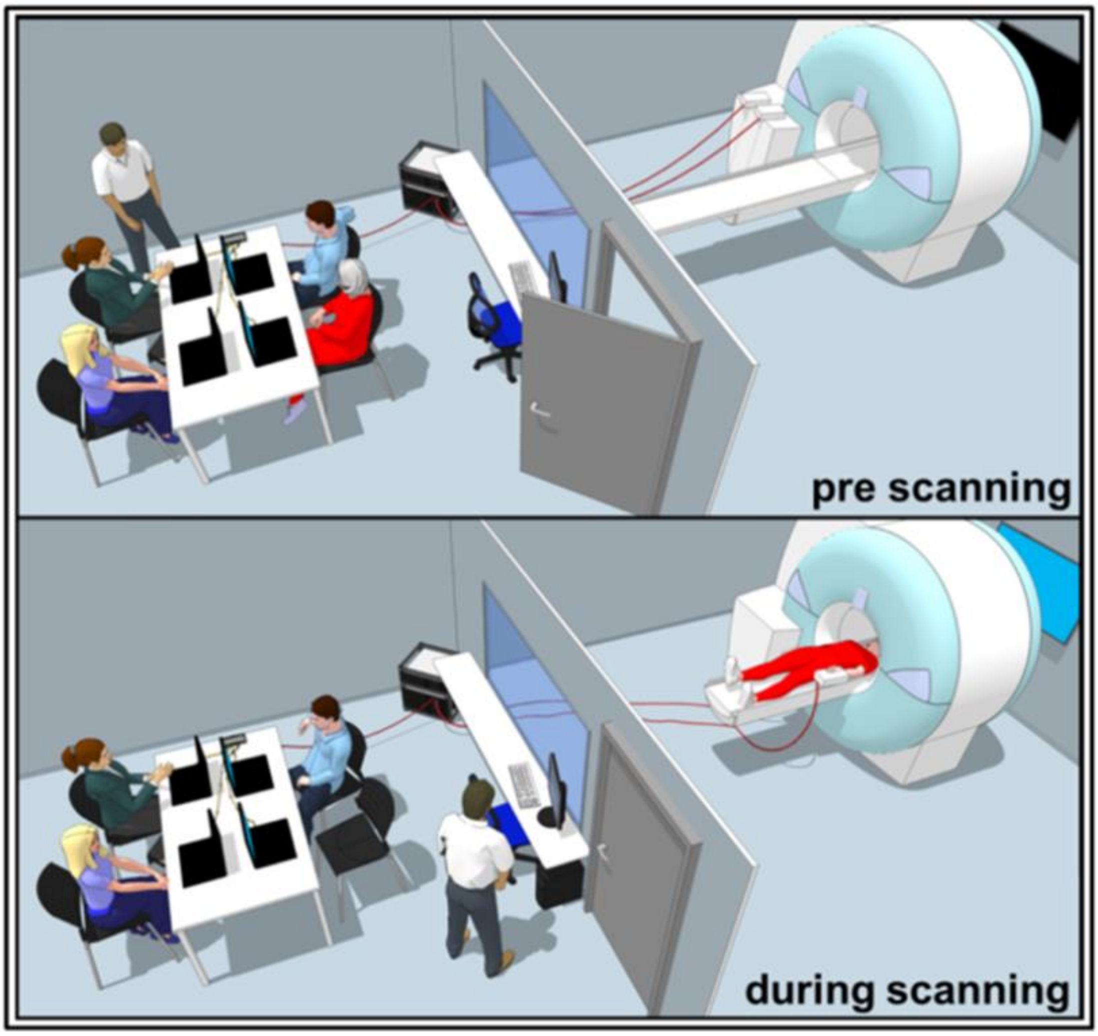
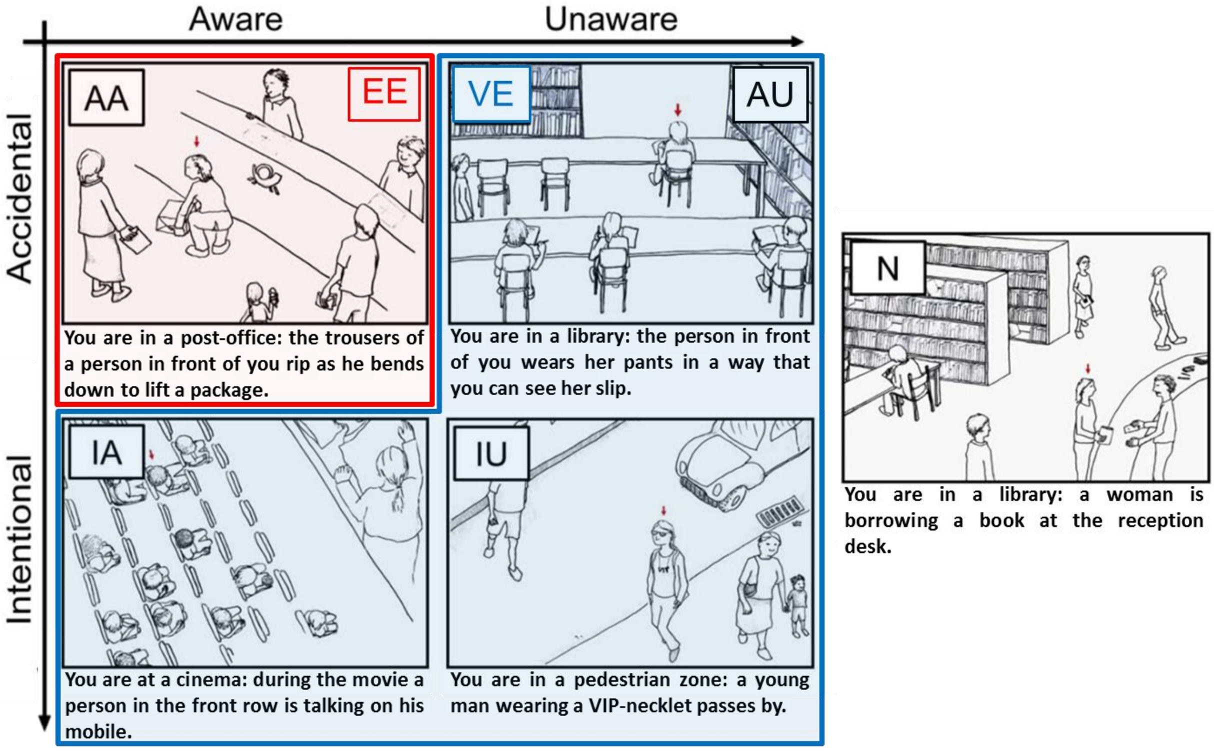


Figure 1. Set-up of the fMRI study on embarrassment. During the pre scanning phase the participant in red is practicing the task with the three confederates. During scanning the participant is immersed into the social situation and believes that in the public condition the three confederates are tracking his/her feedback via the cable connections.

1.3.2. Social situations eliciting vicarious embarrassment

Compared to embarrassment experienced for one's own actions, vicarious embarrassment is elicited by observing embarrassing situations of others and can relatively easy be induced in the fMRI by presenting pictures of social situations since the observer does not have to take part in social interaction. The stimuli for the studies presented in **chapters 3 to 6** concentrated on the aspect of public norm violations as an elicitor of embarrassment (Miller, 1996; Tangney et al., 2007) and depicted social targets during public mishaps and etiquette violations. Empathic and vicarious embarrassment both were characterized by using a broad variety of social situations of our daily lives. If the social target is aware that he/she accidentally violated a social norm, the social target will be embarrassed him- or herself. The observer is then assumed to share the experience of embarrassment with the social target and his/her experience of embarrassment is empathic. Vicarious embarrassment can also be elicited when the social target is unaware about the current norm violation. This is true for example, when someone accidently violates a social norm without recognizing the faux-pas (e.g. walking around with one's flies open). The social target can also intentionally show norm violating behaviors, in some cases not being aware of violating current social standards in other cases he/she might be disrespecting potential observers on purpose (e.g. burping out loud one's own name in a restaurant).

The different categories of vicariously embarrassing situations can be separated by two dimensions, the awareness about the ongoing norm violation (aware vs unaware) and the intentionality of the norm violating behavior (intentional vs accidental). Several situations for each of the four resulting categories were presented in **chapters 3 to 6** (for examples for the different categories see Figure 2). Neutral social scenarios served as control situations. A more detailed description of the stimuli as well as data on their validation can be found in an earlier study (Krach et al., 2011).



You are in a post-office: the trousers of a person in front of you rip as he bends down to lift a package.

You are in a library: the person in front of you wears her pants in a way that you can see her slip.

You are at a cinema: during the movie a person in the front row is talking on his mobile.

You are in a pedestrian zone: a young man wearing a VIP-necklet passes by.

You are in a library: a woman is borrowing a book at the reception desk.

Figure 2. Examples of possibly embarrassing situations used as stimulus material for the studies on vicarious embarrassment. The drawn sketches depict a protagonist, indicated by the red arrow above his/her head, in everyday life situations. Each of the sketches was accompanied by a short sentence below the picture describing the presented situation. EE = empathic embarrassment situation; AA =

accidental and aware; VE = vicarious embarrassment situations; AU = accidental and unaware; IA = intentional and aware; IU = intentional and unaware; N = neutral situation.

1.4. A CONSTRUCTIVIST UNDERSTANDING OF EMOTIONS

As described above, activations of the mentalizing network and the arousal network as well as (para-)limbic areas are supposed to map the components of embarrassment. But very similar networks can be involved in the processing of completely different conditions (Price & Friston, 2005). The AI/ACC network for example is involved in the processing of various emotions (Damasio et al., 2000; Phan et al., 2002), the awareness of one's bodily states (Craig, 2009), during the experience of empathic and own affective states (Eisenberger et al., 2003), and during attention tasks and cognitive functions (Kurth et al., 2010; Touroutoglou et al., 2012). The expected differences on the neural systems level do not have to be evident in separable activation patterns (Iannetti, Salomons, Moayedi, Mouraux, & Davis, 2013). The brain is a neural system, which operates by integrating information across different segregated brain regions and subsystems, and functional integration is thereby thought to better approximate its functioning (Sporns, 2011). In a constructivist understanding of how the brain processes emotions a specific function of a neural network like an emotion arises from interactions and functional integration between brain regions (Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012). Emotion-specific neural processing might therefore be evident only on the level of functional integration within shared networks. To gain insight into the interaction and functional integration of the mentalizing network, the arousal network, and (para-)limbic areas during the experience of embarrassment functional connectivity analyses were implemented in **chapter 2.** By assessing common signal fluctuations of the BOLD-signal between separate brain regions (see e.g. Bedenbender et al., 2011), we hereby were able to draw conclusion about potential functional integration between networks. In **chapter 4** functional connectivity of the pSTS was assessed to highlight its role in sharing others' embarrassment. In **chapter 5** we assessed functional integration of the precuneus and the AI/ ACC in order to gain insight into the modulation of neural network configurations by social closeness.

1.5. OUTLINE

This thesis thus summarizes five studies on the neural and physiological correlates of embarrassment and its vicarious form. The main focus thereby lies on treating both as social phenomena. Therefore, we needed to implement and develop paradigms that are appropriate for their examination. On the neural systems level, the focus is on the activation and interaction between the mentalizing network, potentially mapping the component of thinking about the others' evaluations, and the AI/ACC network, potentially mapping the component of affective arousal. C**hapter 2** investigates embarrassment and its neural correlates from the *first person perspective* using a socially immersive paradigm. In **chapter 3** we focus on the somatovisceral correlates of *vicarious* embarrassment. The following chapters focus again more strongly on the neural systems level. **Chapter 4** compares shared embarrassment *with* another person to vicarious embarrassment *for* a social target that does not experience embarrassment him- or herself. **Chapter 5** then addresses the question of how social closeness affects the experience and processing of *vicarious* embarrassment. **Chapter 6** investigates potentially deficient processing of *vicarious* embarrassment in autism spectrum disorder. All of them broaden our knowledge about the physiological and neural basis of (vicarious) embarrassment and highlight the functioning of specific brain areas in this context. **Chapter 7** then concludes the thesis with a summary of the presented chapters and provides a general discussion.

CHAPTER 2

NEURAL PATHWAYS OF EMBARRASSMENT AND THEIR MODULATION BY SOCIAL ANXIETY

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NEURAL PATHWAYS OF EMBARRASSMENT AND THEIR MODULATION BY SOCIAL ANXIETY

ABSTRACT

While being in the center of attention and exposed to other's evaluations humans are prone to experience embarrassment. To characterize the neural underpinnings of such aversive moments, we induced genuine experiences of embarrassment during person-group interactions in a functional neuroimaging study. Using a mock-up scenario with three confederates, we examined how the presence of an audience affected physiological and neural responses and the reported emotional experiences of failures and achievements. The results indicated that publicity induced activations in mentalizing areas and failures led to activations in arousal processing systems. Mentalizing activity as well as attention towards the audience were increased in socially anxious participants. The converging integration of information from mentalizing areas and arousal processing systems within the ventral anterior insula and amygdala forms the neural pathways of embarrassment. Targeting these neural markers of embarrassment in the (para-)limbic system provides new perspectives for developing treatment strategies for social anxiety disorders.

AUTHOR CONTRIBUTIONS

In this study the author of the thesis contributed to all aspects of the scientific process including the development of the experimental design, data acquisition, data analysis, and presenting the data and writing the paper.

CHAPTER 2

2.1. INTRODUCTION

Since the time of the ancient philosophers (Aristotle; 384–322 B.C.), the distinction between a “public” and a “private” realm has been a central tenet of political theory (Arendt, 1958; Sennett, 1974), jurisprudence (Warren and Brandeis, 1890), and the social sciences (Weintraub, 1997). The presence of others in the public space deeply affects human psychology and the emotional consequences of one’s actions (Gilovich et al., 2000). One of humankind’s most common fears centers around failing to uphold one’s public image within social encounters (Leary and Kowalski, 1995). The expected negative evaluation ‘in the eyes of others’ (Tangney et al., 2007) during ‘public deficiencies’ is the main cause of embarrassment (Miller, 1996). Mental-state attribution is therefore the lynchpin of the emotion of embarrassment, which regulates so many aspects of interpersonal behavior (Tangney et al., 2007) whenever others might potentially act as an audience, be it at school, work or during leisure time (Miller, 1996).

Excessive and persistent concerns about the evaluations of others are a hallmark of social anxiety. While everybody experiences mild forms of social anxiety occasionally (Leary and Kowalski, 1995), social anxiety disorders are a major burden for society (Kessler et al., 2005), and in affected individuals, the fear of embarrassment can even lead to social withdrawal and depression (Schneier, 1992). The neurobiology of how humans process situations that trigger their embarrassment, and how this contributes to social anxiety disorders, remains largely unknown, but would provide akey to understanding the neurobiological mechanisms of social anxieties.

The traditional ‘spectator approach’ in social neuroscience involves measuring the brain activity of participants in isolation while they are viewing photographs or movies of actors, or vignettes of fictional social situations. In these paradigms, the participant cannot interact with the targets of his/her social cognition, and his/her social reputation is not at stake. In typical social interactions, however, we not only perceive what others do, but we also need to (a) react in ways which are appropriate to others’ actions, and (b) maintain our social reputation while we are the focus of other people’s evaluation. The traditional ‘spectator approach’ fails to capture the motor involvement and emotional significance associated with these two aspects of our social world (Hasson et al., 2012; Schilbach et al., 2013). For instance, single cell recordings in monkeys have revealed that a spectator paradigm, in which a monkey watches movies of actions, greatly underestimates premotor mirror responses compared to when the same monkey witnesses a human act 'live', in a shared peripersonal space where direct interactions are possible (Caggiano et al., 2011, 2009).

The limits of the traditional 'spectator approach' are a considerable hindrance in the endeavor to gain a mechanistic understanding of embarrassment (Krach et al., 2013), as embarrassment is defined by the social context: failing in front of a judging audience. To this day, neuroimaging studies have induced *social stress* or *rejection* and were able to overcome this hindrance by implementing interaction paradigms using social or performance feedback (Cooper et al., 2014; Muscatell et al., 2014; Somerville et al., 2006; Wager et al., 2009). However, all we know about the neural substrates of the emotion of *embarrassment* originates from 'spectator approaches', in which the participant did not fail him- or herself, and was not monitored by an audience, but merely read brief fictional stories (e.g. "I was not dressed properly for the occasion"; Finger et al., 2006; Takahashi et al., 2004). We have all, on occasion, confidently said something blatantly incorrect in front of an audience we wished to impress, and the feelings accompanying this can be overwhelmingly intense: blushing, pounding heart, feeling terrible, and a vivid image of how others are mocking us for our failings in their heads. While imagining fictional situations such as "I was not dressed properly for the occasion" might capture some of the rational cognitions that are triggered by real embarrassing situations, the hot emotional rush that is the hallmark of embarrassment (Buss, 1980), and the paralyzing claws of social anxieties, have not been addressed by previous studies.

With this caveat in mind, it is perhaps unsurprising that past experiments using fictional scenarios (Finger et al., 2006; Takahashi et al., 2004) have emphasized the role of the medial prefrontal cortex (mPFC) and the precuneus, so-called "mentalizing areas" which are involved in putting oneself in the mental world of others (Frith and Frith, 1999; Tangney et al., 2007). However, the mPFC and precuneus not only are engaged when we are thinking about another person's mind set, but also when we reflect about ourselves (in the context of others; Müller-Pinzler et al., in revision), we think about future events or just spend time mind-wandering or daydreaming (Critcher and Gilovich, 2010; Schooler et al., 2011). To frame these regions as mentalizing areas is thus simplified and suggests a specificity of processing in these system, that might not generally uphold given more recent evidence. Within the context of the present studies and also the current undertaking in decomposing embarrassment, we will nonetheless keep this term and aim to provide empirical evidence that might be helpful in understanding the ongoing psychological processes.

By contrast to the previous evidence for activity in these mentalizing areas , the limbic system, which is involved in all facets of emotional experiences (Adolphs et al., 1995; Morris et al., 1998; Phan et al., 2002), and the dorsal anterior insula processing the corresponding affective arousal (Critchley, 2005), were not activated in these studies. The lack of evidence for involvement of these regions is surprising but might be due to the previous experimental paradigms that trigger rational cognitions to a greater degree than the hot emotional rush of embarrassing situations. To provide a mechanistic understanding of embarrassment, and to examine its relevance for social anxieties, we therefore need to devise a new paradigm which enables us to capture the emotional dimension of failing in public within a neuroimaging set-up.

According to current models of embarrassment, two factors need to converge to evoke embarrassment. The first factor is a deviation from personal standards, the failure to show appropriate behavior, such as physical pratfalls, loss of control over the body, or cognitive shortcomings (Miller, 1996). The second factor is the publicity of one’s behavior, which motivates individuals to think about others’ evaluations when they are the center of attention. The interaction of both factors, namely the ‘public failure’, is at the core of the “aversive state of abashment, flusterment and chagrin” of embarrassment (Miller, 1996). For this reason, and in line with a ‘psychological constructivist’ approach to emotions (Lindquist et al., 2012), embarrassment should not be localized in one single brain region, but should manifest itself in the interaction of distinct brain systems which integrate the components of failure and publicity.

To explore the interaction between failure and publicity, we set up a staged person-group interaction in which a participant was made to fail in front of three confederates pretending to be fellow research participants (see Fig. 1a, Material and Methods, and Movie A.1). We combined brain imaging with measures of pupillometry and eye-gaze behavior to capture both the neural and physiological correlates of embarrassment and to explore how these variables are related to social anxiety. Participants were required to estimate the properties of objects, i.e. sizes, amounts, or weights, during a restricted period of time. We selected the domain of cognitive abilities to induce embarrassment because they are highly relevant for the human self-concept (Marsh, 1990) and social image, meaning that public cognitive shortcomings are very effective triggers of embarrassment. Participants then received manipulated feedback on their estimation accuracy: a bar chart in the center of the screen displaying the exact percentile of the participant’s performance, and photographs of the three confederates’ faces on the upper left-hand side on the screen. The level of feedback (i.e.

PERFORMANCE) induced failure or achievement through either low (LOW; 1-15%) or high (HIGH; 85-99%) alleged percentiles of accuracy. As a control condition, mediocre feedback was provided (NEUT; 40-60%). Independent of PERFORMANCE, we manipulated the publicity of the feedback (PUBLICITY) by informing the participant whether the feedback on his/her performance was also being presented to the three confederates outside the scanner (PUB; green frame around the photographs, 50% of trials) or was only visible to him/her (PRIV; gray frame around the photographs).

According to the considerations above, we hypothesized that mentalizing areas (mPFC and precuneus) would be involved whenever participants receive public feedback. In addition, we hypothesized that the dorsal aspect of the anterior insula (dAI), which is implicated in the processing of arousal, would be active whenever the participant's performance deviated from his/her expectations; thus especially during perceived failures or achievements (Critchley, 2005; Seeley et al., 2007). There is accumulating evidence demonstrating amygdala involvement in various negative and positive emotions (Adolphs et al., 1995; Morris et al., 1998; Phan et al., 2002), and the amygdala is particularly active in a socially evaluative context (Guyer et al., 2008; Lorberbaum et al., 2004). Additionally, meta-analyses of neuroimaging data consistently show that ventral aspects of the anterior insula (vAI), which are densely connected to the amygdala (Mesulam and Mufson, 1982), are central in human affect (Chang et al., 2013; Deen et al., 2011; Kelly et al., 2012). Thus, we finally expected (para-)limbic regions (vAI and amygdala) to play a critical role in the specific integration of both aspects: the publicity of one's failures.

Based on these assumptions our core hypothesis is that embarrassment should manifest in a unique functional integration in core affect regions of systems involved in mentalizing about the thoughts of the audience and systems involved in the arousal associated with unexpectedly low performance. This hypothesis can be broken down in three specific hypotheses. First, that mentalizing brain regions will show a main effect of publicity, being more active in public than private conditions. Second, that the dAI will show a main effect of performance, in which unusually high or low performance will show stronger activity than neutral performance. Finally, in line with the constructivist understanding of how the brain processes emotions (Lindquist et al., 2012), that the integration of signals from these two systems onto core affect regions (vAI and amygdala) would be particularly high during the failures that trigger the "chagrin of embarrassment" (Miller, 1996).

2.2. MATERIALS AND METHODS

2.2.1. Participants

Twenty-seven healthy naive participants took part in the functional magnetic resonance imaging (fMRI) study (17 females and 10 males; aged 18-28 years; M = 23.11; SD = 2.58). All participants had normal or corrected-to-normal vision, no past neurological or psychiatric history, and were not taking any medication. On average, participants had spent 16.39 years in education (range 12-22; SD = 2.51). All participants received 25 € compensation for approximately 2.5 h involvement in the study. The study was approved by the local ethics committee (AZ 08/10) and written informed consent was obtained from all participants involved in the study.

2.2.2. Pre-scanning procedure and set-up of the cover story

We used a cover story to create a socially immersive environment in which genuine experiences of embarrassment were induced. Together with three confederates, the participant was invited to take part in a study on the neural basis of cognitive estimation. The participant and the confederates arrived at the same time in the preparation room. The room was adjacent to the scanner, which was equipped with four laptop computers that were wired via a local area network. Computers in the preparation room looked like they were also connected to the MRI system (see Fig. 1a for the experimental setting). After signing informed consent forms, the participant and the confederates solved a German translation of the Wonderlic Personnel Test (Wonderlic, 1996) in a shortened period of time (6 min). Based on a faked rank order in the IQ test, providing the participant with the highest score, the participant was selected to enter the MRI and to complete the estimation task in the scanner. The experimenter justified the selection procedure based on the alleged positive correlation of cognitive estimation performance with IQ. The confederates were instructed to complete the same task outside the scanner in the preparation room.

Contenders had to estimate sizes, weights or quantities of pictured objects or living beings in a restricted time period of 10 s (e.g. “How long is this screw?”; see also Fig. 1; see FMRI paradigm and experimental design section for a detailed description of the experimental design). After each trial, the participant then received manipulated feedback on his/her accuracy in the form of a short sentence and a colored bar with a line marking the exact percentile ranging from 0% to 100%. This information indicated how well the participant had performed compared to an alleged reference group of 350 university students who, according to the cover story, had been tested beforehand. In addition, the participant was informed that the three contenders in the adjacent room would be informed about his/her performance during 50% of the trials as a frame of reference to the person with the highest IQ. In these trials, the performance of the participant was projected onto the three screens of the confederates, who thus formed the audience. After careful instructions, the participant and the confederates practiced the estimation task outside the scanner with five example situations. The participant was able to see that his/her performance was displayed on the confederates' screens in the public feedback situations, while in the private feedback situations all contenders received only their own performance feedback. After the instruction period, which lasted approximately 45 min, the participant was then guided into the MRI.

2.2.3. FMRI paradigm and experimental design

Each trial consisted of an estimation period which lasted 10 s and a consecutive feedback period which was presented for 8 s. Estimation and feedback were separated by a fixation cross for 1.5 s, and a low-level baseline period showing a fixation cross for 5 s was interleaved between feedback and the following trial (see Fig. 1B for the timing of the paradigm). During the estimation period, continuous response scales below the pictures determined a range of possible answers, and participants indicated their responses by navigating a pointer on the response scale with button presses of the right and left hands. The upper and lower ends of the response scales were designed such that all answers in between were plausible for the specific object. In this way, it was not possible for participants to know how well they had performed and every kind of feedback they received for their estimation was plausible. Stimuli were presented on an LCD screen with the Presentation 11.0 software package (Neurobehavioral Systems, Albany, CA, USA, http://www.neurobs.com/).

Failures and achievements (i.e. PERFORMANCE) as well as the influence of the audience (i.e. PUBLICITY) were manipulated in a 2x3 factorial within-subject design. Participants received either faked low performance feedback (LOW; e.g. "You are better than 5 % of the reference participants"; percentiles ranging from 1 to 15%), high performance feedback (HIGH; percentiles ranging from 85 to 99%), or mediocre performance feedback (NEUT; percentiles ranging from 40 to 60%) on their estimation performance. Feedback was given either publicly (PUB; performance is exposed to the confederates outside the MRI) or privately (PRIV; performance is visible only to the participant inside the MRI). The feedback screens contained photographs of the three confederates' faces in the upper left corner as a cue for the publicity of an event. Photographs were displayed in black and white, with a gray frame, during PRIV trials, and were colored, with a green frame, during PUB trials (see Fig. 1b for the stimuli). The use of the photographs constituted part of the cover story, as participants had also been asked to send in a photograph of themselves to be used during the experiment. Each performance feedback (LOW, HIGH, NEUT) was either public or private in equal measure.

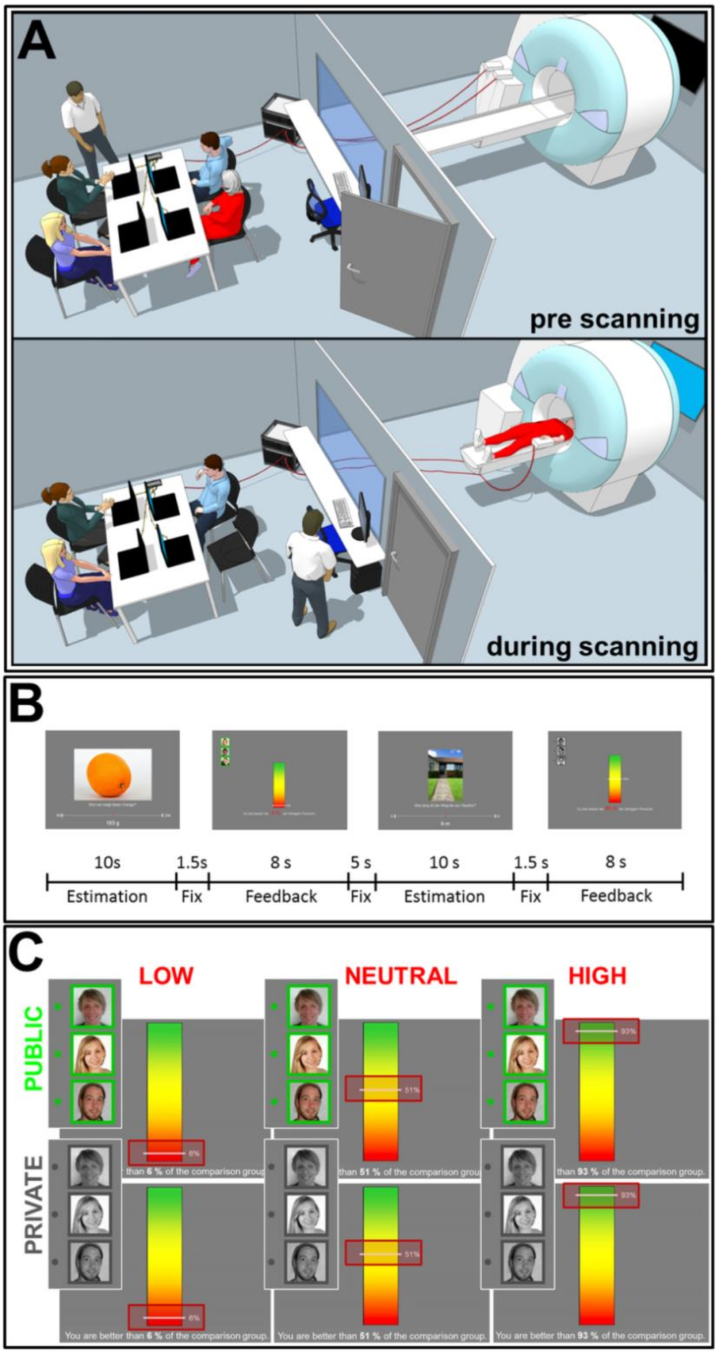

Figure 1. Experimental set-up and design. **A** Set-up of the fMRI experiment. During the pre-scanning phase (upper picture), the participant (red clothes) and the three confederates practice the cognitive estimation task while sitting in front of their notebooks in the preparation room adjacent to the scanner room. During scanning (lower picture), the participant lies in the MRI believing that the three confederates are completing the same task in the preparation room and are able to follow his/her performance on their notebook screens via cable connections. **B** Timing of the fMRI paradigm. Estimation questions are presented for 10 seconds followed by a fixation cross presented for 1.5

seconds and the feedback presented for 8 seconds. After an intertrial interval of 5 seconds, the next trial starts. **C** Design of the fMRI paradigm. There are six different conditions resulting from the PERFORMANCE (3) x PUBLICITY (2) levels. PERFORMANCE is either LOW, mediocre (NEUT) or HIGH and is indicated by a line marking the exact percent value of the relative estimation performance (red frames). Half of the feedback is made public (PUB) and visible to the audience (green frames) and the other half is private (PRIV) and only visible to the participant him- or herself (gray frames). For further details see also Movie A. 1.

Trials were presented in a fixed pseudo-randomized order. The two HIGH and LOW performance conditions included 17 trials for each PUB and PRIV, respectively. The NEUT condition included nine trials each in the PUB and PRIV conditions, resulting in a total of 86 trials which were presented in two consecutive fMRI runs. The duration of the total fMRI experiment was 35.12 min.

2.2.4. Post-fMRI examination

After the fMRI data acquisition, the socially immersive environment was re-established, with the confederates playing their roles until they were guided to adjacent rooms for a post-experimental examination. During the post-experimental examination, the participant provided self-reports of experienced emotions in the MRI for three estimation trials from each condition. Embarrassment and pride (as well as anxiety, anger, sadness, and happiness) were rated on a 9-point unipolar scale (1 = *not at all*, 9 = *very strong*) using descriptive adjectives within a set of emotions. Participants subsequently completed the German version of the social interaction anxiety scale (SIAS; Mattick and Clarke, 1998) and, after verifying that they had not detected the true intention of the study with two suggestive questions (“Did you recognize a systematic in the performance feedback? If you did, what was it?” and “Did you think the performance feedback was related to your performance?”), which none of them had, they were debriefed. Notably, none of the participants indicated having looked through the cover story and revealed that the other “participants” in fact were confederates throughout the post-fMRI examination and after debriefing.

2.2.5. Analyses of behavioral data

All non-imaging data were analyzed with PASW Statistics 18 (Chicago: SPSS Inc.). Post-fMRI self-reports of each emotion were averaged within conditions and analyzed for each emotion separately using analyses of variance (ANOVAs) with PERFORMANCE (LOW, HIGH, NEUT) and PUBLICITY (PUB, PRIV) as within-subject factors. To test the effects on the experience of embarrassment and pride in the MRI, a priori contrasts comparing embarrassment ratings in LOW vs. NEUT and pride ratings in HIGH vs. NEUT were calculated. The specific influence of PUBLICITY on emotions was tested with the PUB vs. PRIV x HIGH vs. LOW interaction with paired t-tests for all self-reports of emotion as obtained in the post-fMRI examination. To compare self-reports of embarrassment, anxiety, anger, sadness, pride and happiness with each other an ANOVA with PERFORMANCE, PUBLICITY and emotion self-reports as additional factor EMOTION was implemented. A priori contrasts were chosen contrasting LOW vs. NEUT and comparing embarrassment ratings versus all other emotion ratings. Additionally self-reports for all emotions in the LOW condition were compared using paired t-tests.

2.2.6. Analyses of pupil dilation

Eye-tracking data were assessed during the fMRI paradigm. Pupil diameter and gaze behavior were recorded non-invasively in one eye at 500 Hz using an MRI-compatible Eyelink-1000 device (SR Research, Kanata, ON, Canada) with manufacturer-recommended settings for calibration and blink detection. Periods of blinks were cut out and values in this gap were interpolated by piecewise cubic interpolation. The pupil trace was subsequently z-normalized over the whole session. To characterize the pupil dilation for each trial by a single value, we subtracted the baseline pupil size during the first 200 ms of each trial from the average value during the last second of each trial. The condition averaged value for the pupil dilation was then entered into a repeated measures ANOVA. A priori contrasts were implemented to compare LOW and HIGH to NEUT, and paired t-tests were implemented in order to test the PUB vs. PRIV x HIGH vs. LOW interaction.

2.2.7. Neuroimaging data

2.2.7.1. Image acquisition.

Participants were scanned at 3T (Siemens Trio, Erlangen) with 36 near-axial slices and a distance factor of 10% providing whole-brain coverage. An echo planar imaging (EPI) sequence was used for acquisition of 503 functional volumes during each of the two sessions of the experiment, resulting in a total of 1,006 functional volumes (TR= 2.2 s, TE = 30 ms, flip angle= 90°, slice thickness = 3 mm, FoV= 192).

2.2.7.2. Analysis of functional imaging data.

FMRI data were analyzed using SPM8 (www.fil.ion.ucl.ac.uk/spm). The first three functional volumes of each of the two sessions were discarded from further analyses, leaving 500 EPI volumes per session. These were corrected for timing differences of the slice acquisition, motion-corrected and spatially normalized to the standard template of the Montreal Neurological Institute (MNI). The normalized volumes were resliced with a voxel size of 2x2x2 mm and smoothed with an 8 mm full-width-at-half-maximum isotropic Gaussian kernel. To remove low-frequency drifts, functional images were high-pass filtered at 1/256.

Statistical analyses were performed in a two-level, mixed-effects procedure. The fixed-effects GLM on the first level included eight epoch regressors modeling the hemodynamic responses to the different performance feedback conditions (6; PERFORMANCE: LOW, HIGH, NEUT X PUBLICITY: PUB, PRIV), the estimation periods as one regressor (1), and the instruction phase (1) for each of the two sessions. Additionally, performance feedback percent values were entered as parametric modulators for the six conditions to explain additional within-subject variance in neural activation within each condition. To account for noise due to head movement, six additional regressors modeling head movement parameters were introduced.

To analyze the effects on the second level, we always kept one of the factors constant and implemented an ANOVA design with the remaining factor. This was done to correctly account for the dependencies of the two repeated factors. To test the effects of PERFORMANCE the ANOVA model on the second level included the three levels LOW, HIGH and NEUT while the contrasts on the first level were computed as the average across both levels of PUBLICITY. To test the effects for PUBLICITY, the ANOVA model on the second level included the two levels PUB and PRIV, while the contrasts on the first level were computed as the average across the three levels of PERFORMANCE. The interaction of PERFORMANCE and PUBLICITY was tested by contrasting the LOW_PUB-LOW_PRIV and HIGH_PUB-HIGH_PRIV on the first level and implementing an ANOVA design on the second level with one factor and two-levels.

For all analyses we conducted planned comparisons in the respective ANOVA design to test the hypothesized effects. First, arousal-related brain regions were identified through a conjunction analysis of both positive and negative deviations from neutral in the PERFORMANCE (LOW-NEUT∩HIGH-NEUT). Effects of the audience were examined by contrasting public with private feedback in the PUBLICITY model (PUB-PRIV). The differential influence of publicity on low compared to high performance feedback was identified by computing a contrast for the respective model for the interaction ((LOW_PUB-LOW_PRIV)-(HIGH_PUB-HIGH_PRIV)).

