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Distinct neural networks underlying empathy for pleasant and unpleasant touch

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ABSTRACT

In spite of considerable progress in the understanding of the neural mechanisms underlying the experience of empathy, the majority of previous investigations have focused on how we share negative affective states (and in particular pain) of others, whereas only few studies have targeted empathy for positive emotions. This bias has precluded addressing one of the central tenets of the shared representations account of empathy, which is that different networks should be engaged when empathizing with emotions that are represented on different neural levels. The aim of the present study was to overcome this limitation and to test whether empathy for pleasant and unpleasant affective touch is underpinned by different neural networks. To this end we used functional magnetic resonance imaging (fMRI), with two independent replication experiments (N = 18, N = 32), and a novel paradigm enabling the joint investigation of first-hand and vicarious responses to pleasant and unpleasant affect induced via visuo-tactile stimulation. This revealed that empathy is subserved by distinct neural networks, with those regions recruited in the first-hand experience of positive or negative affective states also being specifically recruited when empathizing with these respective states in others. More specifically, the first-hand and vicarious experience of pleasant touch commonly recruited medial orbitofrontal cortex (OFC), while unpleasant touch was associated with shared activation in the right fronto-insular cortex. The observation that specifically tailored subsystems of the human brain are engaged to share positive versus negative touch of others brings fresh evidence to one of the major goals of the social neuroscience of empathy: to identify which specific aspects of the affective states of others are shared, and what role this plays in enabling the understanding of the emotions of others.

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1. Introduction

In the past few years, considerable progress has been made in understanding the neural mechanisms underlying the experience of empathy, i.e., the capacity to affectively share the emotions of another person (for review, see Bernhardt & Singer, 2012; Decety, 2011; Singer & Lamm, 2009). Recent image-based as well as coordinate-based meta-analyses of functional magnetic resonance imaging (fMRI) studies show that empathy consistently recruits the anterior medial cingulate cortex and the anterior insular cortex [aMCC and aIns, respectively, (Fan, Duncan, de Greck, & Northoff, 2011; Lamm, Decety, & Singer, 2011)]. For instance, aggregating the individual activation maps of 168 participants of nine different fMRI experiments on empathy, it has been demonstrated that observing others in pain consistently activates parts of the aMCC and of bilateral anterior dorsal insula, including adjacent inferior frontal cortex (Lamm et al., 2011). As these brain areas are also involved in the first-hand experience of pain, their activation has been interpreted as evidence for the "shared representations account" of understanding others. This account posits that one central mechanism enabling empathy is the recruitment of neural structures responses that are engaged during the first-hand experience of the emotions or sensations one is showing empathy for (for recent critical review, see Decety, 2010; Lamm & Majdandzic, 2014).

The majority of previous social neuroscience studies of empathy have focused on how we share negative affective states of others, and in particular pain. Only a handful of investigations targeted empathy for positive emotions (e.g., Ebisch et al., 2011; Jabbi, Swart, & Keysers, 2007; Mobbs et al., 2009; Morelli, Rameson, & Lieberman, 2014). Hence, the consistent engagement of aMCC and AI in empathy studies might have been biased by this disproportionate focus on negative emotions and on empathy for pain. Furthermore, given the strong association between negative stimuli and high arousal, it might well be that activation of this network is limited to empathy for highly arousing responses – which would be in line with arguments associating these areas predominantly with high arousal, uncertainty and anxiety (e.g., Lamm & Singer, 2010; Paulus & Stein, 2006; Singer, Critchley, & Preuschoff, 2009) and the associated negative affect and withdrawal (e.g., Hayes & Northoff, 2011; Marcoux et al., 2013; see also Knutson, Katovich, & Suri, 2014; Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012 for novel concepts of how emotions might be conceptualized and "detected" based on brain imaging).

This bias in empathy research therefore precludes addressing one of the central tenets of the shared representations account. If it is correct that the vicarious activation of the neural networks involved in the first-hand experience of a certain emotion *enables* an accurate empathic sharing of the other person's affect (see Lamm & Majdandzic, 2014 for more extensive discussion), then different networks should be engaged when empathizing with emotions that are represented on different neural levels.

The few former studies assessing empathy for positive affect are limited in several respects. For instance, some studies report activation only for the observation of positive events, but did not include or analyze vicarious responses to negative events (Hennenlotter et al., 2005; Mobbs et al., 2009). In other studies, which included emotions of both valences, analyses were limited to specific subregions of the brain such as the amygdala, fronto-insular cortex, or premotor areas, or predominantly analyzed correlations with trait empathy (Jabbi et al., 2007; van der Gaag, Minderaa, & Keysers, 2007). Other studies, which had included whole-brain analyses of both valences (e.g., Morelli et al., 2014; Perry, Hendler, & Shamay-Tsoory, 2012), were limited by tapping more into "cognitive" aspects of empathy, or by lacking a condition allowing within-subject comparisons of first-hand and vicariously experienced affect.

The aim of the present study was, therefore, to overcome the limitations of previous work and shed new light on the understanding of the brain mechanisms involved in empathy for both positive and negative emotions. In order to achieve these aims, we developed and implemented a novel paradigm enabling the investigation of first-hand and vicarious responses to pleasant and unpleasant affect via visuo-tactile stimulation. Importantly, this paradigm was novel compared to what has been proposed so far in various aspects. First, it was designed in a way that it allowed us to elicit pleasant and unpleasant affective responses of considerable magnitude directly and "online" in participants lying in the MRI scanner. Secondly, these first hand affective responses were compared in a within-subject analysis with empathy for affective responses that were also evoked directly and "online", using the exact same emotion elicitation procedure being applied to another participant. Note that this other participant was not an imaginary or fictitious other, but was present in the imaging lab and had been personally acquainted with the participant in the scanner at the outset of the experiment. The ecological validity of our paradigm was therefore particularly high, as it involved direct interaction of two participants witnessing other's emotions in the very moment they were happening. Finally, to test the robustness of our findings, we performed two consecutive and independent fMRI experiments with a total sample size of 50 participants.

