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Effects of empathic social responses on the emotions of the recipient

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ABSTRACT

Empathy is highly relevant for social behavior and can be verbally expressed by voicing sympathy and concern (emotional empathy) as well as by paraphrasing or stating that one can mentally reconstruct and understand another person's thoughts and feelings (cognitive empathy). In this study, we investigated the emotional effects and neural correlates of receiving empathic social responses after negative performance feedback and compared the effects of emotionally vs. cognitively empathic comments. 20 participants (10 male) underwent functional magnetic resonance imaging while receiving negative performance feedback for a cognitive task. Performance feedback was followed by verbal comments either expressing cognitive and emotional empathy or demonstrating a lack of empathy. Empathic comments in general led to less negative self-reported feelings and calmer breathing. At the neural level, empathic comments induced activity in regions associated with social cognition and emotion processing, specifically in right postcentral gyrus and left cerebellum (cognitively empathic comments), right precentral gyrus, the opercular part of left inferior frontal gyrus, and left middle temporal gyrus (emotionally empathic comments), as well as the orbital part of the left middle frontal gyrus and left superior parietal gyrus (emotionally empathic vs. unempathic comments). The study shows that cognitively and emotionally empathic comments appear to be processed in partially separable neural systems. Furthermore, confirming and expanding on another study on the same subject, the present results demonstrate that the social display of cognitive empathy exerts almost as positive effects on the recipient's feelings and emotions in states of distress as emotionally empathic response does. This can be relevant for professional settings in which strong negative emotions need to be de-escalated while maintaining professional impartiality, which may allow the display of cognitive but not emotional empathy.

1. Introduction

Showing empathy is a highly relevant social interaction pattern, and yet it is one that has almost exclusively been studied with a focus on the sender (i.e. the person feeling empathy for someone else), neglecting the effects on the recipient. What are the effects of empathic social responses on the emotions of the recipient of such responses, and do cognitively and emotionally empathic social responses exert the same effects on the recipient? This important aspect of social interaction has been almost completely neglected in social neuroscience research to date. The present study addresses this gap by exploring emotional effects and neural substrates of processing empathic comments offered by another person in response to an unpleasant situation.

Empathy has been studied from many different angles and under varying definitions, with a commonly accepted definition of empathy still wanting (Bernhardt & Singer, 2012). In the neuropsychological research literature, empathy is most often conceptualized as a complex and composite construct involving several, partially dissociable neuro-cognitive systems with 3 domains: cognitive empathy, emotional empathy, and motor empathy (Blair, 2005; Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Decety & Meyer, 2008). Cognitive empathy, also called theory of mind (ToM) or mentalizing, means the ability to recognize another

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person's mental and emotional state as well as behavioral dispositions by abstract inference. Emotional or affective empathy refers to an observer's emotional response to another person's emotional state (Dziobek et al., 2008). It has been argued that the term empathy presupposes an emotional reaction that is isomorphic to another person's affective state (Vignemont & Singer, 2006), while others define it more broadly as an affective response more appropriate to another's situation than one's own (Hoffman, 2000). Motor empathy is the tendency to automatically mimic and synchronize facial expressions, vocalizations, postures, and movements with those of another person (Blair, 2005). An integrative multidimensional model of empathy has been proposed by Decety (2011), Decety and Jackson (2004) and Decety and Meyer (2008).

Empathy can be verbally expressed by voicing emotional resonance to another's distress (emotional empathy) as well as by paraphrasing or stating that one can mentally reconstruct and understand another person's thoughts and feelings (cognitive empathy). Expressing cognitive empathy through paraphrasing is regularly used in professional counseling settings such as Alternative Dispute Resolution (ADR; Kraybill, Evans, & Evans, 2001; Schreier, 2002). Daily interactions, on the other hand, most often contain verbal demonstrations of emotional empathy. However, we argue that in daily life, this typically expresses itself in verbally offering compassion, sympathy, and concern, rather than an isomorphic reflection of the other person's feelings and emotions (typical responses to another's distress may be "I'm sorry this happened to you" rather than "If you are sad, I am sad, too"). Therefore, and as we were interested in investigating empathic social response close to daily life, we shaped our emotional empathy interventions more toward expressing compassion than isomorphic emotional reactions. It is important to note, however, that emotional empathy and compassion have been associated with different emotional effects and neural activations in the sender (Klimecki, Leiberg, Ricard, & Singer, 2014), and can therefore not be used as interchangeable terms.

To date, very little research has been dedicated to investigating the emotional effects and neuroanatomical basis of processing these social responses and professional interventions expressing empathy. As a starting point, we have been able to show that cognitively empathic social response in the form of paraphrasing can positively influence the recipient's feelings and emotions in social conflict situations (Seehausen, Kazzer, Bajbouj, & Prehn, 2012; Seehausen et al., 2014). In Seehausen et al. (2014), we interviewed participants on a real-life personal conflict and contrasted emotional effects and neural correlates of cognitively empathic vs. unempathic social responses. We found that cognitively empathic social response in the form of paraphrasing positively influenced self-reported feelings, while at the same time increasing autonomic arousal reflected by skin conductance response (SCR). In a similar vein, feeling understood has also been shown to activate neural regions associated with reward and social connection (i.e. ventral striatum and middle insula), while not feeling understood engaged neural regions previously associated with negative affect (i.e. anterior insula) (Morelli, Torre, & Eisenberger, 2014)., Finally, motor empathy in the form of facial mimicry has been repeatedly found to increase affiliation and positive social judgment not only toward the mimicker but also toward other people (Van Baaren, Holland, Kawakami, & Van Knippenberg, 2004; Ashton-James, van Baaren, Chartrand, Decety, & Karremans, 2007; Fischer-Lokou, Martin, Guéguen, & Lamy, 2011; Guéguen, Martin, & Meineri, 2011; Stel & Harinck, 2011). Hence, it seems that empathic social response displaying different types of empathy can have an effect on the recipient's feelings and emotions. The present study directly compared the effects of verbally expressed cognitive and emotional empathy/compassion on the recipient, exploring potential differences in processing these two types of empathic social response at the neural level as well as differences in emotional effects on the recipient.

In general, the processing of empathic and unempathic social response is likely to recruit neural systems involved in social cognition, as the listener tries to decipher the speaker's intention and sincerity, as well as meaning and social adequacy of the utterances. Social cognition is characterized as the acquisition of knowledge about other persons' mental states as well as insight about the meaning of their behavior and verbal expressions (Przyrembel, Smallwood, Pauen, & Singer, 2012). Social cognition research approaches most often focus on the role of the mentalizing network, as well as of shared networks and the putative mirror neuron network (Bernhardt & Singer, 2012; Zaki, Weber, Bolger, & Ochsner, 2009). However, in the absence of visual stimuli, i.e. faces or body movements, subjects seem to rely mostly on the mentalizing system when making inferences about another's inner state (Lamm, Decety, & Singer, 2011).

The present study addressed the following research questions: (1) what are the effects of empathic social response on the feelings and emotions of the recipient during negative performance feedback? (2) How are empathic comments processed at the neural level? (3) How does the processing of emotionally and cognitively empathic comments differ regarding neural substrates and emotional effects?

To answer these questions, cognitively and emotionally empathic and unempathic comments were offered to study participants while they were trying to solve anagrams, and kept receiving negative performance feedback combined with financial loss. This was chosen as the context for empathic social response for three reasons. Firstly, goal failure in this form is relatively easy to create in an experimental setting. Secondly, goal failure has been shown to induce negative affect (Jones, Papadakis, Orr, & Strauman, 2013). And thirdly, failure is a common experience in everyday life, one that often elicits seeking and receiving empathic social support.

Neural data were complemented by self-report ratings of positive or negative feelings, as well as measurements of skin conductance (SCR), pulse, heart rate, and respiration data. These physiological parameters have repeatedly been shown to reflect emotional responses (Critchley, 2002; Kushki, Fairley, Merja, King, & Chau, 2011).

Due to a lack of comparable previous research, the present study was largely exploratory. Negative performance feedback was expected to result in activations in anterior insula and amygdala, as these are core regions of emotion generation and processing (Kober et al., 2008; Ochsner, Silvers, & Buhle, 2012). On a subjective experience level, we predicted less negative feelings following empathic compared to unempathic comments for both types of empathy. We have shown previously that negative feelings can be alleviated by empathic social response in the form of paraphrasing (expressing cognitive empathy) (Seehausen et al., 2012, 2014). We further hypothesized that hearing empathic comments would activate neural networks associated with social cognition, especially the mentalizing network. This is in line with findings from Morelli et al. (2014), who reported that both feeling understood and not feeling understood activated different components of the mentalizing system in their paradigm. Meta-analyses have shown a mentalizing network comprising bilateral ventromedial and dorso-medial prefrontal cortex, precuneus, temporoparietal junction, temporal poles, middle temporal gyrus, posterior superior temporal sulcus, and inferior frontal gyrus, as well as the right MT/V5 (Bzdok et al., 2012; Mar, 2011; Spreng, Mar, & Kim, 2009). In addition, empathic and unempathic comments were expected to stimulate regions associated with emotion generation and processing, involving amygdala, anterior insula, medial orbitofrontal cortex (mOFC) and striatum (Becker, Gandhi, & Schweinhardt, 2012; Ochsner et al., 2012). Furthermore, we expected cognitively empathic comments and emotionally empathic comments to be processed by partially different neural systems. Cognitive and emotional empathy have been shown to involve partially separate neural systems at the experiential level (Fan, Duncan, de Greck, & Northoff, 2011), hence it seems expedient to regard them as non-identical psychological processes that also trigger partially different stimulus processing in the recipient. It also seems likely that social responses such as "I understand why you are angry right now" provoke different emotional reactions from responses such as "I am sorry it is not going well for you", as these convey different messages about the social relationship in question.