2.2.7.3. Correspondence of pupil dilation, gaze behavior, self-reported embarrassment and trait social anxiety with neuroimaging parameters.

To investigate the trial-by-trial association of pupil dilation and neural activation, pupil dilation values were introduced as a parametric modulator in a first-level GLM (see Paulus et al., 2015). The first-level GLM included the hemodynamic responses during feedback (1), the cognitive estimation periods (1), and the instruction phase (1). The parametric modulators of hemodynamic responses during feedback contained first, the exact percent values of PERFORMANCE, second, the deviation from 50% to control for any within-subject variance in neural activation due to PERFORMANCE, and third, the trial-by-trial pupil dilation value. To account for noise due to head movement, six additional regressors modeling head movement parameters were introduced. On the second level, β-maps of the pupil dilation as parametric modulator were analyzed using a one-sample t-test.

Gaze dwell time was calculated as the sum of the time for which the gaze was oriented towards the photographs of the confederates' faces during the feedback in one trial. The association between dwell time on the confederates' faces and neural activation was investigated within a GLM with trial-by-trial dwell time on the confederates' faces as a parametric modulator. In this model the parametric modulators of the hemodynamic responses during feedback were first, the publicity of the performance and second, the trial-by-trial dwell time on the confederates' faces. On the second level, β-maps of the dwell time as parametric modulator were analyzed using a one-sample t-test.

We further explored the association of trait-level social anxiety and self-reported embarrassment during LOW_PUB with neural activation during PUB-PRIV. To account for the influence of potential outliers, robust regressions using M-estimators with Huber weights were calculated. Difference scores for the dwell time on the confederates' faces were then calculated for PUB-PRIV. To assess whether the relationship between social anxiety and differences in neural activation was mediated by differential gaze behavior, Sobel tests were computed, with the dwell time difference scores as mediator. Another mediation analysis was performed for the relationship of dwell time difference scores and self-reports of embarrassment implementing FFA activation as a mediator.

2.2.7.4. Functional connectivity analyses.

Emotion-specific functional connectivity patterns were examined with "psychophysiological interaction" (PPI) analyses as implemented in SPM8. Two seed regions were selected due to their involvement in processing affective arousal, and two seed regions were chosen due to their involvement in mentalizing in the presence of an audience. The left and right dAI peak were defined based on the conjunction of LOW-NEUT∩HIGH-NEUT. The precuneus and an mPFC peaks were defined by the contrast PUB-PRIV. For all regions, time series were extracted as the first eigenvariate from all voxels that showed a positive effect within a sphere of 6 mm radius around the peak voxel. Variance explained by the movement regressors and the hemodynamic responses induced by the estimation period and the instruction were removed with an effects-of-interest correction. To examine embarrassment-specific connectivity patterns, PPI regressors contrasted LOW vs. HIGH performance separately for PUB and PRIV for each time series. For each of the examined regions, a separate fixed-effects GLM was implemented on the first level, including (i) the original time series, (ii) the psychological regressor contrasting the hemodynamic response of LOW and HIGH performances, (iii) the PPI regressor coding the dynamics in the connectivity with the seed region, and (iv) the regressors of the original design matrix. Resulting β-maps of the PPI regressors were analyzed on the second level within an ANOVA design, each including the PUB and PRIV conditions for one of the seed regions.

2.2.7.5. Thresholding procedures.

Both, the effects of neural activation, as well as the dynamics in connectivity were first examined in the whole brain. To do so, we applied a family-wise error (FWE)-correction at $p<.05$, at the voxel level as implemented in SPM8 for all contrasts. In a second step, we restricted our search volume to the predefined brain systems involved in emotional processing, the amygdala and the vAI, to increase our statistical power in these *a priori* regions. These regions within the (para-)limbic system were defined anatomically based on the automated anatomical labeling atlas (AAL; Tzourio-Mazoyer et al., 2002) for the amygdala and based on the parcellation study by Kelly and colleagues (2012) for the vAI. Analyses within this restricted search volume were again thresholded at $p<.05$, FWE-corrected for this search volume.

2.3. RESULTS

2.3.1. Behavioral data and pupil dilation

The feedback given to participants, independent of PUBLICITY, significantly induced the expected emotions. Self-reports after scanning indicated stronger embarrassment experiences in cases of low performance (LOW vs NEUT, $F_{(1,26)} = 88.15$, $p < .001$) and stronger pride experiences in cases of high performance (HIGH vs NEUT, $F_{(1,26)} = 335.32$, p

< .001). Comparisons between self-reports of all emotion assessed after scanning (embarrassment, anxiety, anger, sadness, pride, and happiness) showed that embarrassment was the most prominent emotion during low performance (for means and standard deviations of emotion self-reports for all conditions see Table 1). There was a significant interaction of PERFORMANCE and EMOTION ($F_{(12,312)} = 124.07$, $p < .001$). In the LOW compared to the NEUT condition self-reports of embarrassment were higher than for anxiety, sadness, anger, happiness, and pride (all *ps* < .001). Further, in the LOW performance condition the embarrassment experience exceeded all other emotions (anxiety, sadness, anger, happiness, pride; all *ps* < .005). This suggests that embarrassment was the most prominent emotion that was induced by the low performance feedback in the current task.

The publicity of one's performance affected the experience of embarrassment ($F_{(1,52)} = 7.75$, $p = .010$) but did not affect pride ($F_{(1,52)} = 0.98$, $p = .330$). The effect of PUBLICITY depended on PERFORMANCE. Exposing one's performances to the public increased the self-reported experience of embarrassment ($t_{(26)} = 2.40$, $p = .012$) more during LOW than HIGH performance. There was also a significant triple interaction of PUBLICITY, PERFORMANCE and EMOTION ($F_{(1,26\ )} = 2.841$, $p = .001$). This was mainly driven by differential effects of the PUB and PRIV conditions during HIGH and LOW performances on embarrassment and happiness as indicated by planned comparisons. Whereas embarrassment showed a significantly greater increase in the LOW condition compared to the HIGH condition when the performance was public, happiness showed the opposite effect with greater increase in happiness in response to PUB compared to PRIV performance in the HIGH condition ($t_{(26)} = -2.24$, $p = .017$). For all other emotions, the interaction of PUBLICITY and PERFORMANCE was not significant ($ts_{(26)} < 1.65$, $p > .56$). These findings are in line with the idea that the audience is specifically relevant for embarrassment during failures (Miller, 1996), but is less relevant for the experience of pride during achievements (Seidner et al., 1988).

Pupil dilation, indicating sympathetic arousal (see e.g. Paulus et al., 2015), was also augmented in low and high performances (LOW vs NEUT, $F_{(1,26)} = 14.84$, $p = .001$; HIGH vs NEUT, $F_{(1,26)} = 5.89$, $p = .022$). As for the behavioral data, the effect of PERFORMANCE depended on PUBLICITY. Exposing one's performances to the public increased the pupil dilation ($t_{(26)} = 1.94$, $p = .032$) more during LOW than HIGH performance.

Table 1. Self-reports of emotions for the performance conditions.

Performance condition	PRIV						PUB					
	LOW		NEUT		HIGH		LOW		NEUT		HIGH	
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Emotion Rating												
Embarrassment	3.26	1.84	1.56	1.22	0.40	0.43	4.04	2.00	1.57	1.16	0.45	0.48
Anger	1.79	1.77	1.31	1.40	0.27	0.46	2.04	1.95	1.02	1.10	0.32	0.43
Sadness	2.39	1.80	1.35	1.24	0.40	0.48	2.50	1.85	1.24	1.15	0.33	0.39
Fear	0.74	1.28	0.45	0.78	0.33	0.56	0.70	1.26	0.49	0.83	0.27	0.43
Pride	0.39	0.53	1.54	1.28	5.13	1.76	0.43	0.56	1.83	1.26	5.40	1.71
Happiness	1.21	1.20	1.99	1.37	4.87	1.62	0.98	1.17	2.33	1.44	5.34	1.43

Note. *M* = mean. *SD* = standard deviation. LOW = low performance feedback, HIGH = high performance feedback, NEUT = mediocre performance feedback, PUB = public condition, PRIV = private condition.

2.3.2. FMRI data

Both low and high performances (LOW-NEUT∩HIGH-NEUT) yielded significant increases in bilateral dorsal anterior insula (dAI) activation (right dAI: 40, 24, -10 mm, $t_{(78)} = 5.17$, $p = .020$, corrected; left dAI: -32, 20, -10 mm, $t_{(78)} = 5.56$, $p = .005$, corrected; see Fig. 2c). Trial-by-trial variability in pupil dilation was positively linked to neural activation of the right insula ($t_{(26)} = 8.57$, $p < .001$; see Fig. 2a and Table A. 4) and somatosensory cortex areas ($t_{(26)} = 7.80$, $p = .001$), areas associated with the processing of sympathetic arousal. Compared to low performance, high performance yielded strong and distributed activations including striatal areas (HIGH-LOW, $t_{(52)} = 13.22$, $p < .001$; see Fig. A. 1 and Table A. 1), which is in line with the strong reward potential of positive feedback on cognitive performances (Bandura, 1982; Hattie and Timperley, 2007; Weiner, 1985). However, compared to high performance, low performance showed no specific activation.

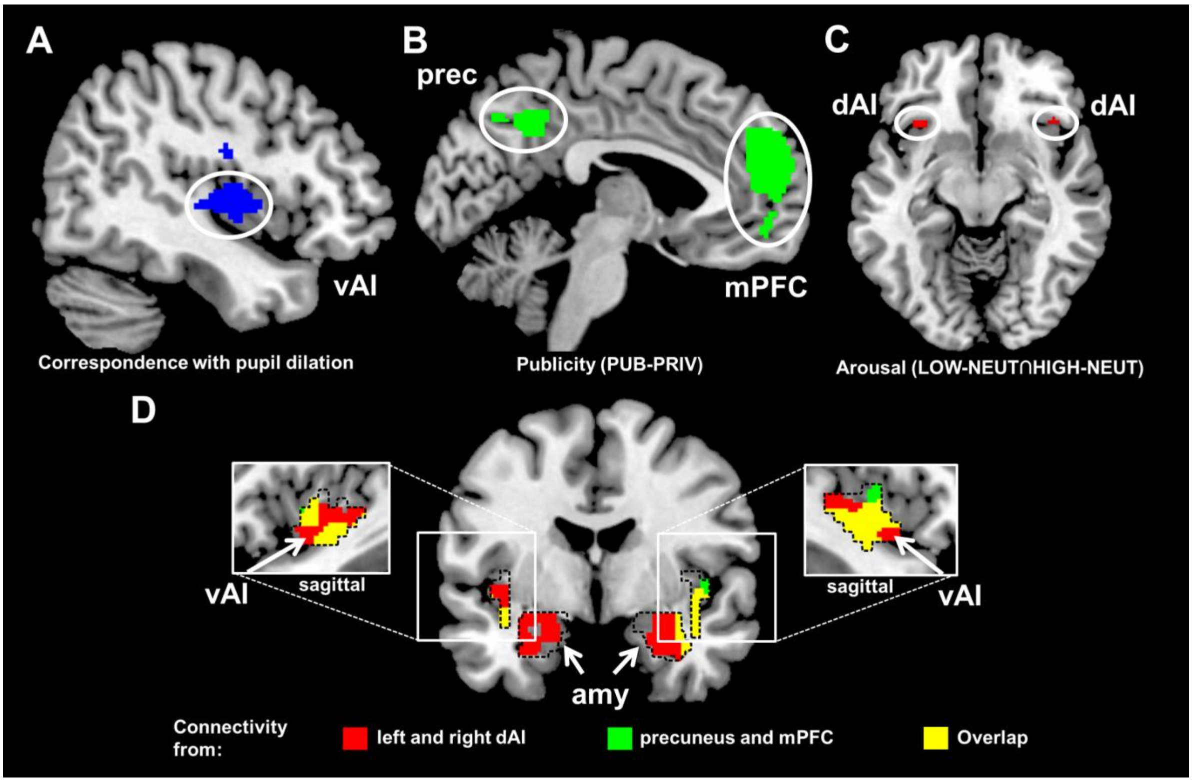

Figure 2. FMRI results. **A** Pupil dilation as indicator of arousal. Increased activation of the ventral anterior insula (vAI) associated with increases in pupil dilation during individual feedback trials across all conditions (p < .05, whole-brain corrected). For further details see also Table A. 4. **B** Audience effect. Increased activation of the medial prefrontal cortex (mPFC) and precuneus during public (PUB) compared to private (PRIV) performance averaged across PERFORMANCE levels was associated with mentalizing processes when thinking about others' evaluations (p < .05, whole-brain corrected, see also Table A. 2) **C** Performance effect. Increased activation of the dorsal anterior insula (dAI) during LOW and HIGH compared to mediocre (NEUT) performance indicating increased processing of affective arousal (conjunction analysis LOW-NEUT∩HIGH-NEUT, p < .05, whole-brain corrected). For further results see also Fig. A. 1 and Table A. 1. **D** Increased functional connectivity during embarrassment. Psychophysiological interaction analyses revealed increased functional connectivity during LOW compared to HIGH performance (p < .05 uncorrected for display purposes, results survive correction within our amygdala and vAI search volumes). Seed regions are based on the arousal (left and right dAIs; results presented in red, for seed regions see Fig. 2c) and mentalizing (precuneus and mPFC; results presented in green, for seed regions see Fig. 2b) networks. Overlap is presented in yellow. Dashed lines illustrate the anatomically defined search volumes including the amygdalae (AAL; Tzourio-Mazoyer et al., 2002) and the functional vAI (Kelly et al., 2012).

PUBLICITY (PUB-PRIV) was associated with a characteristic pattern of activation in the mentalizing network, comprising the mPFC ($t_{(52)}$ = 7.26, *p* < .001, corrected) and the precuneus ($t_{(52)}$ = 6.35, *p* = .001, corrected; see Fig. 2b and Table A. 2), which might be an indicator of increased thinking about others' evaluations (Frith and Frith, 1999). In line with this, participants' gaze dwelled longer on the faces of the confederates ($F_{(1,52)}$ = 18.02, *p* < .001; for means and standard deviations of dwell times see Table A. 3), and the fusiform face area (FFA) was activated more strongly during PUB than during PRIV ($t_{(52)}$ = 6.16, *p* = .002, corrected). Variability in the gaze dwell times on the faces on the within-subject level was also linked to activation of the fusiform gyrus ($t_{(26)} = 9.92$, $p < .001$, corrected; see Fig. A. 1 and Table A. 4).

Table 2. Increased Functional Connectivity During Low Compared to High Performance.

Seed Region Target Region	Side	MNI Coordinates x	y	z	*T*	*p*
right dAI (40, 24, -10 mm)						
amygdala	R	34	0	-24	4.49	.002
amygdala	L	-32	0	-26	4.40	.002
vAI	R	42	6	-10	3.38	.036
vAI	L	-40	0	-14	4.19	.004
left dAI (-32, 20, -10 mm)						
amygdala	R	36	0	-20	4.10	.005
amygdala	L	-32	0	-26	3.67	.015
vAI	R	44	2	-8	4.35	.003
vAI	L	-40	-2	-14	4.27	.003
precuneus (-4, -52, 38 mm)						
amygdala	R	38	-2	-24	3.33	.041
vAI	R	40	-4	-10	3.62	.022
vAI	L	-38	-6	-14	3.88	.009
mPFC (0, 60, 18 mm)						
vAI	L	-40	-4	-16	3.30	.036

Note. Increased functional connectivity between our seed regions (the precuneus and mPFC as well as the left and right dAI) within our a priori search volumes (amygdala and vAI) during low vs high performance (LOW-HIGH). P-values are FWE-corrected within the search volumes. Abbreviations: vAI = ventral anterior insula; mPFC = medial prefrontal cortex; dAI = dorsal anterior insula.

Neural activation of the mPFC (robust regression: $\beta = .35$, $p = .045$), the FFA (robust regression: $\beta = .39$, $p = .021$), and trend-wise of the precuneus ($\beta = .26$, $p = .078$) during PUB compared to PRIV was positively associated with social anxiety scores (see Fig. 3a). These associations were mediated by dwell time of gaze on the pictures of the confederates' faces during PUB compared to PRIV (Sobel tests: mPFC: $p = .04$, FFA: $p = .04$). This finding corroborates the clinical characterization of social anxiety as being related to excessive and maladaptive concerns about being evaluated by others and attentional shifts towards potentially threatening social cues in the environment (Morrison and Heimberg, 2013). Activation of the FFA (robust regression: $\beta = .50$, $p = .001$) and precuneus (robust regression: $\beta = .34$, $p = .050$) in the contrast PUB-PRIV was positively associated with self-reports of embarrassment (as reported during LOW_PUB see Fig. 3b). The robust regression of mPFC activity and self-reports of embarrassment was not significant ($\beta = .25$, $p = .114$). Additionally, participants who reported stronger embarrassment during LOW_PUB feedback also showed increased dwell time of gaze on the confederates' faces (robust regression: $\beta = .37$, $p = .012$). This association of dwell time and self-report of embarrassment was trend-wise mediated by FFA activation in the PUB-PRIV contrast (Sobel tests: FFA: $p = .05$). These findings suggest that paying attention to the audience and engaging in mentalizing about the other's evaluations of one's own situation might increase the own experience of embarrassment during public situations.

The interaction of PERFORMANCE x PUBLICITY did not survive correction for multiple comparison (FWE) at the whole brain level.

We used PPI analyses to explore our hypothesis that embarrassment manifests in a unique pattern of functional connectivity between brain regions processing performance and brain regions processing publicity. To do so we explored whether the precuneus and the mPFC, brain regions involved in publicity, and the arousal related activations in the dAI are also more strongly integrated with regions involved in processing core affect (vAI and amygdala) during low compared to high performances (see Fig. 2d). We indeed found that the mentalizing network revealed increased coupling with the amygdala and ventral aspects of the anterior insula during LOW compared to HIGH performances. The arousal-related left and right dAI showed greater connectivity with the same regions during LOW performance (see Table 2). Accordingly, the concept of embarrassment, as the interaction of failure and publicity, seems to map onto a similar construct in the brain: an increased functional connectivity between regions involved in mentalizing and (para-)limbic structures involved in affect.

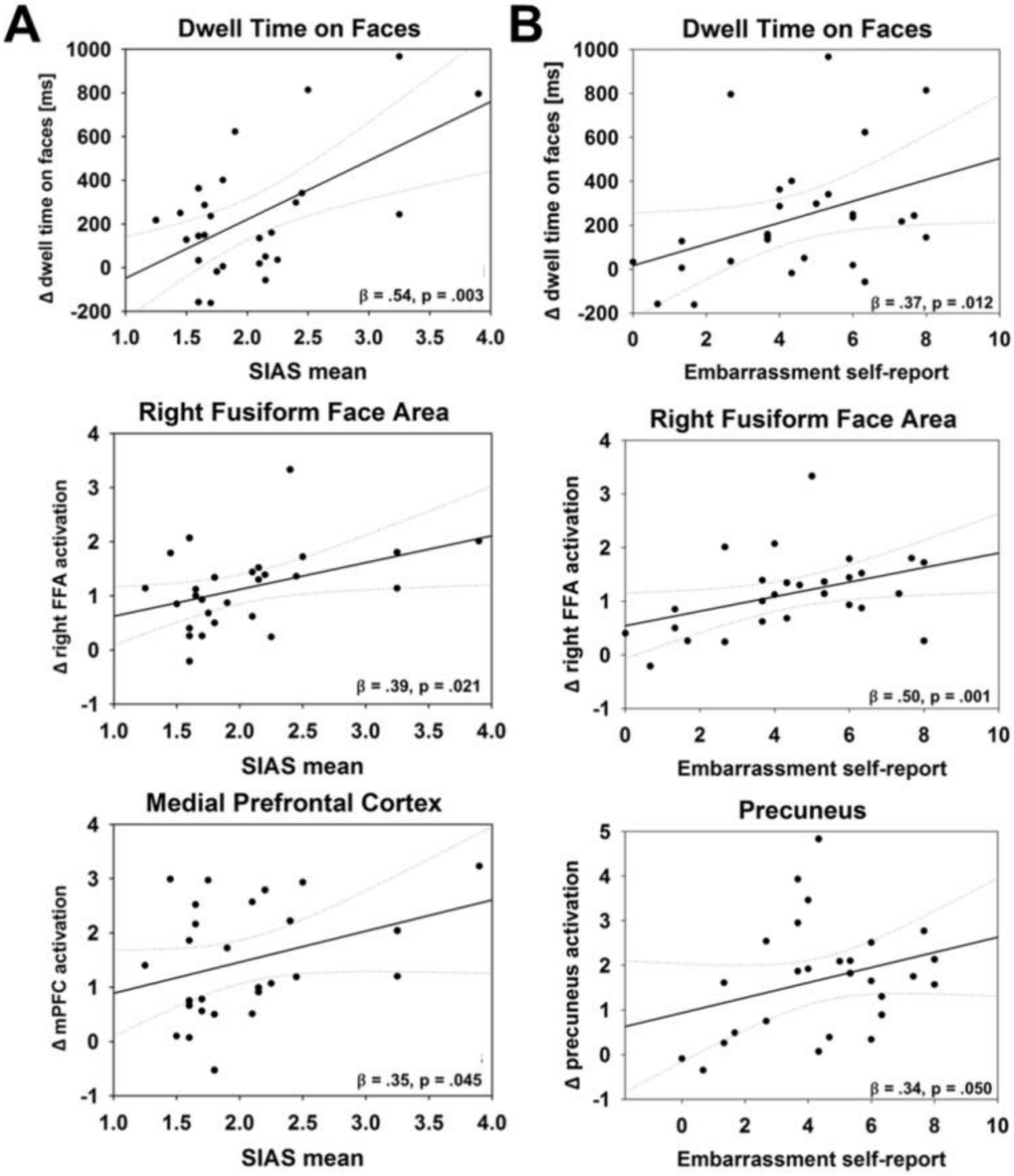

Figure 3. Modulatory effects of social anxiety and self-reported embarrassment. β-values result from robust regression analyses using Huber's M-estimators presented with one-tailed p-values. **A** Scatter plots of trait social anxiety and PUBLICITY effects for gaze dwell times and activation data. There was a positive correlation between social anxiety (mean SIAS scores) and differences in dwell time on the confederates' faces between the public and private conditions (top). Participants with higher social anxiety scores also showed increased activation within the right fusiform face area (FFA, middle) and the mPFC (bottom) during PUB-PRIV (averaged parameter estimates within the FFA and mPFC clusters from the PUBLICITY effect, Fig. 2b). **B** Scatter plots of self-reports of embarrassment and PUBLICITY effects for gaze and activation data. The upper part shows a positive correlation between self-reports of embarrassment during LOW_PUB feedback and differences in dwell time of gaze on the confederates' faces between the public and private conditions. Participants who reported experiencing stronger embarrassment during LOW_PUB feedback also showed increased activation within the right fusiform face area (FFA, middle) and the precuneus (bottom) during PUB-PRIV feedback.

2.4. DISCUSSION

A core goal of our study was to characterize the neurobiological mechanisms of embarrassment while immersing individuals in an authentic social situation that really matters for their social integrity. Through manipulated feedback of failure, we induced a genuine affective experience of embarrassment (as verified by self-report), and triggered physiological and neural responses associated with increased arousal (pupil dilation and stronger activation of the dAI). When participants were informed that their failure was public, they experienced greater embarrassment and showed signs of increased sympathetic activation in terms of pupil dilation. This modulation was not evident for pride in response to feedback of achievements, which yielded distributed activations and strong responses of the brain's reward circuits in the striatum.

According to psychological concepts, and in line with the constructivist understanding of how the brain processes emotions (Lindquist et al., 2012), embarrassment has been suggested to be a unique combination of (a) one's failure and related arousal on the one hand, and (b) mentalizing about how this failure will damage the opinion that others have of oneself on the other hand (Krach et al., 2011; Miller, 1996; Paulus et al., 2014; Tangney et al., 2007). Our neuroimaging data suggest that this functional description of embarrassment as arousal in the context of unfavorable mentalizing maps well onto the brain.

Notably, activations in the mPFC are far from being specific to processes of mentalizing, and have been reported in a multitude of 'tasks' which do not involve embarrassment (Buckner et al., 2008; Critcher and Gilovich, 2010). The role of the mPFC has also been extensively debated in the context of the default mode of the brain where people engage in mind-wandering, self-reflection, or daydreaming (Schooler et al., 2011; Smallwood and Schooler, 2006). Nonetheless, the positive association of mPFC activation with the fixation on the audience's faces supports the notion that the mPFC activity in the present experiment might indeed relate to thinking about the evaluations in-the-eyes-of-others and not mind-wandering or daydreaming.

The significance of this public-private distinction also manifests in the context of social anxiety and thereby contributes to the understanding of its etiology, where excessive and persistent concerns about the evaluations of others are central to the symptomatology (Morrison and Heimberg, 2013; Schneier, 1992). Our correlational data with sub-clinical social anxiety support the notion that in public contexts, persons with greater social anxiety pay increased attention to others which might be related to the clinically well-described negative bias in terms of what the audience might think of them (Morrison and Heimberg, 2013). We found a positive association between social anxiety and increases of gaze dwell time on the social cues in the public relative to the private condition. The co-occurring increase in mentalizing activation was mediated by this attentional bias to the audience. While there is initial evidence for increased mentalizing activity in patients with social anxiety in the context of face perception (Blair et al., 2011a) or negative self-evaluations (Blair et al., 2011b), our integrated perspective on how attentional shifts to the audience induce greater mentalizing activation goes beyond what previous studies on the neural foundations of social anxiety have described. The present paradigm could thus offer a novel perspective to characterize the altered processing of publicity in the pathology of these disorders in a dynamic and interactive setting.

Whenever performances deviated from neutral, we found robust activation of the dAI, a region strongly associated with salience and arousal (Critchley, 2005; Seeley et al., 2007). Given that embarrassment was experienced much more during low than high performances, this dAI activation is not a specific neural marker for the embarrassment experience. Both, the effects for the publicity of an event, as well as this deviation from an anticipated standard of an event, refer to the main effects in our two-factorial design. We further found an interaction of publicity and performance at the behavioral and physiological levels: public failure, i.e. the combination of publicity and low performance, to trigger elevated levels of self-reported embarrassment and pupil dilation as an indicator for sympathetic arousal (Bradley et al., 2008; Paulus et al., 2015). Surprisingly, we did not find a matching interaction between both factors, the public failure, on the level of single voxel BOLD activity. More recent conceptualizations of how the brain processes emotions however depart from a traditional localist approach in which particular voxels are associated with particular emotions. Instead, discrete emotional categories such as embarrassment, shame, guilt, or pride, are thought to be constructed by the concerted dynamics of brain networks, with each network not being specific for one emotion (Lindquist et al., 2012), but the interaction between the brain regions creating a unique configuration. In line with these conceptualizations, we found the conditions of embarrassment to be associated with a unique pattern of functional connectivity. In particular, when we contrast low with high performances, the vAI and amygdala showed increased coupling with distinct brain networks, the bilateral dAI and the mPFC as well as precuneus. The integrated activity across arousal processing and mentalizing networks with these (para-)limbic structures might create a neural ensemble activity that supports the experience we call embarrassment. The dense anatomical connections between the ventral and dorsal aspects of the anterior insula and the amygdala (Cerliani et al., 2012) might constitute the structural underpinning of this integration, in line with accumulated evidence on the integrative role of the vAI in emotion processing (Chang et al., 2013; Kelly et al., 2012). Importantly, activations of the vAI and the amygdala, too, are themselves by no means specific for the experience of embarrassment (Adolphs, 2008; Chang et al., 2013; Kelly et al., 2012), making it highly improbable that the activity in these regions alone would trigger embarrassment.

The present findings provide neurophysiological support for psychological models of embarrassment which state that humans are usually motivated to maintain a positive social image whenever they act in public (Leary and Kowalski, 1990) and feel extreme discomfort if their social integrity is threatened (Miller, 1996). Cognitive shortcomings are among the most common and salient threats to one’s social integrity, and might be especially emphasized in a student setting and under circumstances in which the expectations on one’s cognitive performance are high (Miller, 1996). In the current experiment, this was induced by allegedly selecting participants based on their general mental ability. To understand and reflect on one’s own social image, one needs to model others’ evaluations and their view of oneself, which is relevant for threats to social integrity (Eisenberger et al., 2003). This information processed in the mentalizing network seems to gain particular importance in the context of failure, as we observe a dynamic increase of connectivity of the mentalizing system with (para-)limbic regions for failure as compared to achievement. Together with the concurrent increase in the connectivity with neural systems associated with the processing of arousal, this specific integration of information across both brain systems might explain the publicity effect we found on the behavioral level, which was evident only for the embarrassment in response to public failures. During achievements, there is less integration of mentalizing and arousal-related information in (para-)limbic regions, and hence, publicity does not influence the experience of pride accordingly (Seidner et al., 1988). In conclusion the present paradigm offers a broader perspective to investigate the processing of publicity and its impact on social emotions with the potential to characterize the altered neural pathways in social anxiety disorders in context of a dynamic and socially interactive setting.

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SUPPLEMENTARY MATERIALS

Supplementary Figures and Legends

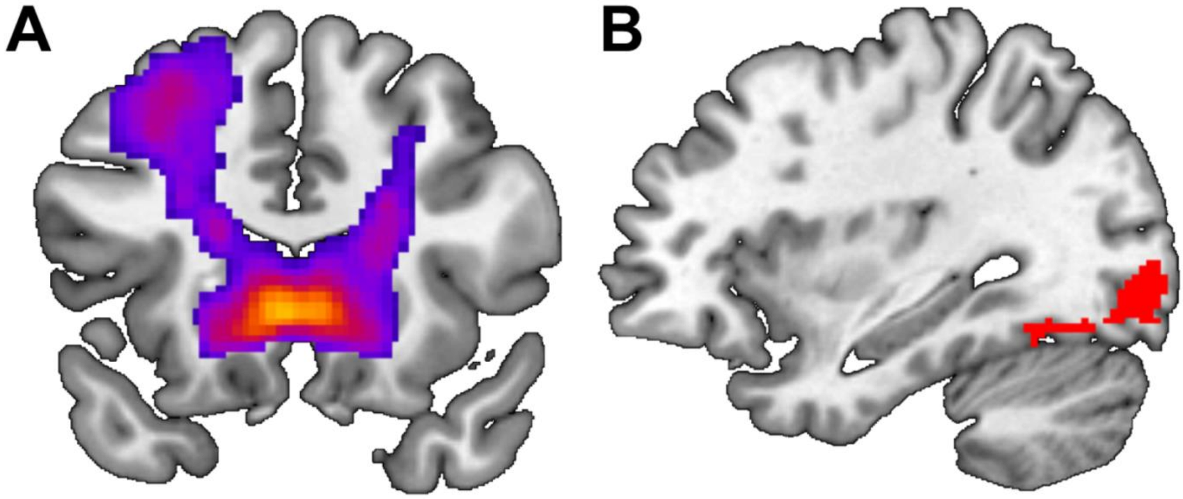

Figure A. 1. **A** Increased activation of striatal areas associated with reward processing during HIGH compared to LOW feedback (p < .05, whole brain corrected). **B** Increased activation of the left fusiform gyrus associated with increased gaze dwell time on the confederates' faces during individual feedback trials (corrected for differences between PUB and PRIV feedback; p < .05, whole brain corrected).

Supplementary Tables

Table A. 1. Activation Associated with Valence of the Feedback.

Brain Region	Side	Cluster Size	MNI Coordinates			*T*	*p*FWE
			x	y	z		
HIGH-LOW							
Caudate Nucleus	R/L	68,087	-4	20	0	13.22	< .001
			4	18	-2	12.04	< .001
			14	28	-2	11.92	< .001
Middle Temporal Gyrus	R	395	62	-8	-12	6.30	< .001
			58	-4	-22	6.18	.001
			60	2	-8	5.65	.004
Superior Frontal Gyrus	R	246	22	36	44	9.19	< .001
			20	32	36	8.83	.007
			20	30	26	8.41	.024
HIGH-NEUT							
Anterior Cingulate Cortex	L/R	9,721	-4	42	12	9.24	< .001
			-4	38	22	7.91	< .001
			-8	28	0	7.85	< .001
Cuneus	R/L	2,595	6	-92	14	8.25	< .001
			8	-92	30	8.01	< .001
			16	-84	8	6.88	< .001
Insula	R	591	32	20	-20	7.79	< .001
			42	24	-12	7.15	< .001
Hippocampus	L	308	-32	-16	-18	7.13	< .001
			-42	-24	-18	5.70	.003
			-52	-30	-12	5.68	.003
Cerebellum	R/L	2,596	-22	-48	-22	7.04	< .001
			-8	-54	-2	6.27	< .001
			10	-70	-14	6.23	< .001
Hippocampus	L	353	-18	-26	-12	6.91	< .001
			0	-18	-16	6.61	< .001
			-10	-16	-16	5.66	.004
Hippocampus	R	174	22	-16	-16	6.26	< .001
			16	-26	-12	6.11	.001
Hippocampus	R	124	30	-32	8	6.19	.001
			40	-40	2	5.00	.035
Middle Temporal	R	53	52	-36	-8	5.67	.003
Linual Gyrus	R	94	8	-54	4	5.48	.007
			6	-44	-2	4.93	.045
Cerebellum	R	110	30	-48	-26	5.47	.007
			22	-54	-20	5.43	.008
			24	-36	-30	5.31	.012

Note. FWE = Family-wise error correction. All statistics for the average effects of HIGH-LOW and HIGH-NEUT are thresholded at p < .05, FWE, whole brain corrected. Clusters with less than 50 voxels are not reported.

Table A. 2. Activation Associated with Publicity of Feedback.

Brain Region	Side	Cluster Size	MNI Coordinates			*T*	*p*FWE
			x	y	z		
PUB-PRIV							
Medial Prefrontal Cortex	L/R	1,180	0	60	18	7.26	< .001
			-4	50	30	7.20	< .001
			2	60	32	6.32	.001
Precuneus	L/R	458	-4	-52	38	6.35	.001
			4	-50	36	6.11	.003
			4	-58	38	5.73	.008
Fusiform Gyrus	R	272	32	-68	-12	6.16	.002
			38	-48	-22	5.62	.012
			26	-74	-18	5.54	.015
Inferior Frontal Gyrus	R	166	46	22	26	5.82	.006
Superior Parietal Lobule	R	50	30	-62	54	5.76	.008

Note. FWE = Family-wise error correction. All statistics for the average effect of PUB-PRIV are thresholded at p < .05, FWE, whole brain corrected. Clusters with less than 50 voxels are not reported.

Table A. 3. Dwell Time on the Confederates' Faces during High and Low Performance Feedback Conditions in ms.

Feedback Condition	Low SIAS		High SIAS		Total Sample	
	M	*SD*	*M*	*SD*	*M*	*SD*
HIGH_PUB	655.1	431.6	754.7	462.3	703.0	440.9
HIGH_PRIV	440.3	313.3	434.0	324.4	437.3	312.5
LOW_PUB	514.5	347.1	668.0	435.6	588.4	392.4
LOW_PRIV	415.1	256.5	431.5	224.9	423.0	237.3
NEUT_PUB	596.7	397.5	897.4	699.3	741.5	572.8
NEUT_PRIV	509.9	331.3	434.6	346.2	473.6	334.1

Note. M = mean; *SD* = standard deviation. SIAS = mean score of the Social Interaction Anxiety Scale; PRIV = private condition, PUB, = public condition. Low and High SIAS refers to the two groups generated by a median split of the SIAS scores.

Table A. 4. Activation Associated with Pupil Dilation and Dwell Time on the Confederates' Faces.

Brain Region	Side	Cluster Size	MNI Coordinates			*T*	*p*FWE
			x	y	z		
Pupil Dilation							
Insula	R	477	48	-8	6	8.57	< .001
			56	2	10	7.64	.002
			54	-4	2	7.62	.002
Precentral Gyrus	R	216	20	-26	62	7.80	.001
			20	-28	70	7.48	.003
			36	-30	64	7.00	.007
Postcentral Gyrus	L	140	-20	-36	64	7.50	.003
Middle Cingulate Cortex	L	66	10	-16	48	7.18	.005
			0	-12	50	6.36	.026
Middle Cingulate Cortex	R/L	58	0	10	38	6.58	.017
Dwell Time on the Confederates' Faces							
Fusiform Gyrus	L	231	-36	-84	-8	9.92	< .001
			-34	-62	-14	8.33	< .001
			-32	-70	-12	7.63	.002
Calcarine Gyrus	L	75	-10	-82	8	7.85	.001
Inferior Occipital	R	138	29	-94	-4	7.52	.002
			32	-86	-12	7.01	.006
			32	-90	-2	6.64	.013

Note. FWE = Family-wise error correction. All statistics for the activation associated with pupil dilation and gaze dwell time on the confederates' faces are thresholded at p < .05, FWE, whole brain corrected. Clusters with less than 50 voxels are not reported.