In summary, this setup enabled the most straightforward test of shared activations during first-hand versus vicariously experienced emotions—as it allowed us to precisely determine for each participant which parts of the brain were activated during the first-hand experience of pleasant and unpleasant touch, and which of these areas were also activated when empathizing with the same types of affective touch.

In line with the predictions of the shared representations of empathy account, we expected to observe two distinct networks as a function of whether subjects were empathizing with unpleasant or pleasant affect elicited via visuo–tactile stimulation, respectively. Hence, empathy for unpleasant touch might distinctly engage areas such as the aIns and the aMCC, given the general role of these areas in coding for negative arousal, their role in empathy for negative emotions, as well as several reports showing the engagement in particular of aIns when witnessing social interactions entailing unpleasant touch (such as hitting a hand or stepping on someone's foot (Decety, Michalska, & Akitsuki, 2008; Grosbras & Paus, 2006)). In contrast, as pleasant touch has been

associated with areas coding for hedonic and pleasant feelings, such as the ventro-medial/medial orbitofrontal cortex (OFC) (e.g., McGlone et al., 2012; Rolls et al., 2003; for review, see Berridge & Kringelbach, 2013; Kringelbach & Rolls, 2004), these areas were predicted to be specifically engaged during empathy for pleasant touch.

2. Material and methods

2.1. Participants

We first performed an exploratory fMRI experiment (fMRI1; N = 18 right handed healthy participants, all female, and mostly students from Zurich and surroundings, age range 18—35), testing the validity and feasibility of our new paradigm as well as exploring for the first time the neural areas involved in it. This experiment was then followed by a second, confirmatory fMRI experiment with an independent sample of N = 32 right handed healthy participants (fMRI2; again, all female, and mostly students from Zurich and surroundings, age range 18—35; in all experiments only participants without past or present neurological or psychiatric disorders, and without contraindications to MRI scanning were included), to determine the robustness of the exploratory findings of fMRI1. Only females were included to increase homogeneity of the sample with respect to behavioral responses and neural activations, as sex/gender differences in empathy and related phenomena have repeatedly been reported (e.g., Singer et al., 2006; Tomova, von Dawans, Heinrichs, Silani, & Lamm, 2014). Note therefore that the conclusions of this study are limited to the female population. All participants gave written informed consent, the study was performed in line with the Declaration of Helsinki, and had been approved by the ethics committee of the University of Zurich.

2.2. Experimental procedures

We developed a new paradigm enabling the repeated elicitation of transient pleasant, neutral, or unpleasant affective responses by means of concurrent visuo-tactile stimulation. Affect was induced, in separate runs, either in participants themselves, or in a confederate acting as a second participant. Participants and confederates were both female and unbeknownst to each other, but had been briefly acquainted to each other at the outset of the experiment when receiving task instructions together. After that, the participant was moved to the scanner, whereas the confederate supposedly underwent visuo-tactile stimulation in an adjacent room of the imaging lab.

Tactile stimulation consisted of touching the left palm with materials that could have, when combined with matching pictures, either a pleasant, unpleasant, or neutral feel — such as a piece of fur, a slimy substance, or a pen. Synchronous to touch, pictures of objects or animals that in reality would feel like the materials with which the participant was being touched were shown to participants. For example, touching the participant's hand with toy slime while she was seeing a picture of a snail was used to elicit unpleasant emotion, while touching the hand with silk and synchronously displaying a

picture of a rose aimed to elicit pleasant emotion (see Fig. 1a, d for a schematic display). The stimuli had been chosen from a larger set validated in a qualitative pretest. Those stimuli that had elicited the highest agreement among participants in terms of congruency between visual stimulus and touch material and emotional responses were selected for final use in the experiments. Note that the emotional valence associated with the visuo-tactile stimulation was specifically related to the *combination* of visual and tactile stimuli. This is so because uni-modal presentation of the stimuli (i.e., visual or tactile only) did not, as revealed when piloting the materials, induce emotional responses of different valence. This also implies that the overlapping neural networks between the self and other conditions cannot be solely attributed to the fact that participants saw similar pictures in these conditions (see Table 1 for a list of the stimuli).

2.3. fMRI experiment 1 (fMRI1)