2. Material and methods

2.1. Participants

20 healthy subjects [10 male; age: mean (M) = 26, standard deviation (SD) = 5.0] participated in this study. All participants were native German speakers, right-handed as assessed using the Edinburgh Handedness Inventory (Oldfield, 1971), and had no current or previous neurological or psychiatric disorder.

The study was carried out in accordance with the Declaration of Helsinki and was approved by the ethical committee of the Charité Universitätsmedizin Berlin. All participants gave written informed consent prior to investigation and received payment for participation.

2.2. Task and stimulus material

To elicit negative emotions in participants, we developed an experimental paradigm deploying a demanding cognitive task (solving anagrams) combined with negative feedback regarding participants' performance, by default given in two thirds of the trials ("That was bad"). In each trial in which participants were given negative feedback, they were informed that they had lost five cents of their study compensation. This was done to enhance negative emotional impact. In addition, a high-level baseline condition with positive feedback ("That was good") instead of negative feedback was included, where participants gained five cents per trial. The negative feedback was followed by either empathic or unempathic interventions. The high-level baseline condition featured empathic interventions only. Half of all interventions featured cognitive and half deployed emotional empathy/non-empathy, resulting in a 2×2 experimental design plus high level baseline. The factor "empathy", refers to empathic/unempathic interventions, the factor "empathy type", means cognitive/emotional empathy. Hence, four types of interventions were given: Cognitive Empathic (CE), Cognitive Unempathic (CN), Emotional Empathic (EE), Emotional Unempathic (EN). Examples[1] for the different types of interventions are: Cognitive Empathic (CE): "I can really understand how you are feeling now." Cognitive Unempathic (CN): "I don't understand what you are feeling right now." Emotional Empathic (EE): "Your feelings in this situation really touch me." Emotional Unempathic (EN): "I don't care what you are feeling right now." Correspondingly, in the high-level baseline condition half of the empathic comments were aligned with cognitive empathy ("I can understand that you are happy now.") and half were geared to emotional empathy ("It makes me happy to see you succeed in this."). This design allowed us to compare the effects of empathic responses with unempathic responses, as well as with a baseline where no negative feelings and emotions were experienced by participants, thus, empathic social support presumably being perceived as less emotionally relevant. Hence, we investigated two different psychological processes: Firstly, the reaction to empathic vs. unempathic social response when in a situation of emotional distress, and secondly, the reaction to empathic social response when in emotional distress vs. when feeling all right. These contrasts were split up into cognitive and emotional empathy and complemented by a direct comparison of CE and EE to differentiate between different types of empathic social response.

For the cognitive task, an anagram pool was generated using the freeware anagram generator Wordpool (http://www.wordpool-home.de). The anagrams were then manually supplemented by alternative wrong solutions similar to the correct solutions (Anagram example[2]: WINTERCOAT. Correct solution: ANTIC TOWER, wrong solution: ANTIQUE TOWER).

We designed 108 empathic and unempathic interventions (18 per experimental condition). The final intervention pool was rated by seven experts (psychologists) regarding the differentiation between cognitive and emotional empathy. The differentiation succeeded with an inter-rater consistency of 92.3%.

The interventions were audio-taped and presented acoustically as well as visually. All interventions were recorded by one female and one male speaker. Each participant was given half of the interventions by a male speaker, and half by a female speaker, with the order of who they heard first being alternated over participants.

2.3. Experimental procedure

Participants were presented with the anagram task and had to choose the correct solution in a maximal time frame of 6 s. Each trial consisted of the anagram task, followed by negative or positive feedback, followed by an intervention, and concluded by a rating phase during which participants rated their present feelings on a scale from -4 to 4 (see Fig. 1). In total, the experiment comprised 108 trials presented in randomized order over two separate runs, with a jittered event-related design and a trial duration of 23 s (plus jitter with a mean of 12 s). Total time spent in the scanner was 57 min.

2.4. Behavioral and psychophysiological data acquisition and analyses

During the fMRI experiment, individual valence ratings were obtained in each trial using an 8-point Likert scale from -4 to 4 ("How positive or negative do you feel right now?"). The subject's pulse was recorded by a pulse plethysmograph placed on the left-hand thumb. Respiration was measured by a respiratory belt placed around the lower rips of the subject. EDA was detected using an MR-compatible ExG-amplifier (Brain Amp ExG MR, Gilching, Germany). Data was acquired with a sampling rate of 5 kHz and recorded with Brain Vision Recorder software (Brain Products, Gilching, Germany). A cup electrode with internal impedance of 15 kΩ was attached to the intermediate phalanges of the index and middle fingers of the subject's left hand. Skin conductance (SCR) was measured with the constant voltage method. SCR data was analyzed in LedaLab V3.3.1, pulse and respiration data were analyzed in MATLAB 7.11.1 (Mathworks Inc., Sherborn, MA, USA). Time frames of analysis were the feedback phase as well as the intervention phase, each comprising six seconds. Parameters for analysis of respiration were tidal volume and respiration rate. Behavioral and psychophysiological data were analyzed with repeated measures ANOVAs (factors were "empathy" and "empathy type") in IBM SPSS Statistics 20.

[1] The actual interventions were in German.

[2] An English example is used in this manuscript for easier comprehension; the experiment deployed German anagrams.

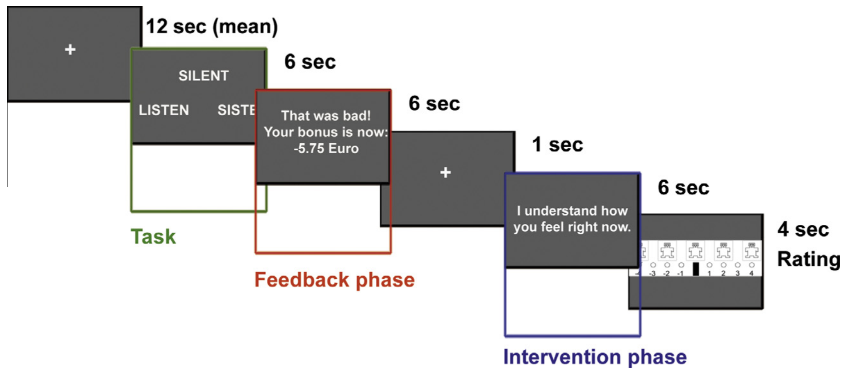

Fig. 1. Experimental paradigm. Participants were presented with the anagram task, followed by positive or negative feedback, followed by an intervention, followed by the rating phase.

2.5. fMRI data acquisition and analyses

fMRI measurements were performed on a 3 T Trio (Siemens, Erlangen) scanner, equipped with a 12-channel coil. The gradient echo sequence (Echo-Planar-Imaging) was used (T_E/T_R/flip angle/bandwidth = 30 ms/2000 ms/70°/2170 Hz) with 3 mm × 3 mm × 3 mm resolution, fat saturation prior to every slice and a GRAPPA acceleration factor of 2. Thirty-seven axially oriented slices with an interslice gap of 0.3 mm were acquired in an interleaved order, providing whole brain coverage. T1-weighted anatomical images (MPRAGE $T_E/T_R/T_I$/flip angle/bandwidth = 2.52 ms/1900 ms/900 ms/9°/170 Hz, 1 mm × 1 mm × 1 mm resolution) were acquired for each subject. Data were recorded in 2 runs each consisting of 752 volumes. The task was programmed in Presentation Software and presented on dual display goggles (VisuaStim, MR Research, USA). A fiber optic response device (2 × 4 Button Diamond, fORP-905, Current Designs Inc., Philadelphia, USA) was used to register the subjects' responses on an 8-point scale.

Data were analyzed using the Statistical Parametric Mapping software (SPM5, Wellcome Dept. of Imaging Neuroscience, London, UK) implemented in MATLAB 7.11.1. Before statistical analyses, functional images were slice-time corrected, realigned, co-registered to the individual anatomical images, segmented, spatially normalized to the Montreal Neurological Institute (MNI) space (voxel size: 3 × 3 × 3 mm^3), and smoothed using an 8 mm full-width at half-maximum Gaussian kernel.

After preprocessing, first-level single subject analyses were conducted to estimate BOLD responses following the general linear model approach. BOLD responses were modeled with 7 event-related regressors of interest (positive/negative feedback, and interventions sorted by the five conditions) and convolved with the canonical hemodynamic response function. As regressors of no interest we included the anagram processing phase terminated by the individual response of the participant, again sorted by conditions; the waiting phase for positive/negative feedback (this was the time left of the 6 s task phase after a participant had solved the anagram); positive/negative prediction error (i.e., deviation of actual feedback from expected feedback based on individual feedback history), and the rating phase. In trials where the actual feedback deviated from the mean feedback history, and therefore presumably from participants' expectations, negative and positive feedback was weighted more in our model than in mean-consistent trials. This was done to reflect the stronger emotional impact of unexpected feedback. Altogether, 17 regressors entered the analysis, modeling all phases of the trials. At second level, estimated beta weights were entered into a repeated measures ANOVA employing a flexible factorial design with the three factors "subject", "empathy" and "empathy type". Only clusters larger than 20 voxels and meeting a threshold of $p < 0.05$ (FWE-corrected) are reported in tables and text. Figures show uncorrected activity ($p < 0.001$). To plot the observed effects, parameter estimates averaged across all voxels in a functional region of interest (ROI; i.e., in a cluster found to be significant at whole brain level), were extracted using the RFXPLOT toolbox (Gläscher, 2009) for SPM.