CHAPTER 3

INCREASED AUTONOMIC ACTIVATION IN VICARIOUS EMBARRASSMENT

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INCREASED AUTONOMIC ACTIVATION IN VICARIOUS EMBARRASSMENT

ABSTRACT

We studied the somatovisceral response pattern of vicarious embarrassment for someone else's inappropriate condition. Participants (N = 54) were confronted with hand-drawn sketches depicting public situations and were instructed to rate the intensity of their vicarious embarrassment. The inappropriate condition varied according to the attribution of intentionality (absent/present) and awareness (absent/present). Irrespective of these attributions, participants reported stronger vicarious embarrassment in comparison to neutral situations. Across a set of eleven somatovisceral variables vicarious embarrassment elicited a pattern of increased autonomic activation which was modulated by the awareness of the protagonist about the ongoing norm violation. The somatovisceral response pattern matches previous findings for the first-person experience of embarrassment. Together, these results support the hypothesis that processes of perspective taking also mediate the vicarious experience of embarrassment.

AUTHOR CONTRIBUTIONS

The author of this thesis contributed to the planning of the experimental design, data acquisition, data analysis, data presentation and writing of the paper.

CHAPTER 3

3.1. INTRODUCTION

Empathic feelings for others have been in the focus of a large body of empirical literature in social psychology and neuroscience. Most of the evidence in these studies is derived from experimental designs confronting participants with the physical pain of others (Lamm et al., 2011; Singer et al., 2004). The main consensus of these efforts was that the empathic simulation of another person's painful state and the subjective experience of pain activate similar physiological processes as evidenced by comparable somatovisceral (Hein et al., 2011; Lamm et al., 2008) and neural response patterns (Craig, 2009; de Vignemont and Singer, 2006; Lamm et al., 2011; Lamm and Singer, 2010).

Although "observing negative *social* experiences [as compared to observing others' *physically* painful experiences] is likely to be a more frequent occurrence" in everyday life (Masten et al., 2011), considerably less investigations have focused on examining physiological correlates of social pain (Eisenberger et al., 2003; Kross et al., 2011) and even less on its vicarious experiences as in studies on compassion (Immordino-Yang et al., 2009), social rejection (Beeney et al., 2011), or embarrassment (Hawk et al., 2011; Krach et al., 2011). Similar to the conceptual understanding of empathy for physical pain (Hein and Singer, 2008), the simulation and mirroring of another person's state are thought to mediate social pain (Hawk et al., 2011; Waytz and Mitchell, 2011). In case of the vicarious embarrassment at another person's cringe-worthy moments Krach and colleagues (2011) have recently demonstrated that observers would feel this form of social pain for protagonists in a broad variety of public social situations. Notably, vicarious embarrassment was also evident when the observed protagonists themselves were not aware of the inappropriateness of their behavior (e.g. walking around in a pedestrian zone with their fly open). Independent of the observation of embarrassment (signs are, e.g. facial blushing or appeasement gestures) the perception of others' public predicaments resulted in cortical activations of the affective and motivational components of the so-called "pain matrix" (Peyron et al., 1999) and, importantly, neural activation within these regions was correlated with individual differences in trait empathy (Krach et al., 2011).

Most research examining the social emotion of embarrassment focused on participants which themselves were exposed to awkward situations. In these studies physiological responses such as blushing (Drummond, 1997; Mulkens et al., 1997; Shearn et al., 1990), electrodermal activity (Gerlach et al., 2003; Hofmann et al., 2006; Mulkens et al., 1997; Shearn et al., 1990), or cardiovascular activity (Gerlach et al., 2003; Harris, 2001; Hofmann et al., 2006; Miller and Fahey, 1991) were investigated. To our knowledge there is no study addressing detailed physiological response patterns of the social emotion of embarrassment as experienced vicariously for another person's inappropriate behavior. The current study aims to close this gap by using a set of physiological measures to systematically investigate cardiovascular and electrodermal activity, peripheral blood flow as well as cheek blood flow and temperature of vicarious embarrassment in a broad variety of situations.

3.1.1. Physiology of Social Emotions

Beside changes in experience and behavior every emotional reaction is accompanied by somatovisceral activation (e. g. Lang, 1993). There has been a longstanding debate about whether emotions produce rather diffuse (Cannon, 1927) or specific somatovisceral responses (Ax, 1953; Fahrenberg, 2001; Stemmler, 2003, 2004). Physiological data indicate that somatovisceral processes are highly patterned and show differences between situations and emotions such as anger or fear (Cacioppo et al., 2000; Fahrenberg, 2001; Stemmler, 1989, 2010; Stemmler et al., 2007; Stemmler et al., 2001). Meta-analytic data (Cacioppo, et al., 2000; Kreibig, 2010; Stemmler, 2004) indicate that anger is associated with increased heart rate, increased number of skin conductance responses, increased skin conductance level, decreased finger temperature and increased facial temperature. Compared to anger, fear is associated with greater increases in heart rate, fewer nonspecific skin conductance responses, a slightly larger decrease in finger temperature, and a smaller increase in facial temperature.

In comparison to the number of studies addressing the somatovisceral basis of anger and fear, there have been only few studies on embarrassment or its vicarious form (Gerlach et al., 2003; Harris, 2001; Hofmann et al., 2006; Miller, 1987; Shearn et al., 1990; Shearn et al., 1999). Moreover, the number of physiological response variables in these studies was rather limited (Kreibig, 2010). Mainly, these studies could show that the induction of embarrassment (Gerlach et al., 2003; Harris, 2001; Hofmann et al., 2006; Miller and Fahey, 1991) or shame (Herrald and Tomaka, 2002) led to increases in heart rate. Further, systolic and diastolic blood pressure increased when embarrassment was elicited (Harris, 2001), as did skin conductance level (Hofmann et al., 2006; Mulkens et al., 1997) and number of skin conductance responses (Gerlach et al., 2003; Shearn et al., 1990). Eliciting embarrassment in a public, but not in a private context, Miller and Fahey (1991) found vasoconstriction as indexed by lower finger temperature. Overall, Kreibig (2010) postulated that the induction of embarrassment consistently resulted in broad sympathetic activation and vagal withdrawal, a response pattern largely overlapping with those of the basic emotions of anger and anxiety.

Only two studies addressed somatovisceral reactions during vicarious embarrassment. In both cases an elevated number of skin conductance responses were reported (Miller, 1987; Shearn et al., 1999).

A potential specific physiological response is *blushing*, according to Buss (1980) the hallmark of embarrassment. Blushing is invoked by increases in blood volume in the subcutaneous surface capillaries, which produces the spontaneous reddening of the face, ears, neck, and upper chest (Leary et al., 1992). The blushing response reaches its peak about 15 to 20 s following the embarrassing incident (Shearn et al., 1990). Previous studies showed that embarrassment was indeed associated with increased temperature and blood flow at the cheek and forehead indicating blushing (Drummond, 1997; Mulkens et al., 1997; Shearn et al., 1990) and persons with higher blushing propensity reported higher levels of social discomfort such as embarrassment (Drummond, 1997; Mulkens et al., 1997). To our knowledge only one study investigated blushing responses during the experience of vicarious embarrassment. Shearn et al. (1999) reported increased cheek blood flow and cheek temperature. Whether blushing propensity is positively related to the experience of vicarious embarrassment has not been studied so far.

3.1.2. A Conceptualization of Vicarious Embarrassment

The studies on the vicarious experience of embarrassment followed the experimental procedure that was first introduced by Miller (1987): While being filmed or observed, the protagonists were requested to dance to recorded music or sing, for example, "The Star Spangled Banner" in front of others. The protagonists were aware of the embarrassing potential of the current situation and showed signs of embarrassment (Marcus et al., 1996; Miller, 1987; Shearn et al., 1999). Krach and colleagues (2011) extended this approach by showing that observers experience vicarious embarrassment in a much broader variety of situations that expose protagonists to the public while violating etiquette and normative social standards. According to this research, it is not necessary that the norm-violating incident is accessible to the protagonist, it is sufficient that the observers are aware of the embarrassing potential (Krach et al., 2011). Similarly, without explicitly testing the hypothesis, Miller (1987) already concluded from the small correlation of the protagonist's embarrassment with the observer's vicarious embarrassment that vicarious embarrassment may occur even if protagonists do not show any signs of embarrassment (e.g. blushing). He suggested that vicarious embarrassment originates from empathic processes in which the observer represents the inner state of the protagonist by drawing on own past experiences (Miller, 1996). This reasoning has been supported by a recent study of Hawk and colleagues which showed that people experience vicarious embarrassment whether or not the exposed protagonists showed observable signs of embarrassment during dancing (Hawk et al., 2011). They further demonstrated that mirroring another person's situation or simulating another person's perspective might both account for the broad scope of situations one might experience vicarious embarrassment in everyday life.

A conceptualization to structure these vicariously embarrassing situations has been developed earlier by Krach and colleagues (2011) who distinguished among situations based on the causation of the social norm violation. In everyday life, embarrassing incidents are usually avoided and often occur accidentally (Miller, 1996). However, social norms can also be intentionally violated and trigger a vicarious emotional reaction in the observer. Whereas accidental norm violations do not inform about the character of the protagonist (Stocks et al., 2011), the attribution of intentionality and hence responsibility clearly does. This differentiation between accidental and intentional norm transgression has also been used before (Berthoz et al., 2002), but there was no focus on the emotion elicited in the observer. Krach and colleagues (2011) have shown that both types of transgressions do elicit vicarious embarrassment and proposed a broader framework which might better correspond to the heterogeneous causes of that feeling in everyday life. The framework includes the above mentioned appraisal dimensions of (1) *intentionality*, representing the accidental versus intentional character of embarrassing situations, and (2) *awareness*, representing the awareness versus unawareness of the norm violating incident by the observed protagonist. On the basis of these dimensions four attribution categories of situations are distinguished (see Figure 1): (1) AA (Accidental/Aware); (2) AU (Accidental/Unaware); (3) IA (Intentional/Aware) and (4) IU (Intentional/Unaware).

3.1.3. *Appraisals of Embarrassing Situations*

The differentiation of these four categories allows to study the consequences of emotion antecedent appraisals of vicarious embarrassment situations. A substantial amount of theoretical and empirical emotion research has focused on appraisal processes (Frijda, 1987; Reisenzein and Hofmann, 1990; Scherer, 2009). Tangney (1996) identified several dimensions of appraisals that are relevant in embarrassing situations. One dimension is common to all attribution categories of vicarious embarrassment: The sense of an observer's evaluation of the protagonist. However, taking into account the observer's attribution of the protagonist's point of view, we expect differences in appraisals across categories which imbue the emotional experience.

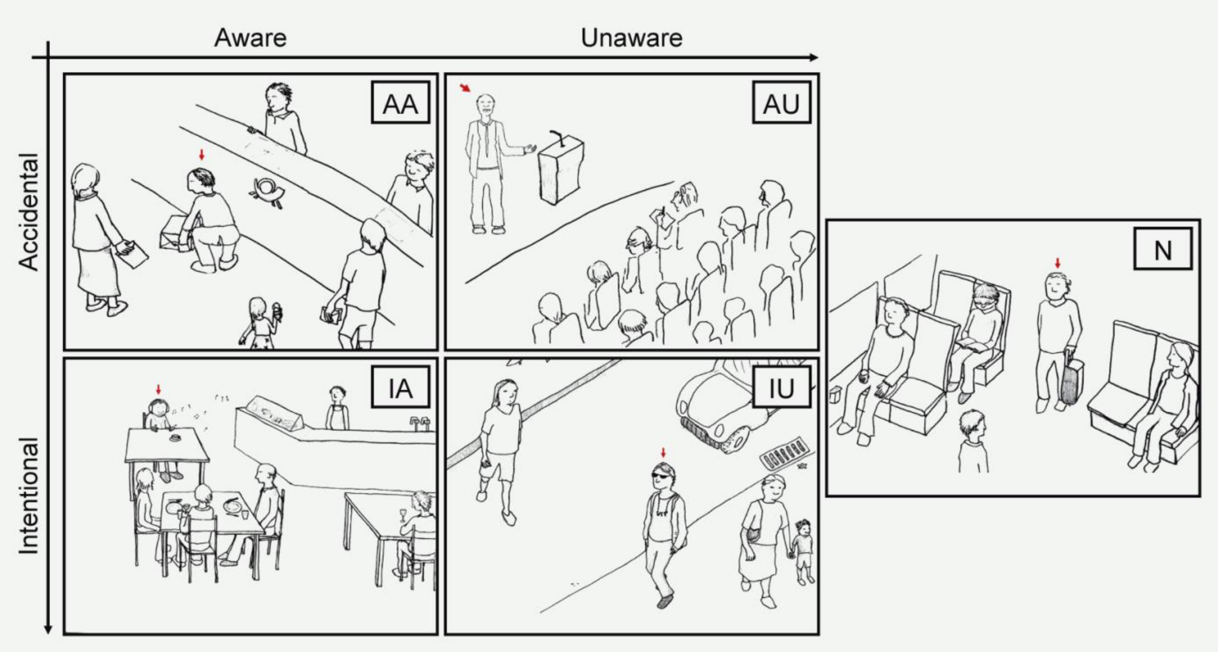

Figure 1. Drawn sketches depicting social situations. Drawn sketches depict a protagonist, indicated by the red arrow above his/her head, in potentially embarrassing situations. During the experiment each sketch was accompanied by a sentence introducing the current scenario. Situations were presented with the following textual vignettes for clarification (in the original version sketches were presented with German textual vignettes): AA: You are at a post-office: the pants of the person in front of you rip as he bends down to lift a package…; AU: You are at a lecture: the lecturer has spinach in his teeth…; IA: You are in a café: the person next to you is listening to music and singing along loudly…; IU: You are in a pedestrian zone: a young man wearing a VIP-necklet passes you…; N: You are on a train: a person is carrying a bag. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

A close relative of vicarious embarrassment is compassion (Stocks et al., 2011). Tangney (1996) pointed out that individuals in embarrassing situations had the sense of little control and personal responsibility for the event. The observer uses these attributions for the protagonist in situations that display accidental norm violations (AA, AU). Such situations do not inform about stable personality traits and are more likely associated with external and uncontrollable causes which evoke the awkwardness of the situation and elicit compassion in the observer (Stocks et al., 2011). Another emotion that could co-occur with vicarious embarrassment is anger. In situations with high awareness (AA, IA) the observer assumes that the protagonist has insight into the embarrassing condition. In category IA, in contrast to AA, the protagonist shows the embarrassing behaviour and intentionally disobeys the observers' expectations and their normative standards. According to Scherer (2009), such situations should elicit anger, in addition to vicarious embarrassment.

3.1.4. Overview and Hypotheses

The social pain of vicarious embarrassment for others' flaws or norm transgressions has attracted growing scientific attention (Hawk et al., 2011; Krach et al., 2011; Stocks et al., 2011). Up to date there is little evidence from previous studies that describe somatovisceral changes related to vicarious embarrassment in diverse everyday life situations. To this end, we use a set of physiological measures to systematically investigate the modulatory role of social context and its cognitive appraisals on somatovisceral responses. Based on previous findings on the somatovisceral responses of embarrassment, we predicted that vicarious embarrassment would lead to a similar pattern of increased autonomic activation characterized by decreased heart period, increased electrodermal activity, and vasoconstriction. We further assessed well-characterized parameters of cardiac activity to describe the somatovisceral response patterns in greater detail (see also Stemmler, 1993; Stemmler et al., 2007; Stemmler et al., 2001). Additionally, we hypothesized vicarious embarrassment to elicit blushing responses as indicated by increased temperature and blood flow at the cheek. The distinction among the attribution categories further allows to examine how the appraisal dimensions affect emotional experience and physiological response patterns. We hypothesized that attribution of awareness and intentionality should affect physiological responses. Finally, we investigated whether individual differences in blushing propensity are associated with the self-reported experience of vicarious embarrassment.

3.2. METHOD

3.2.1. Participants

Fifty-four female subjects, all German native speakers, participated in the study. We recruited female subjects only to minimize potential confounding effects (Wacker et al., in press) resulting from the interaction with the female experimenter (LMP). The sample had a mean age of 23.6 years (range 19-38 yrs., *SD* = 3.8) and a mean body mass index of 22.12 kg/m^2. The majority of 87 % of the participants was university students; the minority worked (7.4 %), received professional training (3.7 %) or was unemployed (1.9 %). On average, participants had spent 16 years in education (range 14-24 yrs., *SD* = 2.51). Participants received compensation of 10 Euros for approximately 2 h of involvement in the study.

3.2.2. Stimuli and Experimental Design

All stimuli, including twenty vicarious embarrassment situations and five neutral ones, were hand-drawn sketches depicting public situations (see Figure 1). Vicarious embarrassment situations varied according to combinations of intentionality (present, absent) and awareness (present, absent) resulting in the four attribution categories each represented by five situations. Stimuli were selected out of a larger set of sketches to best fit the two appraisal dimensions (for a detailed description of the stimulus material the reader is referred to Krach et al., 2011). Stimuli were presented in a fixed pseudo-randomized order. Presentation order was defined so that one situation of each category was presented in a block of five stimuli. The resulting five blocks were presented sequentially constituting the within-subject factor Block.

3.2.3. Setting and Apparatus

The experimental room (4 m × 3.4 m) was sound-attenuated and air-conditioned with a mean temperature of 23.3 °C (range 21.7-23.9 °C, *SD* = 0.08) and had a largely nontechnical appearance. Participants sat comfortably in a reclined position.

Electrodes and transducers were relayed through an input box to a 16-channel MP 100 Biopac (Goleta, CA) system, which was located in an adjacent room, with couplers for electrocardiogram (ECG 100c), skin conductance (GSR 100), skin temperature (SKT 100), and pulse volume (PPG 100). A PC recorded and displayed the signals with the custom software BioRec 3.22 under LabView 8.2. Experimental control was performed with Presentation (Neurobehavioral Systems) on a second PC, which displayed the stimulus material as well as self-report scales on a 15" LCD screen in front of the participant. During the entire experiment participants were alone in the experimental room and communication with the experimenter was established via intercom.

3.2.4. Procedure

After signing the informed consent, participants were instructed to complete personality questionnaires prior to the experiment. Participants were then seated in the experimental room and electrodes and transducers were placed, while the experimenter instructed the participants to sit quietly to prevent movement artifacts. Participants were also informed about the following experimental procedure and that more detailed instruction including a practice trial would follow a rest period for acclimatization to the experimental setting. After a ten-minute rest period, participants were instructed to imagine the displayed situations as if they were observing the situation in everyday life. A situation not used in the experiment was shown during the instruction in the practice trial in order to clarify the experimental procedure.

Each situation was presented after a 20 s baseline period and a subsequent fixation cross-hair indicating that the next situation would be presented on the screen. Vicarious embarrassment and neutral situations were displayed in the center of the screen with a short two-sentence description of the situation below (e.g., "You are in the theater: During the movie the woman next to you calls someone on the phone."). The presentation of the situations had a duration of 20 s which was followed by a self-report of vicarious embarrassment during the latter situation. Ratings were performed on a multi-button response box in front of the participants. Then the next baseline period started. Physiological data were recorded during each baseline period and each presentation of the situations.

Upon completion of the experiment, electrodes were removed and participants were guided to another room for a post-experimental examination. There, situations were presented a second time, but now participants were asked to rate their experienced anger and compassion following the imagination of each situation. Additionally, appraisals of the underlying dimensions of intentionality and awareness were assessed for each situation.

3.2.5. Variables

3.2.5.1. Self-report of emotion and appraisal ratings.

Participants rated vicarious embarrassment ("How strong was your feeling of embarrassment in place of the protagonist?"), anger ("How strong was your feeling of anger about the protagonist?"), and compassion ("How strong was your feeling of compassion for the protagonist?") on a 9-point unipolar scale (1 = *not at all*, 9 = *very strong*). Intentionality of the protagonist's behavior ("To what extent does the person intentionally show this behavior at that specific moment?") and awareness about the underlying inappropriateness of this behavior ("To what extent is the person aware of this situation as being embarrassing at that specific moment?") were assessed on a unipolar 9-point scale (1 = *not at all*, 9 = *very strong*).

3.2.5.2. Somatovisceral variables.

Eleven physiological parameters were derived from the somatovisceral recordings. The electrocardiogram (ECG) was recorded through disposable pregelled Ag/AgCl electrodes (VivoMed, 8 mm sensor diameter, Servoprax, Wesel, Germany) from the sternum and the left leg. A ground electrode was placed on the left forearm. Electrode sites were rubbed with a mild abrasive gel (Every, GVB-geliMED, Germany) and cleansed with alcohol to ensure electrode impedances below 10 kΩ. The signal was sampled at 1000 Hz, amplified by a factor of 1000, filtered with a high-pass filter of 0.5 Hz and a low-pass filter of 35 Hz. Parameterization was performed with the program BodyVision 2.0 (Extra Quality Measurement Systems, Frankfurt, Germany), which for each data recording period formed an R-wave triggered ensemble average for analysis. Parameterization yielded heart period (in milliseconds), P-wave and T-wave amplitudes (in millivolts), P-Q time (end of the P-wave to start of the Q-wave; in milliseconds), relative Q-T time (systolic time in milliseconds: start of the Q-wave to end of the T-wave, corrected for heart period using Sagie's formula Q-T time + 0.154*[1000 - heart period], see Andrassy et al., 2003), and S-T elevation (amplitude of the ECG-curve at a point 80 ms past the J-point, which was defined as the first point with a null potential after the S-peak; in millivolts). Heart period variability (in milliseconds) was calculated as the root mean square of successive heart period differences.

Peripheral pulses were detected at the volar surface of the distal phalanx of the left middle finger and additionally at the cheek to measure blushing responses (TSD 100, Biopac). The signals were amplified by a factor of 50 with filters set to DC and 30 Hz at a sampling rate of 1000 Hz. BodyVision 2.0 extracted pulse volume amplitude (in arbitrary units).

Skin temperature (in degrees Celsius) was measured at the cheek with a TSD 102a fast response thermistor (BIOPAC) to measure blushing responses. Sensitivity was 1.39 °C/V (with a midpoint at 32.2 °C); the frequency range was DC-0.15 Hz; sampling rate was 1 Hz.

Electrodermal activity was recorded with a constant voltage of 0.5 V at the volar surfaces of the proximal phalanxes of the index and ring fingers on the left hand. Skin sites were cleansed with warm soap water. Ag/AgCl electrodes (TSD 103, BIOPAC) had a surface of 0.38 cm^2; they were filled with a 0.05 molar sodium chloride Unibase emulsion. Sensitivity was 100 µS/V with a frequency range of DC-10 Hz and a sampling rate of 100 Hz. For electrodermal activity recorded at the finger phasic responses greater than 0.02 µS (minimal slope of 0.007 µS/s, maximal half recovery time of 10 s) counted as nonspecific skin conductance responses (SCR). BodyVision 2.0 parameterization yielded the number of SCRs per recording period (number per 20 s).

3.2.5.3. Personality questionnaires.

Participants completed nine questionnaires, one of which is relevant here: the Blushing Propensity Scale (Leary and Meadows, 1991). It shows adequate internal and test-retest reliability (Leary and Meadows, 1991). In the present sample the internal consistency was high (α = .89).

3.2.6. Data Analysis

3.2.6.1. Preprocessing of somatovisceral data.

First, the raw data were visually inspected for artifacts and deleted if necessary. Second, outlier detection was performed using Stata 11 (StataCorp LP, 2009). Outliers were set to missing data. Overall, about 4 % of the data were classified as missing. Missing data were replaced with estimates computed from the overall statistical model, which specified Subject and Trial. Third, variables with non-normal distributions were transformed by the natural logarithm (heart period variability, number of skin conductance responses). Finally, difference scores of the preceding baseline and the following stimulus interval were computed and used for statistical data analysis.

3.2.6.2. Statistical data analysis.

Appraisals of attribution categories and self-reports of emotion were analyzed using analysis of variance (ANOVA) with Category (AA, AU, IA, IU, and Neutral) and Block (five blocks of presentation order) as within-subjects factors. To assess awareness and intentionality of the protagonist between attribution categories, a priori contrasts were calculated. For self-reports of vicarious embarrassment, a priori contrasts comparing the neutral category with each of the other four categories of vicarious embarrassment were devised. For self-reports of anger an a priori contrast comparing category IA with the other three categories of vicarious embarrassment was conducted and for self-reports of compassion categories AA and AU were contrasted against categories IA and IU.

To test effects of individual differences in blushing propensity on the self-report of vicarious embarrassment, a 5 (Category) x 5 (Block) ANCOVA with blushing propensity as covariate was implemented. The interaction Category x Blushing Propensity was used to identify differences in correlations between categories. To further examine the effect of individual differences in blushing propensity on ratings of vicarious embarrassment, Pearson correlations were computed separately for each level of Category.

For somatovisceral data, first, as a multivariate test across all variables, a canonical discriminant analysis with all levels of Category was conducted to allow for a characterization of the physiological components showing activation differences and to prevent inflation of the alpha error. To further clarify the results for each somatovisceral variable a 5 (Category) x 5 (Block) ANOVA was computed. The factor Block was included to account for physiological changes over time. To test for the effect of emotion induction, for every somatovisceral variable an a priori contrast comparing the neutral category with all categories of vicarious embarrassment was implemented. A priori contrasts comparing situations with high awareness (AA, IA) vs. low awareness (AU, IU) and high intentionality (IA, IU) vs. low intentionality (AA, AU) were computed to test effects of appraisal dimensions.

3.3. RESULTS

3.3.1. Behavioral Data

Means and standard deviations for appraisals of attribution categories and self-reports of emotion are depicted in Table 1. Ratings of intentionality and awareness validated the classification of vicarious embarrassment situations into the four postulated attribution categories. Category AA had lower intentionality ratings than category IA, $F(1, 212) = 397.76$, $p < .001$, $\eta^2 = .65$, and category IU, $F(1, 212) = 539.76$, $p < .001$, $\eta^2 = .72$. Category AU had lower intentionality ratings than both categories IA, $F(1, 212) = 379.50$, $p < .001$, $\eta^2 = .64$, and IU, $F(1, 212) = 518.46$, $p < .001$, $\eta^2 = .71$. Categories IU and AU had lower ratings of awareness than category AA (IU vs. AA: $F(1, 212) = 503.90$, $p < .001$, $\eta^2 = .70$; AU vs. AA: $F(1, 212) = 534.15$, $p < .001$, $\eta^2 = .72$) and category IA (IU vs. IA: $F(1, 212) = 86.66$, $p < .001$, $\eta^2 = .29$; AU vs. IA: $F(1, 212) = 99.46$, $p < .001$, $\eta^2 = .32$).

In line with the a priori hypotheses the four categories of situations did indeed elicit vicarious embarrassment experiences in the participants. Participants reported higher vicarious embarrassment in category AA, $F(1, 212) = 814.15$, $p < .001$, $\eta^2 = .79$, category AU, $F(1, 212) = 547.84$, $p < .001$, $\eta^2 = .72$, category IA, $F(1, 212) = 428.35$, $p < .001$, $\eta^2 = .67$, and category IU, $F(1, 212) = 246.97$, $p < .001$, $\eta^2 = .54$, than in the neutral category. Ratings of anger and compassion were moderately large, with the exception of category IA eliciting strongest anger reactions compared to the other categories of vicarious embarrassment, $F(1, 212) = 151.68$, $p < .001$, $\eta^2 = .42$, and categories AA and AU eliciting stronger compassion ratings, $F(1, 212) = 466.79$, $p < .001$, $\eta^2 = .69$, in comparison to the categories with high intentionality. Thus, consistent with the prediction derived from the assumed appraisals of categories the feeling of anger was reported predominantly for category IA. Further, the feeling of compassion was elevated in categories AA and AU suggesting compassion to be especially involved when observing another's accidental mishaps.

Table 1. Means (SD) of Self-Reports across Categories

Attribution category	Emotion			Appraisal	
	Vicarious embarrassment	Anger	Compassion	Awareness	Intentionality
Accidental/ Aware	6.21 (2.08)	2.20 (1.93)	7.39 (1.85)	8.09 (1.62)	1.17 (0.74)
Accidental/ Unaware	5.30 (1.89)	2.14 (1.87)	6.15 (2.19)	2.58 (2.57)	1.29 (0.99)
Intentional/ Aware	4.82 (2.14)	4.51 (2.88)	2.78 (2.34)	4.97 (2.50)	6.66 (1.54)
Intentional/ Unaware	3.94 (2.01)	3.09 (2.32)	2.44 (2.04)	2.74 (1.99)	7.56 (2.01)
Neutral	1.14 (0.62)	1.03 (0.27)	1.25 (1.22)		

3.3.2. *Individual Differences in Blushing Propensity*

Individual differences in blushing propensity had a significant impact on self-reported vicarious embarrassment. There was a significant interaction of blushing propensity with Category, $F(4, 208) = 4.45$, $p = .002$, $\eta^2 = .08$. Significant Pearson correlations between blushing propensity and the self-report of vicarious embarrassment were found for all attribution categories of vicarious embarrassment (AA: $r = .43$, $p = .001$; AU: $r = .42$, $p = .002$; IA: $r = .50$, $p < .001$; IU: $r = .28$, $p = .044$), but not for the neutral category ($r = .23$, $p = .10$).

3.3.3. *Somatovisceral Responses*

To characterize activation components discriminating best among the five experimental conditions a canonical discriminant analysis was performed with the eleven somatovisceral variables. There was one significant discriminant function, $F(48, 4659) =$

1.88, $p < .001$. The discriminant function was defined by positive correlations with heart period ($r = .40$), pulse volume amplitude at the finger ($r = .52$) and at the cheek ($r = .41$), and negative correlations with P-wave amplitude ($r = -.43$) and number of skin conductance responses ($r = -.24$). Thus, this function represented an overall autonomic deactivation response. The neutral category was located at the positive pole and the categories AA and IA at the negative pole of the function, showing the strongest activation among the categories.

Following the multivariate analysis, we used contrasts between attribution categories and the neutral category to capture specific embarrassment effects (see Figure 2 and Table 2 and 3 for detailed results). These contrasts at least partially remove effects attributable to all pictorial stimuli: The effect of "outward attention" when, for example, looking attentively at pictures (Lacey, 1967). According to Lacey, a demand for outward attention should lower heart rate and consequently baroreceptor tonus which would lead to a disinhibition of medullary centers facilitating outward attention. The contrasts calculated should capture the additional effects of vicarious embarrassment.

Table 2. Somatovisceral Change Scores for the Average of all Attribution Categories of Vicarious Embarrassment and Contrasts against the Neutral Condition

Variable	Condition					
	Embarrassment		Neutral			
	M	*SD*	*M*	*SD*	*F* (1, 212)	*p*
Heart period [ms]	26.49	19.39	33.72	26.39	5.28	.023
HP-variability [ln (ms)]	0.011	0.17	-0.008	0.212	0.56	.456
P-wave amplitude [mV]	-1.60	6.89	-5.02	12.34	9.35	.003
T-wave amplitude [mV]	3.90	4.89	1.86	7.15	5.23	.023
S-T elevation [mV]	-0.70	1.97	-1.54	3.84	5.36	.022
P-Q time [ms]	-0.12	1.40	-0.69	1.72	6.63	.011
Q-T time [ms]	-3.36	2.62	-4.00	3.67	1.92	.167
# SCR-finger [ln (1/20s)]	-0.15	0.13	-0.21	0.20	3.35	.069
PVA-finger [arb. units]	554.61	634.19	832.75	874.36	8.92	.003
PVA-cheek [arb. units]	3.69	13.38	10.21	18.03	7.14	.008
TMP-cheek [°C]	-0.005	0.033	-0.005	0.079	0.00	.968

Note. Embarrassment = Average of all four Categories of Vicarious Embarrassment. SCR = Number of Skin Conductance Responses. PVA = Pulse Volume Amplitude. TMP = Skin Temperature. AA = Accidental/Aware. AU = Accidental/Unaware. IA = Intentional/Aware. IU = Intentional/Unaware.

There was a difference between the neutral category and the categories of vicarious embarrassment for most of the physiological parameters. The categories of vicarious embarrassment elicited less heart period prolongation than the neutral category, *F*(1, 212) = 5.28, *p* = .023, η^2 = .02, less reduction of P-wave amplitude, *F*(1, 212) = 9.35, *p* = .003, η^2 = .04, and S-T elevation, *F*(1, 212) = 5.36, *p* = .022, η^2 = .03. The T-wave amplitude showed a greater elevation, *F*(1, 212) = 5.23, *p* = .023, η^2 = .02, and P-Q time, *F*(1, 212) = 6.63, *p* = .011, η^2 = .03, was less shortened in comparison to the neutral category. Furthermore, there was less finger vasodilation as indexed by pulse volume amplitude, *F*(1, 212) = 8.92, *p* = .003, η^2 = .04, and less cheek vasodilation, *F*(1, 212) = 7.14, *p* = .008, η^2 = .03, in categories of vicarious embarrassment than in the neutral category. The number of skin conductance responses showed a trend towards less reduction, *F*(1, 212) = 3.35, *p* = .069, η^2 = .02.

Table 3. Contrasts of high vs. low Awareness and Intentionality of Somatovisceral Change Scores

Variable	Contrast Awareness		Contrast Intentionality	
	F (1, 212)	*p*	*F* (1, 212)	*p*
Heart period [ms]	10.84	.001	0.03	.857
HP-variability [ln (ms)]	0.09	.764	<0.01	.987
P-wave amplitude [mV]	4.99	.027	0.98	.324
T-wave amplitude [mV]	2.47	.118	0.87	.351
S-T elevation [mV]	0.44	.507	0.04	.842
P-Q time [ms]	0.02	.881	0.01	.938
Q-T time [ms]	10.38	.002	0.06	.810
# SCR-finger [ln (1/20s]	6.53	.011	0.26	.610
PVA-finger [arb. units]	10.16	.002	1.64	.201
PVA-cheek [arb. units]	4.11	.044	0.52	.473
TMP-cheek [°C]	1.79	.182	1.89	.171

Note. SCR = Number of Skin Conductance Responses. PVA = Pulse Volume Amplitude. TMP = Skin Temperature. Contrast Awareness = AA + IA vs. AU + IU. Contrast intentionality = AA + AU vs. IA + IU.

A comparison of categories with high awareness (AA, IA) to categories with low awareness (AU, IU) showed that the former elicited stronger physiological activation in several physiological parameters. Differences were significant for heart period, *F*(1, 212) = 10.84, *p* = .001, η^2 = .05, P-wave amplitude, *F*(1, 212) = 4.99, *p* = .027, η^2 = .02, relative Q-T time, *F*(1, 212) = 10.38, *p* = .002, η^2 = .05, pulse volume amplitude at the finger, *F*(1, 212) =

10.16, *p* = .002, η² = .05, and at the cheek, *F*(1, 212) = 4.11, *p* = .044, η² = .02, and number of skin conductance responses, *F*(1, 212) = 6.53, *p* = .011, η² = .03 . Situations with high intentionality (IA, IU) did not show any activation differences compared to situations with low intentionality (AA, AU).