Each experiment included two main parts, of which only the first one is reported here [results for the second part, focusing on overcoming emotional egocentricity, are reported elsewhere (Silani, Lamm, Ruff, & Singer, 2013)]. In this first part, two scanning runs were performed (*self* and *other* runs), in which participants either underwent visuo-tactile stimulation themselves, or were instructed to deliver empathic judgments of the feelings of the confederate undergoing visuo-tactile stimulation. Visual stimulus presentation was performed using a back-projection system consisting of a rear-view mirror mounted on the scanner's head coil. Visual stimuli were matched across conditions for luminance and semantic category. Tactile stimulation was manually performed by a female experimenter, who was standing next to the participant to touch her left hand, which was resting with the palm facing upwards on a cushion at the edge of the scanner bore. The frequency of the stimulation was set to 1 Hz, starting from the palm towards the fingertips. Each trial (10 for each condition, with conditions unpleasant/neutral/pleasant, condition order randomly permuted) consisted of 10 sec visuo-tactile stimulation (or visual only, for the run *other*, see below), followed by self-report affect judgments delivered using a Likert-type rating scale with nine discrete values (from -4 = very unpleasant over 0 to $+4$ = very pleasant). Ratings were entered by moving a cursor with right index and middle finger button presses, using a response box attached to the right thigh. Response time was limited to 5 sec. Ratings were subsequently rescaled to range from -10 over 0 to $+10$. A black fixation cross on white background was presented during intertrial intervals, which were randomly jittered between 1000 and 2000 msec (mean ITI = 1500 msec). Following this run, the *other* run was performed. In this run, participants saw only the pictures of the objects shown to the other participant (i.e., the confederate), but did not undergo any sort of tactile stimulation. They were instructed to empathize with the other participants, and to rate their emotions using the same rating scale as in the *self* run. Participants were explicitly instructed as follows for the other condition (translated from German): "In the following condition, put yourself in the shoes of the other person in order to feel what she is feeling. Then, rate how she was feeling during the stimulation."
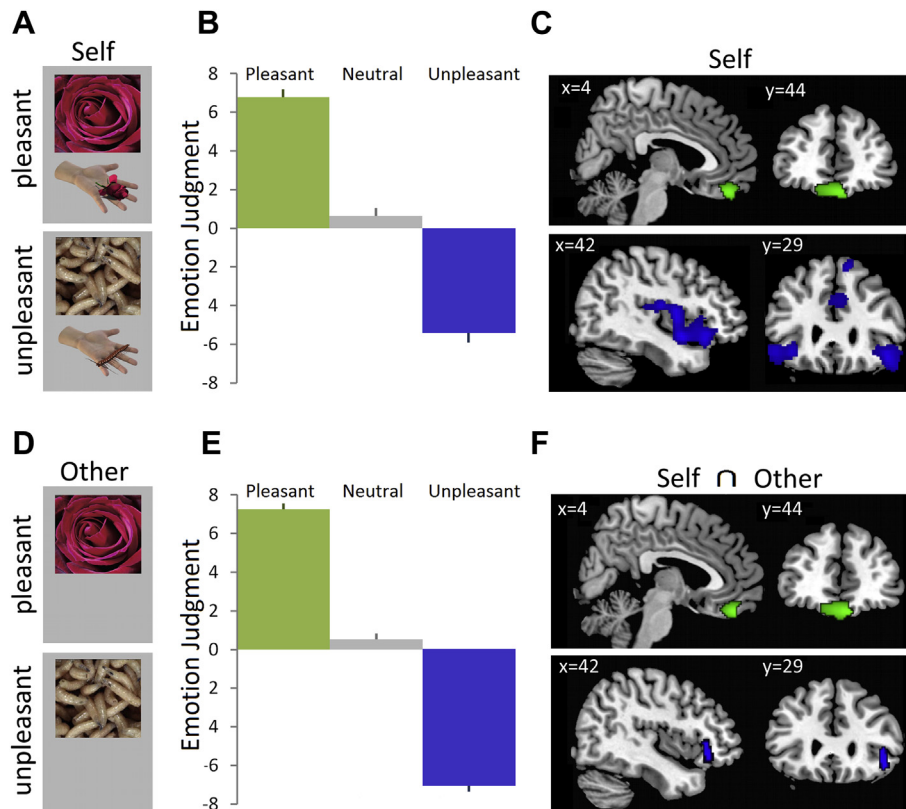
Fig. 1 — **(A) Illustration of the stimulation used in the *self* run. The top row shows the picture participants saw on the screen and the bottom row indicates concurrent touch. During pleasant stimulation, for instance, touch with a soft, rose-like cloth was accompanied by a display of a rose on the screen; for unpleasant stimulation, maggots were shown on the screen while touch was performed using slimy rubber elements designed to feel like maggots. (B) Ratings (mean and SE) of affect during pleasant, neutral and unpleasant visuo-tactile stimulation for fMRI experiment 2. Pleasant stimulation triggered the most positive ratings and unpleasant stimulation the most negative ones. (C) Significant activation for fMRI experiment 2 in mOFC for pleasant (top, green) and in anterior fronto-insular and medial cingulate cortex during unpleasant (bottom, blue) stimulation in the *self* run (contrasts: Self: Pleasant > Unpleasant; Self: Unpleasant > Pleasant; $P_{SVC} = .05$, $k = 10$; numbers indicate stereotactic coordinates of shown slices) (D) Examples for stimuli used in the *other* run. Note that participants did not get touched during these conditions. (E) Ratings of affect (mean and SE) by the other person, during pleasant, neutral and unpleasant stimulation for fMRI experiment 2. (F) Significant clusters (thresholded at $P_{SVC} = .05$, $k = 10$) of the conjunction analysis of activations related to *self* and *other* runs, separately for pleasant (green, top, medial orbitofrontal cortex) and unpleasant affect (blue, bottom, right anterior fronto-insular cortex) (contrasts: Self: Pleasant > Unpleasant ∩ Other: Pleasant > Unpleasant; Self: Unpleasant > Pleasant ∩ Other: Unpleasant > Pleasant) for fMRI experiment 2.**

In both runs, participants were instructed to respond spontaneously, quickly, and accurately. The decision to keep a fixed order (self run before other run) was due to the fact that we first had to provide participants with a direct experience of the combined materials. This was so because only the combined visuo-tactile stimulation was triggering differences in emotional experiences. Hence, participants could only accurately empathize with the other person after having made those emotional experiences themselves.