3. Results

20 subjects entered the fMRI analysis (10 female). Pulse and respiration data of two subjects were lost due to technical reasons, leaving 18 subjects for complete physiological analysis.

3.1. Behavioral data

Valence ratings following experimental conditions (negative feedback) revealed more negative feelings than ratings following the high level baseline condition (positive feedback) [$t(19) = 8.290$, $p = 0.000$]. However, as the 2 ("empathy") × 2 ("empathy type") repeated measures ANOVA showed, participants reported less negative feelings when negative feedback was followed by empathic compared to unempathic comments [main effect of empathy: $F(1,19) = 15.014$, $p = 0.001$]. There was an "empathy" by "empathy type" interaction [$F(1,19) = 26.978$, $p < 0.001$], and post-hoc *t*-tests revealed that the effect of reducing negative feelings was stronger for emotional empathy/compassion [$t(19) = 5.122$, $p < 0.001$, Cohen's $d = 1.15$] than for cognitive empathy [$t(19) = 2.410$, $p = 0.026$, Cohen's $d = 0.54$]. However, both differences were significant and of large effect size (see Fig. 2). Participants needed $M = 2.7$ s to solve the anagrams ($SD = 0.7$ s), averaged over easy and difficult ones, and made one mistake on average.

3.2. Psychophysiological data

Skin conductance response (SCR) was higher during negative feedback than during positive feedback [$t(19) = -2.183$, $p = 0.042$]. No differences were found during the intervention phase, except a strong trend for "empathy type" [main effect of empathy type: $F(1,19) = 4.269$, $p = 0.053$], with SCR being lower during cognitive interventions than during emotional interventions.

Analyzing the respiration data showed that subjects breathed more shallowly during negative feedback than during positive feedback phases. This was visible in a larger amplitude of breath

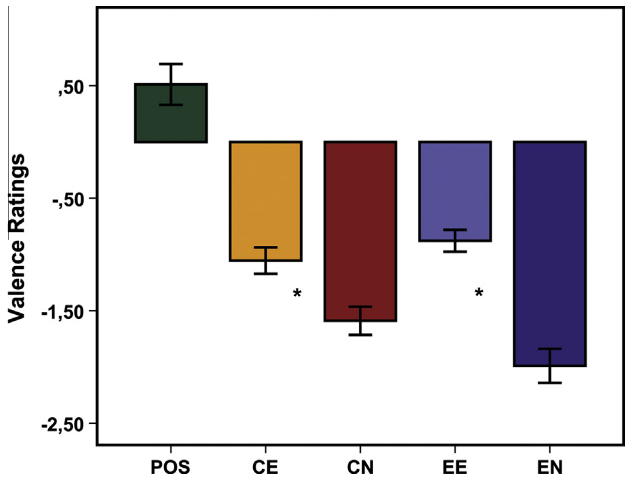

Fig. 2. Valence ratings over the conditions. Participants reported positive feelings in the high level baseline condition, slightly negative feelings after empathic comments (CE, EE), and stronger negative feelings after unempathic comments (CN, EN). Error bars represent standard error of the mean (SEM).

(i.e., tidal volume) during positive feedback [$t(17) = 2.799$, $p = 0.012$] as well as in higher respiratory rate during negative feedback [$t(17 = -3.162$, $p = 0.006$]. The repeated measures ANOVA over the intervention phase showed that tidal volume was also larger during empathic comments than during unempathic comments [main effect of empathy: $F(1,17) = 8.105$, $p = 0.011$], indicating deeper breathing in response to empathic comments. There was no interaction with type of empathy. Furthermore, tidal volume was larger during the intervention phase compared to the negative feedback phase for both types of empathy [cognitive empathy: $t(17) = -3.681$, $p = 0.002$; emotional empathy: $t(17) = -4.355$, $p < 0.001$]. Hence, subjects breathed more shallowly when being criticized, but more deeply when being empathized with. No effects were found for pulse and heart rate, neither in the feedback nor in the intervention phase. Table 1 shows means and standard deviations for all physiological parameters.

3.3. fMRI data

3.3.1. Neural activity during negative vs. positive feedback

Negative feedback compared to positive feedback elicited activity on whole brain level in right anterior insula, left putamen/pallidum, and left supramarginal gyrus, extending to precentral gyrus (see Table 2).

3.3.2. Neural substrates of processing empathic vs. unempathic comments

3.3.2.1. Empathic. Emotionally empathic comments induced activity in the orbital part of left middle frontal gyrus (mOFC) and left superior parietal gyrus (SPG) (EE > EN) (Fig. 3). Cognitively empathic comments (CE > CN) and the combination of both (EE + CE > EN + CN) resulted in no activations.

3.3.2.2. Unempathic. Cognitively unempathic comments activated the medial-orbital part of left superior frontal gyrus (CN > CE). All unempathic comments combined (EN + CN > EE + CE) were processed in left superior temporal gyrus and right putamen.

Activations of empathic comments compared with unempathic comments as well as the high-level baseline are shown in Table 3.

3.3.2.3. Vs. high-level baseline. When empathic interventions were contrasted against the high level baseline condition (CE + EE > base), activity was induced in right postcentral gyrus and left cerebellum. When separated into cognitive and emotional empathy, right postcentral gyrus and left cerebellum responded to cognitively empathic interventions (CE > base) (Fig. 4). Right precentral gyrus, left cerebellum, left opercular inferior frontal gyrus, and left middle temporal gyrus responded to emotionally empathic interventions (EE > base) (Fig. 5).

3.3.3. Neural substrates of processing cognitive and emotional empathy

When cognitive and emotional interventions in general were contrasted, emotional interventions (EE + EN > CE + CN) elicited more activity in the superior temporal gyrus. Contrasting only empathic interventions, emotionally empathic interventions (EE > CE) resulted in activity in the mOFC. Contrasting unempathic interventions only, cognitively unempathic interventions (CN > EN) activated right MFG, and emotionally unempathic interventions (EN > CN) activated left/right superior temporal gyrus. Table 4 shows the results of contrasting emotional and cognitive interventions. Activity resulting from emotional empathy contrasted with cognitive empathy is displayed in Fig. 6.

4. Discussion

The aim of our study was to explore and compare the emotional effects and neural correlates of cognitively and emotionally empathic comments after receiving negative performance feedback. The experiment yielded three main findings: (1) both cognitively and emotionally empathic comments led to less negative feelings and emotions compared to unempathic comments, visible in valence ratings and respiration data. (2) Emotionally empathic/compassion comments activated left mOFC and left SPG when contrasted against unempathic comments. Contrasted against the high-level baseline, cognitively empathic comments were processed in right postcentral gyrus and left cerebellum, whereas emotionally empathic/compassion comments induced activity in right precentral gyrus, left cerebellum, opercular part of left inferior frontal gyrus and left middle temporal gyrus. (3) The two types of expressing empathy were processed in partially separable clusters. Emotional interventions contrasted with cognitive interventions resulted in increased activity in left/right superior temporal gyrus (EE + EN > CE + CN), as well as mOFC for empathic interventions only (EE > CE). The findings are discussed below.

4.1. Emotion induction in the feedback phase

Empathic comments were offered based on the assumption that participants experienced negative feelings and emotions due to the negative performance feedback. The neural activations elicited during the feedback phase suggest that this indeed applied, although contrary to expectations, no amygdala activation was found. Most likely, this is due to the relatively weak stimulus intensity of negative performance feedback.

Negative feedback activated right anterior insula, left putamen/pallidum, and, surprisingly, left supramarginal gyrus, extending to precentral gyrus. Anterior insula activation was anticipated for this contrast, as the anterior insula plays a prominent role in the experience of emotion and physical and mental pain (Jackson, Brunet, Meltzoff, & Decety, 2006; Lamm, Batson, & Decety, 2007; Lamm & Singer, 2010). The right anterior insula has been suggested to be critical for the subjective awareness of feelings and involved in processing signals from the body (Craig, 2004, 2009; Kober et al., 2008). Anterior insula activation has been related to negative affective states such as disgust (Jabbi, Bastiaansen, & Keysers, 2008; Wicker et al., 2003), social exclusion (Eisenberger, Inagaki, Rameson, Mashal, & Irwin, 2009; Eisenberger, Lieberman, & Williams, 2003), and the rejection of unfair offers (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003).

Table 1
Physiological measures in the feedback phase and during the different interventions. (a) Means and standard errors (S.E.) for tidal volume (amplitude) and respiration rate (breathing cycle). (b) Mean SCR with standard errors (S.E.).

	Pos. feedback	Neg. feedback	CE	CN	EE	EN
(a) Amplitude (mean)	2558.28	2492.77	2638.41	2576.75	2640.59	2538.77
(S.E.)	403.43	410.73	437.02	466.75	466.85	430.84
Breathing cycles (mean)	1.73	1.80	1.75	1.80	1.76	1.78
(S.E.)	0.44	0.38	0.41	0.51	0.41	0.44
(b) SCR (mean)	0.57	0.68	0.55	0.46	0.59	0.64
(S.E.)	0.51	0.60	0.50	0.48	0.73	0.57

Table 2
Negative vs. positive performance feedback.