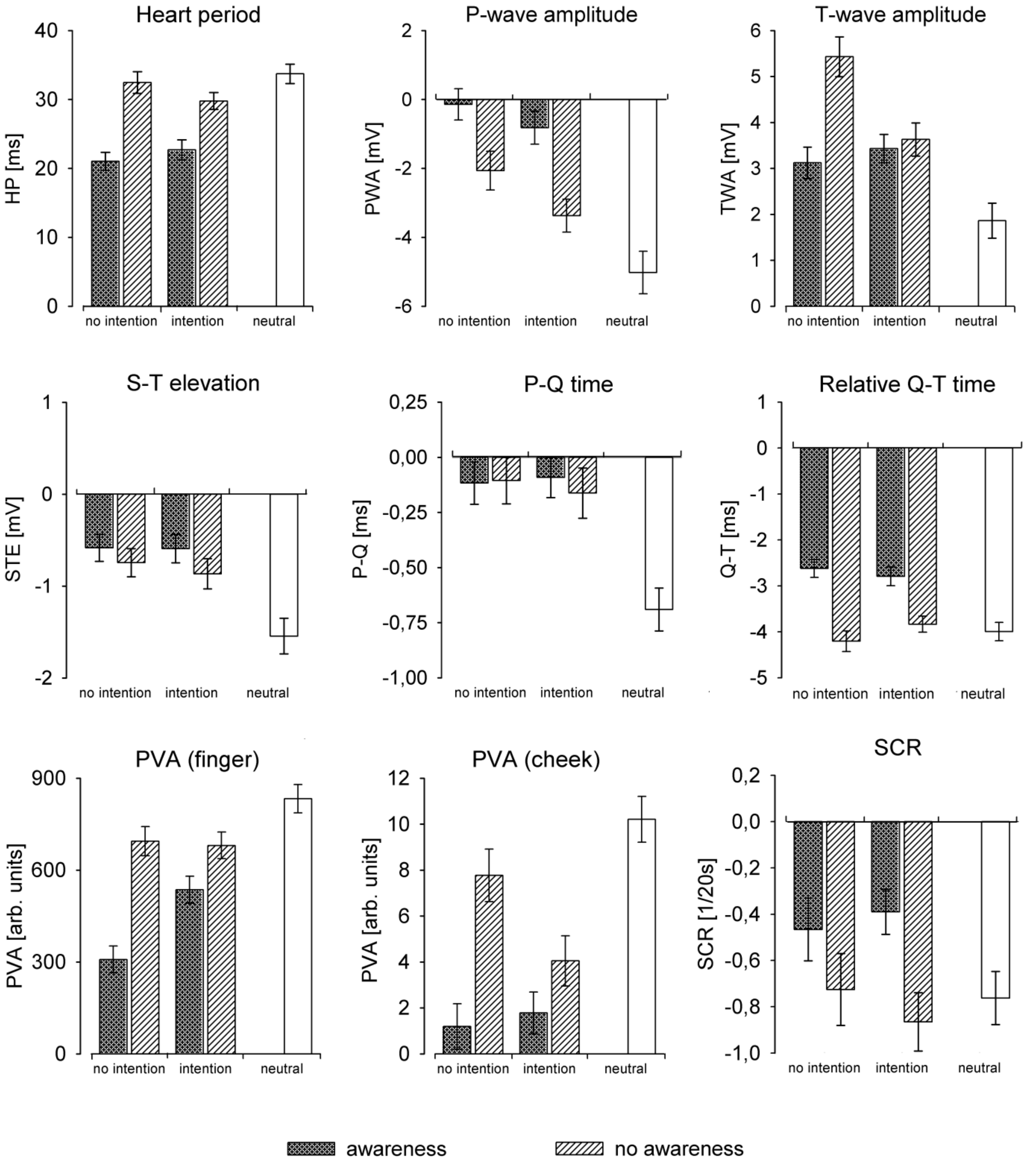

Figure 2. Means of baseline differences of responses in somatovisceral variables for the four attribution categories and the neutral category. Error bars indicate standard errors. HP = Heart period. PWA = P-wave amplitude. TWA = T-wave amplitude. STE = S-T elevation. P-Q = P-Q time. Q-T = Relative Q-T time. PVA = Pulse volume amplitude. SCR = Skin conductance responses.

3.4. DISCUSSION

The objective of the present study was to investigate the somatovisceral responses that accompany the social pain of vicarious embarrassment. Therefore we recorded physiological measures including cardiovascular and electrodermal activity, peripheral blood flow as well as cheek blood flow and temperature while observing others' social predicaments. The present findings confirmed our hypothesis, for the first time showing a broad pattern of autonomic activation accompanying vicarious embarrassment.

3.4.1. Physiology of Vicarious Embarrassment

Embarrassment is typically associated with decreased heart period, increased electrodermal activity, and peripheral vasoconstriction (Gerlach et al., 2003; Harris, 2001; Hofmann et al., 2006; Miller and Fahey, 1991; Shearn et al., 1990). We expected comparable physiological reactions to be related to the vicarious experience of embarrassment in the attribution categories of social situations. This has proven to be true especially for situations in which the protagonist was aware of the ongoing norm transgression (AA, IA). Somatovisceral responses of vicarious embarrassment included a greater number of skin conductance responses at the finger, a finding replicating earlier reports of increased electrodermal activity during vicarious embarrassment (Miller, 1987; Shearn et al., 1999). Further, categories of vicarious embarrassment compared to neutral elicited shortened heart period and finger vasoconstriction. According to our expectations, these findings indicate that responses of vicarious embarrassment are comparable to those reported for embarrassment (Gerlach et al., 2003; Harris, 2001; Hofmann et al., 2006; Miller and Fahey, 1991; Mulkens et al., 1997; Shearn et al., 1990). In addition, we found larger P-wave amplitudes, which have previously not been examined. These results provide clear support for the notion that vicarious embarrassment is associated with an increased autonomic activation.

Overall, Kreibig (2010) interpreted comparable physiological responses in case of first person embarrassment as a pattern of sympathetic activation and vagal withdrawal and argued that they have a considerable overlap especially with physiological responses of anger. This might arguably also apply for vicarious embarrassment. However, in contradiction to this we found unique physiological indicators for this kind of social pain in form of prolonged P-Q time and increased S-T elevation and T-wave amplitude. In other experimental settings these changes were considered as indicators for reduced autonomic activation and not associated with anger (Fahrenberg, 2001; Stemmler et al., 2001). These findings illustrate that vicarious embarrassment and possibly also embarrassment-induced physiological responses are complex, context dependent, and need to be assessed within a comprehensive set of response variables.

The autonomic activation in the context of vicarious embarrassment may be explained with respect to its functions during first-person experiences of embarrassment. It has been suggested that embarrassment serves an appeasement function, conciliating observers of social norm transgressions in order to restore social relations (Keltner, 1995; Keltner and Buswell, 1997). Embarrassment elicits the motivational state to repair one's own social pratfalls and social bonds following a norm violation (Darby and Harris, 2010; Keltner and Buswell, 1997). This motivation may drive individuals to actively discern the emotional reactions of others to gain access to the information needed to repair the situation (Darby and Harris, 2010). Increased autonomic activation could therefore be functional in preparing reparative actions. The autonomic activation in response to another's plight likely results from imagining oneself in this situation and thus could facilitate the understanding of the situation. In this process one also draws on information about the embarrassing potential of the on-going norm transgression which is exclusively accessible from one's own perspective (Epley and Caruso, 2009).

3.4.2. Modulation of Physiological Response Pattern by Awareness and Intentionality

Although participants experienced vicarious embarrassment in all four attribution categories, the pattern of increased autonomic activation seems to be predominantly confined to categories AA and IA. There was a significant activation differences between situations with high and low awareness for all physiological parameters that also showed an effect for vicarious embarrassment, except for T-wave amplitude, S-T elevation, and P-Q time. Additionally, Q-T time was increased in categories with high awareness compared to low awareness. The single significant discriminant function of overall autonomic activation which differentiates between categories with higher activation of the high-awareness situations (AA, IA) and with lower activation in low-awareness situations (AU, IU) supports the notion that there is a pattern of increased autonomic activation predominantly in categories AA and IA. These results therefore suggest that the attribution of awareness to a protagonist about his or her predicament modulates the emotional meaning of situations and somatovisceral effects of vicarious embarrassment.

One explanation could relate to differences in the state of awareness itself. Both categories of situations display a protagonist who is aware about the underlying norm violation of the situation. The observers might simulate the dissonance between the protagonist's situation and the perceived expectations of the social environment. As we typically try to avoid norm deviating behaviors dissonant with the expectations of the social environment (Miller, 1996), attributed awareness of the dissonance might induce stronger physiological responses. Based on the dimensional classification of vicariously embarrassing situations, this is the first time to identify a moderating influence of awareness of one's predicament.

An alternate explanation for the physiological response pattern might relate to other appraisals of categories, which drive different processes in the observer. On the one hand, only category AA situations expose a protagonist to the experience of embarrassment (Krach et al., 2011) and lead to the display of this emotion via appeasement gestures, such as hands covering the face (Keltner, 1995). The observer can simulate this emotional experience, as suggested by Miller's concept of empathic embarrassment (Miller, 1987). Triggered by the observation of embarrassment, stronger vicarious embarrassment and according somatovisceral effects should be elicited in category AA. On the other hand, the stronger somatovisceral effects in category IA could relate to the observer's experience of anger in response to such situations. The results of earlier studies indicated that the emotion of anger goes along with somatovisceral changes overlapping with, but not identical to, the pattern of autonomic activation during vicarious embarrassment (Cacioppo et al., 2000; Stemmler et al., 2007; Stemmler et al., 2001). In part, the experience of anger could therefore explain the observed stronger responses in category IA. Based on our results, however, it is not possible to ascribe the physiological responses to either one of the two emotional states.

3.4.3. Blushing

Contrary to our expectation, we did not find indications for a blushing response induced by vicarious embarrassment. In constrast, vasoconstriction at the cheek was increased, matching the responses recorded at the finger, and cheek temperature did not show any signs of blushing. These results rather support the notion of an increase in autonomic activation. One explanation for this finding could be that the experimental induction of vicarious embarrassment was not intense enough. Prior studies used a social setting, such as video-recordings (Shearn et al., 1999) or an in-vivo exposition (Miller, 1987), which may have induced a stronger blushing response. Further, Keltner (1995) argued that blushing, as an appeasement gesture, should be especially important in the presence of others (similar to Fridlund's functional interpretation of facial affective expressions; Fridlund, 1991). This might be important for vicarious embarrassment, too. Depending on the characteristics of the social situation empathic blushing could signal empathic understanding or help observers to dissociate themselves from the norm-violation. The presence of a real audience in vicarious embarrassment situations might increase effects of blushing also in the observer. Notably, two studies which could find blushing responses in embarrassing situations made use of this audience effect (Shearn et al., 1990; Shearn et al., 1999). The current experimental set-up which used an imagined audience depicted in the sketches might not be sufficient to trigger blushing responses in the observer. Future studies should address this issue and consider more interactive (Schilbach et al., in press) and immersive (Krach et al., in press) experimental settings to elicit strong vicarious embarrassment.

Based on the seminal work of Leary and colleagues (1992), however, the lack of blushing response in observers might not even be unexpected. The authors did not consider blushing as a hallmark feature of embarrassment (cf. Buss, 1980), but rather resulting from undesired social attention. Our study participants did not attract social attention of an audience, thus besides their experience of vicarious embarrassment no blushing would have been expected according to Leary and colleagues (1992). However, previous studies provided evidence for empathic blushing in observers (Shearn et al., 1999). Future research should therefore address the role of social attention on empathic blushing.

Here it might be important to also consider personality characteristics. The positive correlation of individual differences in blushing propensity with vicarious embarrassment ratings in our study at least indicated that blushing propensity might not only relate to one's own embarrassability (Leary and Meadows, 1991), but also to the vicarious experience of embarrassment.

3.4.4. Conclusion and Outlook

We describe the somatovisceral response pattern of increased autonomic activation during the experience of the social pain of vicarious embarrassment. Using a set of social situations we further demonstrate that the experience of vicarious embarrassment and its autonomic activation is not limited to situations in which an observed protagonist is a victim of embarrassment. Instead, the physiological response pattern is modulated by the awareness of the protagonist about the inappropriateness of the situation, underscoring the effect of perspective taking in this process.

This finding shows that the examination of the social context as well as observers' appraisals are important issues in order to better understand the potential heterogeneity of the experience of vicarious emotions and their corresponding physiological responses. The importance of the social context and observer appraisals has already been acknowledged in studies on vicarious physical pain (Hein and Singer, 2008; Lamm et al., 2007). For the experience of vicarious social pain the configuration of the social scene is even more relevant, thus demanding a thorough analysis of context variables. Controlling for appraisal processes and assessing them in greater detail might enable specific predictions about the emotional processes and the corresponding physiological patterns in such complex social situations. Future research could address the impact of other emotions like anger and compassion on the psychophysiological effects of social situations and specifically manipulate the social context. To broaden the perspective a promising approach might be to investigate other self-conscious emotions and their vicarious experience such as guilt or pride.

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CHAPTER 4

MENTALIZING AND THE ROLE OF THE POSTERIOR SUPERIOR TEMPORAL SULCUS IN SHARING OTHERS' EMBARRASSMENT.

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CHAPTER 4

ABSTRACT

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 fMRI, we show that the embarrassment on behalf of others engages the temporal pole and the mid-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, 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-superior temporal sulcus in sharing others' affective state.

AUTHOR CONTRIBUTIONS

In this study the author of this thesis contributed to the data analysis as well as the writing of the paper.

MENTALIZING AND THE ROLE OF THE POSTERIOR SUPERIOR TEMPORAL SULCUS IN SHARING OTHERS' EMBARRASSMENT

4.1. 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[1] – 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). 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 doesn't realize that their zip is open. A perceiver, however, notes the open zip and is

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[1] The shared etymological background of the terms embarrassment and pain provides intriguing evidence for the common nature of embarrassing and physically painful experiences. The High-German term for embarrassment "peinlich" [ˈpaɪnˌlɪç] 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" [ˈpaɪnˌlɪçə ˈʃtʀaːfən], 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.

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; Keltner 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 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 mid-prefrontal cortex (mPFC), the tempo-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 to pain empathy (Immordino-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/SII) (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; Saarela et al. 2007; Akitsuki 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 (Immordino-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 twofold 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 suggests 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 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 whilst observing the scene.

4.2. MATERIALS AND METHODS

4.2.1. Participants and Data Acquisition

Thirty-two naive right-handed subjects (undergraduates from the Philipps-University Marburg, 17 female, aged 20-28 years, mean age = 22.81 ± 2.19 years) participated in the functional MRI study. Other aspects of this sample's data have been published previously (Krach et al. 2011). All subjects were native German speakers, had normal or corrected-to-normal vision, and gave written informed consent in accordance with the requirements of internal review boards at Philipps-University Hospital Marburg. Subjects were scanned at 3T (Siemens Trio, Erlangen) with 36 near-axial slices and a distance factor of 10% providing whole brain coverage. An echo planar imaging (EPI) sequence was used for acquisition of 553 functional volumes during the experiment (TR = 2.2 s, TE = 30 ms, flip angle = 90°, slice thickness = 3 mm, FoV = 192).

4.2.2. 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; (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 out 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]. In order 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 ten situations each. For control purposes, ten 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 Fig. 1a.

4.2.3. 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 non-serif 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*[2]*?*"]). Responses were made on a scale ranging from 1 ('not at all') to 5 ('very strong') 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 pseudo-randomization of the inter-trial interval between ± 150 ms with an *SD* = 100 ms. Stimuli were presented in a pseudo-randomized 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 Presentation 11.0 software package (Neurobehavioral Systems, Albany, CA, USA, http://www.neurobs.com/).

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

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[2] 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' [ˈfʀɛmt̩ʃɛːmən] 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 condition.

were observing the situations in everyday life with the following instruction: "*Imagine **you** are observing <u>the person</u> 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**").

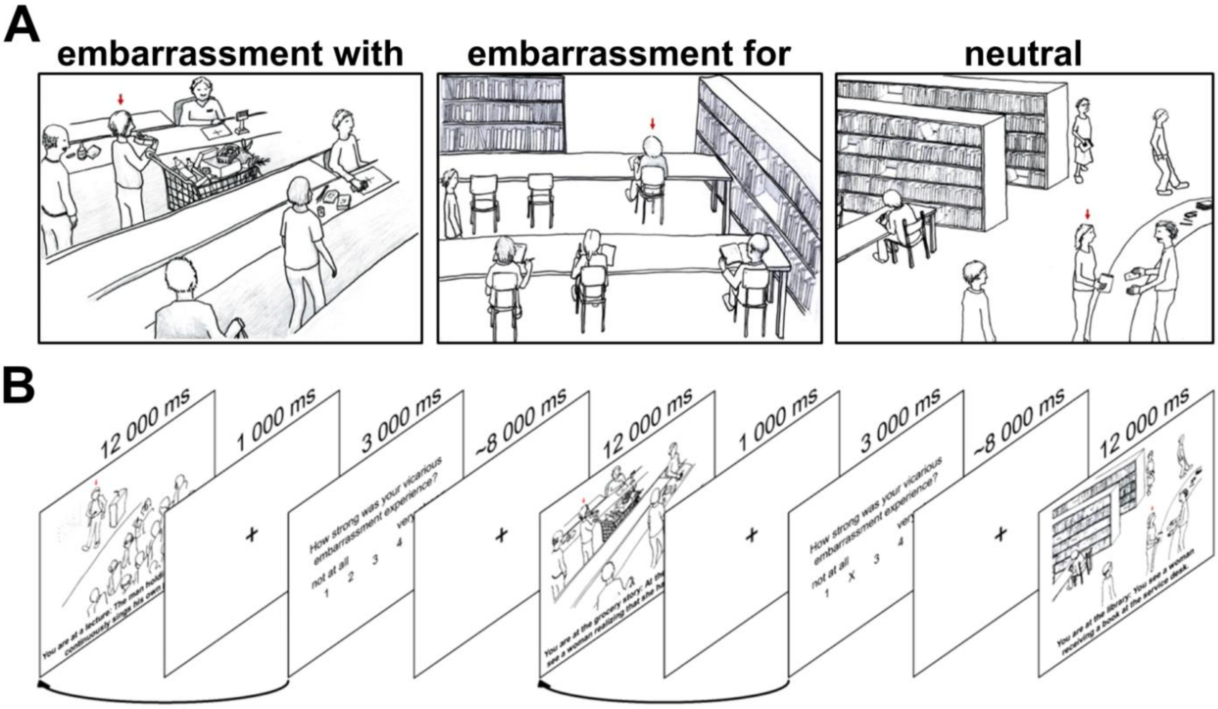

Figure 1. Stimulus material and experimental paradigm. (**a**) Examples of displayed situations. Subjects see social targets in different scenarios, being embarrassed (embarrassment *with*, EMB WITH) or not (embarrassment *for*, EMB FOR), as well as in neutral scenarios (NEUT). The sketches were displayed 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). (**b**) 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.

4.2.4. Functional MRI 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 re-sliced 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 after 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 *ß*-maps of activation differences between the embarrassing and neutral situations, as well as *ß*-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 to NEUT was able to identify activated brain regions irrespective of the emotional state of the social target. Second, 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 in the intensity ratings *between* the EMB WITH and EMB FOR conditions. Finally, we analyzed the average effect of the parametric weights within EMB WITH and EMB FOR, thus explaining intra-subject variability of hemodynamic responses associated with subjectively reported intensity of the embarrassment experience. Two subjects showed no variability in one of the EMB WITH or EMB FOR conditions and these *ß*-maps were thus excluded from the random-effects analysis. To account for influences of variance restriction on the individual subject level, the random-effects GLM of the parametric modulators contained inter-individual differences in the intra-subject standard deviations of the intensity of the perceivers' embarrassment responses to each type of situation as covariates.

4.2.5. Psychophysiological Interaction Analyses

To examine the context-dependent contributions of the pSTS region to blood-oxygen-level-dependent (BOLD) responses in other brain regions, "psycho-physiological interaction" (PPI) analyses were conducted as implemented in SPM8 (Gitelman et al. 2003). Left and right pSTS masks were created based on the conjunction of EMB WITH specific effects on the group level as described above. The activation map for the left and right pSTS was smoothed with 8mm and with a 50 % intensity cut-off threshold. For each subject, the pSTS seed region was centered at the global maximum within this mask of the equivalent contrast to that of the ANOVA model. Individual time series were then extracted as the first eigenvariate from all of the voxel time series showing a positive effect ($p < .50$) 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: (i) the original pSTS time series, (ii) the PPI time series coding the dynamics in the connectivity of pSTS, (iii) the corresponding difference in the hemodynamic response between EMB WITH and EMB FOR, (iv) the task-induced hemodynamic responses, and (v) the six head movement parameters. Resulting beta-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 to 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, Woolrich, Behrens, Smith, & Johansen-Berg, 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 $p < .005$. All anatomical coordinates are reported in MNI standard space.

4.3. 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 s.d.) compared to EMB FOR (2.84±0.78 s.d., repeated measures ANOVA, post-hoc contrast comparing EMB WITH to EMB FOR, $F(1,31) = 53.35$, $p < .001$). Individual differences in the intensities of the corresponding embarrassment reactions from the perceiver's perspective were thus controlled for in the fMRI data analyses. Reaction times did not differ between the two experimental conditions (EMB WITH 1,039±312ms s.d. and EMB FOR 1,003±325ms s.d., repeated measures ANOVA, post-hoc contrast comparing EMB WITH to EMB FOR, $F(1,31) = 1.18$, $p = .286$), but were significantly slower compared to NEUT (716±158ms s.d., post-hoc contrast comparing EMB WITH and EMB FOR to NEUT, $F(1,31) = 28.15$, $p < .001$).

4.3.1. 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], $t(120) > 4.62$, $p < .05$, corrected, see Fig. 2, 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 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 and colleagues (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 Figure 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, $t(118) > 4.64$, $p < .05$, 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, Table 1). No statistically significant negative associations were found.

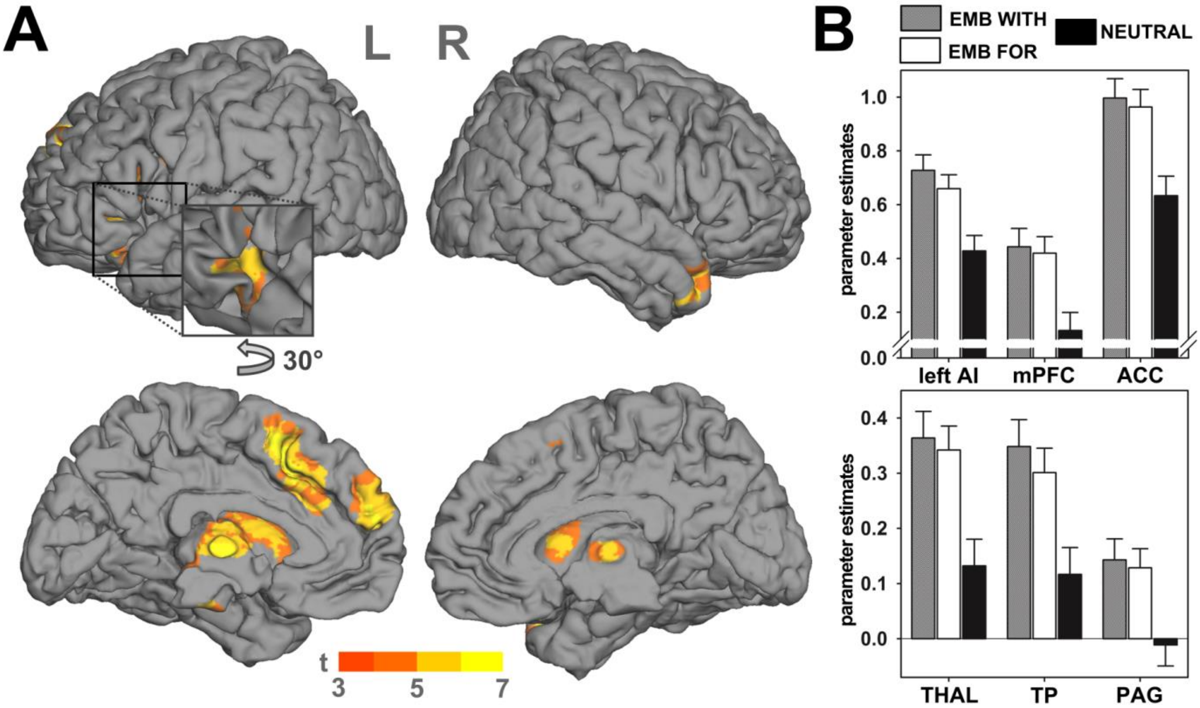

Figure 2. Common activation of embarrassment on behalf of others' mishaps. (**a**) Activation of the medial prefrontal cortex (mPFC), anterior cingulate cortex (ACC), left anterior insula (AI), and sub-cortical structures during observation of threats to the social integrity of target person. Render 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 $t(120) > 4.62$, $p < .05$, FWE corrected. (**b**) Parameter estimates at the peak of significant effects for the EMB WITH and EMB FOR condition. Parameter estimates show mean±s.e.m.

Table 1. Vicarious embarrassment-related neural activation and associations with the self-reported intensity of the social pain experiences.

Anatomical region	Cyto Area	Side	Cluster Size	MNI Coordinates			*T*	*p*
				X	Y	Z		
Activation								
SMA	BA6	L	234	-3	14	55	7.51	<.001
Anterior cingulate		L		-9	29	28	5.72	<.001
Thalamus	Th-Prefrontal	L	189	-6	-10	7	6.73	<.001
Pallidum		L		-15	-1	-5	5.91	<.001
Caudate nucleus		L		-15	5	13	5.56	.001
Inferior frontal gyrus		L	130	-36	26	-2	6.49	<.001
Insula lobe		L		-27	17	-14	4.91	.018
Superior medial gyrus		L	141	-6	56	22	6.24	<.001
Superior frontal gyrus		L		-12	50	34	5.87	<.001
Temporal pole		R	32	45	17	-29	5.80	.001
Cerebellum	Lobule VI	R	60	33	-61	-26	5.74	.001
Brainstem		L	23	-3	-22	-17	5.37	.003
Inferior frontal gyrus	BA44	L	44	-48	14	22	5.35	.003
Caudate nucleus		R	35	12	11	10	5.32	.004
Cerebellum	Lobule VI	L	31	-39	-55	-26	5.28	.004
Hippocampus		L	23	-30	-16	-8	5.20	.006
Parametric Modulations								
Precentral gyrus	BA6	R	63	51	2	46	6.83	<.001
Insula lobe		L	50	-30	23	7	6.06	<.001
Superior temporal gyrus		R	47	69	-37	22	6.56	<.001
Supramarginal gyrus		R		66	-37	37	5.19	.007
SMA	BA6	R	198	3	-1	61	5.78	.001
Middle cingulate		R		3	14	34	5.31	.004
Supramarginal gyrus	IPC(PFcm)	L	26	-54	-37	28	5.37	.003
Middle temporal gyrus		R	24	51	-37	4	5.32	.004
Insula lobe		R	17	33	26	7	5.07	.011
Anterior cingulate		L	4	-9	23	28	4.92	.019
Inferior parietal	IPC(PFop)	L	1	-51	-31	25	5.07	.035

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. Anatomical labels were derived respectively.

4.3.2. 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 to EMB FOR and NEUT. The results showed a specific reactivity of the bilateral pSTS (repeated measures GLM, post-hoc contrast [EMB WITH - EMB FOR] ∩ [EMB WITH - NEUT], $t(123) > 4.61$, $p < .05$, corrected, see Fig. 4, Table 2, and Supplementary Figure 2). We also explored the reverse contrast and found stronger activation of the left amygdala in EMB FOR compared to EMB WITH and NEUT (repeated measures GLM, post-hoc contrast [EMB FOR - EMB WITH] ∩ [EMB FOR - NEUT], $t(123) > 4.61$, $p < .05$, 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 condition (see Methods).

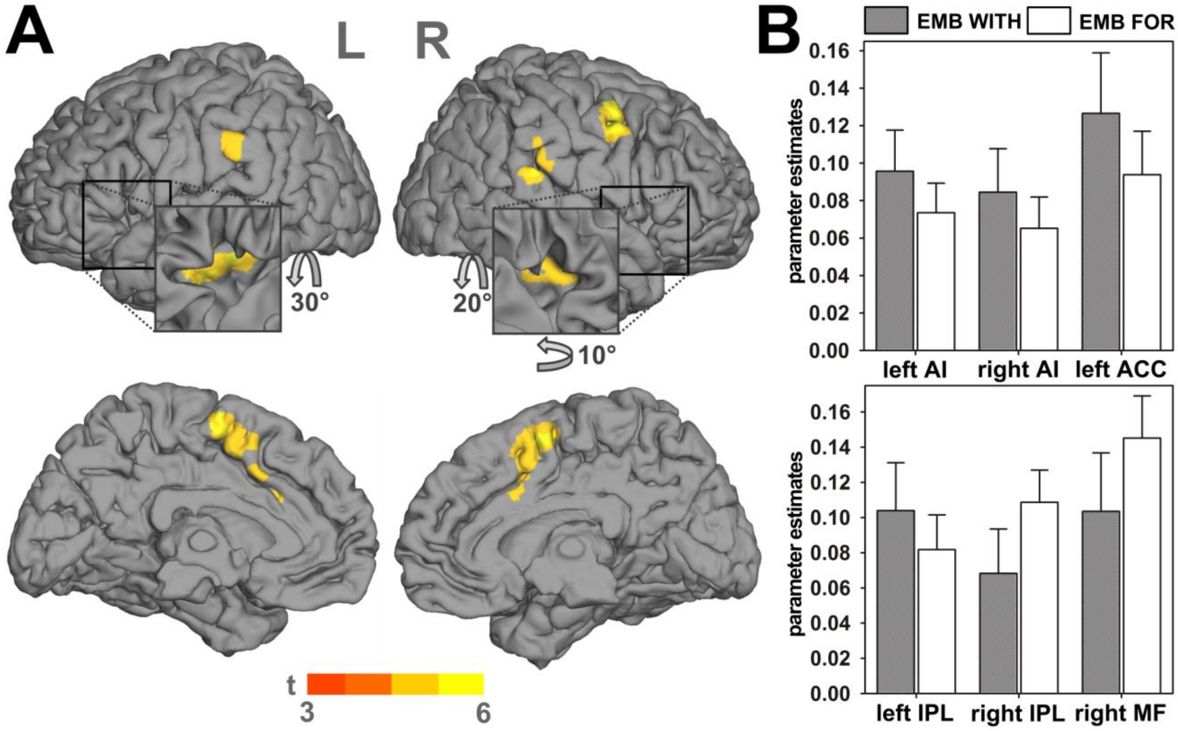

Figure 3. Variability in the hemodynamic responses positively related to the intensity of the self-reported embarrassment participants felt while watching the situation. (**a**) Render images display the average effect of a GLM random-effects analysis of the parametric weights with a threshold at $t(118) > 4.64$, $p < .05$, FWE corrected. Significant associations were found in the anterior cingulate cortex (ACC), bilateral anterior insula (AI), bilateral inferior parietal cortex (IPL), and the right dorsolateral prefrontal cortex (DLPFC). (**b**) Parameter estimates at the peak of the effects for the embarrassment *for* and the embarrassment *with* condition. Parameter estimates show mean±s.e.m.

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 inferior parietal lobe, and the left posterior and middle insular cortex in the EMB WITH condition (see Fig. 5, Table 2). These clusters were sufficiently large to survive the corrected cluster extent threshold (one-sample *t*-test, $t(31) > 2.74$, $p < .005$ uncorrected, $k \geq 415$). A region of interest (ROI) analysis within the brain regions activated by the conjunction ([EMB WITH – NEUT] ∩ [EMB FOR - NEUT]) also revealed stronger correlations of the BOLD response with the left AI (one-sample *t*-test, $t(31) = 3.28$, $p = .025$, 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.

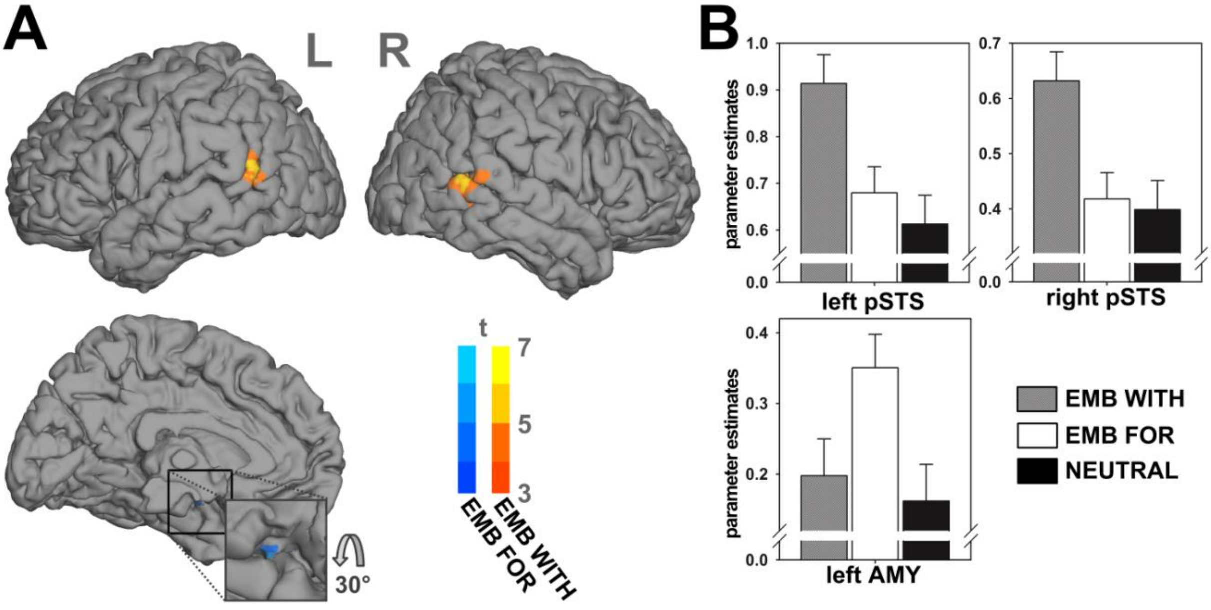

Figure 4. Dissociation of embarrassment *with* [EMB WITH] and embarrassment *for* [EMB FOR] another. (**a**) Render images depict specific activation for embarrassment *with* and embarrassment *for* another and show the results of the post-hoc contrasts EMB WITH - NEUT ∩ EMB WITH - EMB FOR, as well as EMB FOR - NEUT ∩ EMB FOR - EMB WITH, using a threshold at $t(123) > 4.61$, $p < .05$, FWE corrected. The stronger activation for EMB WITH in the bilateral posterior superior temporal sulcus (pSTS) is coded in red/yellow and the stronger activation in response to EMB FOR in the left amygdala (AMY) is coded in blue. (**b**) Parameter estimates at the peak of the corresponding effect in the bilateral pSTS and the left AMY for EMB WITH and EMB FOR. Parameter estimates show mean±s.e.m.

Table 2. Specific neural activation in response to observing another's social pain experience and dynamics in the functional integration of the right posterior temporal sulcus.

Anatomical region	Cyto Area	Side	Cluster Size	MNI Coordinates			*T*	*p*
				X	Y	Z		
Embarrassment With > Embarrassment For Another								
Middle temporal gyrus		L	75	-54	-58	16	6.47	<.001
Middle temporal gyrus		R	94	51	-49	7	5.88	<.001
Superior temporal gyrus		R		66	-43	13	4.86	.021
Superior occipital gyrus	BA17	L	17	-15	-88	7	5.54	.002
Embarrassment For > Embarrassment With Another								
Amygdala	Amy(SF)	L	5	-21	-7	-14	5.22	.005
Increased Right pSTS Connectivity during Embarrassment With Another								
Inferior parietal	IPC(PF)	L	502	-51	-21	20		<.001
Rolandic operculum		L		-48	-1	10	4.17	
Inferior parietal	IPC(PF)	L		-66	-31	31	4.02	
Rolandic operculum	BA44	L		-60	8	4	3.89	
Insula lobe		L		-39	2	7	3.88	
Insula lobe	Insula(lg2)	L		-39	-16	1	3.74	
Inferior parietal	IPC(PF)	R	415	56	-31	25		.002
Middle temporal gyrus		R		60	-50	12	5.09	
Heschl's gyrus	OP1	R		45	-29	18	4.62	
Supramarginal gyrus	IPC(PFt)	R		60	-29	45	4.46	
Superior temporal gyrus		R		51	-31	16	3.85	
Supramarginal gyrus	BA3b	R		45	-19	31	3.08	
Anterior insula ROI		L	5	-30	26	4	3.28	.025

Note. Activation differences for *embarrassment with* and *embarrassment for* were thresholded at $p < .05$, family-wise error-corrected for whole-brain analyses. The region of interest (ROI) analysis was family-wise error-corrected within the anterior insula. All remaining results of the psychophysiological interaction (PPI) analysis were thresholded at $p < .005$, $k > 414$, corresponding to the family-wise error-corrected cluster-extent threshold of whole-brain analyses. The Cyto Area column indicates the assigned cytoarchitectonical area as indicated by the SPM ANATOMY toolbox v1.8 if available. Anatomical labels were derived respectively.

4.4. DISCUSSION

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 sociality 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.