A 3 T Philips Achieva whole-body MR Scanner at the University Hospital Zurich, equipped with an 8-channel head coil, was used for MRI scanning. Structural images were acquired as 180 T1—weighted transversal images (.75 mm slice thickness). Functional images were acquired using a T2*-weighted echo-planar imaging (EPI) sequence with 33 transversal slices covering the whole brain (slice thickness 3.2 mm; interslice gap 0.5 mm; TR/TE = 2000/35 msec; flip angle = 82°, field of view = 220 x 220 mm^2; matrix size = 128 × 128, SENSE factor 2). A total of 300 volumes was obtained for each run. Data were analysed with SPM8 (Wellcome Department of Imaging Neuroscience, London, UK). All functional volumes were realigned to the first volume, spatially normalized to the standard EPI template, and smoothed using a Gaussian kernel with full width at half maximum (FWHM) of 10 mm^3 (6 mm smoothing at first, 8 mm at second level). Following preprocessing, statistical analysis was carried out using the general linear model. High-pass temporal filtering with a cut-off of 128 sec was used to remove low-frequency drifts. Regressors of interest were convolved with the canonical hemodynamic response function (hrf), and coded the type of trial (pleasant, unpleasant, or neutral stimulation, in self- or other-related runs). A separate regressor was defined for the

Table 1 – List of the stimuli.

Pictures	Materials	Valence
Puppy Dog	Wool	Pleasant
Cotton plant	Cotton	Pleasant
Kitten	Synthetic Fur	Pleasant
Brush	Soft Brush	Pleasant
Sheep	Wool	Pleasant
Rabbit	Synthetic Fur	Pleasant
Swan	Feather	Pleasant
Cotton ball	Cotton	Pleasant
Rose	Silk	Pleasant
Chick	Feather	Pleasant
Mushroom 1	Slimy mushroom	Unpleasant
Cow tongue	Softened Velcro	Unpleasant
Stinkbug	Plastic stinkbug	Unpleasant
Mushroom 2	Gelatine	Unpleasant
Catfish	Small Toy Slime	Unpleasant
Maggots	Toy worms	Unpleasant
Liver	Toy Slime	Unpleasant
Spider	Plastic Spider	Unpleasant
Slug	Plastic slug	Unpleasant
Oyster	Toy Slime	Unpleasant
Box	Cardboard	Neutral
Branch	Branch	Neutral
Dog	Hard Brush	Neutral
Elk	Horn	Neutral
Walnut	Walnut	Neutral
Peanut	Peanut	Neutral
Pen	Plastic Pen	Neutral
Stork	Ivory	Neutral
Tartle	Ivory	Neutral
Wild boar	Hard Brush	Neutral

rating window. The intertrial intervals (fixation) constituted the implicit baseline. Residual effects of head motion were corrected by including the six estimated motion parameters of each participant as regressors of no interest in the design matrix. Given the exploratory nature of this first imaging study, a finite impulse response (FIR) model was implemented in order to explore the time course of the effects. The model showed significant activation restricted to the first seconds of the trial. The 10 sec stimulation window was therefore split into two regressors, one modeling early responses during the first 5 sec of the trial and one regressor of no interest modeling the remaining 5 sec.

Neural activation resulting from contrasts of interest was determined by entering the parameter estimates for each regressor corresponding to the pleasant, unpleasant and neutral conditions from the first-level analyses into 2nd level random effects linear contrasts, allowing for statistical inference at the group level (Penny & Holmes, 2004; for review). Whole-brain random effects conjunction analyses (Nichols, Brett, Andersson, Wager, & Poline, 2005) of contrasts from the *self* and *other* runs were performed in order to identify brain regions activated during both the first-hand and the vicarious experience of pleasant and unpleasant emotions.

The Anatomy Toolbox [version 2.0, (Eickhoff et al., 2005)] and an anatomical atlas (Duvernoy, 1991) were used for anatomical and cytoarchitectonic localization. Given the exploratory nature of fMRI1 we performed whole-brain analyses with thresholds of *p*-values < .005, uncorrected for multiple comparisons, and a cluster size criterion of k = 10

contiguous voxels. This threshold was chosen to minimize the probability of false negatives rather than of false positives—as this was the first and still exploratory fMRI experiment using our newly developed paradigm, which therefore mainly aimed to generate hypotheses rather than testing them with high specificity.

2.4. fMRI experiment 2 (fMRI2)

32 right handed female participants were recruited for fMRI experiment 2 (fMRI2). Based on the exploration of our new paradigm in fMRI1, we made two changes to the paradigm. We shortened the duration of stimulation to 3 sec, as exploratory analyses of fMRI1 had indicated that this was sufficient to observe robust neural activations. The resulting reduction in scanning time per trial enabled us to add additional four trials per condition and therefore to increase efficiency and reliability of the neural and behavioral measures. Second, affect ratings were entered in a more fine-grained manner, using a visual analogue scale. Responses on this scale were entered by moving a cursor using an MRI-compatible track ball device, and the selected screen co-ordinates were converted offline to range from −10 over 0 to +10 (−10 = very unpleasant; +10 = very pleasant; with two decimals resolution).

MRI scanning was performed in the Laboratory for Social and Neural Systems Research, Zurich, using a scanner and head coil of the same make and configuration as the one in fMRI1. 26 transversal slices covering the whole brain with a slice thickness of 3.5 mm were acquired (interslice gap of 0.5 mm; TR/TE = 1500/35 msec; flip angle = 82°; field of view = 220×220 mm^2; matrix size = 80×80, SENSE factor 2). A total of 300 volumes were scanned for each run. Preprocessing and first-level analyses were identical to fMRI1.