Anatomical region	Side	MNI-coordinates			*z*-Score of local maximum	Number of voxels in cluster
		x	*y*	*z*		
Putamen/pallidum	L	−27	−6	−3	5.37	84
Supramarginal gyrus (extending to precentral gyrus)	L	−54	−24	33	5.20	4883
Insula	R	45	18	−9	5.16	1693

$p < 0.05$, FWE-corrected.

Ochsner (2008) concludes that the anterior insula plays a general role in negative affective experience. The putamen has also been implicated in negative emotions (Sass et al., 2012) as well as in the intention to suppress emotions and motor responses (Vanderhasselt, Kühn, & De Raedt, 2012). The left supramarginal gyrus together with left dorsal premotor gyrus has been associated with action reprogramming in response to environmental cues demanding rapid action reprogramming (Hartwigsen et al., 2012). In a study by Lamm et al. (2007), the supramarginal gyrus responded to subjects imagining the experience of a visually displayed painful injury together with insula, putamen, precentral gyrus, caudate nucleus, supplementary motor area, superior

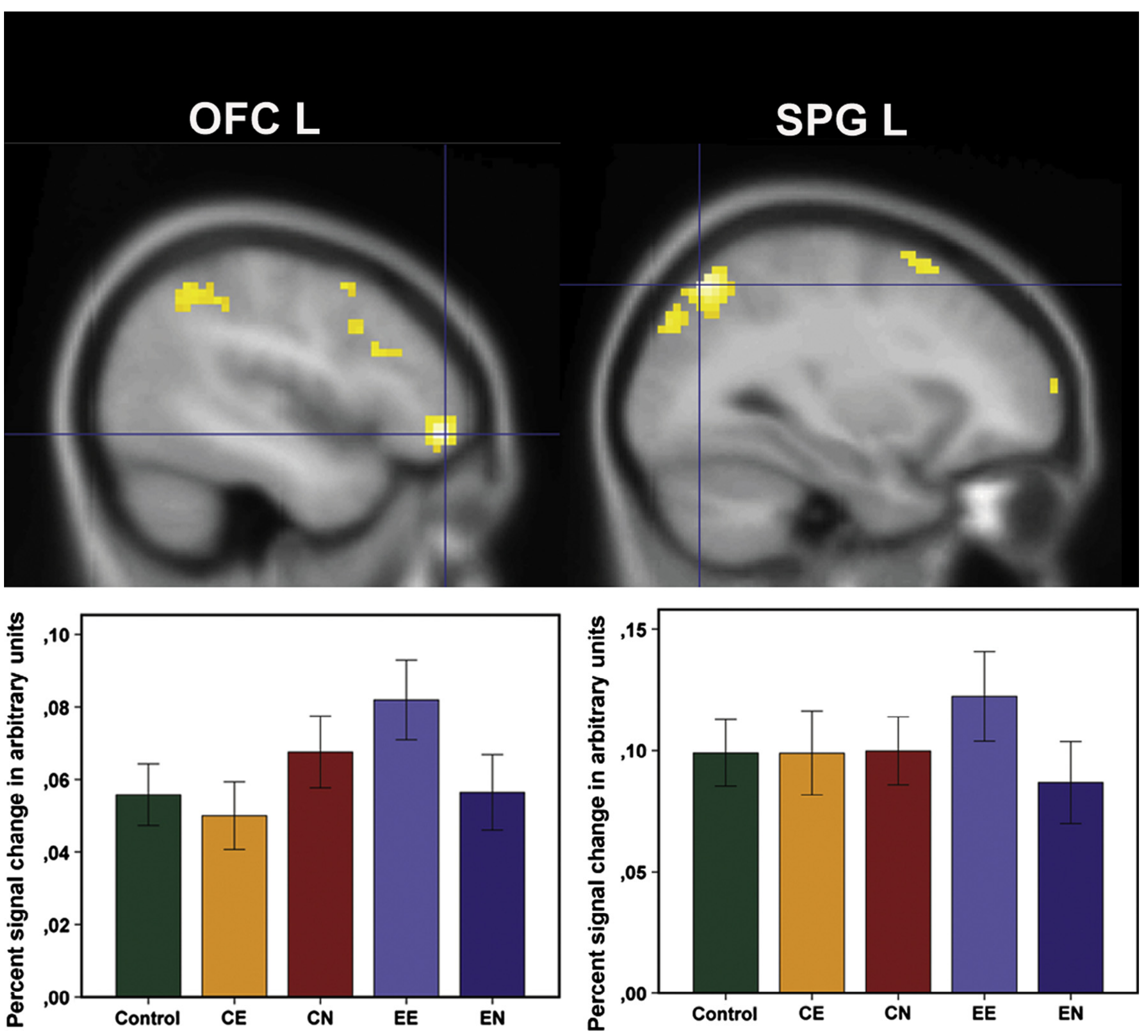

Fig. 3. Emotionally empathic > emotionally unempathic. For emotional empathy, contrasting empathic against unempathic comments resulted in activity in left OFC and left SPG (figure shows activations at $p < 0.001$).

Table 3
Effects of empathic comments.

Anatomical region	Side	MNI-coordinates			z-Score of local maximum	Number of voxels in cluster
		x	y	z		
(A) Emotional empathic (EE) > emotional unempathic (EN)						
Middle frontal gyrus, orbital part	L	−45	45	−9	4.98	58
Superior parietal gyrus	L	−30	−72	51	4.73	284
(B) Unempathic (EN + CN) > empathic (EE + CE)						
Superior temporal gyrus	L	−51	3	−9	4.98	208
Putamen	R	27	−3	3	4.86	1197
(C) Cognitive unempathic (CN) > cognitive empathic (CE)						
Superior frontal gyrus, medial-orbital	L	−6	45	−15	4.82	22
(D) Empathic (EE + CE) > high level baseline						
Postcentral gyrus	R	39	−21	45	5.77	617
Cerebellum/ Hemisphere/ Lobule 4–5	L	−21	−51	−21	5.37	230
(E) Emotional empathic (EE) > high level baseline						
Precentral gyrus	R	39	−21	42	5.12	498
Cerebellum/ Hemisphere/ Lobule 4–5	L	−21	−51	−21	5.48	175
Inferior frontal gyrus, opercular part	L	−36	9	27	4.71	281
Middle temporal gyrus	L	−57	−33	−3	4.69	218
(F) Cognitive empathic (CE) > high level baseline						
Postcentral gyrus	R	39	−21	45	4.96	297
Cerebellum/ Hemisphere/ Lobule 4–5	L	−18	−48	−21	4.69	126

$p < 0.05$, FWE-corrected.

temporal gyrus, middle frontal gyrus, and rolandic operculum. In view of these findings, the involvement of the supramarginal gyrus in response to negative feedback in our paradigm is, while unexpected, not entirely implausible.

Overall, the neural activations caused by the negative performance feedback in combination with financial loss suggest that the induction of negative feelings and emotions was successful. This conclusion is also supported by the valence ratings, the higher respiration rate and lower tidal volume during negative compared to positive performance feedback, as well as by skin conductance data, which shows that participants had a higher SCR during negative than during positive feedback. Increased SCR is commonly associated with emotion-related sympathetic arousal, often in correspondence with negative emotions (Critchley, 2002; Kreibig, Wilhelm, Roth, & Gross, 2007).

4.2. Emotional effects of empathic comments

For both types of empathy, empathic comments led to less negative self-reported feelings in recipients. This was complemented by respiration data. While negative performance feedback induced faster and shallower breathing, empathic interventions re-established deeper breathing. Tidal volume has been repeatedly shown to decrease and respiration rate to increase with negative emotion such as anxiety (Kreibig et al., 2007), while pleasant emotions and relaxation decrease respiration frequency and increase tidal volume (Masaoka, Koiwa, & Homma, 2005; Masaoka, Sugiyama, Katayama, Kashiwagi, & Homma, 2012).

Hence, both types of empathic social response seem to have influenced the recipient's feelings and emotions in a positive way, slightly more so with emotionally empathic/compassion comments than cognitively empathic comments. However, it should be noted that the interaction with empathy type in the valence data seems to be primarily driven by a stronger reaction to emotionally unempathic comments than to cognitively unempathic comments. This suggests that social messages like "I don't care what you feel" induce negative feelings and emotions in the recipient, and to a larger degree than social messages along the lines of "I don't understand what you feel". Due to the design and exploratory nature of the study, we cannot at this point draw conclusions on the extent feelings and emotions were actually down- or up-regulated by the interventions. We propose that most likely a combination of two effects took place: While the unempathic interventions seem to have exacerbated the negative feelings and emotions induced by the negative feedback, empathic interventions alleviated them.

While the effects on feelings and emotions of the recipient may not be surprising for emotional empathy, it is notable in the case of cognitive empathy. Cognitive empathy offers no sympathy or help, but mainly displays that an observer is capable of reconstructing the thoughts and feelings of somebody in distress. The results confirm previous findings where expressing cognitive empathy through paraphrasing led to more positive feelings compared to an unempathic intervention, and that participants felt better after paraphrasing than before and worse after an unempathic intervention, compared to before. (Seehausen et al., 2012, 2014). One possible explanation for this effect is that subjects feel validated in their perception of a given situation when somebody else is able to see it the same way. Another possibility is that another person making an effort to understand someone's perspective communicates a message of social solidarity and connection. Several studies have suggested that feeling understood enhances both personal and social well-being (Cahn, 1990; Oishi, Krochik, & Akimoto, 2010; Reis, Clark, & Holmes, 2004; Reis, Sheldon, Gable, Roscoe, & Ryan, 2000; Swann, 1990).

