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## Q1 Neural pathways of embarrassment and their modulation by 2 social anxiety

Q2 L. Müller-Pinzler<sup>a,b</sup>, V. Gazzola<sup>c,d</sup>, C. Keysers<sup>d</sup>, J. Sommer<sup>e</sup>, A. Jansen<sup>e</sup>, S. Frässle<sup>b,e</sup>, W. Einhäuser<sup>f</sup>,  
4 F.M. Paulus<sup>a,b,1</sup>, S. Krach<sup>a,b,\*,1</sup>

5 <sup>a</sup> Department of Psychiatry and Psychotherapy, Social Neuroscience Lab, University of Lübeck, Ratzeburger Allee 160, D-23538 Lübeck, Germany

6 <sup>b</sup> Department of Child and Adolescent Psychiatry, University of Marburg, Schützenstr. 49, D-35033 Marburg, Germany

7 <sup>c</sup> Department of Neuroscience, University Medical Center Groningen, 9713 AW Groningen, The Netherlands

8 <sup>d</sup> Social Brain Laboratory, The Netherlands Institute for Neuroscience, Royal Netherlands Academy for the Arts and Sciences, 1105 BA Amsterdam, The Netherlands

9 <sup>e</sup> Department of Psychiatry, University of Marburg, Rudolf-Bultmann-Straße 8, D-35033 Marburg, Germany

10 <sup>f</sup> Department of Neurophysics, University of Marburg, Karl-von-Frisch-Straße 8a, D-35043 Marburg, Germany

### 1 1 A R T I C L E I N F O

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### A B S T R A C T

While being in the center of attention and exposed to other's evaluations humans are prone to experience 23  
embarrassment. To characterize the neural underpinnings of such aversive moments, we induced genuine 24  
experiences of embarrassment during person–group interactions in a functional neuroimaging study. Using a 25  
mock-up scenario with three confederates, we examined how the presence of an audience affected physiological 26  
and neural responses and the reported emotional experiences of failures and achievements. The results indicated 27  
that publicity induced activations in mentalizing areas and failures led to activations in arousal processing 28  
systems. Mentalizing activity as well as attention towards the audience were increased in socially anxious partic- 29  
ipants. The converging integration of information from mentalizing areas and arousal processing systems within 30  
the ventral anterior insula and amygdala forms the neural pathways of embarrassment. Targeting these neural 31  
markers of embarrassment in the (para-)limbic system provides new perspectives for developing treatment 32  
strategies for social anxiety disorders. 33

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### 39 Introduction

40 Since the time of the ancient philosophers (Aristotle; 384–322 B.C.), 56  
41 the distinction between a “public” and a “private” realm has been a 57  
42 central tenet of political theory (Arendt, 1958; Sennett, 1974), jurispru- 58  
43 dence (Warren and Brandeis, 1890), and the social sciences (Weintraub, 60  
44 1997). The presence of others in the public space deeply affects human 61  
45 psychology and the emotional consequences of one's actions (Gilovich 62  
46 et al., 2000). One of humankind's most common fears centers around 63  
47 failing to uphold one's public image within social encounters (Leary 64  
48 and Kowalski, 1995). The expected negative evaluation ‘in the eyes of 65  
49 others’ (Tangney et al., 2007) during ‘public deficiencies’ is the main 66  
50 cause of embarrassment (Miller, 1996). Mental-state attribution is 67  
51 therefore the lynchpin of the emotion of embarrassment, which regu- 68  
52 lates so many aspects of interpersonal behavior (Tangney et al., 2007) 69  
53 whenever others might potentially act as an audience, be it at school, 70  
54 work or during leisure time (Miller, 1996).

Excessive and persistent concerns about the evaluations of others 55  
are a hallmark of social anxiety. While everybody experiences mild 56  
forms of social anxiety occasionally (Leary and Kowalski, 1995), social 57  
anxiety disorders are a major burden for society (Kessler et al., 2005), 58  
and in affected individuals, the fear of embarrassment can even lead 59  
to social withdrawal and depression (Schneier, 1992). The neurobiology 60  
of how humans process situations that trigger their embarrassment, and 61  
how this contributes to social anxiety disorders, remains largely un- 62  
known, but would provide a key to understanding the neurobiological 63  
mechanisms of social anxieties. 64

The traditional ‘spectator approach’ in social neuroscience involves 65  
measuring the brain activity of participants in isolation while they are 66  
viewing photographs or movies of actors, or vignettes of fictional social 67  
situations. In these paradigms, the participant cannot interact with the 68  
targets of his/her social cognition, and his/her social reputation is not 69  
at stake. In typical social interactions, however, we not only perceive 70  
what others do, but we also need to (a) react in ways which are appro- 71  
priate to others' actions, and (b) maintain our social reputation while 72  
we are the focus of other people's evaluation. The traditional ‘spectator 73  
approach’ fails to capture the motor involvement and emotional signif- 74  
icance associated with these two aspects of our social world (Hasson 75  
et al., 2012; Schilbach et al., 2013). For instance, single cell recordings 76

\* Corresponding author at: University of Lübeck, Department of Psychiatry and  
Psychotherapy, Social Neuroscience Lab, Ratzeburger Allee 160, 23538 Lübeck, Germany.

E-mail address: [krach@snl.uni-luebeck.de](mailto:krach@snl.uni-luebeck.de) (S. Krach).

<sup>1</sup> These authors contributed equally to this work.

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., 2009, 2011).

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, has 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., n.d.), 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 systems, 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, Materials 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).

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