We performed contrast analyses targeting our main hypotheses about distinct valence-specific networks (contrasts: self: unpleasant > pleasant; other: unpleasant > pleasant, and vice versa, and conjunction contrasts self & other). In these contrasts, we always directly compared the two different valences against each other (i.e., unpleasant > pleasant, and vice versa) in order to maximize the sensitivity of the analysis for detecting differences in valence (as opposed to contrast each valence against the neutral condition, which, however, yielded similar results). In order to increase the sensitivity of our analyses, we pursued a small volume correction approach (SVC). This entailed using the results of each corresponding contrast in fMRI1 to define an *a priori* search space (consisting of a volume of interest/VOI, including several distinct regions of interest/ROIs, see results), within which activation in the respective contrast of fMRI2 was assessed using a threshold of $p(\text{SVC}) = .05$, k = 10. The motivation of using the SVC approach was that in the presence of strong hypotheses derived from fMRI1, correction for multiple comparisons across the whole brain would have resulted in too conservative statistical testing. Hence, this represents a two-tier strategy in which the sensitivity and the robustness of analyses is increased by assessing fMRI2 findings with strict control of false positives, but only within a more liberally identified network of areas based on fMRI1 (see Poldrack, 2007, as well as Silani, Lamm, Ruff, & Singer, 2013).

2.5. Behavioral data

Behavioral data were analyzed using repeated measures ANOVAs, implemented in SPSS 18.0, with factor valence (pleasant, neutral, unpleasant), calculated separately for the self and other runs, and followed up by a priori linear contrasts and pairwise comparisons. Violations of the sphericity assumption were corrected according to Greenhouse & Geisser (GG).

3. Results

3.1. Behavioral data

Behavioral data of fMRI1 showed that participants clearly and in line with the valence of stimulations distinguished between the three different valence conditions, both when judging first-hand affective experiences [F(2,29.891) = 288.318, $p < .001$, $\eta_p^2 = .944$], and when empathically judging affect felt by the other person [F(2,28.816) = 451.434, $p < .001$, $\eta_p^2 = .964$]. Results of fMRI2 replicated these findings [self: F(2,47.857) = 141.710, $p < .001$, $\eta_p^2 = .821$; other: F(2,44.339) = 409.190, $p < .001$, $\eta_p^2 = .930$; Fig. 1b and e]. Notably, pairwise comparison of pleasant and unpleasant stimulation (using paired samples t-tests, performed separately for self and other judgments) revealed strong significant differences in both experiments (all p-values << .001). Moreover, comparing the intensity of affect ratings revealed that pleasant and unpleasant affect ratings did not differ in intensity both for the self and other runs for fMRI2 [paired t-test of absolute values, self run: t(31) = .457, $p = .651$; other run: t(31) = .286, $p = .776$] while for fMRI1, pleasant stimuli for the self were judged to be more intense than the negative ones [paired t-test of absolute values, self run: t(17) = 3.799, $p = .001$; other run: t(17) = 1.215, $p = .241$]. Ratings showed strong correlations between self and other in both experiments as well (fMRI1/2 pleasant: r = .762/0.684, fMRI1/2 unpleasant: r = .826/0.748; all p-values < .00001; see Fig. 2).
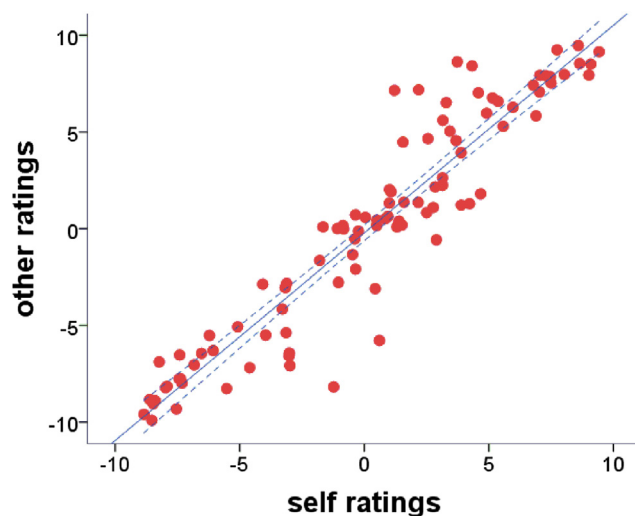

Fig. 2 — Correlation between ratings of affect for pleasant, neutral and unpleasant visuo-tactile stimulation during *self* and *other* runs (in fMRI experiment 2).

3.2. fMRI data

As outlined in the methods section, all results are from experiment fMRI2, with search volumes restricted by the clusters obtained from experiment fMRI1 in the same contrasts. The first-hand experience (run *self*) of pleasant and unpleasant emotions resulted in two clearly distinct neural networks (Fig. 1c and Table 2). While only bilateral medial orbitofrontal cortex (mOFC) was differentially activated during the first-hand experience of pleasant touch (contrast *self: Pleasant > Unpleasant* of fMRI2, $p < .05$ small volume corrected using ROI from fMRI1), being touched by unpleasant stimuli recruited a larger network of areas including the right amygdala, middle and anterior fronto-insular cortex (aIns), and anterior middle cingulate cortex (aMCC; *self: Unpleasant > Pleasant*).