4.3. Neural substrates of empathic comments

Empathic comments induced activations in right postcentral gyrus and precentral gyrus, left cerebellum, the opercular part of the left inferior frontal gyrus and left middle temporal gyrus when compared to the high level baseline. When contrasted with unempathic comments, emotionally empathic/compassion comments activated the mOFC and left SPG. This differentiation is interesting because it reflects different effects of empathic comments in relation to context, i.e. emotional state and necessity of social support.

Being empathized with vs. being denied empathy while being in a negative emotional state activated mOFC and SPG. The mOFC is part of the reward network and central for hedonic experience (Becker et al., 2012; Fett, Gromann, Giampietro, Shergill, & Krabbendam, 2012; Kringelbach, 2005). It has been suggested that the mOFC specifically processes magnitude of a received reward, or computes the subjective value of rewards, respectively (Diekhof, Kaps, Falkai, & Gruber, 2012; Padoa-Schioppa & Cai, 2011). In addition, the mOFC is involved in regulation of motivation and affect (Arnsten & Rubia, 2012), and in cultivating compassion (Beauregard, Courtemanche, Paquette, & St-Pierre, 2009; Immordino-Yang, McColl, Damasio, & Damasio, 2009; Klimecki, Leiberg, Lamm, & Singer, 2012). The engagement of mOFC in the processing of empathic comments in our study cannot be regarded as evidence that being empathized with held a rewarding value for participants, as there was no correlation between emotional valence ratings and mOFC activation. However, it should be noted that feeling understood has recently been shown to activate

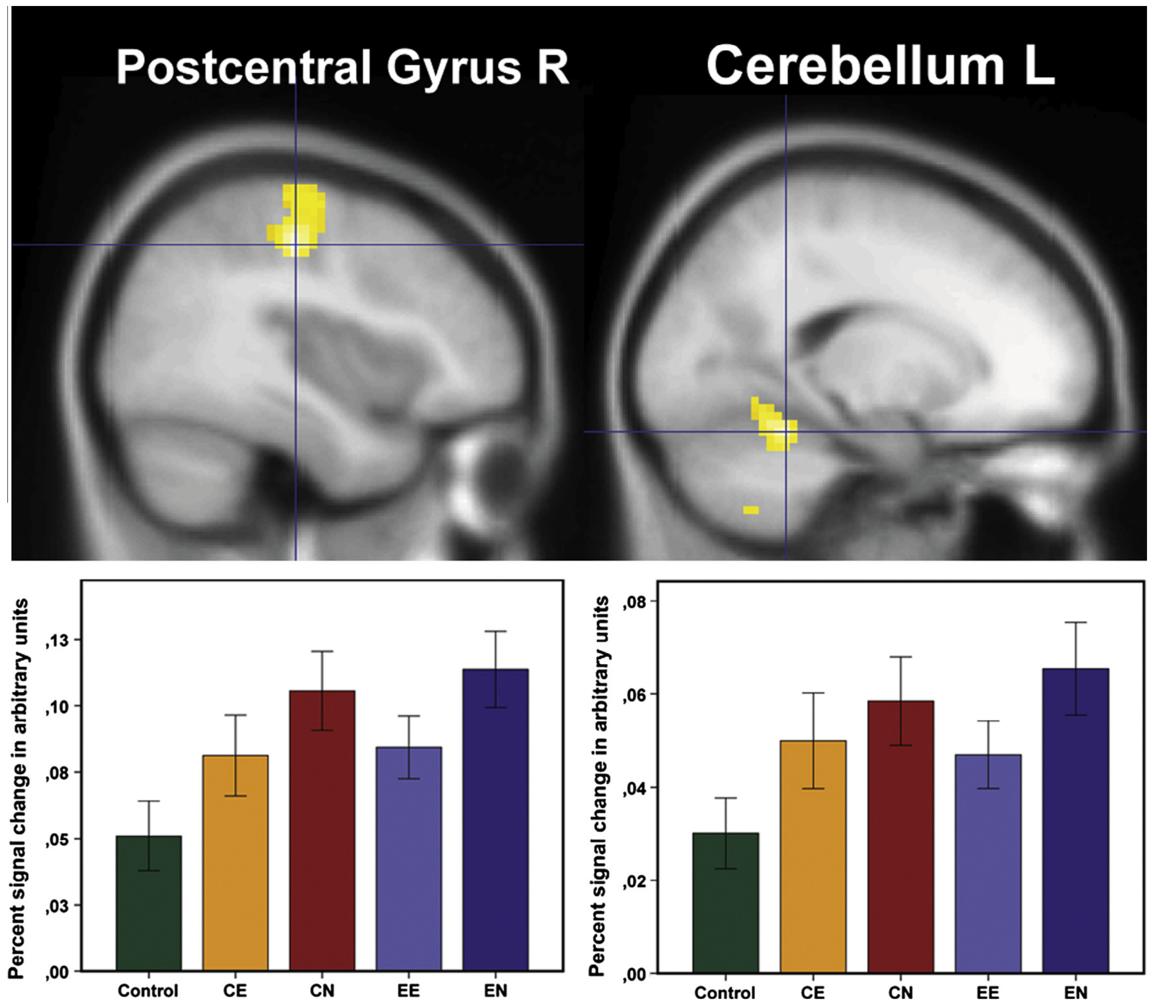

Fig. 4. Cognitively empathic > baseline. Cognitively empathic comments produced activity in right postcentral gyrus and left cerebellum when compared with the high level baseline (figure shows activations at $p < 0.001$).

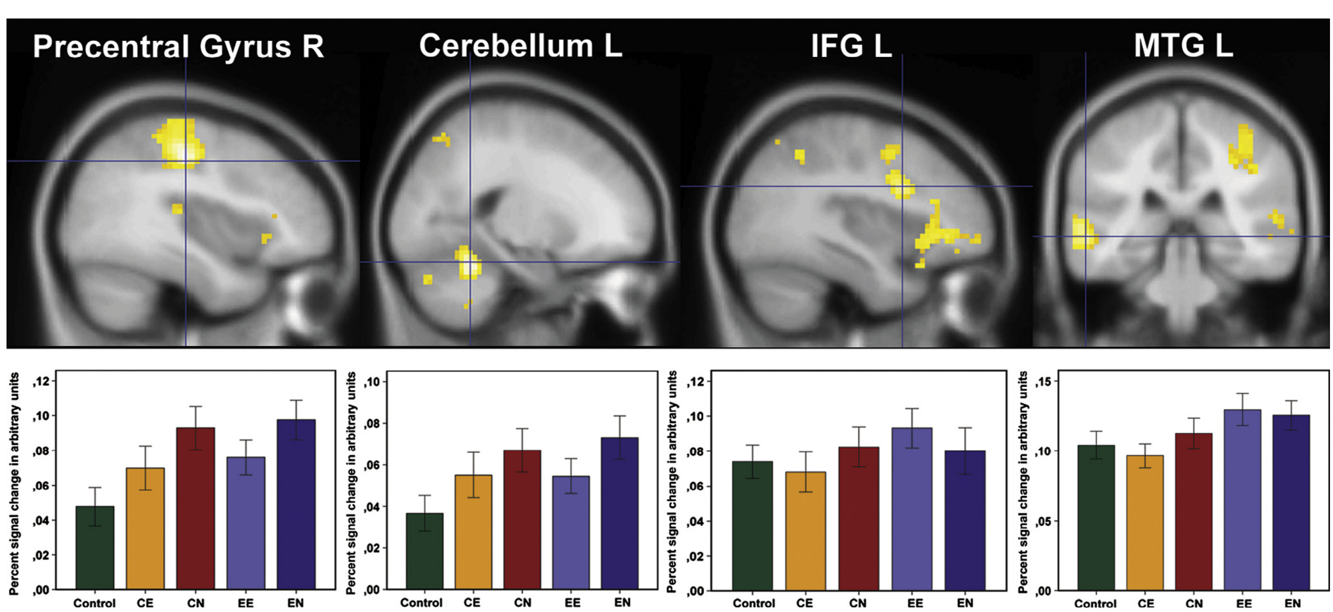

Fig. 5. Emotionally empathic > baseline. Emotionally empathic comments activated right precentral gyrus, left cerebellum, left inferior frontal gyrus and left middle temporal gyrus when contrasted against the high level baseline (figure shows activations at $p < 0.001$).

Table 4
Emotional vs. cognitive comments.

Anatomical region	Side	MNI-coordinates			z-Score of local maximum	Number of voxels in cluster
		x	y	z		
(A) Emotional (EE + EN) > cognitive (CE + CN)						
Superior temporal gyrus	L	−63	−24	3	5.93	298
Superior temporal gyrus	R	60	−3	−3	5.30	317
(B) Emotional empathic (EE) > cognitive empathic (CE)						
Middle frontal gyrus, orbital part	L	−45	45	−3	4.73	229
(C) Emotional unempathic (EN) > cognitive unempathic (CN)						
Superior temporal gyrus	L	−57	−6	−3	5.14	121
Superior temporal gyrus	R	60	−6	−3	4.87	139
(D) Cognitive unempathic (CN) > emotional unempathic (EN)						
Middle frontal gyrus	R	36	9	51	4.87	170

$p < 0.05$, FWE-corrected.

regions associated with reward and social connection (ventral striatum and middle insula) in a similar study, whereas not feeling understood engaged the anterior insula, which has been linked to negative emotions (Morelli et al., 2014).