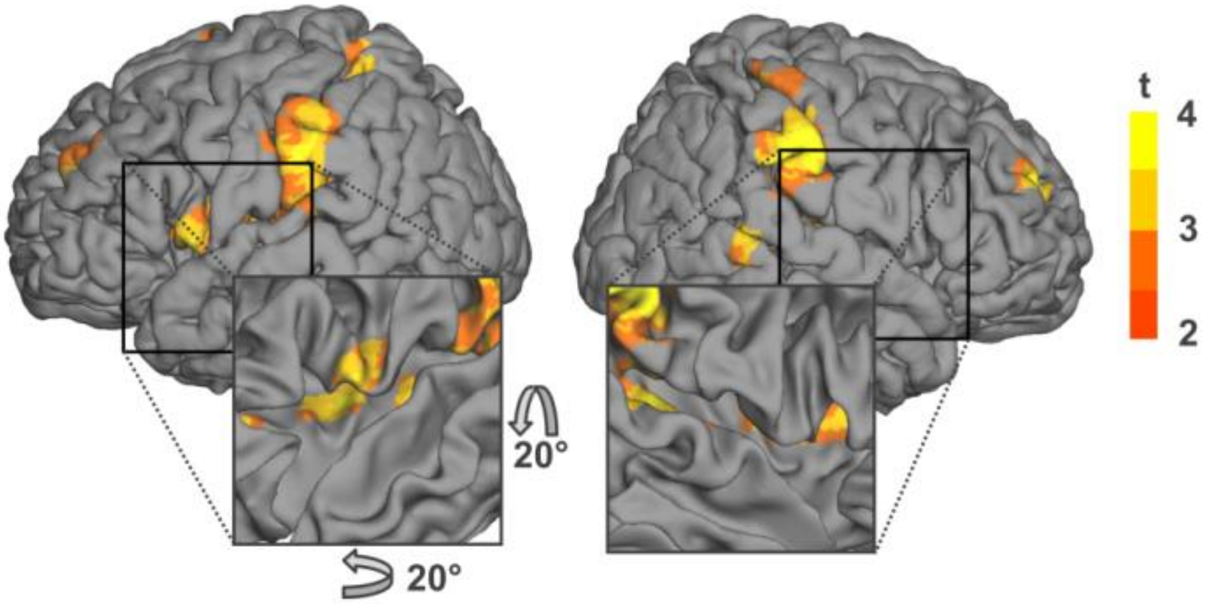

Figure 5. Increased functional connectivity with the right posterior superior temporal sulcus (pSTS) during embarrassment *with* [EMB WITH] as compared to embarrassment *for* [EMB FOR] another. Render images show the results of a psychophysiological interaction analysis on the group level, with a threshold at $t(31) > 2.74$, $p < .005$, uncorrected. Clusters with a significant increase in function coupling with the right pSTS during EMB WITH were found in the bilateral inferior parietal lobe, as well as posterior, middle, and frontal aspects of the left insula.

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 areas 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 (Eisenberger et al. 2003; Dewall et al. 2010; Kross et al. 2011) and empathically from the third-person perspective (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 shows 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 likewise 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 reproduce the results previously found for empathy for physical pain (Saarela et al. 2007) and extend these findings to the domain of social pain. This evidence supports the notion that neural activation of these regions – and specifically the AI – form 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 is 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 and colleagues (2010) as well as Zaki and colleagues (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, i.e. 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 (Cerliani 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.

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AUTHOR 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.

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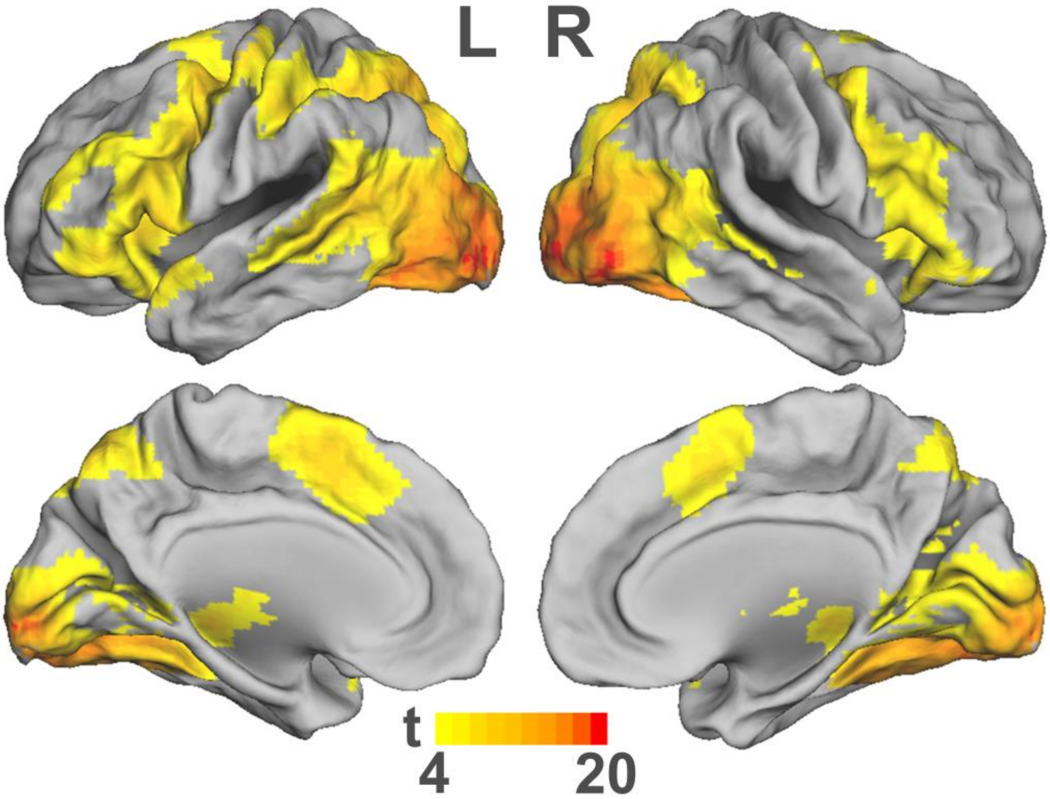
SUPPLEMENTARY MATERIALS

Supplementary Methods

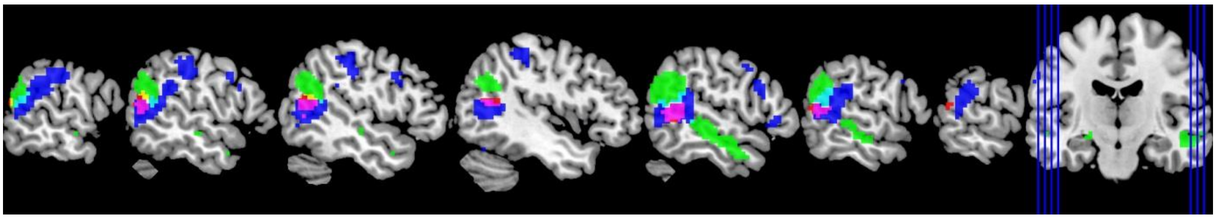
Psychophysiological Interaction Analysis of the left Amygdala.

In order to examine the context-dependent contributions of the left amygdala region to blood-oxygen-level-dependent (BOLD) responses in other brain regions a "psycho-physiological interaction" (PPI) analysis was conducted as implemented in SPM8. The left amygdala mask was created based on the EMB FOR specific effects [EMB FOR-EMB WITH ∩ EMB FOR-NEUT] on the group level. The resulting activation map of the amygdala was smoothed with 8mm with a 50 % intensity cut-off threshold. Individual time series were then extracted as the first eigenvariate from all the voxel time series within this mask. Thereby, time series were high-pass filtered at 1/256 Hz, mean-adjusted, and variance explained by the movement regressors as well as 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 FOR to EMB WITH. For each subject the fixed-effects connectivity GLMs each contained (i) the original amygdala time series, (ii) the PPI time series coding the dynamics in the connectivity of left amygdala, (iii) the corresponding difference in the hemodynamic response between EMB FOR and EMB WITH, (iv) the task-induced hemodynamic responses, and (v) the six head movement parameters. The resulting beta-maps of the PPI regressors were analyzed on the group level with a one-sample *t*-test. Positive and negative effects were examined in order to identify brain regions having a stronger functional integration with the left amygdala during EMB FOR compared to EMB WITH or vice versa.

Supplementary Data



Supplementary Figure 1. Activation during the observation of neutral scenarios. Render images display the positive effects of a GLM random-effects analysis of the neutral situations with a threshold at *t*(155) > 4.58, *p* < .05, corrected.



Supplementary Figure 2. Overlap of the pSTS activation with a Theory of Mind (ToM) and mirroring of affective touch. Red areas depict the pSTS activation for sharing another’s embarrassment (EMB WITH) in the present study. Dark blue areas display activation related to mirroring of affective touch (AT) as used in (Meffert et al. 2013) and green areas illustrates activation of the temporo-parietal junction and middle and anterior STS during a classical ToM task (Thioux & Keysers, unpublished). The depicted activation of the STS in green relates to ToM activity and is a distinct cluster to the TPJ region. It shows now overlap with the pSTS during the EMB WITH condition. Overlap between activations is coded by additive colors so that EMB WITH∩AT = pink, EMB WITH∩ToM = yellow, AT∩ToM = light blue, and EMB WITH∩AT∩ToM = white.

Reference

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MENTALIZING AND THE ROLE OF THE POSTERIOR SUPERIOR TEMPORAL SULCUS IN SHARING OTHERS' EMBARRASSMENT

Supplementary Table 1. Stimulus properties as identified in a pre-test for validation purposes and item selection.

	Embarrassment with			Embarrassment for									Neutral		
	low Int ∩ high Aw			low Int ∩ low Aw			high Int ∩ high Aw			high Int ∩ low Aw					
	Mn	M (SD)	Mx	Mn	M (SD)	Mx	Mn	M (SD)	Mx	Mn	M (SD)	Mx	Mn	M (SD)	Mx
Embarrassment	3.2	**3.8** (0.3)	4.3	3.4	**3.6** (0.2)	3.9	2.1	**3.1** (0.5)	3.8	1.6	**2.6** (0.5)	3.4	1.0	**1.0** (0.0)	1.1
Intentionality	1.1	**1.2** (0.2)	1.9	1.1	**1.3** (0.2)	1.6	2.8	**3.6** (0.6)	4.4	3.9	**4.3** (0.3)	4.7	3.7	**4.0** (0.2)	4.2
Awareness	3.7	**4.1** (0.2)	4.5	1.5	**1.8** (0.2)	2.1	2.5	**2.9** (0.4)	3.6	1.7	**2.1** (0.2)	2.4	1.0	**1.1** (0.1)	1.2
Shame	2.5	**2.9** (0.3)	3.4	2.7	**3.1** (0.2)	3.4	2.0	**2.8** (0.4)	3.4	1.5	**2.4** (0.4)	3.2	1.0	**1.0** (0.0)	1.1
Anger	1.2	**1.7** (0.7)	3.5	1.1	**1.6** (0.6)	3.3	1.4	**2.7** (1.1)	4.8	1.4	**2.0** (0.6)	3.2	1.0	**1.0** (0.0)	1.1
Pity	1.8	**3.8** (0.7)	4.5	2.5	**3.1** (0.3)	3.7	1.3	**1.7** (0.3)	2.2	1.2	**1.7** (0.3)	2.1	1.0	**1.0** (0.0)	1.1
Schadenfreude	1.2	**1.9** (0.6)	3.1	1.5	**1.9** (0.2)	2.3	1.2	**1.6** (0.5)	2.9	1.2	**1.6** (0.3)	2.1	1.0	**1.0** (0.0)	1.0
Humor	1.3	**2.4** (0.9)	4.1	1.2	**2.5** (0.6)	3.1	1.1	**2.3** (0.8)	3.4	1.9	**2.4** (0.3)	2.8	1.0	**1.1** (0.0)	1.2
Clarity	4.5	**4.6** (0.1)	4.8	4.2	**4.4** (0.1)	4.7	3.7	**4.1** (0.2)	4.3	3.9	**4.1** (0.2)	4.5	4.4	**4.7** (0.1)	4.8
# Bystanders	3	**6.6** (3.3)	12	3	**6.8** (3.1)	13	3	**6.5** (4.0)	17	3	**5.9** (2.5)	11	4	**5.4** (1.2)	7

Note. Mn = minimum, Mx = maximum, Int = intentionality of the depicted action, Aw = the social target's awareness of the embarrassing potential of the present situation. All ratings were obtained on a likert type scale ranging from 1 = 'not at all' to 5 = 'very strong'. Embarrassment indicates the intensity of the embarrassment from the observer's perspective. The embarrassment from the observer's perspective, intentionality of the depicted action, and awareness of the social target about the ongoing norm violation were selection criteria of stimuli used in this study. All emotions were rated from the observer's perspective. Clarity indicates how well the observers understand the action depicted in the situation. The amount bystanders do not significantly differ between stimulus classes ($p > 0.30$).

Supplementary Table 2. Positive effects for the neutral situations within the task activated network.

Anatomical region	Cyto Area	Side	Cluster Size	# Voxels with positive effect in neutral condition	MNI Coordinates		
					X	Y	Z
Activation							
SMA	BA6	L	234	234 (100%)	-3	14	55
Anterior cingulate		L			-9	29	28
Thalamus	Th-Prefrontal	L	189	164 (87%)	-6	-10	7
Pallidum		L			-15	-1	-5
Caudate nucleus		L			-15	5	13
Inferior frontal gyrus		L	130	130 (100%)	-36	26	-2
Insula lobe		L			-27	17	-14
Superior medial gyrus		L	141	140 (99%)	-6	56	22
Superior frontal gyrus		L			-12	50	34
Temporal pole		R	32	32 (100%)	45	17	-29
Cerebellum	Lobule VI	R	60	60 (100%)	33	-61	-26
Brainstem		L	23	17 (74%)	-3	-22	-17
Inferior frontal gyrus	BA44	L	44	44 (100%)	-48	14	22
Caudate nucleus		R	35	35 (100%)	12	11	10
Cerebellum	Lobule VI	L	31	31 (100%)	-39	-55	-26
Hippocampus		L	23	23 (100%)	-33	-19	-11

Note. Cluster sizes for the activation were obtained with a conjunction analysis contrasting embarrassment with and embarrassment for another to the neutral condition using a $p < .05$, corrected threshold. Using this set of clusters as a mask, the baseline contrast for the neutral condition was examined with a one-sample t-test and a threshold of $p < .50$, thus illustrating all effects within the clusters greater than zero for the neutral condition. The 'Cyto Area' column indicates the assigned cytoarchitectonical area as indicated by the SPM ANATOMY toolbox v1.8 if available. Anatomical labels have been derived respectively.

CHAPTER 5

WHEN YOUR FRIENDS MAKE YOU CRINGE: SOCIAL CLOSENESS MODULATES VICARIOUS EMBARRASSMENT RELATED NEURAL ACTIVITY

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CHAPTER 5

ABSTRACT

Social closeness is a potent moderator of vicarious affect and specifically vicarious embarrassment. The neural pathways of how social closeness to another person affects our experience of vicarious embarrassment for the other's public flaws, failures and norm violations are yet unknown. To bridge this gap we examined the neural response of participants while witnessing threats to either a friend's or a stranger's social integrity. The results show consistent responses of the anterior insula (AI) and anterior cingulate cortex (ACC), shared circuits of the aversive quality of affect, as well as the medial prefrontal cortex and temporal pole, central structures of the mentalizing network. However, the ACC/AI network activation was increased during vicarious embarrassment in response to a friend's failures. At the same time, the precuneus, a brain region associated with self-related thoughts, showed a specific activation and an increase in functional connectivity with the shared circuits in the frontal lobe while observing friends. This might indicate a neural systems mechanism for greater affective sharing and self-involvement while people interact with close others that are relevant to oneself.

AUTHOR CONTRIBUTIONS

In this study the author's contribution lies in analyzing and presenting the data as well as the writing the paper.

WHEN YOUR FRIENDS MAKE YOU CRINGE: SOCIAL CLOSENESS MODULATES VICARIOUS EMBARRASSMENT RELATED NEURAL ACTIVITY

5.1. INTRODUCTION

Most human affect is rooted in the social ties with the environment that we are living in. This applies for the pain we feel at others' injuries (Singer et al., 2004), the joy when witnessing the success of a colleague (Mobbs et al., 2009), the disgust when listening to others' nauseating stories (Jabbi et al., 2008; Wicker et al., 2003), and the embarrassment we feel on behalf of others' blunders and pratfalls (Krach et al., 2011; Paulus et al., 2015). The social relation to the target person thereby is an important modulator of such vicarious responses to the emotional events in the environment (Cheng et al., 2010; Singer et al., 2006). This is particularly true for vicarious embarrassment as can be illustrated in everyday life situations. For example, parents cringe only if their children, but not others' children, act out in public or one flushes only to a fellow student's blatant ignorance while a similar incident happening to an unrelated other rather evokes amusement (see e.g. Fortune & Newby-Clark, 2008). In this study we investigate how our social ties and friendship in particular affect the experience of vicarious embarrassment and propose novel neural pathways for how vicarious affect is modulated by social relation.

Earlier studies showed that vicarious embarrassment on behalf of unrelated others' public flaws, blunders or norm violations is a form of vicarious social pain (Krach et al., 2011, 2015; Melchers et al., 2015; Müller-Pinzler et al., 2012; Paulus et al., 2015). Similar to how physical pain signals injuries of the bodily integrity, social pain signals threats to the social integrity – which undoubtedly is in danger in embarrassing moments (Eisenberger, 2012; Macdonald and Leary, 2005; Paulus et al., 2015). In the case of embarrassment the integrity threat results from the expected negative evaluations in the eyes of others (Keltner and Buswell, 1997) and can also be experienced vicariously (Krach et al., 2011; Müller-Pinzler et al., 2012). The vicarious experience of embarrassment is associated with neural activation of the anterior cingulate cortex (ACC), the anterior insula (AI) and, if induced strong enough, higher-order somatosensory cortex areas (Paulus et al., 2015). This network of brain regions is also linked to the experience of vicarious physical pain (de Vignemont and Singer, 2006; Lamm et al., 2011) and other forms of vicarious social pain (Immordino-Yang et al., 2009; Masten et al., 2011). These neural pathways are also fundamentally involved in the first-hand experiences of social and physical pain (Eisenberger et al., 2003; Kross et al., 2011; Wager et al., 2013), supporting the notion that activity of the AI and ACC network represents consciously accessible bodily affect in shared-circuits (Keysers and Gazzola, 2006) that can then somehow be articulated in the course of social interactions (Hein et al., 2010).

Besides the involvement of these shared circuits in vicarious embarrassment, one needs to have the capacity to read and understand the potentially negative evaluations of bystanders. Only then one will be able to understand the threats to another’s social integrity. This process of so-called ‘mentalizing’ about others’ evaluations, thoughts and intentions refers to a rather reflective process of perspective taking (Frith and Frith, 2003). The medial prefrontal cortex (mPFC) and the temporal poles (TP) thereby are part of a well-defined neural pathway that is engaged when we construct internal models about another person’s mental state (Hein and Singer, 2008; Lieberman, 2007) or experience embarrassment on behalf of another’s public flaws, blunders or norm violations (Paulus et al., 2015).

As outlined above, the perceived relation to the social target is a highly potent moderator for one’s vicarious emotional responses (Cheng et al., 2010; Singer et al., 2006). Negative experiences of physical or social pain (Meyer et al., 2012; Singer et al., 2006) as well as positive experiences like vicarious reward are modulated by the relations to the social target (Leng and Zhou, 2010; Mobbs et al., 2009). Behavioral data demonstrated that with increasing closeness to a social target participants showed more intense vicarious experiences of physical (Cheng et al., 2010) and social pain (Meyer et al., 2012) and also embarrassment (Chekroun and Nugier, 2011; Fortune and Newby-Clark, 2008). On the level of neural systems, the effect of social closeness on physical and social pain was accordingly accompanied by increased shared circuit activity within the ACC and AI (Beeney et al., 2011; Cheng et al., 2010; Meyer et al., 2012) and increased mPFC engagement (Meyer et al., 2012). It has been argued that the perceived social closeness strengthens the affective link to the other person, which results in the more intense caring for the other’s affect (Cheng et al., 2010). Further, the mental representations of close others are considered to be more vivid and rich and might therefore boost the affective consequences that follow a friend’s social deconstruction during embarrassing moments (Cheng et al., 2010; Meyer et al., 2012).

Another rationale for the increase of vicarious embarrassment by the perceived social closeness to the target is that observers might be particularly concerned about their own social image. This notion is supported by behavioral studies on vicarious embarrassment, which indicated that social closeness increases the observers’ concerns about their own images while observing inappropriate behaviors of e.g. friends (Fortune and Newby-Clark, 2008). The psychological literature on social identity and group processes has recently characterized comparable effects. There, wrongdoings or inadequate behaviors (e.g. racist attitudes or behaviors) of in-group members pose a threat to one’s own group’s social integrity and yield vicarious shame or guilt to in-group members even in case one is neither involved nor responsible for the other's norm transgressions (Chekroun and Nugier, 2011; Lickel et al., 2011, 2005). The increased concerns about one's own social image and the degree of overlap between cognitive representations of self and others (Aron et al., 1991) should thereby enhance self-related thoughts when observing a close other. On the neural systems level, this notion should manifest in greater involvement of the precuneus, a structure known to be involved in self-related thoughts, self-referential processing, representation of the self, as well as the assessment of self-relevant sensations (Cavanna and Trimble, 2006; Mazzola et al., 2010; Northoff et al., 2006). Accordingly, if perceivers are concerned about their friend's actions to reflect negatively upon themselves, the integration of the precuneus in the neural systems' pathways that convey vicarious embarrassment should increase.

According to this there are two potential models for how social closeness modulates vicarious embarrassment. In the first model social closeness strengthens the affective link to the other person leading to richer mental representations of close others and a potential increase in mentalizing about the other person's mind. In the second model the perceived social closeness to the target might induce concerns about one's own social image. Based on the above outlined research and theoretical considerations we hypothesized a greater response within the shared circuits of the AI and ACC when cringing in response to the wrongdoings of friends compared to strangers. Second, as one's friend's wrongdoings more strongly reflect on oneself compared to those of a stranger we expected the precuneus, a brain region that is involved in the processing of self-related thoughts, to show greater activity while observing your friends' misbehaviours.

5.2. METHOD

5.2.1. Ethics Statement

We confirm that the research has been conducted in compliance with the ethical guidelines of the American Psychological Association (APA). The study protocol was approved by the local ethics committee at the local faculty of medicine at Philipps-University Marburg and all subjects gave written informed consent.

5.2.2. Participants

All participants (*N* = 64) were fluent in German and had normal or corrected to normal vision. The majority of the participants (87.5 %) were university students. A minority of participants worked (7.8 %) or attended high school (3.1 %). On average participants had spent 15.85 years in education (range 12-22 years, *SD* = 2.38). Participants were assigned either to a “friend” or a “stranger” condition. Data of the sample in the “stranger” condition has been published previously (Krach et al., 2011; Paulus et al., 2015). These *N* = 32 participants (17 female; aged 20-28 years; *M* = 22.81; *SD* = 2.19) were age and sex-matched to *N* = 32 participants who received the “friend” instruction (17 female; aged 18-31 years; *M* = 23.56; *SD* = 3.30, *ps* ≥ .288).

5.2.3. Stimuli, Experimental Design, and Procedure

Social closeness was manipulated in a between-subjects design with one group being assigned to the “stranger” and the other one to the “friend” condition. Both groups viewed a set of 36 previously validated hand-drawn sketches representing vicarious embarrassment situations and nine neutral sketches serving as control situations. Situations that elicited vicarious embarrassment displayed a social target while he or she was violating a social norm in public and thus threatened his or her social integrity. Neutral control stimuli displayed the social target in a public context without violating socially normative standards. For clarification each sketch was accompanied by a two-sentence description of the current situation (e.g. "You are at the grocery store: You observe a woman at the cashier realizing that she cannot pay her purchase…", see **Fig. 1**). Notably, in the “stranger” condition, the social target was introduced as a stranger (e.g. "You observe a *person* ...") while in the “friend” condition the social target was referred to as a friend (e.g. "You observe your *friend* ..."). To cover a broad variety of public norm violations that elicit embarrassment on behalf of others in everyday life, situations modelled four different types of scenarios, varying the degree of intentionality and awareness of the social target’s behaviour (see Krach, et al., 2011 for a detailed description). For the means of the present study the four types of situations were collapsed into one and compared to the neutral control situations.

After providing written informed consent, participants were carefully instructed about the experimental procedure. Therefore, participants received two exemplary situations that were not displayed during the fMRI session and asked to mentally visualize the displayed situations as vividly as possible. In the friend condition participants were instructed to imagine that the social target, which was marked by a red arrow above the persons head, is their friend and in the stranger condition they were instructed to imagine that they observe an unknown person. Participants were also informed that a sentence below the particular picture will inform them about the social target (friend vs stranger). In the MRI, all sketches were presented for 12 s together with the description of the situation. The text was presented in a black 24-point non- serif font (Arial) on a white background in two to three rows below the sketches. The stimulus presentation was followed by a blank screen for 1 s and a subsequent rating period of 3 s.

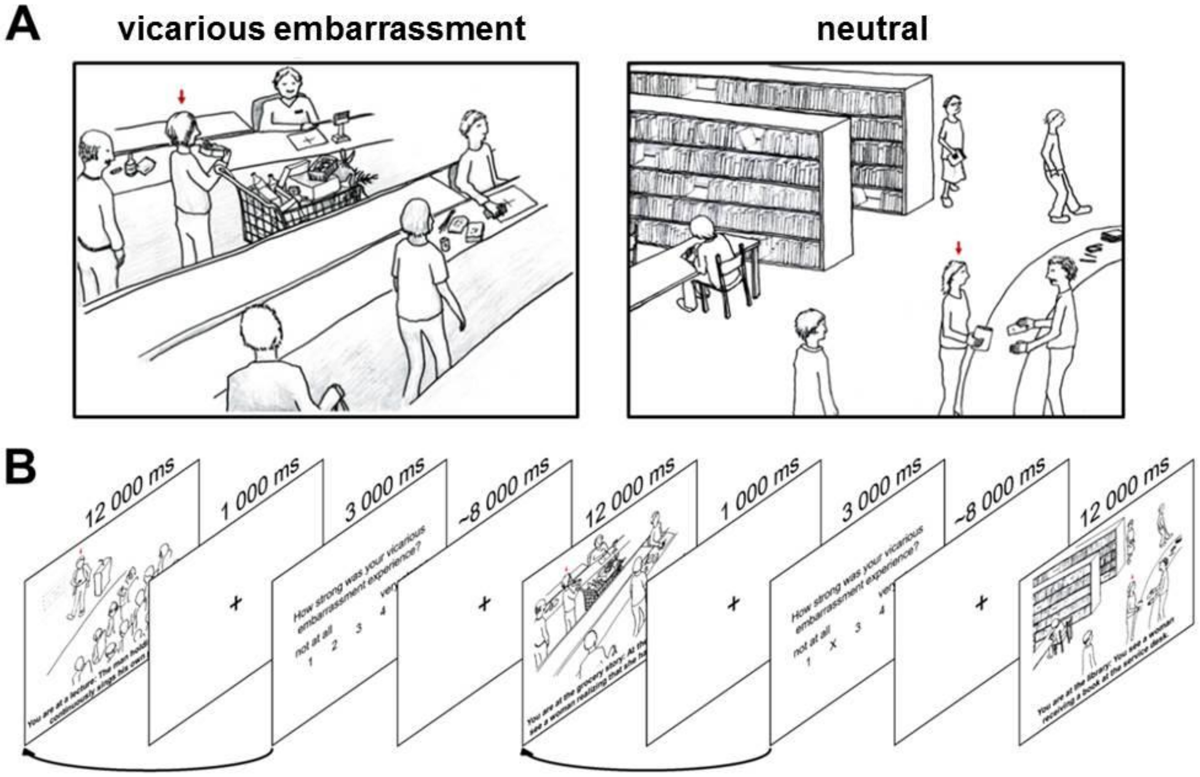

Figure 1. Stimulus material and timing of the experimental paradigm. **A** Examples of the presented stimuli. Social targets (friends and stranger) are exposed during public flaws, blunders or norm violations in different situations (vicarious embarrassment, VE) as well as in neutral scenarios (NEUT). The sketches were presented together with a short description of the situation that describes the observed person either as a stranger or a friend. In the ‘friend’ condition these are ‘You are at the grocery store: your friend realizes at the cashier that she cannot pay her purchase…’ (VE) and ‘You are at the library: your friend returns some books at the service desk…’ (NEUT). In the ‘stranger’ condition the sentences read ‘You are at the grocery store: a woman realizes at the cashier that she cannot pay her purchase…’ (VE) and ‘You are at the library: a man returns some books at the service desk…’ (NEUT) **B** Timing of the experimental paradigm. The arrows pointing from the rating period to the preceding stimulus presentation indicate that the intensity of the self-report was used as parametric weight for the preceding stimulus.

During the rating period, participants were asked to evaluate the intensity of their preceding vicarious embarrassment experiences (“How strong was your experience of vicarious embarrassment?”). Responses were made on a scale ranging from 1 (‘not at all’) to

5 (‘very strong’) 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. Stimuli were presented in a pseudo-randomized 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 18.28 min.

5.2.4. Data Acquisition

Participants were scanned at 3T (Siemens Trio, Erlangen) with 36 near-axial slices and a distance factor of 10% providing whole brain coverage. An echo planar imaging (EPI) sequence was used for acquisition of functional volumes during the experiment (repetition time = 2.2 s, echo time = 30 ms, flip angle= 90°, slice thickness = 3 mm, field of view = 192). Stimuli were presented on an LCD screen with Presentation 11.0 software package (Neurobehavioral Systems, Albany, CA, USA).

5.2.5. Data Analysis

5.2.5.1. Behavioral Data.

Data were analyzed with PASW Statistics 18 (SPSS, 2009, Chicago, IL). The average self-reports in the different vicarious embarrassing (VE) and neutral situations (NEUT) were analyzed using analysis of variance (ANOVA) with Group as a between-subject factor (stranger vs. friend) and Condition as a within-subject factor (VE vs. NEUT). Main effects and interactions were examined in order to identify effects of the emotion induction and group differences in the vicarious embarrassment self-report.

5.2.5.2. Functional MRI Data.

FMRI data were analyzed using SPM8 (www.fil.ion.ucl.ac.uk/spm). Four images were dummy scans and 51 scans comprising the presentation of the first five stimuli (one for each type of VE situation and NEUT) were discarded from further analyses. This had to be done because of delayed onsets of the EPI image acquisition in a sub-sample of participants in the “friend” condition. To maintain similar statistical power and within-subject models for all participants and achieve valid group comparisons we discarded the amount of scans for all participants prior to the analyses. The remaining 494 EPI volumes were corrected for timing differences of the slice acquisitions, motion-corrected and spatially normalized to the standard template of the Montreal Neurological Institute (MNI) using the EPI template. The normalized volumes were resliced with a voxel size of 2x2x2 mm, smoothed with an 8 mm full-width half-maximum isotropic Gaussian kernel and high-pass filtered at 1/256 Hz to remove low frequency drifts.

5.2.5.2.1. Vicarious Embarrassment related Activation.

Statistical analysis was performed in a two-level, mixed-effects procedure. The fixed-effects generalized linear model (GLM) on the first level included six epoch regressors modeling hemodynamic responses to the vicariously embarrassing situations (4), neutral situations (1), and rating phase (1) with the abovementioned stimulus durations. The vicarious embarrassment ratings after each situation of vicarious embarrassment were entered as parametric modulators to explain additional variance in neural activation due to differences in emotional responses on the within-subject level. Six additional regressors modeling head movement parameters were introduced to account for noise.

Beta-maps of activation in the vicarious embarrassment and the neutral situations were analyzed on the second level. The second-level analysis of activation differences was conducted with a random-effects GLM. The GLM contained one factor for the friend and stranger condition and a second factor for the five dependent levels of VE and the NEUT situations. The second-level analysis was controlled for individual differences in the self-report of vicarious embarrassment within each category and group by introducing subjects' averaged ratings within each category as covariates in the GLM. In order to identify brain regions that are generally involved in vicarious embarrassment we conducted a conjunction-analysis across both groups and contrasted the VE against the NEUT condition ((friend_VE–friend_NEUT) ∩ (stranger_VE–stranger_NEUT)). The results of the conjunction-analysis were thresholded at $p < .05$ applying family-wise error (FWE) correction for a whole brain analysis. To find brain regions that show stronger vicarious embarrassment related activation when observing a friend compared to a stranger the interaction of both factors was calculated ((friend_VE–friend_NEUT) – (stranger_VE–stranger_NEUT)). The reverse comparison was calculated to investigate increased effects when observing a stranger compared to a friend ((stranger_VE–stranger_NEUT) – (friend_VE–friend_NEUT)). Both analyses were first conducted in the whole brain and in a second step restricted to the regions of interest (ROIs) activated during vicarious embarrassment as defined by the results of the prior conjunction-analysis. Finally, to examine how our friends' misbehaviors could endanger our own social integrity, and accordingly enhance self-reflective thoughts at their wrongdoings, we contrasted the friend with the stranger condition (friend_VE–stranger_VE). For this contrast, we applied FWE correction on the cluster extent threshold.

To examine the correspondence between hemodynamic responses and the behavioral reports of vicarious embarrassment we additionally tested the parametric weights for the different VE facets (Paulus et al., 2015). Therefore β-images of the four parametric weights were computed and analyzed at the group level. In the random-effects GLM we implemented a 4x2 repeated measures ANOVA with the parametric weights of the four VE facets as repeated factor. We first tested the average effect of the parametric modulators within each group and second calculated the difference between the friend and the stranger condition in order to identify brain regions that show greater correspondence between brain and behavior in either condition. Both analyses were restricted to the ROIs activated during vicarious embarrassment as defined by the results of the prior conjunction analysis. All results are reported in MNI space.

5.2.5.2.2. Functional Connectivity Analysis of the Precuneus.

To examine context dependent modulations of the connectivity pattern of the precuneus we conducted a functional connectivity analysis in both groups. To do so, we selected the area within the precuneus that had stronger activation in the friend compared to the stranger condition as seed region (see Figure 3; friend_VE–stranger_VE, $p < .0005$, uncorrected, within the anatomical boundaries of precuneus and posterior cingulate cortex). Timeseries were mean centered and task induced hemodynamic responses were removed by applying an effects-of-interest correction with an F-contrast set to the six movement parameters (Paulus et al., 2014). Because we expected differences in connectivity profiles to emerge while participants processed the social stimuli, only those periods of the timeseries that represent hemodynamic signal during stimulus presentation were included in the analyses. To do so, the timeseries when participants did not attend to the stimuli (i.e. low-level baseline, rating period) were fixed to zero, so that variability of blood oxygenation level dependent (BOLD) signal of the precuneus during these periods could not contribute to explain variance in the target timeseries. To account for the delay of the hemodynamic response, valid stimulus intervals of the BOLD timeseries were set to 2.2 seconds after stimulus onset until 3.4 seconds after the end of stimulus presentation corresponding to a total duration 13.2 seconds of BOLD signal per stimulus. The so derived timeseries covered the variability in the BOLD response for all situations where participants observed a social target being it in a VE or NEUT situation. To account for noise, two additional timeseries were extracted for each subject from the first eigenvariates of all voxels within masks covering medial cerebrospinalfluid regions (CSF) or white matter (WM) (Bedenbender et al., 2011). The fixed-effects GLM for the connectivity analysis on the first-level thus included the modified timeseries of the precuneus, the WM and CSF noise regressors, and the above described regressors of the original design matrix including the regressors modeling head movement parameters. Beta-maps of the precuneus timeseries were analyzed on the group-level with a random-effects GLM. Standard deviations of the six head movement parameters of each subject were included as covariates to reduce the influence of different amplitudes of head movement between and within groups on connectivity profiles. In addition the averaged ratings of vicarious embarrassment within each category were included as covariates as previously described. Differences in functional connectivity profiles of the precuneus between the friend and the stranger group were investigated within the brain regions that were consistently activated during vicarious embarrassment in both conditions. The results were family-wise error (FWE) corrected within a ROI of regions consistently activated during vicarious embarrassment defined by the results of the prior conjunction analysis (friend_VE–friend_NEUT ∩ stranger_VE–stranger_NEUT; see Fig. 2 and Table 1).

5.3. RESULTS

5.3.1. *Behavioral Data*

As expected, participants self-reported vicarious embarrassment was significantly stronger for all categories of vicarious embarrassment ($M = 3.04$, $SD = 0.61$ (stranger), $M = 3.10$, $SD = 0.50$ (friend)) compared to the neutral condition ($M = 1.04$, $SD = 0.11$ (stranger), $M = 1.02$, $SD = 0.07$ (friend)) across both groups, $F_{(1,\ 62)} = 861.37$, $p < .001$. There was no main effect of Group indicating overall similar responses (F(1, 62) = 0.12, p = .733) and no significant interaction between Group and Condition (F(1, 62) = 0.31, p = .578).