Empathizing (run *other*) with pleasant and unpleasant visuo-tactile stimulation also revealed two distinct neural networks (Table 3). Empathy for pleasant touch predominantly activated the mOFC and areas of the occipital and parietal visual cortex (contrast: *other: Pleasant > Unpleasant*, $p < .05$ SVC), whereas empathy with negative emotions recruited fronto-insular and distinct parts of visual cortex. Notably, parts of these networks specifically overlapped with activations observed during the corresponding pleasant and unpleasant first-hand emotion experiences (Fig. 1f, Table 4). More specifically, conjunction analyses revealed shared activation in the mOFC for pleasant stimulation (conjunction contrast: *Pleasant > Unpleasant: self ∩ other*), and in the right

Table 2 — Significant activations related to direct emotional experiences.

	k	x	y	z	Z scores
Self: Pleasant > Unpleasant					
Orbito-Frontal Cortex	485	10	48	−22	5.03
Orbito-Frontal Cortex	485	6	46	−22	5.01
Orbito-Frontal Cortex	485	−12	38	−16	4.38
Self: Unpleasant > Pleasant					
Superior frontal Gyrus	98	24	56	16	4.53
Supplementary Motor Area	3999	14	16	66	5.18
Middle Cingulate Cortex	3999	8	0	40	4.82
Precentral Gyrus S1	360	26	−24	70	4.28
Rolandic Operculum	7919	62	14	18	4.36
Middle Insula	7919	36	−2	−16	5.57
Middle Insula	2985	−38	0	−10	4.63
Posterior Insula S2	7919	36	−14	16	5.52
Posterior Insula	2985	−36	−20	16	4.74
Superior Temporal Gyrus	7919	58	−14	4	4.62
Superior Temporal Gyrus	2985	−56	−6	4	4.62
Temporal Pole	7919	54	14	−12	5.84
Temporal Pole	2985	−44	18	−16	5.70
Thalamus	7919	6	−18	6	4.81
Thalamus	7919	−8	−16	12	4.60
Amygdala/Parahippocampus	7919	20	0	−22	4.67
Middle Occipital Gyrus	6034	−34	−98	4	6.45
Calcarine Cortex	216	20	−100	−2	4.21
Calcarine Cortex	101	−20	−72	8	4.53
Cerebellum	6034	−24	−68	−24	5.21

k = cluster size, x/y/z = MNI Cartesian coordinates; all clusters from fMRI2, surviving $p < .05$ small-volume multiple comparisons correction on specific masks from fMRI1.

Table 3 – Significant activations related to vicarious emotional experiences.

	k	x	y	z	Z scores
Other: Pleasant > Unpleasant					
Orbito-Frontal Cortex	69	−16	40	−16	6.37
Orbito-Frontal Cortex	19	16	42	−6	4.45
Precentral Gyrus	44	−36	−24	56	5.21
Angular Gyrus	35	48	−68	44	4.14
Sup Temporal Gyrus	13	−60	0	2	3.58
Middle Temporal Gyrus	22	68	−8	−22	3.90
Cuneus	24	10	−92	26	4.48
Lingual Gyrus	200	−4	−94	16	5.86
Other: Unpleasant > Pleasant					
Inferior Frontal Gyrus/ Anterior Insula	34	44	30	−10	3.59
Middle Occipital Gyrus	479	36	−86	18	6.00
Middle Occipital Gyrus	1068	−36	−94	14	5.81
Inf Occipital Gyrus	237	−44	−70	−8	3.68
Fusiform Gyrus	237	−30	−70	−10	4.30
Calcarine Cortex	479	20	−102	−2	4.40

k = cluster size, x/y/z = MNI Cartesian coordinates; all clusters from fMRI2, surviving p < .05 small-volume multiple comparisons correction on specific masks from fMRI1.

anterior fronto-insular cortex (*Unpleasant > Pleasant: self ∩ other*) and the medial occipital cortex for unpleasant stimulation (Fig. 1f).

4. Discussion

The main aim of our study was to test whether empathy for affective touch differing in valence is subserved by shared activations in distinct neural networks. This enabled us to investigate a central claim of the shared representations account of empathy. We used a newly developed visuo-tactile stimulation paradigm tailored to perform a within-subject comparison of activations triggered by the first-hand experience of pleasant or unpleasant touch with activations elicited when vicariously experiencing such touch. Notably, speaking for the robustness of the results, our findings were replicated across two independent fMRI experiments, in a total sample of 50 participants.

The behavioral results indicate that our paradigm was able to trigger first-hand affective experiences of clearly distinct

Table 4 – Shared activations for direct and vicarious emotional experiences.

	k	x	y	z	Z scores
Conjunction Self ∩ Other: Pleasant > Unpleasant					
Orbito-Frontal Cortex	15	−14	38	−16	4.20
Orbito-Frontal Cortex	15	−10	42	−18	4.08
Conjunction Self ∩ Other: Unpleasant > Pleasant					
Inferior Frontal Gyrus/ Anterior Insula	18	44	3230	−10	3.59
Middle Occipital Gyrus	848	−34	−96	12	5.44
Middle Occipital Gyrus	58	34	−86	18	4.48
Fusiform Gyrus	124	−28	−72	−12	4.11

k = cluster size, x/y/z = MNI Cartesian coordinates; all clusters from fMRI2, surviving p < .05 small-volume multiple comparisons correction on specific masks from fMRI1.

valence, and with considerably intensity—as participants on average rated the intensity of their affective responses to be around 70–80 % of the maximum possible intensities. Importantly, as shown by direct statistical comparison, pleasant and unpleasant stimulation were also experienced to be of equal intensities. Hence, comparisons between the two valence categories was not confounded by the frequent phenomenon that negative stimuli trigger more intense responses than positive ones (e.g., Bradley & Lang, 2007). Crucially, when asked to empathize "online" with a confederate undergoing affective stimulation identical to the one they had experienced just before, participants were able to correctly judge the valence of the confederate's emotions, and the intensity of the empathic judgments did not differ between valences either. Moreover, self-related and empathic affect judgments were of similar mean intensity as well, and showed substantial positive correlations. This hints at the interpretation that empathic judgments were based on a simulation of the affective responses of the other.