The left SPG was not among our hypothesized regions, and its emergence in this contrast was surprising. Yet, our study being largely exploratory, unexpected activations are likely to be found to some extent. That being said, a parallel study done by our group on the same subject yielded engagement of the left inferior parietal gyrus in the processing of cognitive empathy in the form of paraphrasing during a live interview on social conflict in the MRT (Seehausen et al., 2014). Hence, both studies indicate the involvement of parietal regions in the processing of empathic social response. Our second study also found activation in the left middle frontal gyrus for the processing of cognitively empathic response, similar to the activation of the left mOFC in the present study. Both studies suggest the significance of a fronto-parietal network for the neural processing of empathic social behavior. Also, both studies located activation in a fronto-temporal network associated with the processing of unempathic social response. In the present study, unempathic comments engaged left superior temporal gyrus and right putamen, as well as left superior frontal gyrus for cognitively empathic comments. In our second study, unempathic responses stating that the listener found it impossible to understand the narrator's perspective involved peak activation in the left inferior frontal gyrus, pars triangularis, and right temporal pole (Seehausen et al., 2014).

Processing empathic social response during the experience of negative feelings and emotions compared to during the experience of positive feelings and emotions (high-level baseline) recruited clusters implicated in social cognition. Inferior frontal gyrus and middle temporal gyrus are part of the mentalizing network (Bzdok et al., 2012); pars opercularis and cerebellum have been associated with the putative mirror neuron network (Decety & Meyer, 2008; Molenberghs, Cunnington, & Mattingley, 2012; Rizzolatti & Sinigaglia, 2010). Hence, these activations are in line with our initial assumption that hearing empathic comments while in a negative emotional state fuels social-cognitive processes involving inferences about the speaker's intention, possibly combined with interpretation of meaning, comparison with social norms and weighing emotional significance of the empathic comments. In line with our results, Morelli et al. (2014) likewise found that both feeling understood and not feeling understood activated parts of the mentalizing system, although the precise location of the activations differed (feeling understood: precuneus and temporoparietal junction, not feeling understood: dorsomedial prefrontal cortex). It seems likely that the emotional impact of empathic comments depends significantly on their sincerity as well as their suitability to the given situation. Therefore, it can be assumed that hearing empathic statements fuels social judgment and inference processes. Social judgment, such as rating someone's trustworthiness, has been previously shown to rely on inferior frontal gyrus together with dorsomedial prefrontal cortex (Bzdok et al., 2012). Furthermore, Blackwood et al. (2000) demonstrated that left inferior frontal gyrus (BA 47) is recruited when pondering whether or not verbal statements of differing emotional valence are relevant to oneself.

The increased activation of these neural regions in processing empathic comments when subjects experienced negative feelings and emotions might be due to the above mentioned social-cognitive processes being more relevant for recipients of empathic support who are actually in need of such support. When individuals are in a balanced emotional state, empathic utterances from other people may easily be dismissed as nice but not particularly relevant. In contrast, when someone experiences negative affect, social support becomes a crucial source of emotional recovery. Hence, it is possible that the social cognition processes related to receiving empathic social support are triggered only, or to a greater extent, when the recipient experiences negative feelings and emotions, as indicated by our results. Empathic comments did not recruit the complete mentalizing network, however. Rather, empathic comments appear to stimulate social-cognitive processes partly relying on mentalizing regions, while simultaneously invoking emotion processing regions.

This may also account for the activation of right postcentral gyrus and precentral gyrus by empathic comments. These regions were also engaged in the processing of cognitive empathy in the form of paraphrasing in the above-mentioned second study (Seehausen et al., 2014). Hence, two studies using different paradigms consistently found activation in right precentral gyrus and postcentral gyrus for the processing of empathic social response during the experience of negative feelings and emotions. Postcentral gyrus and cerebellum have been linked to social emotion processing in connection with an embodied affective style (Saxbe, Yang, Borofsky, & Immordino-Yang, 2012). Right precentral and postcentral gyri, as well as the left frontal operculum, have also been previously implicated in recognizing other people's emotions (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000).

4.4. Processing cognitively vs. emotionally empathic comments

As hypothesized, cognitively and emotionally empathic comments for negative emotions were processed by partially separate neural clusters. Both stimulated cerebellar and post-/precentral activity when contrasted against the high-level baseline, but emotional empathy/compassion in addition yielded activations in left inferior frontal gyrus (opercular part), and left middle temporal gyrus. Emotionally empathic comments may have been evaluated as more salient or socially relevant by participants, which would explain the increased involvement of social cognition regions. However, as these activations resulted from a comparison with the high-level baseline condition and not a direct contrast of emotional and cognitive empathy, it is difficult to draw conclusions on this basis. In direct comparison with cognitive empathy,

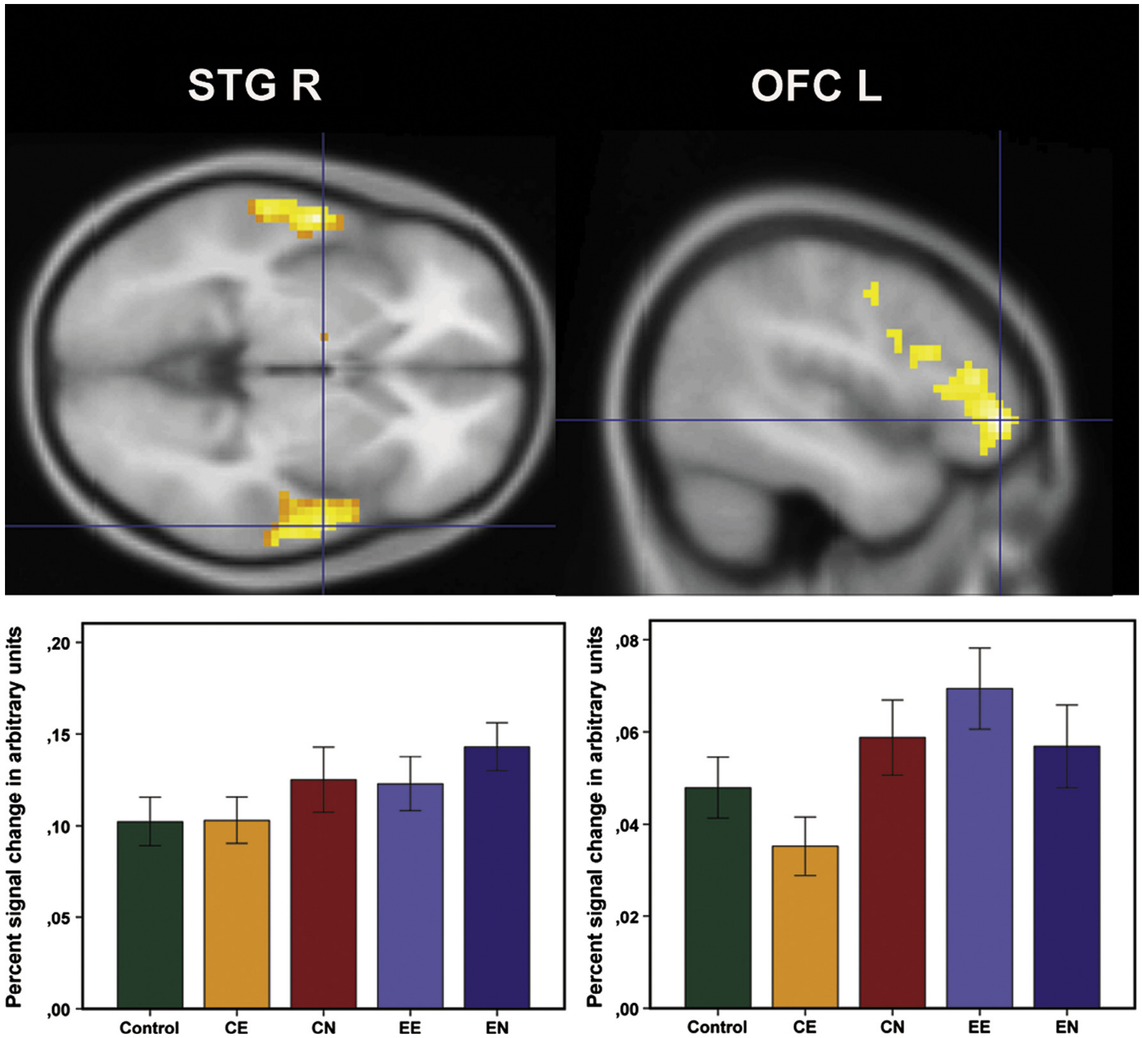

Fig. 6. Emotional > cognitive (left) and emotionally empathic > cognitively empathic (right). All emotional interventions contrasted against all cognitive interventions activated left and right superior temporal gyrus (left). Contrasting only empathic emotional vs. empathic cognitive comments stimulated left OFC (figure shows activations at $p < 0.001$).

emotionally empathic/compassion comments predominantly invoked the left mOFC.

Emotional interventions, contrasted with cognitive interventions, recruited right and left superior temporal gyrus, the latter of which was also activated by unempathic comments compared to empathic comments. The superior temporal cortex plays a critical role in hearing as well as speech, and contains multiple interconnected auditory areas (Howard et al., 2000). Blair (2005) argues that theory of mind, motor empathy, and emotional empathy all rely on the integrity of superior temporal regions. Our results suggest this region is also involved in processing empathic and unempathic behavior, especially unempathic verbal statements. However, this needs to be further explored.