5.3.2. *Neuroimaging Data*

According to our expectations and prior studies on vicarious embarrassment (Krach et al., 2011; Paulus et al., 2015), we found stronger shared circuits activity in the ACC ($t_{(302)} = 6.09$, $p < .001$; corrected for whole brain analyses) and the AI ($t_{(302)} = 6.34$, $p < .001$; corrected for whole brain analyses) as well as mentalizing regions in the mPFC ($t_{(302)} = 6.23$, $p < .001$; corrected for whole brain analyses) and the temporal pole ($t_{(302)} = 4.86$, $p = .022$; corrected for whole brain analyses) during VE compared to NEUT situations for both groups (see also **Fig. 2** and **Table 1**). In addition and irrespective of the social relation to the target, the thalamus ($t_{(302)}$ = 5.99, p < .001; corrected for whole brain analyses) and brainstem ($t_{(302)}$ = 5.96, p < .001; corrected for whole brain analyses) confirmed the typical activation in response to social pain.

In both groups there was a positive correspondence of vicarious embarrassment ratings with neural activations of the left AI (stranger: $t_{(246)}$ = 5.68, p < .001; x = -32, y = 22, z = 6; friend: $t_{(246)}$ = 3.40, p = .008; x = -28, y = 26, z = 4) and activation of the ACC was positively associated with vicarious embarrassment ratings in the stranger group ($t_{(246)}$ = 5.06, p < .001, x = -8, y = 24, z = 30) but not in the friend group ($t_{(246)}$ = 2.01, p = .153, x = -6, y = 28, z = 26). Comparing both groups revealed a greater correspondence of vicarious embarrassment ratings and neural activations in the stranger group vs friend group for the ACC ($t_{(246)}$ = 2.63, p = .041, x = -10, y = 24, z = 30) and trend-wise also for the left AI ($t_{(246)}$ = 2.62, p = .070, x = -38, y = 18, z = 6).

As hypothesized, there was an interaction effect revealing that vicarious embarrassment associated activity was stronger in the friend compared to the stranger condition for the ACC ($t_{(302)}$ = 2.84, p = .026; corrected for ROI analyses) and the left AI ($t_{(302)}$ = 2.81, p = .047; corrected for ROI analyses). A whole-brain analysis did not reveal any additional significant clusters. The opposed contrast did not show any significant differences, neither in the ROI analyses nor in the whole-brain analysis.

When directly contrasting the activation while observing friends' wrongdoings compared to those of a stranger (friend_VE–stranger_VE) we found an increased BOLD response in the precuneus ($t_{(302)}$ = 4.72; k= 1016; p = .006; corrected for whole-brain analyses) (see **Fig. 3**). The subsequent functional connectivity analyses showed increased functional integration of the precuneus timeseries with the ACC ($t_{(48)}$ = 4.21, p = .046; corrected for ROI analyses) in the friend compared to the stranger condition (see **Fig. 3b**).

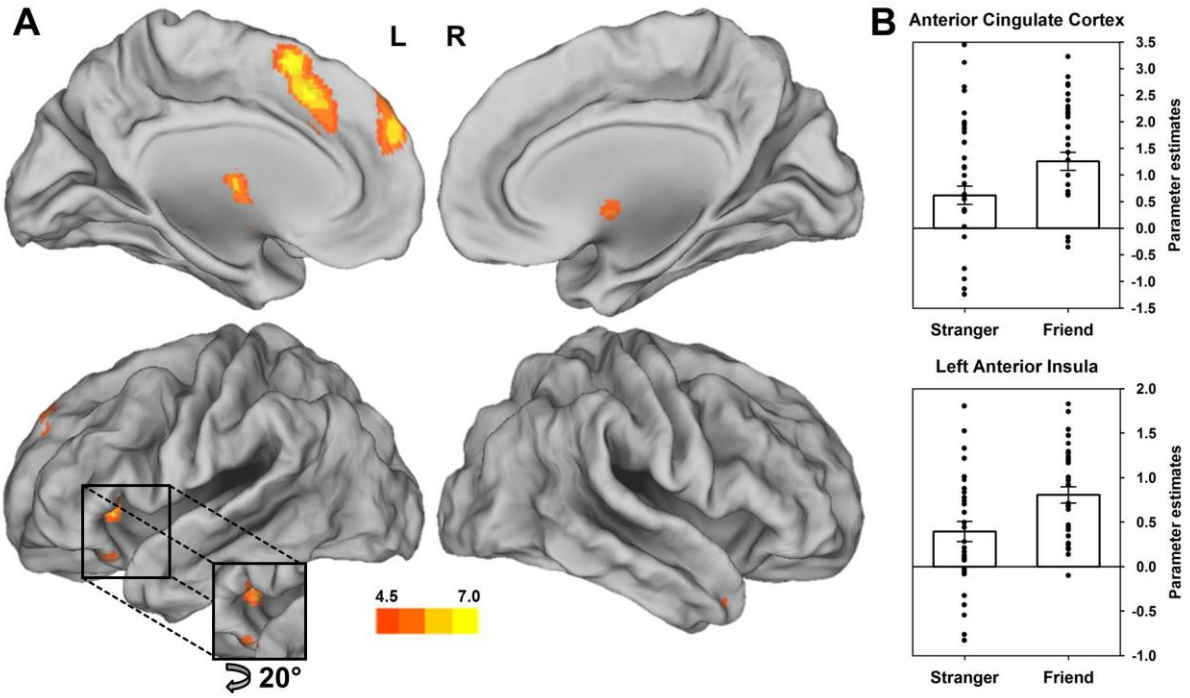

Figure 2. Increased activation during the experience of vicarious embarrassment for friends and strangers exposed in public situations. **A** The conjunction analysis ((friend_VE-friend_NEUT) ∩ (stranger_VE-stranger_NEUT)) reveals increased activation of the ACC, left anterior Insula, mPFC, brainstem and right temporal pole while observing friends and stranger in embarrassing situations ($p < .05$, FWE corrected). The color gradient illustrates the corresponding t-vaules. **B** Activation of the ACC and AI is specifically increased during vicarious embarrassment for friends versus strangers (see results section). Parameter estimates are plotted for the peak voxel of the interaction effect ((friend_VE-friend_NEUT)-(stranger_VE-stranger_NEUT)) within the ACC (-4, 30, 28 mm) and left anterior insula (-28, 20, 2 mm).

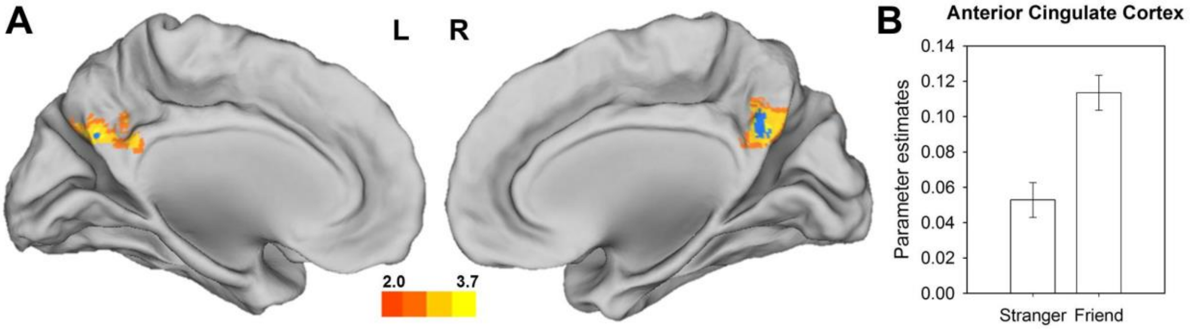

Figure 3. Increased activation and functional connectivity while observing a friend versus stranger in vicarious embarrassment situations . **A** Increased activation of the precuneus for friend_VE-stranger_VE is depicted with a yellow color gradient ($p < .05$, corrected on cluster extend level; the color gradient illustrates the corresponding t-vaules) and the constricted precuneus area used as seed region for the functional connectivity analysis is depicted in blue ($p < .0005$, uncorrected, masked with an anatomical precuneus and PCC mask). **B** Increased connectivity of the precuneus with the ACC while observing a friend versus stranger during social situations. Bar charts indicate the mean parameter estimates at the peak voxel of the connectivity effect within the ACC (-10, 22, 42 mm).

Table 1. Vicarious embarrassment related activation while observing a friend or a stranger.

	Side	MNI Coordinates			Cluster size	*T*	*p*
		x	y	z			
(friend_VE-friend_NEUT) ∩ (stranger_VE-stranger_NEUT)							
ACC/SMA	L	-4	14	56	581	7.25	<.001
		-6	22	42		6.57	<.001
		-10	26	34		6.09	<.001
Anterior Insula	L	-32	24	0	146	6.34	<.001
		-40	24	4		5.76	<.001
mPFC/superior medial gyrus	L/R	-2	56	30	375	6.23	<.001
		-6	52	40		5.69	.001
Thalamus	L/R	-8	-6	4	370	5.99	<.001
Putamen		-14	10	2		5.95	<.001
		-16	2	-6		5.24	.004
Brainstem	L/R	-2	-20	-22	144	5.96	<.001
Nucleus caudatus	R	12	10	2	163	5.54	.001
		10	2	-2		5.43	.001
		6	-6	-12		4.88	.013
Inferior Frontal Gyrus	L	-36	26	-18	28	5.46	.001
Inferior Temporal Gyrus	L	-42	-40	-16	20	5.06	.006
Medial Temporal Pole	R	40	14	-36	13	4.86	.022

Note. Results for the conjunction-analysis ((friend_VE-friend_NEUT) ∩ (stranger_VE-stranger_NEUT)). All p-values are family wise error corrected for the whole brain. Clusters with less than 10 voxels are not reported.

5.4. DISCUSSION

Is it always favorable to keep your friends close? In the present study we examined how the social ties with others affect the vicarious embarrassment on behalf of their flaws, failures or norm violations and unravel pathways that help to understand vicarious embarrassment on the neural systems level. We predicted that vicarious embarrassment would trigger activity within shared circuits as a measure for an empathic sharing of others' unbearable moments and that this activation would be modulated by the social closeness to the target person. Further, as humans are concerned about their social images, we expected that the cringe worthy behaviors of close friends would trigger precuneus activity as a neural measure of increased self-referential processing.

5.4.1. Empathizing with others' predicaments

Confirming earlier studies on the unpleasant emotional experience of vicarious embarrassment (Krach et al., 2011; Paulus et al., 2015), the shared circuits within the AI and ACC (Keysers and Gazzola, 2006), were involved either if participants observed their friends or unrelated strangers in embarrassing conditions. Similarly, activations within the brainstem and thalamus were increased when participants observed a friend or stranger. These activations might reflect how information of bodily arousal going along with vicarious embarrassment is relayed. However, activity within the shared circuits of the AI and ACC was specifically increased if participants observed threats to their friends' social integrity, supporting the notion that social closeness modulates empathic processes on the level of shared circuits. Further, we corroborated earlier findings that the subjective experience of vicarious embarrassment is indeed linked to AI and ACC activation (Krach et al., 2015; Paulus et al., 2015). However, in the friend condition, the link between neural response and behavior was lower compared to the stranger condition.

In a classic study, Shearn and coworkers could nicely demonstrate that participants showed stronger blushing when observing a friend as compared to a stranger in an embarrassing situation (Shearn et al., 1999) and argued that empathic blushing, such as proper empathy (Davis, 1996), would be particularly influenced by the increased empathic accuracy within friendship and kinship relations (Ickes, 1997; Ickes et al., 1990; Zaki et al., 2009). Our findings are also in line with recent studies on the effect of social closeness on vicarious physical (Cheng et al., 2010) and social pain (Beeney et al., 2011; Meyer et al., 2012) that reported increased shared circuit activity within the ACC and AI if friends compared to strangers were observed. Meyer and colleagues (2012) made participants observe friends and strangers during social exclusion as a form of social pain, which likewise activated affective pain regions in the ACC and AI (Meyer et al., 2012) - the very same regions that were previously shown to be associated with the direct and firsthand experience of social exclusion (Eisenberger, 2012; Eisenberger et al., 2003). In line with the present findings of an upregulation within shared circuits during the observation of friends vs. strangers in embarrassing predicaments, Meyer and colleagues reported a 'social closeness effect' on the experience of social exclusion. Similarly, Cheng and colleagues found a comparable 'social closeness effect' in the ACC and AI for sharing the physical pain of loved ones compared to strangers' (Cheng et al., 2010). Independent of the (social) pain of others being observed the fact that we have more vivid and rich mental representations of our close friends' feelings compared to unrelated others eases sharing their affect and accordingly could lead to increased activity in empathy networks. This should be particularly true for sharing a close friend’s embarrassing moments, which are triggered by deviations from social norms. Gaining access to a stranger’s emotionality during such moments is much more effortful compared to sharing a close friend’s thoughts and feelings with whom we spend time on a daily basis and where we thus have more intuitive access to the other’s mind (Ickes, 1997; Zaki and Ochsner, 2011; Zaki et al., 2009). Shared past emotional moments or experiences (e.g. shared grief upon the death of a friend or joint cheering in a sports event) as well as common norms or attitudes (e.g. shared rejection of racism) contribute to a better and more accurate mental representation of close others and accordingly ease empathizing with their situations.

5.4.2. Role of Mentalizing

In order to gain access to another person’s affect, participants need to form a representation of the other’s mental states (Frith and Frith, 2006). Thus, apart from the direct sharing of the other person’s affective state through mirroring, participants engage in perspective taking to build a model of another’s mind, a process that is associated with neural activity of the mPFC and the TP. Accordingly, in the present study we could show that the mPFC and TP were consistently involved during vicarious embarrassment, also while witnessing friends. This involvement however, was not modulated by social closeness. We have previously argued that mentalizing should be viewed as a general underlying process to understand vicarious embarrassment. Without mentalizing on others’ minds it is not possible to discern the evaluations in the eyes of bystanders that constitute the threat to the social integrity of the target (Paulus et al., 2015) and to experience this complex social emotion. This is why it was not surprising that we found an upregulation in the mentalizing network independent of the social relation to the humiliated social target.

5.4.3. Role of Self-Referential Processing

A large body of literature in social psychology has shown that people have a strong motivation to feel good about themselves (Baumeister, 1994; Tesser, 1988) and accordingly are concerned about the portrayal of their social images (Leary and Kowalski, 1990; Mead, 1934). Importantly, the own social images are not only fixed and stable across time, but are also continuously (re)constructed and adjusted to the social context. Self-portrayals can thus be highly heterogeneous and incorporate past, present, and future selves (Markus & Nurius, 1986; Wilson & Ross, 2001) or differentiate between private (personal) and public (relational, social, and collective) aspects of the self (Robins, Norem, & Cheek, 1999) which in total constitute a person's identity. One component that is continuously shaping our social images is the feedback of others (Leary et al., 1995). People give feedback for one's behaviors and attitudes and their acceptance or rebuttal shapes the social image that one aims to represent. However, also one's close friends' (mis)behaviors can impact and endanger our own social images as the social ties to a person may communicate a sharing of certain attitudes, norms, and values (Fortune and Newby-Clark, 2008). Observing a friend's norm violating behavior in a public context (e.g. yelling at the restaurant waiter) thereby may elicit concerns about one's own social image (Chekroun and Nugier, 2011; Fortune and Newby-Clark, 2008), however, only if one disagrees with the friend's behavior in that particular moment. Such concerns about one's own portrayed social image elicit the emotional reaction of embarrassment (Eisenberg, 2000; Macdonald and Leary, 2005; Tangney and Dearing, 2002). Previous research could show that people react to others' embarrassing circumstances, which also constituted a threat to their own social integrity, by showing signs of appeasement gestures and restitution behavior with the aim to restore their own social image (Keltner and Buswell, 1997; Semin and Manstead, 1982). Interestingly, concerns about the social image evolve relatively early in the human development. Children have a concept of an extended identity from around 8 years onwards and spontaneously report feeling embarrassed on behalf of another child or toddler in their care who commits a faux pas (Bennett et al., 1998). With increasing age children even appear to have a greater preoccupation with their social images and increasingly make judgments concerning others' evaluations. Around that time a passive audience is already sufficient to induce first-person experiences of embarrassment following rule violations (Bennett et al., 1998). Interestingly, opposed to vicarious embarrassment, first-person experiences of embarrassment are experienced as less devastating in front family members and friends compared to strangers (Keltner and Buswell, 1997; Lewis et al., 1991; Macdonald and Davies, 1983). Likewise, young children were more likely to show displays of embarrassment when dancing in front of strangers as compared to dancing in front of their mothers (Lewis et al., 1991).

In a similar way people tend to exert social control over deviant in-group members in order to avoid embarrassment and damage to their own and the group's social integrity (Chekroun and Nugier, 2011). Studies in the field of group-based emotions have brought up the concept of identity threat which could also mediate the effect of others' wrongdoings on the personal experience of vicarious embarrassment. Lickel and colleagues showed that group-based emotions such as shame or guilt were elicited when people were afraid of maintaining a positive group identity (Lickel et al., 2005, 2004). Hence people felt ashamed for another's wrongdoing when that person's behavior was relevant to their own social identity and when they feared that the other person's behavior would negatively reflect upon themselves (Lickel et al., 2005).

Taken together, concerns about one's own social image might pose a potent additional factor increasing embarrassment related activation of the ACC and AI in response to a friend's public failures. The increased activity within the precuneus, which is considered to be a neural correlate of ongoing self-related thoughts and representation of the self (Cavanna and Trimble, 2006; Mazzola et al., 2010; Northoff et al., 2006) might indicate the greater overlap between the cognitive representations of self and others, increased social image concerns and engagement in self-referential processing, while observing a friend's norm violating behaviors. The increased functional coupling of the precuneus with the ACC could thus represent a neural pathway that further explains, how the affective response in shared circuits is modulated the social relation by own image concerns.

5.4.4. Limitations

One limitation of the present study is the lack of the expected significant differences on the behavioral level, while finding coherent differences on neural activation and connectivity measures. Several factors could explain this observation. First, the lack of findings on the behavioral level might be explained by diminished statistical power for the behavioral effects. The level of neural activation is closer to the actual psycho-physiological process that we are interested in, e.g. the affective arousal of vicarious embarrassment that is mapped in the AI and ACC activation. Second, social desirability might influence the validity of the participants' self-report on their emotional experiences during the fMRI study. Specifically when it comes to emotions, which are related to judgments of another person's condition, people tend to adjust their explicit rating, to correspond to societal norms, standards and the expectations of the experimenter. This specifically could have affected the ratings in the friend condition, since participants might rather support friends than strangers and defend their social integrity in front of others in order to decrease negative affect (Cohen & Wills, 1985), maintain self-esteem (Major et al., 1991) and enhance well-being (Cohen and Hoberman, 1983). In case of strangers it might be easier and more socially accepted to explicitly express negative emotions such as vicarious embarrassment. These thoughts are supported by the correspondence between the behavioral report and the neural activation measures in the AI and ACC. Importantly, the association was not as strong for observing friends compared to strangers. The reduced coupling in the friend condition could be explained by effects of social desirability and adjustments of the behavioral report to align with the expectations of the environment.

5.4.5. Conclusion and Outlook

The present data opens up new perspectives for how social closeness affects brain processes related to vicarious affect. Earlier studies on empathy for various negative and positive states could provide evidence for involvement of cognitive processes and showed increased functional connectivity of mentalizing areas and shared circuits of affect processing (Leng and Zhou, 2010; Meyer et al., 2012; Mobbs et al., 2009). During social interaction the relationship to the social target modulates cognitive and mentalizing processes that influence shared circuit activations and the empathic response, similar to how the responsibility for anothers' suffering or ingroup-membership upregulate shared circuit activity (Cui et al., 2015; Hein et al., 2010). We initially described two models of how social closeness modulates vicarious embarrassment. Based on the present data we, however, cannot prefer one of the two provided models. Precuneus activation might map increased mentalizing about the other person's mind as well as be related to increased concerns about one's own social image during vicarious embarrassment for a close other. Nonetheless, the notion of self-referential processing to mediate affect experienced on behalf of others is a novel in the neurosciences. Our finding thus might help integrating and informing findings from social psychology on group processes, where the identification of oneself with a social group is the key concept in the phenomenon of vicarious affect (Lickel et al., 2005). Future studies on the neural foundations of various forms of social pain (e.g. embarrassment, guilt, exclusion, relational devaluation) however would benefit from more ecologically plausible environments, which are, however, difficult to realize in the restricted fMRI settings (Krach et al., 2013).

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CHAPTER 6

EVIDENCE FROM PUPILLOMETRY AND FMRI REVEALS REDUCED EMPATHY FOR SOCIAL PAIN BUT NOT PHYSICAL PAIN IN AUTISM

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CHAPTER 6

ABSTRACT

Autism spectrum disorder (ASD) is characterized by substantial social deficits. The notion that dysfunctions in neural circuits involved in sharing another's affect explain these deficits is appealing but has received only modest experimental support. Here we evaluated a complex paradigm on the vicarious social pain of embarrassment to probe social deficits in ASD as to whether it is more potent than paradigms currently in use. To do so we acquired pupillometry and fMRI in young adults with ASD and matched healthy controls. During a simple vicarious physical pain task no differences emerged between groups in behavior, pupillometry, and neural activation of the anterior insula (AIC) and anterior cingulate cortex (ACC). In contrast, processing complex vicarious social pain yielded reduced responses in ASD on all physiological measures of sharing another's affect. The reduced activity within the AIC was thereby explained by the severity of autistic symptoms in the social and affective domain. Additionally, behavioral responses lacked correspondence with the anterior cingulate and anterior insula cortex activity found in controls. Instead, behavioral responses in ASD were associated with hippocampal activity. The observed dissociation echoes the clinical observations that deficits in ASD are most pronounced in complex social situations and simple tasks may not probe the dysfunctions in neural pathways involved in sharing affect. Our results are highly relevant because individuals with ASD may have preserved abilities to share another's physical pain but still have problems with the vicarious representation of more complex emotions that matter in life.

AUTHOR CONTRIBUTIONS

In this study the author of the thesis contributed to the data analysis and writing of the paper.

EVIDENCE FROM PUPILLOMETRY AND FMRI REVEALS REDUCED EMPATHY FOR SOCIAL PAIN BUT NOT PHYSICAL PAIN IN AUTISM

6.1. INTRODUCTION

One of the core symptoms in high-functioning individuals with autism spectrum disorder (ASD) is their reduced capacity to intuitively represent their own and others' mental states [Levy et al., 2009; Lombardo et al., 2007; Lombardo et al., 2010]. This affects many aspects of life, but predominantly alters experience and behavior within complex social situations [American Psychiatric Association, 2013; Klin et al., 2007]. A frequent explanation for this impairment is based on the patients' often described deficit in embodying another's affective states [Gallese et al., 2013; Hill et al., 2004]. The deficient embodied representation has been attributed to malfunctions of the interoceptive cortex [Craig, 2002; Craig, 2003], a network comprising the anterior insula cortex (AIC) and the anterior cingulate cortex (ACC) [Bird et al., 2010; Silani et al., 2008]. This network, and specifically the AIC, provides a salient representation of one's own bodily states and has been suggested to be a correlate of one's conscious experience of emotion [Gu et al., 2013]. The observation that the same regions are activated while witnessing the affect of other individuals led to the idea that the representation of another's affect is reached through the embodied simulation of our own states [Gallese and Sinigaglia, 2011; Keysers and Gazzola, 2009]. Such embodied representations of emotions are thought to underlie and motivate socially competent behavior [Eisenberg and Miller, 1987; Hein et al., 2010]. Emotional resonance can occur for others' primary emotions such as physical pain [Singer et al., 2004] or disgust [Wicker et al., 2003], as well as for more complex social emotions such as rejection and embarrassment [Beeney et al., 2011; Krach et al., 2011; Paulus et al., 2014].

Embarrassment on behalf of others' mishaps (e.g., observing a waiter in a fully occupied restaurant stumbling and dropping dishes to the floor) constitutes a form of vicarious social pain [Krach et al., 2011; Müller-Pinzler et al., 2012; Paulus et al., Paulus et al., 2014] . The experience of vicarious embarrassment from the perceiver's perspective thereby has a conceptual and neurobiological overlap with vicarious physical pain (henceforth PP). The negative affect induced by witnessing another person's PP is thought to provide strong signals for the injuries of another's bodily integrity [Singer et al., 2004]. Likewise, the experience of vicarious social pain (henceforth SP) – and particularly embarrassment – is thought to serve a similar function, thereby signaling threats to another's social integrity [Macdonald and Leary, 2005; Krach et al., 2011; Paulus et al., 2014]. Vicarious responses for SP result in cortical activation comparable to those associated with vicarious PP [Immordino-

Yang et al., 2009; Krach et al., 2011; Masten et al., 2011], and are coupled with increased autonomic activation [Müller-Pinzler et al., 2012].

Most of the previous neuroimaging studies have framed social pain rather narrow and used paradigms of social exclusion [Eisenberger, 2012a; Eisenberger, 2012b; Eisenberger and Lieberman, 2004]. However, the concept of social pain has been conceptualized much broader, also including negative affective states such as shame, guilt, or embarrassment because they provide signs that one might not live up to others' standards [Macdonald and Leary, 2005]. In the aforementioned example the waiter attracts the attention of the audience in a situation which is severely unfavorable for his social image. The situation poses a threat to his social integrity and might potentially result in devaluation by desired partners or groups. The conceptualization of embarrassment as a form of social pain has been discussed in several earlier studies [Müller-Pinzler et al., 2015; Paulus et al., 2013a; Paulus et al., 2014][1]. Although the emotion of embarrassment is conceptually different from the experience of social exclusion, both share the underlying threat to one's social integrity which justifies integrating embarrassment in the broader construct of social pain.

To generate the vicarious emotional response for SP, however, contextual demands such as knowledge about norms and values, expectations of the social environment, and appraisals of the social target need to be dynamically integrated [Paulus et al., 2013b; Paulus et al., 2014]. In contrast, contextual demands are less complex for understanding and experiencing others' PP. This distinction is supported by the faster neural response of the AIC for PP as compared to SP [Immordino-Yang et al., 2009]. Basically, while witnessing others' PP, the individual's own body provides sufficient input to build an adequate model of

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[1] In many neuroscience studies the term 'empathy' has been used to circumscribe embodied representations of others' emotions and mostly empathy for physical pain [Batson, 1981; Engen and Singer, 2012; Hein and Singer, 2008; Lamm et al., 2007; Pfeifer et al., 2008; Zaki and Ochsner, 2012]. However, from a conceptual point of view, the term 'empathy' reflects incidents where perceivers (i.e. participants involved in our study) and social targets (i.e. protagonists displayed in the often painful situations) have a shared affective experience, with the perceivers being fully aware that the source of their own affective experience is the other's emotion [de Vignemont and Singer, 2006]. This does not always account for the experiences of embarrassment on behalf of others. For example, the experience of embarrassment would not be shared in an 'isomorphic fashion' [Engen and Singer, 2012] between attendees of a scientific conference observing a presenter with an open zipper and the presenter him- or herself [Paulus et al., 2013]. Thus, the term 'vicarious emotion' offers a wider scope and also includes non-shared affective experiences. For this reason we decided to use the term 'vicarious pain' instead of 'pain empathy' in the present manuscript.

another’s affect. Thus, contrasting SP with PP offers a unique opportunity to test the hypothesis of domain-general deficiencies of embodied representation in ASD. If domain-general deficiencies in embodied representations exist in ASD, these should affect PP and SP alike. In contrast, if it is the contextual demand of the social situation that defines whether individuals with ASD are able to rely on conscious access to their emotional representation, then alterations should specifically surface in SP. If difficulties in embodying SP exist in ASD, we would expect them to manifest within the circuit involved in such an embodiment, in particular in the AIC and ACC [Gallese and Sinigaglia, 2011; Keysers and Gazzola, 2009].

A longstanding theory in autism research suggests that from the time of their early childhood onwards, patients with ASD try to compensate for their lack of social intuition by adhering to learned social rules and conventions – often in an inflexible or stereotyped manner [Baron-Cohen et al., 2003; Klin et al., 2003]. Using this strategy, patients with ASD learn to navigate the complex social world being less dependent on social intuition. If this is truly the case, we would, in turn, expect activity in regions involved in such processes to be more pronounced in ASD individuals. Neuropsychological data, imaging and lesion studies show that the hippocampus is highly implicated in memory formation [Squire, 1992; Squire and Zola-Morgan, 1991]. Similar to tasks that require different elements to be remembered as a pair, such as a name and a face [Squire et al., 2004], social norms, conventions, and etiquettes are culturally learned connections of certain behaviors with certain social occasions (e.g., wearing a black suit at a funeral). We therefore hypothesize hippocampal involvement in the experience of SP, specifically in ASD individuals, and tested these hypotheses using combined pupillometry and functional magnetic resonance imaging (fMRI) within a sample of 16 young, male adults with ASD and 16 matched controls (see Table 1).

6.2. MATERIALS AND METHODS

6.2.1. Participants

Patients (N=16) were older than 18 years, male, and had a verbal IQ>85; matched the DSM IV criteria for ASD; had a confirmed ICD-10 diagnosis of autism (n=1), Asperger Syndrome (n=14), or Atypical Autism (n=1); had undergone standardized diagnostic procedures with either Module 3 or Module 4 of the Autism Diagnostic Observation Schedule (ADOS) [Lord et al., 2000; Lord et al., 2012; Rühl et al., 2004, see supplemental Methods for further details], the Wechsler Intelligence Scale for Children [Wechsler, 2003], and, if parental informants were available (n=11), the Autism Diagnostic Interview-Revised (ADI-R)

Table 1. Sample Characteristics, Behavioral Data and Pupil Dilation

		ASD		HC		*p* <	
ADOS-SA		9.47±4.5	9.36±4.8				
ADOS-RRB		1.80±1.4	1.64±1.3				
ADOS Comparison Score		6.27±2.9	6.18±3.1				
ADI-R Com		14.27±4.4	(12.88±3.9)	--	--	--	--
ADI-R Soc		18.00±5.2	(18.00±6.1)	--	--	--	--
ADI-R Stereo		5.82±2.8	(4.63±1.6)	--	--	--	--
Age		21.50±2.9	(20.90±1.8)	24.31±2.9	(24.27±3.3)	0.012	(0.008)
Age at diagnosis		14.76±3.1	(14.07±2.3)	--	--		--
Verbal IQ		117.5±14.4	(116.8±15.9)	113.3±10.7	(113.5±9.1)	0.368	(0.550)
AQ		30.06±8.8	(28.64±9.0)	11.91±5.7	(11.28±5.7)	<0.001	(<0.001)
TAS-20		55.53±14.3	(56.80±14.1)	44.93±10.0	(44.56±12.0)	0.030	(0.059)
Rating	PN	1.29±0.3	(1.18±0.2)	1.23±0.3	(1.26±0.4)	0.603	(0.565)
	PP	3.68±0.7	(3.67±0.6)	3.56±0.4	(3.69±0.4)	0.531	(0.937)
	SN	1.14±0.2	(1.14±0.3)	1.04±0.7	(1.04±0.1)	0.120	(0.258)
	SP	2.82±0.8	(2.83±0.8)	2.99±0.6	(3.00±0.7)	0.502	(0.607)
RT	PN	753.5±233.2	(729.6±124.2)	597.6±125.1	(590.0±122.7)	0.025	(0.015)
	PP	851.7±297.2	(871.5±302.6)	787.0±144.2	(760.3±156.5)	0.440	(0.331)
	SN	807.8±274.2	(752.3±195.0)	755.5±194.8	(725.4±143.0)	0.539	(0.715)
	SP	1016.6±416.1	(941.4±298.3)	954.4±259.6	(931.9±230.0)	0.616	(0.934)
Pupil dilation	PN	(0.69±0.60)		(0.55±0.31)		(0.498)	
	PP	(1.06±0.52)		(1.11±0.34)		(0.255)	
	SN	(-0.09±0.65)		(-0.05±0.43)		(0.849)	
	SP	(0.04±0.63)		(0.50±0.41)		(0.055)	

Note. ASD = Autism Spectrum Disorder; HC = Healthy Controls; ADOS = Autism Diagnostic Observational Schedule [Lord et al., 2000; Rühl et al., 2004]; ADOS-SA = ADOS Social Affect; ADOS-RRB = ADOS Restrictive and Repetitive Behavior; ADI-R = Autism Diagnostic Interview-Revised [Bölte and Poustka, 2001; Lord et al., 1994]; ADI-R COM = Communication and Language; ADI-R SOC = Reciprocal Social Interaction; ADI-R STEREO = Patterns of Behavior; PP = Physical Pain; PN = Physical Neutral; SP = Social Pain; SN = Social Neutral; RT = Reaction Time. Verbal IQ was assessed using the German Wechsler Adult Intelligence Scale [Tewes, 1991]. The German version of the Autism Spectrum-Quotient questionnaire (AQ) [Freitag et al., 2007] was used to assess autistic symptoms and the Toronto Alexithymia Scale (TAS-20) to assess symptoms of alexithymia [Taylor et al., 1997]. Numbers indicate means and standard deviations for the whole group. For the sub-group of participants (*N*=11) for which valid eye-tracking data was available, numbers are indicated in parentheses. P-values result from two-sample t-tests for mean differences.

[Bölte and Poustka, 2001; Lord et al., 1994]. Healthy controls (HC; N = 16) were matched for sex, age (ASD: M = 21.5 years; HC: M = 24.3 years; t(30) = 2.68; $P < 0.012$), and verbal IQ (ASD: M = 117.4; HC: M = 113.3; t(28) = 0.93; $P = 0.368$) using the Wechsler Adult Intelligence Scale [Tewes, 1991] (see Table 1).

Healthy controls had no history of mental or neurological disorders or cases of ASD in first- or second-degree relatives and all participants had normal or corrected-to-normal vision. The study was approved by the local ethics committee and written informed consent was obtained from all participants involved in the study.

6.2.2. Stimuli and paradigm

In two consecutive experiments we induced PP and SP with stimuli and paradigms that have been previously described [Krach et al., 2011; Paulus et al., 2015]. To induce PP, 56 digital color photographs depicting another person’s left or right hand or foot from a first-person perspective in either painful or non-painful (physical neutral - PN) situations were presented to the participants (see Figure 1a, upper row). PP and PN were matched in number and for semantic content and luminance (t(27) = 0.26, $P = 0.79$). Participants were instructed to attend to each photograph for 4.5 seconds and to estimate the intensity of physical pain that the depicted protagonist would experience in the respective scenario on a trial-by-trial basis (i.e., 1 = no suffering, 5 = very strong suffering). A fixation cross followed the rating phase (3s) for an average of 6.1s (see Figure 1b, upper row). In total, the experiment lasted 14.48min.

To induce SP, 50 validated hand-drawn sketches displaying a protagonist in either socially undesirable (SP; 40 sketches) or neutral public scenarios (socially neutral - SN; 10 sketches) were presented to the participants (see Figure 1a, lower row). SP stimuli consisted of four facets of previously established and validated vicarious social pain situations [Krach et al., 2011]. SP and SN stimuli did not differ regarding their luminance (t(48) = 1.54, $P = 0.13$). Participants were instructed to attend to each sketch for 12s and to evaluate the intensity of their vicarious embarrassment experience on a trial-by-trial basis (i.e., 1=no suffering, 5=very strong suffering). A blank screen with a fixation cross (1s) was interleaved between the presentation of the sketch and the rating period (3s) which was followed by a 8s low-level baseline separating the trials (see Figure 1b, lower row). The total experiment lasted 20.28min.