Directly comparing the first-hand experiences of pleasant and unpleasant touch revealed two distinct neural networks. Pleasant touch, compared to unpleasant touch, was associated with higher mOFC activation, which is well in line with the role of this area in coding pleasant feelings resulting from being touched (e.g., Francis et al., 1999; McCabe, Rolls, Bilderbeck, & McGlone, 2008; McGlone et al., 2012; Rolls et al., 2003). For instance, Rolls & colleagues showed that stimulating the left hand (as we did) using similar materials as used here resulted in activation of a subdivision of mOFC overlapping with the activation identified by our analysis (Rolls et al., 2003). Interestingly, another fMRI study by the same group indicated that activation of mOFC during pleasant touch seems to be modulated by cognitive representations, indicating that the responses of mOFC to pleasant touch might relate to the encoding of subjective pleasure, based on learned associations, rather than being a predisposed, non-learned response driven by the sensory stimulation (McCabe et al., 2008; see also McGlone et al., 2012). This interpretation is also in agreement with the view associating medial OFC with pleasant affect in various domains other than somatosensation (Berridge & Kringelbach, 2013; Kringelbach & Berridge, 2009).

As for MCC, aIns and amygdala which all showed higher activation during the first-hand experience of unpleasant touch, this network has been repeatedly associated with highly arousing and in particular negative-aversive affective states. For instance, MCC and aIns are conjointly activated when the organism needs to flexibly respond to external events requiring autonomic homeostatic and behavioral regulation (e.g., Lamm & Singer, 2010; Medford & Critchley, 2010). Moreover, anterior insula and its interoceptive functions (Craig, 2009) have been specifically linked to highly arousing feeling states, such as anxiety (Paulus, Rogalsky, Simmons, Feinstein, & Stein, 2003; Paulus & Stein, 2006), or the anticipation of negative events (Knutson et al., 2014), and have also being linked to experiencing and imagining gentle touch (Lucas, Anderson, Bolling, Pelphrey, & Kaiser, 2014). While such regulation might in principle also be required for positive events, negative events even when equated for intensity might trigger higher arousal and hence might also

carry higher regulatory and adaptive requirements. Moreover, the current consensus on amygdala function seems to be that this area is predominantly involved in the detection of salient events and the ensuing preparation of autonomic and behavioral responses to them (e.g., Sergerie, Chochol, & Armony, 2008; see also Lindquist et al., 2012). Taken together, the stronger engagement of these areas when undergoing unpleasant touch oneself might suggest a higher salience of the aversive stimulation and the ensuing arousal and mobilization of putative defensive responses to it. Unpleasant compared to pleasant first-hand touch also showed stronger involvement of the primary and secondary visual and somatosensory cortices. The reason for this could be twofold. For one, as just discussed, the negative stimuli's higher salience and arousal might have caused stronger attention in visual and somatosensory areas. On the other hand, the different physical properties of the materials used in the two conditions might account for the activation differences in somatosensory areas. While more soft and light materials (such as down feathers) had been used to induce pleasant affect, more dense and heavier materials had been used to induce unpleasant touch (such as toy slime). These differences could possibly have elicited differential responses on the level of the somatosensory receptors in the stimulated hand (but see also Gazzola et al., 2012 for the specific role of SI during pleasant touch).

It is crucial to note that our paradigm was able to engage two distinct networks associated with the first-hand experience of pleasant and unpleasant touch — which was a precondition for testing our hypothesis that distinctly shared neural networks also underlie the experience of empathy. The conjunction analyses confirmed our main hypothesis that empathy is subserved by two distinct and valence specific neural networks, with those regions recruited in the first-hand experience of positive or negative affect also being specifically recruited when empathizing with these respective states in others. More specifically, the first-hand and vicarious experience of pleasant touch commonly recruited mOFC, while unpleasant stimulation led to shared activation in the right fronto-insular cortex.

It is, moreover, important to stress that this overlap was identified by a within-subject comparison, using a conjunction analysis which directly compares activation obtained during empathy with activation when directly experiencing the very emotions participants were empathizing with. Furthermore, both the first-hand emotion experience and their empathic sharing were induced online, hence eliciting affect and empathy in an immediate and naturalistic fashion—which is in contrast to previous work based on more "cognitive" or "offline" and probably memory-based induction methods (such as vignettes or affective memories) to induce the empathic responses for positive and negative affect (e.g., Perry, Hendler, & Shamay-Tsoory, 2011, 2012; see also Lamm & Majdandzic, 2014; Shamay-Tsoory, 2011; Singer, 2006, for the distinction between the neural networks related to "cognitive" and "affective" empathy).