4.5. Limitations of the current study

Due to lack of previous research on this topic, the present study was mainly exploratory. Results need to be repeatedly confirmed by several comparable studies before they can be regarded as definite. In particular, the present study cannot account for the actual online regulation of negative feelings and emotions. In order to not overstrain the participants with too many valence ratings, we did not collect any ratings directly following negative performance feedback, in addition to following the subsequent interventions. Therefore, no direct comparison can be made between participant's feelings before and after the interventions. The present study should be understood as laying a foundation for more field-oriented surveys. In addition, our emotional empathy interventions reflected compassion more than a narrow definition of emotional empathy as an isomorphic reaction to another's emotion. While we believe that this enhanced external validity, this needs to be kept in mind when appraising the neural findings caused by emotionally empathic and unempathic interventions.

5. Conclusion

Our study confirms and expands on the results of a parallel study by our group (Seehausen et al., 2014) on the effects of empathic social response. Both studies indicate the engagement of a fronto-parietal network in the processing of empathic social response, and the involvement of a fronto-temporal network in the processing of unempathic social response. In both studies, social cognition regions appear to play an important role in the processing of empathic and unempathic social response. The present study furthermore showed that cognitively and emotionally empathic comments engage partially different neural networks, however, both types of empathy exert a positive influence on feelings and emotions. This is potentially relevant for all professional groups who deal with and have to de-escalate strong negative feelings and emotions on a regular basis, e.g. lawyers, judges, mediators, and physicians. As has been discussed in Seehausen et al. (2014), it can be difficult for the above-mentioned groups to reconcile the often-needed display of empathy with the impartial stance their professional role requires. However, demonstrating cognitive empathy, e.g. in the form of paraphrasing the perspective of another person, is almost always acceptable, and, as has been shown here, also effective in de-escalating negative feelings and emotions.

Conflict of interest statement

The authors are not aware of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

Adolphs, R., Damasio, H., Tranel, D., Cooper, G., & Damasio, A. R. (2000). A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *The Journal of Neuroscience, 20*(7), 2683–2690.

Arnsten, A. F. T., & Rubia, K. (2012). Neurobiological circuits regulating attention, cognitive control, motivation, and emotion: Disruptions in neurodevelopmental psychiatric disorders. *Journal of the American Academy of Child and Adolescent Psychiatry, 51*(4), 356–367. http://dx.doi.org/10.1016/j.jaac.2012.01.008.

Ashton-James, C., van Baaren, R. B., Chartrand, T. L., Decety, J., & Karremans, J. (2007). Mimicry and me: The impact of mimicry on self-construal. *Social Cognition., 25*, 518–535.

Beauregard, M., Courtemanche, J., Paquette, V., & St-Pierre, E. L. (2009). The neural basis of unconditional love. *Psychiatry Research, 172*, 93–98.

Becker, S., Gandhi, W., & Schweinhardt, P. (2012). Cerebral interactions of pain and reward and their relevance for chronic pain. *Neuroscience Letters, 520*(2), 182–187. http://dx.doi.org/10.1016/j.neulet.2012.03.013.

Bernhardt, B. C., & Singer, T. (2012). The neural basis of empathy. *Annual Review of Neuroscience, 35*, 1–23. http://dx.doi.org/10.1146/annurev-neuro-062111-150536.

Blackwood, N. J., Howard, R. J., ffytche, D. H., Simmons, A., Bentall, R. P., & Murray, R. M. (2000). Imaging attentional and attributional bias: An fMRI approach to the paranoid delusion. *Psychological Medicine, 30*(4), 873–883.

Blair, R. J. R. (2005). Responding to the emotions of others: Dissociating forms of empathy through the study of typical and psychiatric populations. *Consciousness and Cognition, 14*(4), 698–718. http://dx.doi.org/10.1016/j.concog.2005.06.004.

Bzdok, D., Schilbach, L., Vogeley, K., Schneider, K., Laird, A. R., Langner, R., & Eickhoff, S. B. (2012). Parsing the neural correlates of moral cognition: ALE meta-analysis on morality, theory of mind, and empathy. *Brain Structure & Function, 217*(4), 783–796.

Cahn, D. D. (1990). Perceived understanding and interpersonal relationships. *Journal of Social and Personal Relationships, 7*(2), 231–244.

Carr, L., Iacoboni, M., Dubeau, M.-C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proceedings of the National academy of Sciences of the United States of America, 100*(9), 5497–5502. http://dx.doi.org/10.1073/pnas.0935845100.

Craig, A. D. (Bud) (2004). Human feelings: Why are some more aware than others? *Trends in Cognitive Sciences, 8*(6), 239–241.

Craig, A. D. B. (2009). How do you feel-now? The anterior insula and human awareness. *Nature Reviews Neuroscience, 10*(1), 59–70. http://dx.doi.org/10.1038/nrn2555.

Critchley, H. D. (2002). Electrodermal responses: What happens in the brain. *The Neuroscientist, 8*(2), 132–142.

Decety, J. (2011). Dissecting the neural mechanisms mediating empathy. *Emotion Review, 3*(1), 92–108. http://dx.doi.org/10.1177/1754073910374662.

Decety, Jean., & Jackson, P. L. (2004). The functional architecture of human empathy. *Behavioral and Cognitive Neuroscience Reviews, 3*(2), 71–100. http://dx.doi.org/10.1177/1534582304267187.

Decety, J., & Meyer, M. (2008). From emotion resonance to empathic understanding: A social developmental neuroscience account. *Development and Psychopathology, 20*(4), 1053–1080. http://dx.doi.org/10.1017/S0954579408000503.

Diekhof, E. K., Kaps, L., Falkai, P., & Gruber, O. (2012). The role of the human ventral striatum and the medial orbitofrontal cortex in the representation of reward magnitude – An activation likelihood estimation meta-analysis of neuroimaging studies of passive reward expectancy and outcome processing. *Neuropsychologia, 50*(7), 1252–1266. http://dx.doi.org/10.1016/j.neuropsychologia.2012.02.007.

Dziobek, I., Rogers, K., Fleck, S., Bahnemann, M., Heekeren, H. R., Wolf, O. T., & Convit, A. (2008). Dissociation of cognitive and emotional empathy in adults with Asperger syndrome using the Multifaceted Empathy Test (MET). *Journal of Autism and Developmental Disorders, 38*(3), 464–473. http://dx.doi.org/10.1007/s10803-007-0486-x.

Eisenberger, N. I., Inagaki, T. K., Rameson, L. T., Mashal, N. M., & Irwin, M. R. (2009). An fMRI study of cytokine-induced depressed mood and social pain: The role of sex differences. *Neuroimage, 47*(3), 881–890. http://dx.doi.org/10.1016/j.neuroimage.2009.04.040.

Eisenberger, N. I., Lieberman, M. D., & Williams, K. D. (2003). Does rejection hurt? An FMRI study of social exclusion. *Science, 302*(5643), 290–292. http://dx.doi.org/10.1126/science.1089134.

Fan, Y., Duncan, N. W., de Greck, M., & Northoff, G. (2011). Is there a core neural network in empathy? An fMRI based quantitative meta-analysis. *Neuroscience and Biobehavioral Reviews, 35*(3), 903–911. http://dx.doi.org/10.1016/j.neubiorev.2010.10.009.

Fett, A.-K. J., Gromann, P. M., Giampietro, V., Shergill, S. S., & Krabbendam, L. (2012). Default distrust? An fMRI investigation of the neural development of trust and cooperation. *Social Cognitive and Affective Neuroscience, 9*(4), 395–402. http://dx.doi.org/10.1093/scan/nss144.

Fischer-Lokou, J., Martin, A., Guéguen, N., & Lamy, L. (2011). Mimicry and propagation of prosocial behavior in a natural setting. *Psychological Reports, 108*(2), 599–605. http://dx.doi.org/10.2466/07.17.21.PR0.108.2.599-605.

Gläscher, J. (2009). Visualization of group inference data in functional neuroimaging. *Neuroinformatics, 7*(1), 73–82. http://dx.doi.org/10.1007/s12021-008-9042-x.

Guéguen, N., Martin, A., & Meineri, S. (2011). Mimicry and helping behavior: An evaluation of mimicry on explicit helping request. *The Journal of Social Psychology, 151*(1), 1–4. http://dx.doi.org/10.1080/00224540903366701.

Hartwigsen, G., Bestmann, S., Ward, N. S., Woerbel, S., Mastroeni, C., Granert, O., & Siebner, H. R. (2012). Left dorsal premotor cortex and supramarginal gyrus complement each other during rapid action reprogramming. *Journal of Neuroscience, 32*(46), 16162–16171. http://dx.doi.org/10.1523/JNEUROSCI.1010-12.2012.

Hoffman, M. L. (2000). *Empathy and moral development: Implications for caring and justice*. Cambridge University Press.

Howard, M. A., Volkov, I. O., Mirsky, R., Garell, P. C., Noh, M. D., Granner, M., ... Brugge, J. F. (2000). Auditory cortex on the human posterior superior temporal gyrus. *Journal of Comparative Neurology, 416*(1), 79–92.

Immordino-Yang, M. H., McColl, A., Damasio, H., & Damasio, A. (2009). Neural correlates of admiration and compassion. *Proceedings of the National academy of Sciences of the United States of America, 106*, 8021–8026.

Jabbi, M., Bastiaansen, J., & Keysers, C. (2008). A common anterior insula representation of disgust observation, experience and imagination shows divergent functional connectivity pathways. *PLoS One, 3*(8), e2939. http://dx.doi.org/10.1371/journal.pone.0002939.

Jackson, P. L., Brunet, E., Meltzoff, A. N., & Decety, J. (2006). Empathy examined through the neural mechanisms involved in imagining how I feel versus how you feel pain. *Neuropsychologia, 44*(5), 752–761. http://dx.doi.org/10.1016/j.neuropsychologia.2005.07.015.