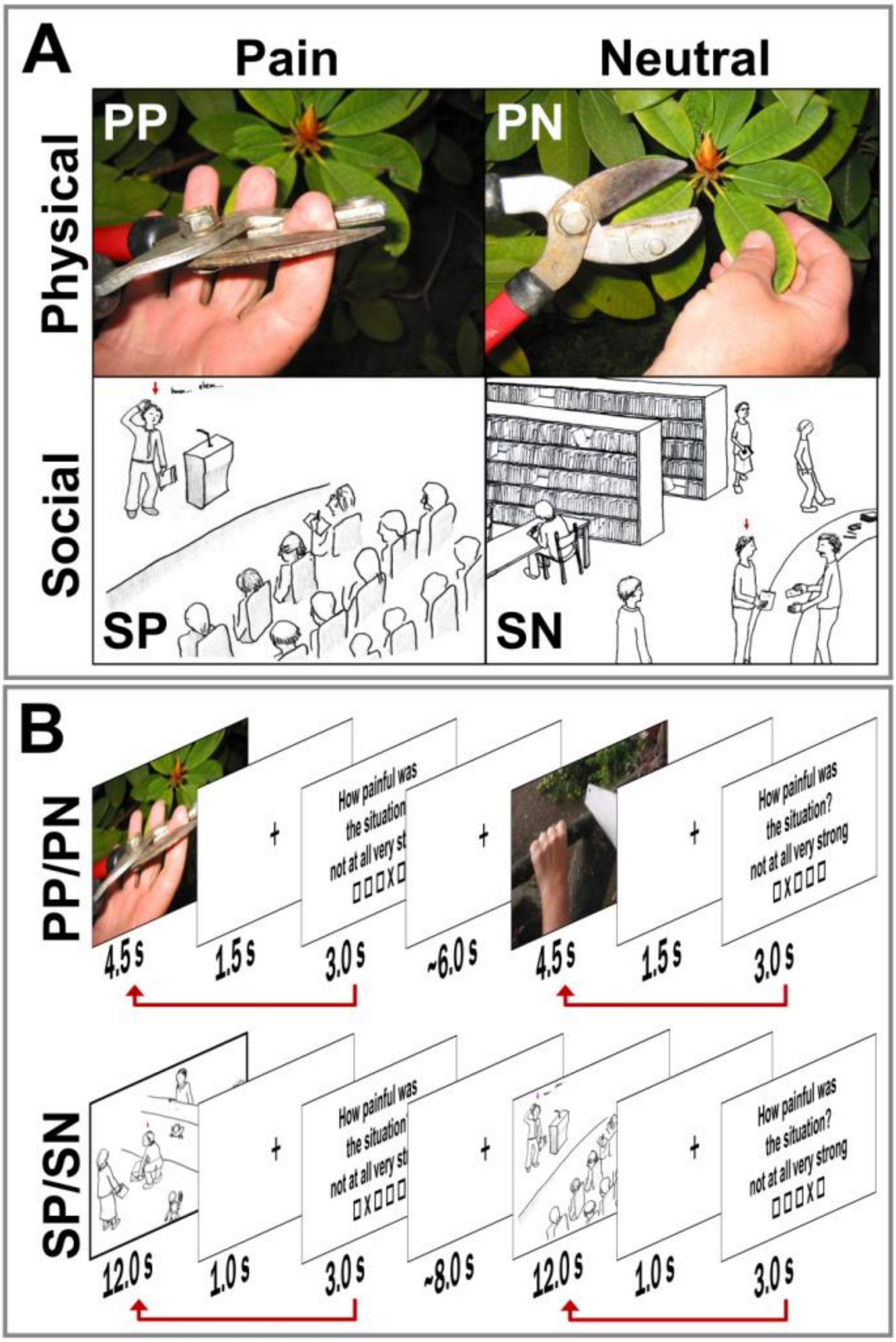

Figure 1. Experimental paradigms to induce physical pain (PP) and social pain (SP). A. The upper row illustrates one example stimulus of the experimental paradigm to induce PP (left) and one of the neutral control condition (PN, right, stimuli were taken from Jackson et al., 2005). The lower row illustrates one example stimulus of the experimental paradigm to induce SP (left) and one of the neutral control condition (SN, right[Krach et al., 2011]. Sketches depict a protagonist, indicated by the red arrow above his/her head, in potentially embarrassing or neutral situations. During the fMRI measurements, each sketch was accompanied by a sentence introducing the current scenario. B. The sequence of events during the functional MRI scanning is exemplified for PP/PN (upper row) and SP/SN (lower row) together with the subsequent rating periods and low-level baselines. The red arrow illustrates the weighting procedure of the PP and SP events with the intensity ratings provided after stimulus presentation.

6.2.3. Acquisition and analyses of pupil diameter

Pupil dilation is considered to be a measure of autonomic arousal which provides an additional and directly observable quantitative measure of the temporal pattern of brain reactivity to emotional stimuli [Silk et al., 2007]. Pupil diameter was continuously recorded at 500Hz using an MRI-compatible Eyelink-1000 device (SR Research, Kanata, ON, Canada) during both fMRI paradigms. Valid pupil measurements were available for eleven ASD patients and eleven healthy controls (see Table 1). To characterize each trial by a single value, we determined the sustained increase in pupil size during the picture presentation of PP and SP (see Supplemental Methods). Trial-specific estimates of pupil dilation were included in the respective fMRI models to test the association of the pupil dilation with the hemodynamic signal during PP and SP (see Figure 1b and below).

6.2.4. Functional MRI data acquisition and analyses

Participants were scanned at 3T (Siemens Trio, Erlangen, Germany) with 36 near-axial slices and a distance factor of 10% providing whole brain coverage. An echo planar imaging (EPI) sequence was used for acquisition of functional volumes (TR = 2.2s, TE = 30ms, flip angle = 90°, slice thickness = 3mm, FoV = 192). Overall, we obtained 395 volumes for PP and 553 volumes for SP. The first seven (PP) and four (SP) volumes of each session were discarded from further analyses. To rule out potential anatomical abnormalities, we acquired high resolution images with a T1-weighted 3D FFE sequence (TR: 25ms; TE: 4.59ms; NS: 170 (sagittal); ST: 2mm; IG: 1mm; FOV: 256x256 mm2; voxel size:1x1x2 mm3). For two participants of the control group anatomical images were either not available or distorted.

Data were analyzed using SPM8 (www.fil.ion.ucl.ac.uk/spm). For each session brain volumes were corrected for slice timing, head motion and spatially normalized to the standard EPI template of the Montreal Neurological Institute (MNI) using linear and non-linear transformations of the mean EPI images of each time session. The normalized volumes were resliced with a voxel size of 2x2x2 mm, smoothed with an 8 mm full-width half-maximum isotropic Gaussian kernel and high-pass filtered at 1/192Hz for the PP and 1/256 for the SP task. Group differences in head motion were examined using the translations and rotations for each session to control for potential biases between ASD and HC. For each, the average as well as the variance during SP and PP a multivariate analysis of variance (MANOVA) was conducted including all six parameters (i.e. three translations and three rotations) as dependent variables. The four MANOVAs revealed no significant differences in subject's head motion between groups both for the averages (SP: F(6,25) = 1.36, *P* = 0.269; PP: F(6,25) = 1.07, *P* = 0.407) and the variances (SP: F(6,25) = 2.26, *P* = 0.070; PP: F(6,25) = 2.01, *P* = 0.102).

Two separate fixed-effects general linear models (GLMs) were calculated at the within-subject level each for PP and SP (as detailed below) in order to test for (1) activation differences and differences in the correspondence of the ratings with hemodynamics and (2) the association of pupil dilation with the hemodynamic response within ASD and HC.

6.2.5. Vicarious Physical Pain

6.2.5.1. Hemodynamic Response and Correspondence with Behavior.

The first model for PP included three regressors modeling the hemodynamic responses to PP and the corresponding neutral control condition (PN), and the rating period with the aforementioned stimulus durations. The PP events were additionally weighted with the corresponding rating response to examine the relationship between neural activation and behavior. Weighted β-images contrasting PP to PN and the effect of the parametric weights on PP were computed and analyzed at the group level.

6.2.5.2. Association of Hemodynamic Response and Pupil Diameter.

The second model tested the association of the pupil dilation with the hemodynamic response. Therefore the trial specific pupil dilation was entered as an additional parametric weight in the subsample of n=11 participants for whom valid eye-tracking data were available. β-images of the parametric modulators of the pupil dilation during the painful and neutral condition were analyzed at the group level.

6.2.5.3. Group-Level Analyses of PP.

Three random-effects GLMs were computed for PP at the group level. The first model compared PP related neural activation in the ASD and HC group. The second model tested the association of trial-by-trial variability in the pupil slope and the hemodynamic response with a 2x2 repeated measures design including the parametric weights within PP and PN as repeated factor. To control for potential confounds due to group differences in pupil dynamics, this model included the intra-individual standard deviations of the pupil slope as a covariate for each group. The third model tested the association of trial-by-trial variability in PP self-reports with hemodynamic responses in both groups. To control for potential confounds due to group differences in the variance of the self-report, this model included the intra-individual standard deviations of ratings as a covariate for each group. All three random-effects group-level models also included the participants' age as an additional covariate in order to control for potential age-related confounds in the group comparisons.

6.2.6. Vicarious Social Pain

All GLMs for SP were built in an identical fashion with two separate models on the within-subject level and three random-effects GLMs on the group level.

6.2.6.1. Hemodynamic Response and Correspondence with Behavior.

The first GLM for SP included six regressors, with four epoch regressors modeling the hemodynamic responses to the SP facets, one for the neutral control condition (SN), and one for the rating period with the aforementioned stimulus durations. The SP events were additionally weighted with the corresponding rating response to examine the relationship between neural activation and behavior [Paulus et al., 2014]. Weighted β-images contrasting each SP condition to the SN and the effect of the four parametric weights on SP were computed and analyzed at the group level.

6.2.6.2. Association of Hemodynamic Response and Pupil Diameter.

The second model tested the association of the pupil dilation with the hemodynamic response. Therefore the trial-specific pupil dilation was entered as an additional parametric weight for all SP and SN conditions in the subsample of n=11participants for whom valid eye-tracking data were available. β-images of the parametric modulators of the pupil dilation during the painful and neutral condition were analyzed at the group level.

6.2.6.3. Group-Level Analyses of SP.

Three random-effects GLMs were computed for SP at the group level. The first model compared the SP related neural activation in the ASD and HC group by implementing a 4x2 repeated measures ANOVA with the four SP facets as repeated factor. The second model tested the association of trial-by-trial variability in pupil dilation and the hemodynamic response with a 5x2 repeated measures design including the parametric weights within the SP facets and SN as repeated factor and the ASD and HC group. To control for potential confounds due to group differences in pupil dynamics, this model included the intra-individual standard deviations of the pupil slope as a covariate for each group. The third model tested the association of trial-by-trial variability in SP self-reports with hemodynamic responses in both groups with a 4x2 repeated measures ANOVA with the parametric weights of the four SP facets as repeated factor. To control for potential confounds due to group differences in the variance of the self-report, this model included the intra-individual standard deviations of ratings as a covariate for each group. All three random-effects models also included the participants' age as an additional covariate in order to control for potential age-related confounds in the group comparisons and average effects were estimated across the four SP facets. All results were family-wise error (FWE)-corrected for multiple comparisons either in whole-brain or regions of interest (ROI) analyses using Gaussian-random field theory as implemented in SPM8.

6.2.7. Regions of interest analyses

Previous results stress the AIC and the ACC as key regions in processing PP and SP. Accordingly, two sets of functional ROIs were used in the present study: First, for PP, the bilateral AIC and ACC were defined in an independent sample contrasting PP-PN [Paulus et al., 2015], and second, the left AIC and ACC during SP were derived from another independent sample with the respective contrast SP-SN [Krach et al., 2011] (see Supplemental Figure S2 for an illustration of the ROI volumes for PP and SP). Additionally, because individuals with ASD were hypothesized to compensate for their social deficits by adhering to learned social rules, we expected regions associated with associative learning and memory retrieval to be involved in processing complex social scenarios. We therefore generated an anatomical mask of the hippocampus including the parahippocampal gyrus - a key region for memory processes [Squire et al., 2004] - as defined by the anatomical labeling atlas with a dilation factor of one [Tzourio-Mazoyer et al., 2002]. All ROI analyses were conducted using the small-volume correction as implemented in SPM8.

To examine the relationship between brain activity and autistic symptoms we extracted the mean parameter estimates within the AIC ROIs for SP-SN and PP-PN for each individual in the ASD group. The activation parameters for each condition were then correlated with the two ADOS subscales for social affect (ADOS-SA) and restricted and repetitive behaviors (ADOS-RRB). We calculated Spearman's rho as a non-parametric measure for the association since the sample size for this group was rather small (n=15). All analyses and the statistical analyses of the pupil dilation and behavioral data were conducted using IBM SPSS Statistics 22 (Armonk, NY: IBM Corp. Released 2013).

6.3. RESULTS

6.3.1. Vicarious Physical Pain (PP)

On the behavioral level, PP was successfully induced in both groups, as indicated by a significant main effect of Condition (PP: M = 3.62, SD = 0.57; PN: M = 1.26, SD = 0.34; F(1,30) = 401.06; $P < 0.001$; repeated measures ANOVA) and non-significant effects of Group (F(1,30) = 0.66; $P = 0.422$) and Group x Condition (F(1,30) = 0.075; $P = 0.787$, see Table 1) on the pain ratings. Additionally, there was a significant main effect for increase in pupil diameter, indicating arousal-related sympathetic activation [Bradley et al., 2008; Paulus et al., 2015] during PP compared to PN in both groups (F(1,20) = 32.65; $P < 0.001$; repeated measures ANOVA, see Table 1) and no significant effects of Group (F(1,20) = 0.68; $P = 0.797$) or Group x Condition interaction (F(1,20) = 1.21; $P = 0.284$). Furthermore, whole brain analyses indicated PP to induce strong and consistent activations of brain regions typically associated with the processing of one's own or others' pain in ASD and HC [Lamm et al., 2011] (see Figure 2a and Table 2). This multimodal evidence for preserved affective reactivity in the ASD group was supported by a trial-specific correspondence of increase in pupil diameter and hemodynamic changes in the ROIs of the AIC (right: t(39) = 4.33; $P_{\text{FWE}} = 0.003$; left: t(39) = 3.53; $P_{\text{FWE}} < 0.032$) and ACC (t(39) = 4.42; $P_{\text{FWE}} < 0.008$) as indicated by a conjunction of the effects in both groups (see Supplemental Figure S1 and Table 3 for results on the average effect), thus integrating both measures for arousal related activation [see also Paulus et al., 2015].

6.3.2. Vicarious Social Pain (SP)

The SP task revealed a very different picture. On the behavioral level, SP was successfully induced in both groups, as indicated by a significant main effect of Condition (SP: M = 2.90, SD = 0.73; SN: M = 1.09, SD = 0.18; F(1,30) = 216.78; $P < 0.001$; repeated measures ANOVA) and no significant effects of Group (F(1,30) = 0.07; $P = 0.791$) or Group x Condition interaction (F(1,30) = 1.25; $P = 0.272$, see Table 1). However, the groups differed markedly on all neurobiological parameters. First, while there was a significant main effect of Condition on pupil dilation (F(1,20) = 16.05; $P < 0.001$) there was no main effect of Group (F(1,20) = 1.41; $P = 0.250$). Importantly, the Group x Condition interaction was significant

(F(1,20) = 6.05; P = 0.023). Direct comparisons of the conditions within groups showed greater pupil dilation during SP in the HC group (t(10)=5.15; P < 0.001), which was not evident in ASD individuals (t(10) = 0.99; P = 0.344, see Table 1).

In accordance with the results of the pupillometry, in HCs, whole brain analyses revealed SP to elicit significant cortical activations of the ACC, AIC, thalamus, cerebellum, inferior frontal and temporal gyrus [Krach et al., 2011; Paulus et al., 2014] (see Table 2 and Figure 2b). In patients with ASD brain activation was overall less pronounced (see Figure 2b) and ROI analyses showed a specific decrease compared to HCs within the left AIC (x = -28, y = 24, z = 2; t(118) = 2.74; P_{FWE} = 0.032) and the ACC at trend level (x = -4, y = 22, z = 48; t(118)=2.71; $P_{uncorrected}$ = 0.004, see Figure 2c). To ensure that the obtained results were not affected by potential outliers, we examined the parameter estimates for each individual and also computed robust regressions using Huber's M-estimator on the extracted parameters. Visual inspection of the parameter estimates revealed no influential data points in the direction of our hypothesis (see Figure 2c) and the robust regression showed stable t-values, specifically in the AIC (t(30) = 2.78; P = 0.005) with a less substantial trend in the ACC (t(30) = 1.99; P = 0.028). Notably, the trial-by-trial variability in the pupil dilation again corresponded to the dynamics in hemodynamic response in the ROIs of the left AIC (x = -34, y = 26, z = 0; t(99) = 2.56; P_{FWE} = 0.040) and the ACC (x = -10, y = 18, z = 38; t(99) = 3.13; P_{FWE} = 0.041) in the HC group (see Supplemental Figure S1 and Table 3 for the results of the average effect). These data thus provide multimodal evidence for reduced embodied representation of SP in ASD.

Table 2. Brain Activation during Physical Pain (PP) and Social Pain (SP) and Group Differences.

Anatomical region	Cyto area	Side	Cluster Size	MNI Coordinates x	y	z	*T*	*P*
Physical Pain								
HC: PP – PN								
Cingulate/ SMA		L/R	1,495					< .001
SMA				-2	22	44	8.25	
Middle Cingulate				2	26	34	6.56	
SMA				2	12	56	6.51	
Somatosensory		L	783					< .001
Supramarginal Gyrus	PFt			-56	-26	38	6.75	
Postcentral Gyrus	PFop			-58	-20	22	5.62	
Postcentral Gyrus	BA1			-54	-34	54	4.78	

Anterior Insula		L	296					.005
Insula Lobe				-36	16	6	6.01	
Insula Lobe				-30	26	0	3.89	
Anterior Insula		R	310					.004
Insula Lobe				34	20	-4	5.71	
Insula Lobe				44	16	-2	4.74	
Insula Lobe				32	20	6	4.47	
ASD: PP – PN								
Somatosensory		L	1,580					< .001
Postcentral Gyrus	PFt			-58	-22	32	7.64	
Supramarginal Gyrus	PFt			-62	-28	38	6.86	
Inferior parietal Lobe	PFt			-46	-34	42	5.72	
Cingulate/ SMA		L/R	1,548					< .001
Superior Medial Gyrus				-2	20	42	6.89	
Posterio-Medial Frontal				0	12	56	6.11	
Middle Cingulate Cortex				-6	24	34	5.76	
Somatosensory		R	1,267					< .001
Postcentral Gyrus	PFt			52	-26	40	6.67	
Supramarginal Gyrus	PFop			64	-18	28	6.06	
Postcentral Gyrus	BA2			46	-32	52	5.80	
Anterior Insula		R	554					< .001
Insula Lobe				40	4	14	5.40	
Pars Opercularis	BA44			58	10	16	4.76	
Inferior Frontal		L	177					.035
Pars Triangularis				-34	20	10	4.99	
Pars Orbitalis				-36	22	-10	4.15	
Anterior Insula		L	326					.003
Insula Lobe				-38	-2	16	4.82	
Pars Opercularis				-50	8	4	4.55	
Social Pain								
HC: SP – SN								
Cingulate / Insula		L/R	7,787					< .001
Posterior-Medial Frontal				-4	20	48	8.81	
Middle Frontal Gyrus				-50	14	36	6.40	
Insula Lobe				-26	26	2	6.16	
Caudate / Thalamus		L	2,058					< .001
Caudate Nucleus				-14	6	12	5.78	
Thalamus	Temporal			-4	-10	8	5.08	
Cerebellum		R	180					.043
Cerebellum	Lobule VI			30	-60	-28	5.39	
Cerebellum	Lobule VI			26	-74	-24	3.99	
Inferior Temporal Gyrus		R	459					<.001
Inferior Temporal Gyrus				-46	-58	-14	5.03	
Inferior Temporal Gyrus				-44	-44	-18	4.15	

Somatosensory		L	655					< .001
Postcentral Gyrus	BA2			-38	-38	54	4.85	
Inferior Parietal Lobe	BA1			-52	-30	50	4.39	
Inferior Parietal Lobe				-32	-36	42	4.16	
Inferior Frontal Gyrus		R	181					.043
Pars Opercularis	BA44			56	10	20	4.62	
Pars Triangularis	BA45			62	16	22	4.53	
Occipital Cortex		L	240					.018
Middle Occipital Gyrus	hOc2			-12	-102	6	4.24	
Calcarine Gyrus	hOc1			-14	-102	-4	4.14	
Lingual Gyrus	hOc4v			-32	-90	-14	3.53	
ASD: SP – SN								
Posterior-Medial Frontal		R/L	288	-6	12	52	5.71	.008
Interaction: [HC - ASD] - [SP - SN]								
Anterior Insula		L	13	-28	24	2	2.74	.032

Note. ASD = Autism Spectrum Disorder; HC = Healthy Controls; PP = Physical Pain; PN = Physical Neutral; SP = Social Pain; SN = Social Neutral; all statistics for the PP/SP > PN/SN effects are family-wise error (FWE) corrected for whole-brain analyses at cluster level. The interaction effect was examined in an anterior insula region of interest (ROI) which was derived from an independent study on SP [Krach et al., 2011]. All *p* values represent the corresponding FWE corrected value. The 'Cyto Area' column indicates the assigned cytoarchitectonical area as indicated by the SPM ANATOMY toolbox v2.1 [Eickhoff et al., 2005] if available. Anatomical labels were derived respectively.

The inspection of individual activation parameters showed substantial heterogeneity during the SP task within the ASD group and the inter-individual differences of the AIC activation during SP were somewhat larger in individuals with ASD compared to healthy controls (ASD: SD = 0.19, HC: SD = 0.13, see Figure 2c). The observed heterogeneity in the neural response during the SP condition could relate to differences in the severity of autistic symptoms. To test this assumption and explain the heterogeneity of the neural responses in the ASD group, we correlated the two ADOS scales for SA and RRB with the average activation within the AIC ROIs for SP and PP. Non-parametric analyses revealed a significant negative association of the ADOS-SA with SP activation (Spearman's rho = -.482; *P* = 0.034) indicating less SP induced activation with increasing symptom severity in the social affect domain. However, this association was not observed for the PP condition (Spearman's rho = 0.297; *P* = 0.141) and the correlations with the ADOS-SA were significantly different between the SP and PP conditions (*P* = 0.007; see Figure 3 left). Such dissociation was not found for the ADOS-RRB (SP: rho = -0.007; *P* = 0.490, PP: rho = .321; *P* = 0.122, see Figure 3 right) and notably the ADOS-RRB correlation was significantly less pronounced than the association of SP activation with the ADOS-SA domain (*P* = 0.035).

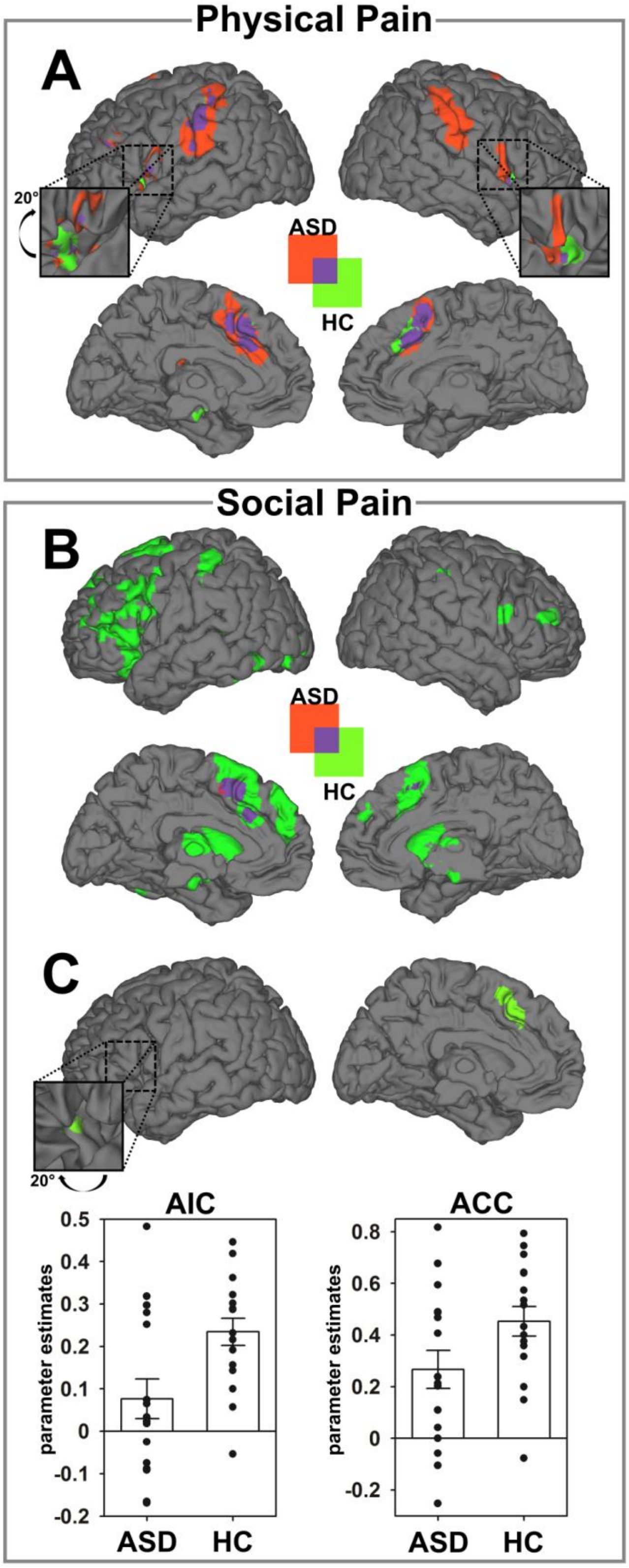

Figure 2. Brain activation during physical pain (PP) and social pain (SP)**. A.** Brain activation for main effect of task (PP-PN) for patients with autism spectrum disorders (ASD) and healthy controls (HC). **B.** Brain activation for main effect of task (SP-SN) for patients with ASD and HCs. **C.** Parameter estimates of the left anterior insula cortex (AIC) and the anterior cingulate cortex (ACC) show reduction of SP-related activation in the ASD group. Parameter estimates are plotted together with standard errors at the peak voxel and illustrate the contrast of SP-SN for each group within the left AIC and the ACC (see also Supplemental Figure S2 and Table 2).

Table 3. Association of Hemodynamic Response with Variability in the Pupil Dilation during Physical Pain (PP) and Social Pain (SP).

Anatomical Region	Cyto Area	Side	Cluster Size	MNI Coordinates			*T*	*p*
				x	y	z		
Physical Pain								
Cingulate SMA		L/R	3,641					< .001
Posterior-Medial Frontal				-2	14	44	7.50	
Anterior Cingulate	BA33			6	14	28	6.93	
Middle Cingulate				8	22	34	6.64	
Insula		R/L	7,180					< .001
Insula Lobe				34	22	-4	7.44	
Insula Lobe				-34	16	6	6.72	
Insula Lobe				40	18	2	6.69	
VLPFC		L	357					.004
Inferior Frontal Gyrus				-40	42	6	5.45	
Middle Frontal Gyrus				-36	52	6	4.90	
Somatosensory		R	567					< .001
SupraMarginal Gyrus	PFt			48	-32	38	5.14	
Supramarginal Gyrus	PFt			56	-28	36	4.77	
Postcentral Gyrus	BA3b			30	-20	376	4.09	
Precuneus		R/L	2,098					< .001
Cuneus	BA7M			8	-84	40	5.13	
Precuneus	BA7A			6	-66	60	4.74	
Cuneus	BA7M			-2	80	40	4.74	
Superior Frontal		L	300					< .008
Superior Frontal Gyrus				-14	2	74	4.89	
Superior Frontal Gyrus				-20	-6	70	4.00	
Superior Frontal Gyrus				-28	-10	66	3.89	
Precentral Gyrus	BA6	L	194	-48	2	44	4.30	< .038
Social Pain								
Anterior Insula		L	38	-32	26	-4	2.56	.046

Note. Effects represent the average effect of the parametric weights for physical (PP and PN) and social pain (SP and SN) across the ASD and HC group. All PP/PN effects are family-wise error (FWE) corrected at the cluster level for whole brain analyses. The SP/SN effect was examined in the anterior insula region of interest (ROI) which was derived from an independent sample on SP [Krach et al., 2011]. All *p* values represent the corresponding FWE corrected value. The 'Cyto Area' column indicates the assigned cytoarchitectonical area as indicated by the SPM ANATOMY toolbox v2.1 [Eickhoff et al., 2005] if available. Anatomical labels were derived respectively.

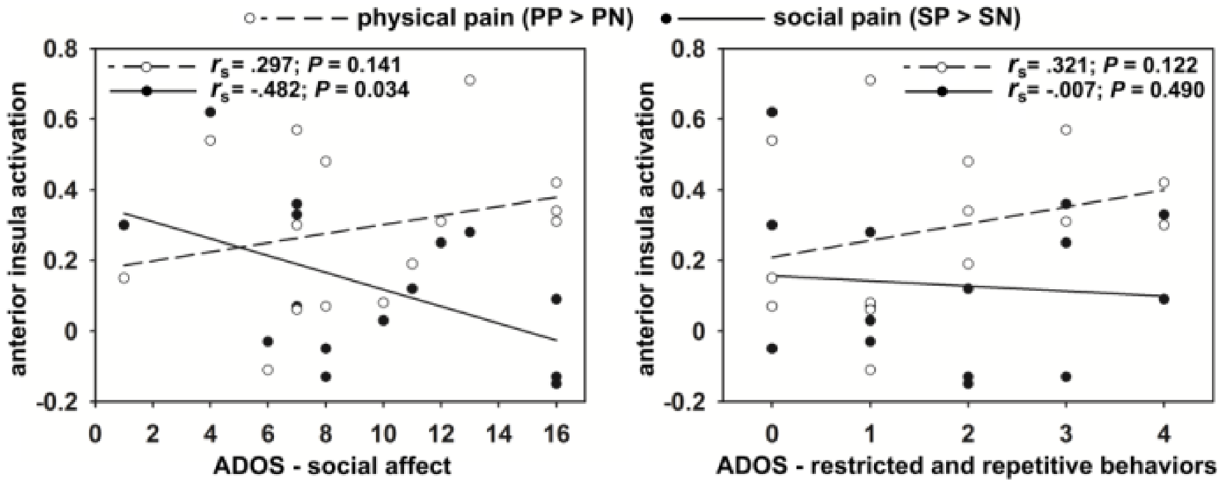

Figure 3. Association of anterior insula (AIC) activation with individual differences in symptom severity as measured with the autism diagnostic observational schedule (ADOS). Spearman's rho correlation coefficients are depicted together with the slope of the linear fit between symptom severity and AIC activation. The association of symptom severity in the domain of social affect with AIC activation significantly differs between physical and social pain (p=.007) and individuals with autism spectrum disorders show less pronounced AIC activation with stronger symptom severity.

6.3.3. Correspondence of brain and intensity ratings

The contradiction between the non-findings on the behavioral level and the differences on the level of neurobiological parameters, specifically during SP, could be explained by regressing the intensity of the obtained self-reports with hemodynamic responses on a trial-by-trial level. In the HC group, the intensity of the SP self-reports positively correlated with the hemodynamic response in the ROIs of the AIC (t(113) = 3.31; P_{FWE} = 0.007) and ACC (t(113) = 3.36; P_{FWE} = 0.022, see Table 4 and Figure 4b). This positive association of behavior with neural activation in the AIC was also present during PP in HC (t(27) = 3.68; P_{FWE} = 0.030; see Table 4 and Figure 4a). In ASD, the correspondence of brain and behavior was not significant for either PP and SP and, compared to the HC group, a significantly smaller association of the hemodynamic response with the intensity of the SP self-report was found in the ROI of the ACC (t(113) = 3.21; P_{FWE} = 0.032, see Figure 4c). In contrast, patients with ASD showed greater correspondence of SP self-reports with activity of the hippocampus (right: x = 20, y = -34, z = -10; t(113) = 3.76; P_{FWE} = 0.031 and left at trend level: x = -28, y = -44, z = -6; t(113) = 3.21; $P_{uncorrected}$ = 0.001, see Figure 4c), which is a key region for memory processes [Squire et al., 2004; Squire and Zola-Morgan, 1991].

Table 4. Correspondence of Within-Subject Variability in the Intensity of Physical Pain (PP) and Social Pain (SP) with Hemodynamic Response.

Anatomical Region	Side	Cluster Size	MNI Coordinates			*T*	*p*
			x	y	Z		
Physical Pain							
HC							
Anterior Insula	L	143	-34	30	4	3.68	.030
Social Pain							
HC							
Anterior Insula	L	62	-36	24	0	3.31	.007
Anterior Cingulate	L/R	280	-2	10	56	3.36	.022
			-6	20	38	3.15	.038
HC – ASD							
Anterior Cingulate	L/R	75	-2	18	58	3.21	.032
ASD – HC							
Hippocampus	R	673	20	-34	-10	3.77	.031

Note. ASD = Autism Spectrum Disorder; HC = Healthy Controls; effects represent the effect of the parametric weights for physical (PP) and social pain (SP) within the HC group and the direct comparison between groups for SP. No significant effects were found for the main effect of task in the ASD group. Effects were examined in the regions of interests (ROI) which were derived from independent studies on PP [Paulus et al., 2015] and SP [Krach et al., 2011] and the *p* values represent the corresponding FWE corrected value within the ROIs (for functional ROIs see **Supplemental Figure S2**). The ROI analysis for the hippocampus was conducted within an anatomically defined mask from the anatomical labeling atlas (AAL) [Tzourio-Mazoyer et al., 2002] and the *p* value represents the corresponding FWE corrected value within the ROI.

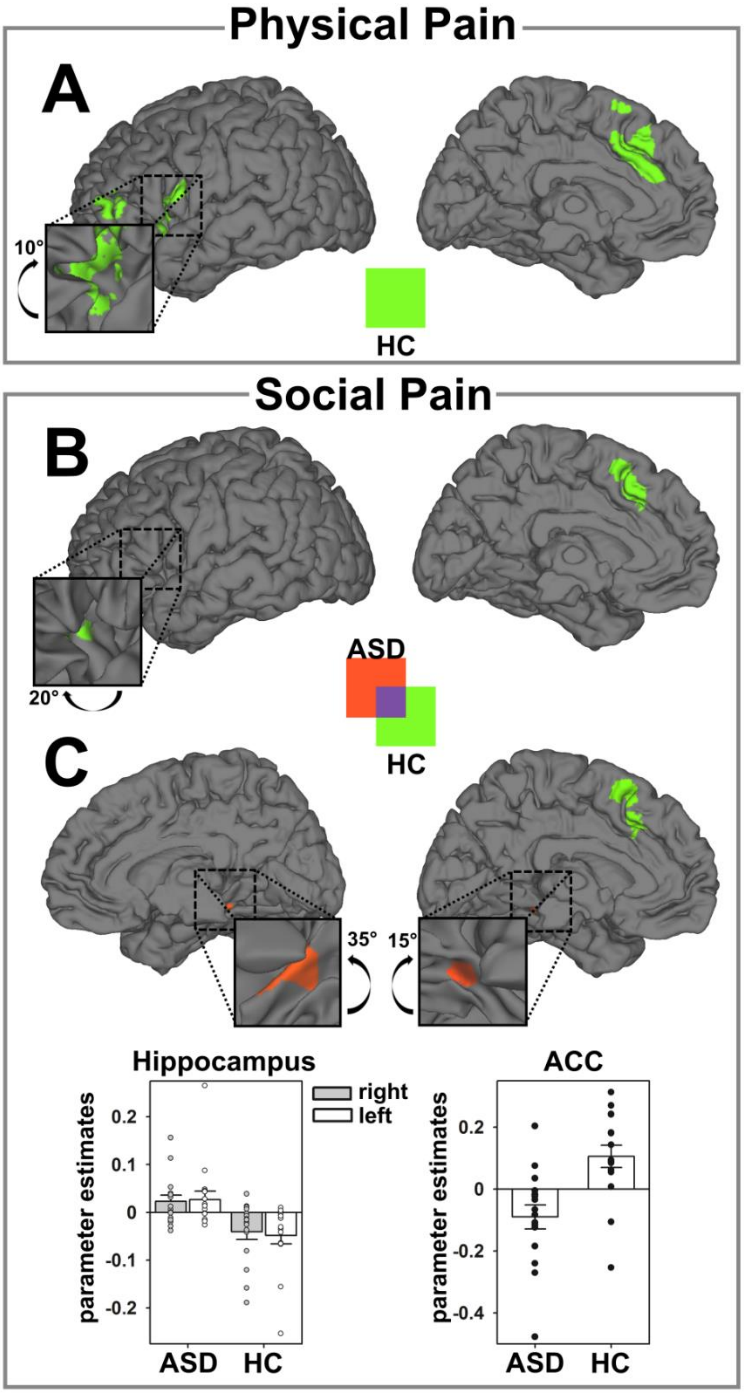

Figure 4. Association of within-subject variability in the intensity of the vicarious physical pain (PP) and social pain (SP) with hemodynamic responses in both groups. A. Neural network comprising the left anterior insula cortex (AIC) and the anterior cingulate cortex (ACC) that was significantly associated with the intensity of the self-report during PP in the healthy control (HC) group. In patients with autism spectrum disorders (ASD) there was no significant correspondence between the intensity of the self-report and the hemodynamic response during PP. B. Neural network comprising the left AIC and the ACC that was significantly associated with the intensity of the self-report during SP in the HC group. In patients with ASD there was no significant correspondence between the intensity of the self-report and the hemodynamic response during SP. C. Direct comparison between ASD and HC in terms of correspondence between SP self-report and hemodynamic response. Stronger associations in ASD are coded in red, stronger associations in HC are coded in green. Parameter estimates of areas showing significant differences between groups are plotted together with standard errors at the peak voxel (see also Supplemental Figure S2 and Table 4).