Jones, N. P., Papadakis, A. A., Orr, C. A., & Strauman, T. J. (2013). Cognitive processes in response to goal failure: A study of ruminative thought and its affective consequences. *Journal of Social and Clinical Psychology, 32*(5).

Klimecki, O. M., Leiberg, S., Lamm, C., & Singer, T. (2012). Functional neural plasticity and associated changes in positive affect after compassion training. *Cerebral Cortex*. http://dx.doi.org/10.1093/cercor/bhs142.

Klimecki, O. M., Leiberg, S., Ricard, M., & Singer, T. (2014). Differential pattern of functional brain plasticity after compassion and empathy training. *Social Cognitive and Affective Neuroscience, 9*, 873–879. 2014.

Kober, H., Barrett, L. F., Joseph, J., Bliss-Moreau, E., Lindquist, K., & Wager, T. D. (2008). Functional grouping and cortical-subcortical interactions in emotion: A meta-analysis of neuroimaging studies. *Neuroimage, 42*(2), 998–1031. http://dx.doi.org/10.1016/j.neuroimage.2008.03.059.

Kraybill, R. S., Evans, R. A., & Evans, A. F. (2001). *Peace skills: Manual for community mediators*. San Francisco: Jossey-Bass.

Kreibig, S. D., Wilhelm, F. H., Roth, W. T., & Gross, J. J. (2007). Cardiovascular, electrodermal, and respiratory response patterns to fear- and sadness-inducing films. *Psychophysiology, 44*(5), 787–806. http://dx.doi.org/10.1111/j.1469-8986.2007.00550.x.

Kringelbach, M. L. (2005). The human orbitofrontal cortex: Linking reward to hedonic experience. *Nature Reviews Neuroscience, 6*(9), 691–702. http://dx.doi.org/10.1038/nrn1747.

Kushki, A., Fairley, J., Merja, S., King, G., & Chau, T. (2011). Comparison of blood volume pulse and skin conductance responses to mental and affective stimuli at different anatomical sites. *Physiological Measurement, 32*(10), 1529–1539. http://dx.doi.org/10.1088/0967-3334/32/10/002.

Lamm, C., Batson, C. D., & Decety, J. (2007). The neural substrate of human empathy: Effects of perspective-taking and cognitive appraisal. *Journal of Cognitive Neuroscience, 19*(1), 42–58. http://dx.doi.org/10.1162/jocn.2007.19.1.42.

Lamm, C., Decety, J., & Singer, T. (2011). Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. *Neuroimage, 54*(3), 2492–2502. http://dx.doi.org/10.1016/j.neuroimage.2010.10.014.

Lamm, C., & Singer, T. (2010). The role of anterior insular cortex in social emotions. *Brain Structure & Function, 214*(5–6), 579–591. http://dx.doi.org/10.1007/s00429-010-0251-3.

Mar, R. A. (2011). The neural bases of social cognition and story comprehension. *Annual Review of Psychology, 62*, 103–134. http://dx.doi.org/10.1146/annurev-psych-120709-145406.

Masaoka, Y., Koiwa, N., & Homma, I. (2005). Inspiratory phase-locked alpha oscillation in human olfaction: Source generators estimated by a dipole tracing method. *The Journal of Physiology, 566*(Pt 3), 979–997. http://dx.doi.org/10.1113/jphysiol.2005.086124.

Masaoka, Y., Sugiyama, H., Katayama, A., Kashiwagi, M., & Homma, I. (2012). Slow breathing and emotions associated with odor-induced autobiographical memories. *Chemical Senses, 37*(4), 379–388. http://dx.doi.org/10.1093/chemse/bjr120.

Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2012). Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies. *Neuroscience and Biobehavioral Reviews, 36*(1), 341–349.

Morelli, S. A., Torre, J. B., & Eisenberger, N. I. (2014). The neural bases of feeling understood and not understood. *Social Cognitive and Affective Neuroscience, 2014* (9), 1890–1896.

Ochsner, K. N. (2008). The social-emotional processing stream: Five core constructs and their translational potential for schizophrenia and beyond. *Biological Psychiatry, 64*(1), 48–61. http://dx.doi.org/10.1016/j.biopsych.2008.04.024.

Ochsner, K. N., Silvers, J. A., & Buhle, J. T. (2012). Functional imaging studies of emotion regulation: A synthetic review and evolving model of the cognitive control of emotion. *Annals of the New York Academy of Sciences, 1251*(1), E1–E24. http://dx.doi.org/10.1111/j.1749-6632.2012.06751.x.

Oishi, S., Krochik, M., & Akimoto, S. (2010). Felt understanding as a bridge between close relationships and subjective wellbeing: Antecedents and consequences across individuals and cultures. *Social and Personality Psychology Compass, 4*(6), 403–416.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97–113. http://dx.doi.org/10.1016/0028-3932(71)90067-4.

Padoa-Schioppa, C., & Cai, X. (2011). The orbitofrontal cortex and the computation of subjective value: Consolidated concepts and new perspectives. *Annals of the New York Academy of Sciences, 1239*, 130–137. http://dx.doi.org/10.1111/j.1749-6632.2011.06262.x.

Przyrembel, M., Smallwood, J., Pauen, M., & Singer, T. (2012). Illuminating the dark matter of social neuroscience: Considering the problem of social interaction from philosophical, psychological, and neuroscientific perspectives. *Frontiers in Human Neuroscience, 6*, 190. http://dx.doi.org/10.3389/fnhum.2012.00190.

Reis, H. T., Clark, M. S., & Holmes, J. G. (2004). Perceived partner responsiveness as an organizing construct in the study of intimacy and closeness. In D. J. Mashek & A. Aron (Eds.), *Handbook of closeness and intimacy* (pp. 201–225). Mahwah, NJ: Lawrence Erlbaum Associates Publishers.

Reis, H. T., Sheldon, K. M., Gable, S. L., Roscoe, J., & Ryan, R. M. (2000). Daily well-being: The role of autonomy, competence, and relatedness. *Personality and Social Psychology Bulletin, 26*(4), 419–435.

Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience, 11*(4), 264–274.

Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the ultimatum game. *Science, 300* (5626), 1755–1758. http://dx.doi.org/10.1126/science.1082976.

Sass, K., Habel, U., Kellermann, T., Mathiak, K., Gauggel, S., & Kircher, T. (2012). The influence of positive and negative emotional associations on semantic processing in depression: An fMRI study. *Human Brain Mapping, 35*(2), 471–482. http://dx.doi.org/10.1002/hbm.22186.

Saxbe, D. E., Yang, X.-F., Borofsky, L. A., & Immordino-Yang, M. H. (2012). The embodiment of emotion: Language use during the feeling of social emotions predicts cortical somatosensory activity. *Social Cognitive and Affective Neuroscience, 8*(7), 806–812. http://dx.doi.org/10.1093/scan/nss075.

Schreier, L. (2002). Emotional intelligence and mediation training. *Conflict resolution quarterly* (vol. 20(1), pp. 10). Wiley Periodicals Inc.

Seehausen, M., Kazzer, P., Bajbouj, M., Heekeren, H. R., Jacobs, A. M., Klann-Delius, G., ... Prehn, K. (2014). Talking about social conflict in the MRI scanner: Neural correlates of being empathized with. *Neuroimage, 84*, 951–961. http://dx.doi.org/10.1016/j.neuroimage.2013.09.056.

Seehausen, M., Kazzer, P., Bajbouj, M., & Prehn, K. (2012). Effects of empathic paraphrasing – Extrinsic emotion regulation in social conflict. *Frontiers in Psychology, 3*, 482. http://dx.doi.org/10.3389/fpsyg.2012.00482.

Spreng, R. N., Mar, R. A., & Kim, A. S. (2009). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: A quantitative meta-analysis. *Journal of Cognitive Neuroscience, 21* (3), 489–510. http://dx.doi.org/10.1162/jocn.2008.21029.

Stel, M., & Harinck, F. (2011). Being mimicked makes you a prosocial voter. *Experimental Psychology, 58*(1), 79–84. http://dx.doi.org/10.1027/1618-3169/a000070.

Swann, W. B. Jr., (1990). To be adored or to be known: The interplay of self-enhancement and self-verification. In R. M. Sorrentino & E. T. Higgins (Eds.). *Handbook of motivation and cognition*: *Foundations of social behavior* (vol. 2, pp. 408–448). New York: Guilford.

Van Baaren, R. B., Holland, R. W., Kawakami, K., & Van Knippenberg, A. (2004). Mimicry and prosocial behavior. *Psychological Science, 15*(1), 71–74. http://dx.doi.org/10.1111/j.0963- 7214.2004.01501012.x.

Vanderhasselt, M.-A., Kühn, S., & De Raedt, R. (2012). "Put on your poker face": Neural systems supporting the anticipation for expressive suppression and cognitive reappraisal. *Social Cognitive and Affective Neuroscience*. http://dx.doi.org/10.1093/scan/nss090.

Vignemont, F., & Singer, T. (2006). The empathic brain: How, when and why? *Trends in Cognitive Sciences, 10*(10), 435–441.

Wicker, B., Keysers, C., Plailly, J., Royet, J. P., Gallese, V., & Rizzolatti, G. (2003). Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron, 40*(3), 655–664.

Zaki, J., Weber, J., Bolger, N., & Ochsner, K. (2009). The neural bases of empathic accuracy. *Proceedings of the National academy of Sciences of the United States of America, 106*(27), 11382–11387. http://dx.doi.org/10.1073/pnas.0902666106.