6.4. DISCUSSION

The present study analyzed behavioral and neurobiological markers of embodied representations of another's physical and social pain in ASD. Integrating pupillometry with fMRI, in ASD, we found domain-specific decrements in the neurobiological response of vicarious social but not physical pain. The data suggest that in ASD, the behavioral response to SP dissociates from the neurobiological embodiment of others' affect. This evidence provides support for previous findings in patients with ASD that verbal responses may not be sufficient to unravel altered mechanisms in intuitively representing another person's state. This has been documented, for example, in the context of different theory-of-mind tasks showing that persons with ASD were likely to give correct verbal reports that did not correspond to their spontaneous behavior [Abell et al., 2000; Castelli, 2002; Kana et al., 2009; Klin, 2000] or anticipatory looks [Ruffman et al., 2001; Senju et al., 2009]. Here, we show that persons with ASD use an alternative route to obtain the same behavior and we provide the first evidence for differences in the underlying neurobiological mechanisms that link neural activation with behavior.

In healthy controls, the self-reports on the intensity of their SP experience showed significant coupling with activity of the ACC and AIC, brain regions associated with embodied affects (for a replication of this effect in an independent sample, see Paulus et al., 2014). In contrast, ASD individuals did not base their self-report on the embodied representations of affect in this network, but instead showed a stronger association with the hippocampus, which is a key region for memory processes [Squire, 1992; Squire and Zola-Morgan, 1991]. This echoes with clinical observations that people with ASD compensate for their reduced ability to access embodied signals by means of rigidly learning and memorizing social rules and conventions [Baron-Cohen et al., 2003; Klin et al., 2003]. This gains relevance for the social pain of vicarious embarrassment which, in particular, relies on a conceptual understanding of social norms that can be thought of as culturally learned connections of specific social occasions with specific behaviors. Thus, the present data suggest different pathways to report on one's own vicarious emotions in complex social environments. Individuals with ASD seem to compensate for dysfunctions in the interoceptive route that give access to the embodied representation of others' affect by retrieving memorized representations of learned rules and conventions.

The lack of reliance on the interoceptive route in ASD also manifests in diminished embodied affect as represented by reduced activation of the ACC and AIC as well as by the pupillary responses. This finding is specific to complex social scenarios in which one has to dynamically integrate intuitive judgments about contextual demands and the expectations of the social environment [Paulus et al., 2013]. In the context of vicarious physical pain, no peculiarities were found in any of the neurobiological markers of embodied affect. The neural response of the AIC and ACC as well as the pupil response of the ASD group were very similar compared to HC, thereby replicating recent findings on vicarious physical pain in ASD [Bird et al., 2010; Hadjikhani et al., 2014]. This suggests the absence of domain-general disturbances in embodying affect in ASD, but points to a gradient regarding the complexity of social situations. In simple situations, in which one's own body is sufficient to represent the totality of others' affect, persons with ASD are not compromised. In more complex social situations, however, in which the representation of another's affective experience necessitates the extraction of the gist of the social setting by integrating contextual demands with the expectations of the social environment patients with ASD lack the intuitive access to the embodied representation of affect. This might help to explain the often observed odd and eccentric behaviors and difficulties during social interactions [Carter et al., 2005] and also suggests that the ability to share another's affect is not fundamentally compromised in ASD [Bird et al., 2010; Keysers and Gazzola, 2014]. Instead, other factors such as the complexity of the situation [Paulus et al., 2013b] and motivational aspects [Chevallier et al., 2012] might impact the vicarious response.

ASD is a highly heterogeneous disorder not only at the level of behavior and the expressed clinical symptoms but also at the underlying neural systems' functional architecture. This is supported by previous studies which reported significant correlations between individual differences in trait markers for social behavior and empathy related brain activity in individuals with ASD [see e.g., Greimel et al., 2010; Schulte-Rüther et al., 2011]. In this line, we observe the neural response during vicarious SP to be related to the ADOS-SA which additionally substantiates the finding for reduced neural responses in more complex social situations. The activation within the AIC was thereby inversely related to autism symptom severity in the domain of social affect, suggesting a central role of embodiment of others' affect for the emotional and social impairments in ASD. Conversely, no such significant correlation was found for restricted and repetitive behaviors. This might be due to the small degree and variance of observed behaviors in this domain or the relatively small sample size of individuals with ASD but could also indicate that dysfunctions within neural systems that process social cognition specifically relate to clinical symptoms in the similar domain, thus helping to understand the heterogeneity of the ASD phenotype.

The present findings of impaired embodiment of others’ affective states might have implications for therapeutic interventions in ASD. First, interventions focusing on the understanding and sharing of basic emotions in simple social scenarios might not help to improve social intuition and enable the transfer to complex everyday life situations. Second, social skills training [Frith, 2004; Rao et al., 2008] that conveys strategies to avoid maladjusted behavior might reduce potential stigmatization and personal distress of affected individuals, but will not necessarily ease social interactions. Finally, the present data might inspire treatment options to anchor therapeutic interventions in very simply structured social situations and then gradually increase their social complexity. Repeated access to intact embodied measures of affect, and training of neural routes that are not fundamentally impaired, could be transferred to increasingly complex social situations that were previously not directly accessible. As oxytocin has been identified as a significant enhancer of behavioral performance but also neural activity related to empathy and social cognition (Aoki et al., 2014), innovative therapeutic approaches could also aim to combine oxytocin treatment with the training of social skills in order to improve therapeutic outcome.

In conclusion, the present study stresses the relevance for the neurosciences to focus on more refined experimental paradigms to reveal the peculiarities in the neural systems functional architecture of ASD. In line with developments towards using sophisticated tasks to test theory of mind deficits in autism [Baron-Cohen et al., 1997; Happé, 1994; Kaland et al., 2002], more complex paradigms on vicarious emotions are crucially needed to characterize the specific alterations in brain function related to social affect. This is evidenced by the specific association of activation with the symptom severity in the social affect domain of the ADOS only for the more complex vicarious social pain task where the gist of the depicted social situations is more difficult to grasp. The here-presented dissociation between vicarious social and physical pain in ASD on the neural systems level seems particularly valuable, since, to the best of our knowledge, it provides the first neural evidence for long-hypothesized differential strategies in dealing with complex social situations in ASD: while HCs rely on intuitively embodying others' affect, the hippocampal involvement suggests that ASD patients access explicit memory representations of socially appropriate behavior to surpass interoceptive routes.

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SUPPLEMENTARY MATERIALS

Supplementary Methods

Participants

The initial diagnoses dated back to the patients' early childhood or adolescence (mean age at time of diagnosis = 14.76 y, SD = 3.1) and patients had received ASD-specific therapy in the interim time. Notably, one subject was initially examined in a different outpatient clinic so that ADOS scores of the diagnoses were not available for the purpose of this study. The intensity of present ASD symptoms was measured by the AQ [Freitag et al., 2007], and the symptoms of alexithymia were assessed with the TAS-20 [Parker et al., 2003]. As co-morbidities are common in ASD [Lugnegård et al., 2011; Matson and Nebel-Schwalm, 2007; Mazzone et al., 2012], only individuals displaying no psychiatric or neurological comorbidity (e.g., psychotic disorders, epilepsy) were included.

Vicarious Physical Pain

Participants were instructed to attend to the presented pictures and to estimate the strength of pain that the displayed person would feel ("*Please attend carefully to each of the presented pictures. Concentrate on the person in focus, guess his or her reactions to that situation and estimate how strongly the person experiences pain.*"). The stimulus presentation was followed by a blank screen for 1.5 s and a subsequent rating period (button press with the participant's right hand) lasting 3 s. Painful and non-painful images were presented in a pseudo-randomized (no more than two painful or non-painful consecutive stimuli in a row) order, which was the same for each participant.

Vicarious Social Pain

Each drawing was explained with a written vignette that introduced the social context of the situation (e.g. "You are at a lecture:") and the condition of the social target (e.g. "the lecturer forgets his/her lines during the speech…"). For control, neutral scenarios depicting comparable public contexts in the absence of threats to another's social integrity complemented the stimulus set. 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 observer and social target could be assumed; (3) the sex of the social target is counterbalanced; (4) the actors are single persons with two exceptions, where a couple is used instead; (5) no emotional facial expressions such as smiles or gestures of appeasement are present in the sketches. The text was presented in a black sans-serif font on a white background below the drawings. Participants were instructed to watch the scenarios as if they were observing the situations in everyday life and to indicate their vicarious embarrassment experience ("*Imagine that* ***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 by using bold face font ("**you**") and underlining ("the person").

The stimulus presentation (12 s) was followed by a blank screen (1 s) and a subsequent rating period (3 s). Stimuli were presented in a fixed pseudo-randomized order, ensuring that no class of situation was immediately repeated and different situations had equal frequency throughout the entire fMRI time series.

All stimuli were presented on an LCD screen using the Presentation 11.0 software package (Neurobehavioral Systems, Albany, CA, USA, http://www.neurobs.com/). Before entering the fMRI scanner, participants received careful instructions about both experiments using two example situations for each experiment, which were not displayed again during the actual scanning sessions.

Procedure

After providing written informed consent, participants received instructions and practiced the experimental paradigms outside the scanner. Brief instructions were then provided again for each task and potential remaining questions about the procedures were clarified. In a post-scanning experiment, participants rated the SP stimuli presented during the fMRI experiment on three different dimensions in order to verify equal comprehension of the social scenarios during SP in both groups. To this end, all stimuli were presented on a notebook and participants were asked to rate (i) the degree of intentionality of the social target's behavior, (ii) the awareness of the embarrassing potential of the situation and (iii) the current experience of embarrassment in the social target [Krach et al., 2011]. All items were rated on a scale from 1 '*not at all*' to 5 '*very strongly*' with the keyboard of the notebook. Data of these ratings were available for a total of N = 27 (ASD = 16, HC = 11) participants. For each of the three appraisal dimensions, a 5 x 2 repeated measures ANOVA was computed with 5 levels in the repeated factor 'Stimulus' coding the different stimulus classes including the neutral situations (see Krach et al. 2011) and 2 levels for the between-subject factor ‘Group’.

Acquisition and analyses of pupil diameter

The pupil’s response to emotional stimuli is triggered by increased arousal and upregulation of the sympathetic system that innervates the iris dilator, a radial muscle that dilates the pupil [Bradley et al., 2008]. Accordingly, a characteristic pattern of sustained pupil dilation has been observed for viewing negative emotional pictures [Bradley et al., 2008; Janisse, 1974] or listening to emotionally engaging sounds [Partala and Surakka, 2003]. Arousal-related activation within the ACC and the brainstem has also been associated with sustained pupil dilation [Critchley et al., 2005]. Based on the coupling of activity in brain areas that internally code another person’s bodily and social pain experiences with sustained pupil dilation, we suggest that PP- and SP-related arousal on the neural system’s level also manifest in the pupil responses.

Pupil dilation is considered to be a measure of autonomic arousal which provides an additional and directly observable quantitative measure of the temporal pattern of brain reactivity to emotional stimuli [Silk et al., 2007]. Pupil diameter of one eye was continuously recorded during both fMRI paradigms. Periods of blinks were detected by the eye-tracker's built-in algorithm, and subsequently pupil time series were manually inspected for remaining blink-related artifacts. Periods of blinks were interpolated by piecewise cubic interpolation and the pupil trace was subsequently z-normalized over the whole experiment. For the PP paradigm, the slope of the pupil size during each image presentation (4.5 s) was estimated by fitting an optimal least-square linear regression to the pupil trace [Paulus et al., 2015; Stoll et al., 2013]. Due to the substantially increased duration of the stimulus presentation, for the SP paradigm, we computed the trial-specific estimate of the pupil dilation by subtracting the average pupil size until 500 ms after trial onset from the average pupil size between 6,000 ms and 10,000 ms after trial start. Further, repeated measures ANOVAs were conducted with the condition averaged pupil dilation in order to test the condition and group effects and their interactions for each PP and SP.

Supplementary Results

Stimulus comprehension

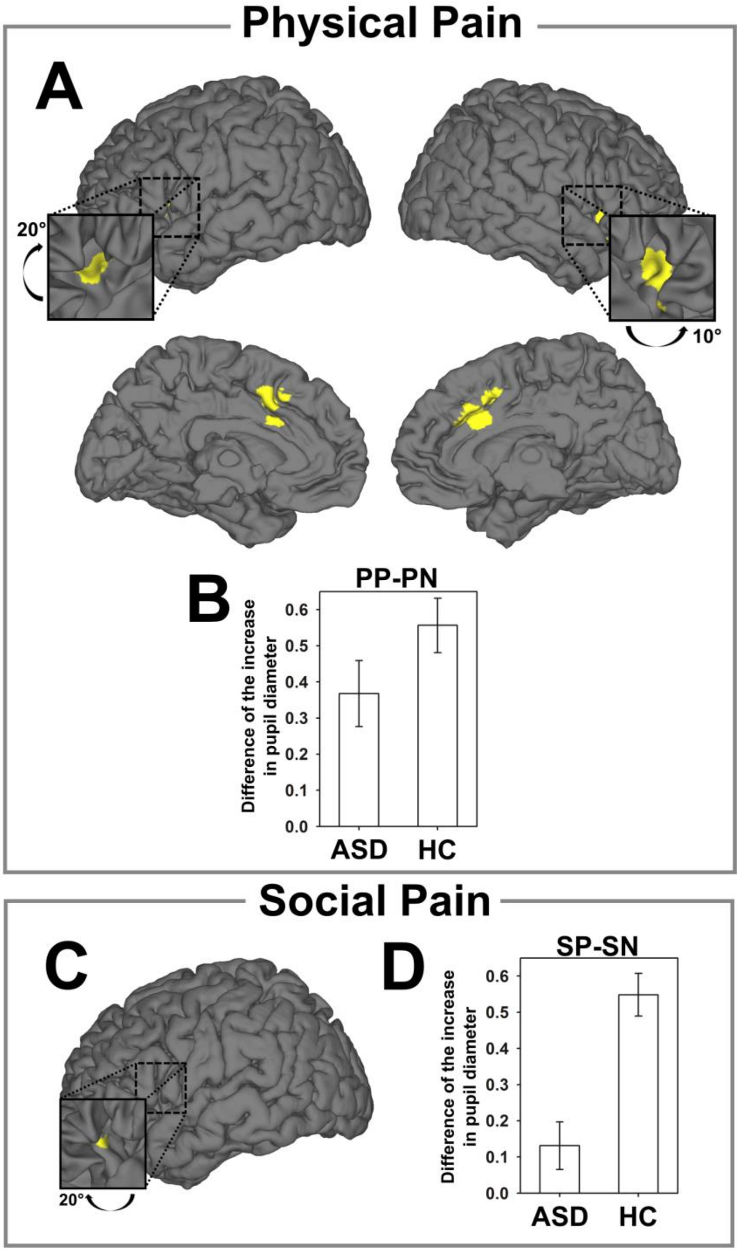
The post-fMRI rating revealed no significant differences in the comprehension of the SP stimuli. The three repeated measures ANOVAs showed significant main effects of Stimulus (Fs(4, 100) > 166.29, ps < .001), indicating significantly different appraisals for the SP conditions and replicating our initial study on vicarious embarrassment (Krach et al. 2011). However, there was no statistically significant main effect of Group (Fs(1, 26) < .69, ps > .414) and no Stimulus x Group interaction even at the trend level (Fs(4,100) < 1.81, ps > .179), suggesting comparable comprehension of the social scenarios presented in the SP paradigm.

Gaze Behavior

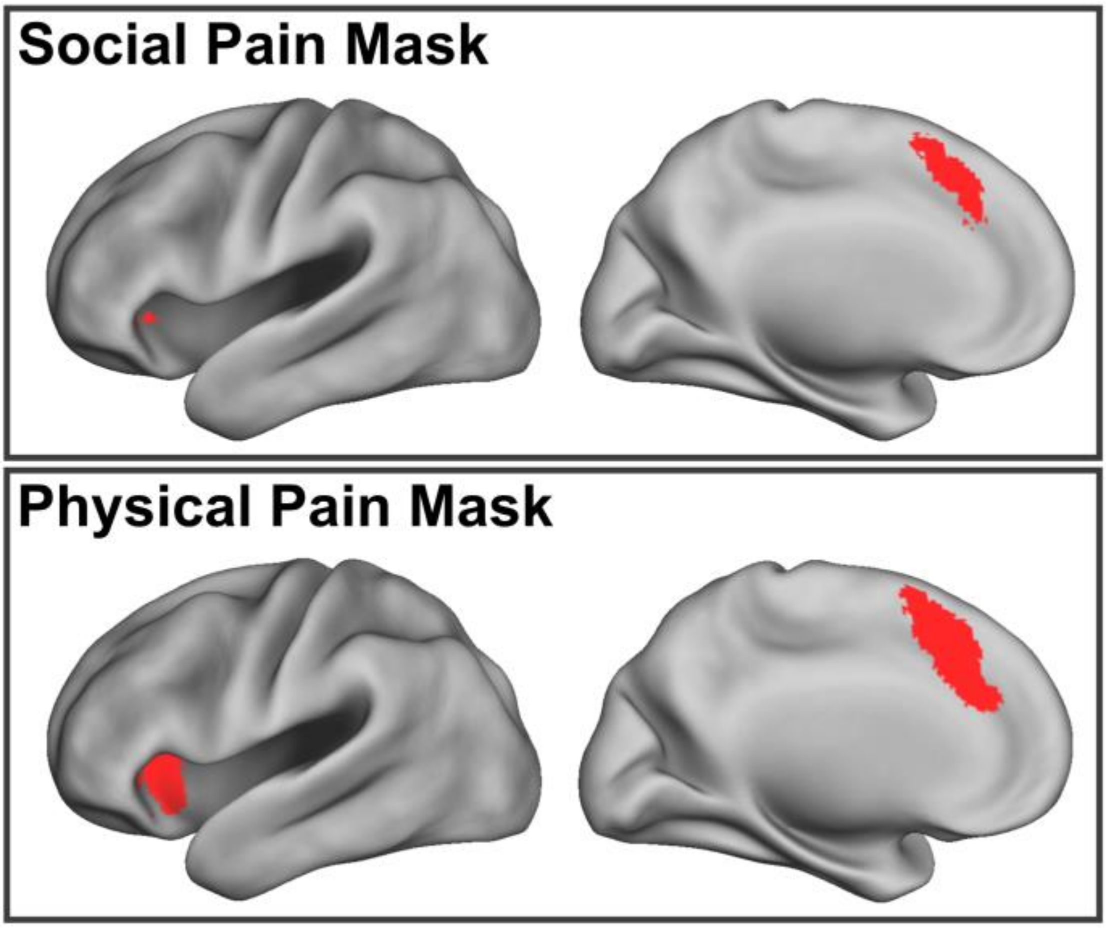
We found no evidence for group differences in gaze behavior during PP. There was a significant effect of Condition on the duration of fixations, which increased during PP compared to PN (PP: mean = 366ms, SD = 76ms; PN: mean = 325ms, SD = 63ms, F(1,20) = 37.19, p < .001) but no significant effect of Group (p=.804) and no Group x Condition interaction (p = .276). Accordingly, the number of fixations was significantly smaller during PP (PP: mean = 8.92, SD = 1.90; PN: mean = 10.26, SD = 1.81, F(1,20) = 56.34, p < .001), group level.

During SP, there was no significant effect of either Condition (p = .559), Group (p = .999) or Condition x Group interaction (p = .852) in the duration of fixations (SP: mean = 286ms, SD = 43ms; SN: mean = 283ms, SD = 47ms). Likewise, the number of fixations (SP: mean = 35.82, SD = 4.86; SN: mean = 36.19, SD = 5.36) during SP did not differ between Groups (p = .707) and Conditions (p = .508) and there was no Condition x Group interaction (p = .956). To rule out that groups used different strategies for understanding the relatively complex social scenarios (i.e. reading the text describing the situation vs. visually scanning and analyzing the depicted scene), we examined the percentage of fixations on the text relative to total amount of fixations for each presented stimulus. We found no evidence for differences between groups in relative fixations on the text; there was a significant effect of Condition (SP: mean = 51.5%, SD = 7.6%; SN: mean = 48.7%, SD = 8.9%, F(1,20) = 5.35, p = .032), but no effect of Group (p = .557) and no Condition x Group interaction (p = .355).

Supplementary Figures



Supplemental Figure 1. Pupil dilation and association with hemodynamic responses during vicarious physical pain (PP) and vicarious social pain (SP). **A.** Brain areas where the hemodynamic signal was positively associated with the pupil dilation during vicarious physical pain (PP/PN) task across healthy controls (HC) and patients with autism spectrum disorder (ASD). The average effect of the parametric weights of the pupil dilation during PP/PN was family-wise error (FWE)-corrected at the cluster level for whole brain analyses at p<.05. **B.** Difference of the increase in pupil diameter during the presentation of PP versus PN stimuli in HC and ASD. Bars represent the mean for each group and are plotted together with the standard error. **C.** Brain areas where the hemodynamic signal was positively associated with the pupil dilation during vicarious social pain (SP/SN) task across HC and ASD. The average effect of the parametric weights of the pupil dilation during SP and SN was FWE-corrected in the anterior insula region of interest (ROI) which was derived from an independent sample on SP [Krach et al., 2011]. **D.** Difference of the increase in pupil diameter during the presentation of SP versus SN stimuli in HC and ASD. Bars represent the mean for each group and are plotted together with the standard error.



Supplemental Figure 2. Vicarious social and physical pain activations from previous studies. Upper part: Neural activation of the anterior cingulate cortex (ACC) and the anterior insula (AI) during vicarious embarrassment [Krach et al., 2011]; Lower part: Neural activation of the ACC and AI during vicarious physical pain [Paulus et al., 2015].

Supplementary References

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CHAPTER 7

DISCUSSION

CHAPTER 7

This thesis summarizes five studies on the social emotion of embarrassment and its vicarious form. The aim of these studies was to further our understanding of the neurobiological foundations of these emotions and of the neural networks involved.

7.1. VICARIOUS EMBARRASSMENT

In **chapter 3** we could show that vicarious embarrassment was associated with a specific physiological response pattern of increased autonomic arousal, particularly in situations in which the social target was aware about the violation of others' expectations. We did also find unique physiological indicators for vicarious embarrassment (prolonged P–Q time, increased S–T elevation and T–wave amplitude) differentiating the response pattern from other emotions eliciting a pattern of sympathetic activation like anger (Stemmler et al., 2001). We typically try to avoid norm deviating behavior that is dissonant with the expectations of the social environment (Miller, 1996). The observer might simulate the dissonance of the social target's situation being aware about the ongoing norm violation and this might induce stronger responses of autonomic arousal in the observer. During situations in which the social target intentionally disobeyed the observers' normative standards participants experienced anger in addition to vicarious embarrassment. Increased physiological responses could therefore be explained by the shared embarrassment during accidental norm violations but partially also by the experienced anger in addition to vicarious embarrassment, when the social target violates others' expectations on purpose. These findings illustrate that vicarious embarrassment and possibly also embarrassment-induced physiological responses are complex and can be differentiated from those of other emotions. They are also context dependent, and need to be assessed within a comprehensive set of response variables. Only this will help to find subtle differences and effects of situational appraisals.

In **chapter 4**, **chapter 5**, and **chapter 6** we could show that on the neural systems level these physiological changes of vicarious embarrassment go along with constant activations of the arousal network independent of the social target's affective state, which is thought to contribute to the conscious experience of vicarious embarrassment. The activations within the mentalizing network at the same time could map how the observer tries to make sense of the social target's state of mind and thinks about the evaluations of the deviant behavior in-the-eyes-of-others. **Chapter 4** showed that there was a specific activation of the pSTS region and increased functional integration of pSTS with parts of the arousal network during shared embarrassment compared to vicarious embarrassment. The pSTS is a region sensitive to multimodal social stimuli and involved in processing of bodily and facial expressions (Puce & Perrett, 2003; Zaki et al., 2010). Bodily and facial movements as well as eye-gaze behavior possibly contain an emotional connotation when the social target experiences embarrassment him- or herself (Keltner, 1995). Hence, the increased activation and functional connectivity of the pSTS might indicate that observers more strongly rely on this kind of emotional information during shared embarrassment. These results therefore might support the assumption of enhanced mirroring of affective information in shared embarrassment.

7.1.1. Vicarious embarrassment for close others

Chapter 5 replicated the findings of **chapter 4** showing an involvement of the mentalizing network and AI and ACC during vicarious embarrassment. Additionally, we found that social closeness with the observed target enhanced the activations within the “shared circuits” of the AI and ACC. Observing a friend compared to a stranger additionally elicited increased activations of the precuneus independent of the type of situation. Due to the role of the precuneus in self-referential processing (Cavanna & Trimble, 2006; Mazzola et al., 2010; Northoff et al., 2006), this activation could represent increased concerns about the own social image while observing a close other (Chekroun & Nugier, 2011; Fortune & Newby-Clark, 2008). Functional connectivity analyses of the precuneus showed increased functional coupling with the ACC when observing a friend compared to a stranger. When people interact with close others they are more strongly involved themselves. The increased integration of information between both networks could reveal a mechanism that explains how self-related information from the precuneus can be integrated in the respective situations. Similarly, the precuneus might map self-related thoughts during embarrassment from the first person perspective in **chapter 2**. Embarrassment from the first person perspective involves self-reflection or concerns about the evaluation of one’s behavior in-the-eyes-of-others. The precuneus activation could therefore map the component of self-relevance of the situation during the experience of own embarrassment as well. In contrast, earlier studies revealed that precuneus activation was associated with mentalizing about another person’s mental state that does not need to be related to the self (Lombardo et al., 2010). Since both, the experience of embarrassment and vicarious embarrassment for a close other involve mentalizing processes as well, the question of whether precuneus activation is rather related to self-referential processing or mentalizing in general is therefore a very interesting endeavor for future studies (see **Future research 1**). However, increased functional integration of information between the mentalizing and arousal processing networks underline the importance of both in processing of vicarious embarrassment for a close other.

Future research 1

An interesting endeavor for future studies would be to investigate the role of the precuneus during embarrassment and vicarious embarrassment. Assessing appraisal processes in greater detail will clarify the precuneus' role in mentalizing in general and processing of self-referential thoughts specifically.

7.1.2. Interoceptive representations of vicarious embarrassment in autism spectrum disorder

In **chapter 6** individuals with ASD seemed to show no impairments in sharing another person's bodily pain and interoceptive processing associated with bodily pain. This supports the assumption that there are no domain-general deficiencies in interoceptive representations in ASD. Likewise, when contextual demands were increased and individuals with ASD were asked to evaluate their affective experience during vicariously embarrassing situations they showed no deficits. However, there were clear differences to healthy subjects on all neurobiological parameters. In response to vicarious embarrassment healthy subjects showed greater pupil dilation and greater activations within the AI and ACC than individuals with ASD. This supports the notion of specific deficiencies in interoceptive representations in ASD when contextual demands gain complexity. While in healthy subjects variability in vicarious embarrassment self-reports was associated with activations of the AI and ACC, the associations of activation and self-report were reduced in the ASD. In contrast, individuals with ASD showed a greater correspondence of vicarious embarrassment self-reports with activity of the hippocampus, which is associated with memory processes (Squire & Zola-Morgan, 1991; Squire, 1992). These results indicate that healthy subjects are able to rely on their interoceptive representations when evaluating their experience of shared emotions. Individuals with ASD might not be able to rely on these markers in the same way. Instead they might recruit compensatory strategies involving retrieval of learned norms and social rules from memory (Baron-Cohen et al., 2003; Klin et al., 2003) when evaluating emotional experiences. The data also indicate that in individuals with ASD behavioral responses dissociate from the embodied representations of other's affect. Previous studies could show that individuals with ASD give correct verbal reports in theory-of-mind tasks but do not adapt their behavior accordingly (Abell, Happé, & Frith, 2000; Castelli, 2002). In line with this the present results support the assumption that verbal responses are not sufficient to characterize deficiencies in intuitively representing another person's state. Overall, the results indicate that there are deficiencies in interoceptive processing in ASD that are specific to the context of complex social situations. This can help to explain ASD specific difficulties during situations involving social interactions that have an inherent complexity. Social paradigms including more complex situations might therefore be an appropriate way to investigate deficits in ASD (see also **Future research 2**).

Future research 2

Individuals with ASD less frequently refer to an audience when describing embarrassment (Capps, Yirmiyat, & Sigmant, 1992). Hence, the procedure described in **chapter 2** in which a private and a public context are distinguished can offer a novel way to assess if and how affected individuals rely on public feedback during complex social situations by directing their attention towards the audience.

7.2. EMBARRASSMENT

In **chapter 2** we were able to induce a genuine experience of embarrassment in the first person. Making participants fail by presenting low feedback on their estimation performance induced activations of the arousal network and activations within the mentalizing network were increased during public feedback. The positive correlation of pupil diameter and AI activation across all conditions thereby underlined the AIs role in arousal processing. The construct of embarrassment as a unique combination of arousal related to one's failures and mentalizing related to how these failure could damage other's opinions of oneself, was well reflected in the activation data. However, in line with the constructivist understanding of how the brain processes emotions (Lindquist et al., 2012) there were no voxels showing an embarrassment specific response. Instead, **chapter 2** revealed increased functional integration of both, the mentalizing and arousal processing networks, with (para-)limbic, emotion-coding systems during embarrassment compared to the positive social emotion of pride. Embarrassment is supposed to be the unique combination of one's failure related to physiological and affective arousal and mentalizing about how this failure is evaluated in-the-eyes-of-others (Miller, 1996; Tangney et al., 2007). This is reflected in the converging integration of information from mentalizing areas and arousal processing systems possibly forming the neural pathways of embarrassment. Participants that experienced stronger embarrassment also paid increased attention to the audience during public feedback, as indicated by a positive correlation with gaze dwell time on the face stimuli. Additionally precuneus activation increased along with the experience of embarrassment between subjects. The results therefore validate that attention towards and thoughts about others' evaluations as well as activation of the mentalizing network seem to be an important component of embarrassment.

Current models describe embarrassment as a response to public failure (Miller, 1996). In **chapter 2** participants also experienced embarrassment during private failures, possibly because they were unable to withdraw from the public setting of the whole study. Nevertheless, the experience of embarrassment, along with arousal related increases in pupil diameter, was stronger when failures were made public. The dynamic increase of connectivity of the mentalizing network with (para-)limbic regions during low feedback shows that information processed in the mentalizing network gains particular relevance in the context of failure. This might explain the publicity related increase in the experience of embarrassment when increased mentalizing activation potentially is integrated with information of arousal in response to public failure. During achievements publicity did not influence the experience of pride in the same way (see also Seidner, Stipek, & Feshbach, 1988), which is in line with the decreased integration of mentalizing and arousal-related information in (para-)limbic regions.

7.2.1. The role of the insula cortex in embarrassment

When experiencing embarrassment the vAI might have a key role as a hub-region integrating information from separated brain networks to generate the global feeling state of embarrassment. There is accumulating evidence on the role of the vAI in emotion processing (Chang et al., 2013; Kelly et al., 2012) and the AI's "hub"-role in different functional networks (Craig, 2009), making it suitable to integrate information of affect with context information (Engen & Singer, 2012). Ventral and dorsal aspects of the AI and the amygdala are densely anatomically connected (Cerliani et al., 2012; Mesulam & Mufson, 1982) and this could constitute the structural underpinning of the functional coupling of mentalizing and arousal processing regions with the vAI. In **chapter 2** we might have been able to specify the vAI's role in the context of embarrassment by revealing its integrative functioning.

The AI's role as a neural substrate that may translate bodily states into feelings is also supported by studies showing that awareness of one's own heart beat is associated with increased activation of the insula (Critchley, 2009). Activity within the AI may therefore be associated with emotion-specific autonomic response patterns measured within and between bodily organs (Critchley, 2009). The positive association of arousal related pupil diameter and activation of the AI during embarrassment supports this notion. Emotion-specific physiological response patterns generate physiological preparedness of the body. They are assumed to shape the adaptive modulation of particular behaviors while cognitive and emotional processes are linked via the insula cortex (Critchley, 2009; Engen & Singer, 2012; Keltner, 1995). The anatomical substrate for this could lie in the AIs anatomical connections with networks associated with decision-making including areas implicated in response selection such as orbitofrontal cortex, nucleus accumbens, ACC, and dorsolateral prefrontal cortex (Singer, Critchley, & Preuschoff, 2009). Ideas for future research on the role of the insula cortex in embodiment are presented in **Future research 3**.

Future research 3

Future studies will be needed to shed further light onto the role of the insula cortex in embodiment and emotion processing. Identifying common and specific underlying processes induced by a specific task might help differentiating emotion- and task-specific activation patterns within sub-regions of the AI. One idea would be to simultaneously assess well-characterized somatovisceral response patterns and neural activation data.

Interactive settings like the one implemented in **chapter 2** can also allow investigating specific appeasement gestures for one's own mishaps and helping behavior triggered when observing other's mishaps. This will shed light onto the role of specific somatovisceral and neural response patterns in the preparation and modulation of these behaviors.

7.2.2. A constructivist understanding of emotions

In the constructivist understanding complex functions like an emotion are constructed psychologically by basic psychological operations. This suggests that a given brain region can perform multiple functions depending on the areas with which it interacts (Price & Friston, 2005). In line with this we did not find emotion-specificity on the voxel level of activation but on the level of functional integration of mentalizing areas and arousal processing areas with vAI and amygdala. It might thus be that the uniqueness of embarrassment triggered by public failure derives not from the activation of a specific part of the cortex, but from the unique pattern of integration of activation across these regions. Of course, finding overlapping activation patterns across emotions and no specific activations for embarrassment does not exclude alternate explanations. FMRI is generally considered to have a high spatial resolution for a non-invasive imaging technique. However, its spatial resolution limits the analysis of the neural systems architecture to a macroscopic scale (Sporns, 2011). Specificity of neural activations may be driven by fine-grained differences in activation patterns in regions activated by separate conditions, like activations of distinct neuronal populations within the same regions. Methods like multivariate pattern analysis (MVPA) are more sensitive than univariate analyses and might be able to detect such fine-grained differences even in the spatial patterns of fMRI activity, as studies on physical pain could show (see Iannetti et al., 2013). Emotion-specificity might also be evident at a more refined level of spatial and temporal analysis, when using other methods, e.g. single cell recording (see Lindquist et al., 2012).

7.2.3. Effects of publicity in social anxiety

Finally, the distinction between a private and a public context is an essential part of the emotion of embarrassment and also manifests itself in the context of social anxiety where excessive and persistent concerns about the evaluations of others are central to the symptomatology (Morrison & Heimberg, 2013; Schneier, 1992). However, most studies investigated social anxiety in social isolation (Etkin & Wager, 2007). In **chapter 2** we found a positive correlation of activation of the mPFC and the FFA during publicity with trait level social anxiety scores. These associations were mediated by gaze dwell time on the pictures of the confederates' faces during public feedback. This finding corroborates the clinical characterization of social anxiety as being related to maladaptive concerns about being evaluated by others and attentional shifts towards potentially threatening social cues in the environment (Morrison & Heimberg, 2013). The paradigm presented in **chapter 2** could therefore offer a novel perspective to an understanding of the etiology of social anxiety disorders. It might help characterizing the altered processing of publicity in these disorders in a dynamic and interactive setting and contribute to our understanding of the etiology of social anxiety disorder (for further perspectives and fields of application see **Future research 4**).

Future research 4

With the social immersion paradigm presented in **chapter 2** a genuine experience of the social emotion embarrassment was elicited in the MRI for the first time. The paradigm therefore offers a reasonable starting point for future studies.

In this study setting embarrassment and its vicarious form can be elicited within the same participants. When embarrassment and empathic embarrassment are compared directly, activations of “shared circuits” and distinctive neural networks may give insights into the role of mirroring and mentalizing processes.

Anchoring and adjustment processes during vicarious embarrassment can be investigated in more detail by the use of this paradigm. Therefore the discrepancy between the observer’s perspective and the social target’s perspective needs to be assessed and gradually manipulated.

Future studies could also be interested in social emotions like guilt. Guilt is common in everyday life but eliciting it in a restricted setting is challenging like it is for other social emotions. Literature on the neural foundations of guilt is therefore sparse. The presented social immersion paradigm could easily be adapted to elicit guilt in the participants by implementing shared goals with other participants and responsibility for collective punishments (see Cui, Abdelgabar, Keysers, & Gazzola, 2015).

Another field of application is the school context where the public failure is related to children’s test anxiety which affects school performance (Cassady & Johnson, 2002). Using the cognitive estimation task in a social context constitutes a performance situation similar to children’s daily experience at school and allows investigating the interaction of test anxiety and performance on the neural systems level.

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