Interestingly, there were also some differences between the type and amount in which shared activations were engaged. Empathy for pleasant touch was subserved by the only area that was also significantly activated during the first-hand experience of pleasant touch, i.e., the mOFC. Apart from its specific role in coding pleasant touch, this part of the brain has been consistently linked to reward and positive valuation. For instance, a meta-analysis of 87 neuroimaging studies has shown that medial OFC is specifically related to representing pleasure or hedonic value of a variety of both primary (e.g., taste, sound, and touch) and secondary reinforcers (Berridge & Kringelbach, 2008, 2011; Kringelbach & Berridge, 2009; Kringelbach & Rolls, 2004). More recent evidence also suggests that ventromedial prefrontal cortex (vmPFC), i.e., a brain area encompassing mOFC, is not only involved in the coding of self-related rewards, but also engages in social decision making paradigms that require considering the consequences of one's own actions on the affective responses of others (Ruff & Fehr, 2014; for review). Similarly, two recent studies focusing on compassion training showed that activation in mOFC was increased after such training of positive social affect, and that this effect was associated to an increase in feelings of affiliation and positive affect towards another (Klimecki, Leiberg, Lamm, & Singer, 2013; Klimecki, Leiberg, Ricard, & Singer, 2014). Furthermore, Janowksi & colleagues observed increased activation in a very similar subdivision of mOFC to our study when participants were deciding to buy DVDs either for themselves, or for another person (Janowski, Camerer, & Rangel, 2013). This required representing the positive value of DVDs that were liked and therefore should be invested in, in contrast to DVDs that were disliked and on which no money should be spent. Interestingly, other areas of the reward circuitry, such as the ventral striatum, which has been linked to first-hand reward and vicarious reward alike (e.g., Mobbs et al., 2009), have not been identified in our experiment—neither during the direct nor during the vicarious experience of pleasant touch. This might be explained in two ways. For one, since the first-hand experience of pleasant touch did not activate these areas either, the empathic experience of pleasant touch might have closely matched that first-hand experience. Second, their lack of activation might be attributed to the absence of motivational or incentive-driven processes in our paradigm—which in contrast to the typical reward paradigms did not require decisions or responses enabling participants to achieve a reward or a hedonic outcome.

In contrast to the positive domain, empathy for unpleasant touch only involved fronto-insular cortex, i.e., a subset of the full neural network engaged during the direct experience of unpleasant visuo-tactile stimulation. Activation in the amygdala, the aMCC, and in motor areas (which were involved during the first-hand experience of unpleasant touch) was not shared during empathy for unpleasant touch. This selectivity in sharing only parts of the neural processes underlying the direct emotion experience may be explained by the higher arousal and possibly a higher withdrawal tendency in response to the first-hand experience of the unpleasant stimuli.

There seems to be increasing consensus that the anterior subdivision of insular cortex is related to interoception and the sense of bodily awareness, and a large body of evidence suggests that this area is recruited during both social and non-social emotions (e.g., Craig, 2009; Lamm & Singer, 2010; for review). It has also been proposed that anterior insular cortex

plays an integrative role in the generation of predictive models about other's feeling states, grounded in one's own representation of the same feeling states (Singer et al., 2009). Surprisingly, though, this model only seems to apply to unpleasant touch in the present study. This at first sight might be counterintuitive as positive affect is also known to induce bodily responses that require interoception, and as the anterior fronto-insular cortex in a very similar part as the one detected here has even been associated with empathy for pleasant gustatory experiences (Jabbi et al., 2007). On the other hand, fronto-insular cortex was not even activated during the first-hand experience of pleasant touch (not even when contrasted against the low-level fixation baseline, data not shown). Hence, one explanation for this finding might be that while the unpleasant stimulation was sufficiently arousing, both for its first-hand and vicarious experience, pleasant touch had a rather soothing quality and limited bodily arousal. This hypothesis needs to be tested by future studies though as we did not include behavioral or psychophysiological measures of arousal or its modulation.

Interestingly, empathizing with unpleasant and pleasant affective touch differentially engaged neither primary nor secondary somatosensory cortex. This observation is surprising in light of several recent reports and theoretical models assigning a prominent role to somatosensory cortex in empathy and affect sharing (Keysers, Kaas, & Gazzola, 2010; for review). For instance, observing the body parts of others being touched recruits S1 and S2 (e.g., Blakemore, Bristow, Bird, Frith, & Ward, 2005; Ebisch et al., 2011; Keysers et al., 2010, for review), and activation in right S1 even plays a causal role in sharing affective touch (Bolognini, Rossetti, Convento, & Vallar, 2013). Apart from the fact that these studies have not been tailored to compare different valences of touch, the possible discrepancy between our and previous results might be addressed in a similar way as a comparable controversy in the literature on empathy for pain. While earlier findings (Singer et al., 2004) had suggested that only the affective component of pain is empathically shared, later reports had documented somatosensory sharing as well (e.g., Bufalari, Aprile, Avenanti, Di Russo, & Aglioti, 2007; Riecansky, Paul, Kolble, Stieger, & Lamm, 2014). This discrepancy lately has been attributed to the way in which empathy was experimentally evoked (Keysers et al., 2010; Lamm et al., 2011). More specifically, showing pictures of body parts in pain did more consistently activate somatosensory areas, while conveying the pain of others by means of abstract visual cues did not. The same logic might apply to the domain of affective touch, as we — in contrast to most previous work on empathy for touch—did not show touched body parts to participants, but only used pictures of objects from which their somatosensory "feel" for the other person had to be inferred.

Notably, the present results rely on female participants only. While folk psychology seems to predict that the two sexes/genders strongly differ in empathy, recent meta-analysis of neuroimaging data (Lamm et al., 2011) and large sample questionnaire studies (Koller & Lamm, 2014) suggest that these differences are absent or small. Based on this evidence, it may seem unlikely that males will engage radically different neural mechanisms to share another person's affective touch than females. However, other studies using specific experimental manipulations such as modulating the perceived fairness of interaction partners or stressing participants have reported significant sex/gender differences (Singer et al., 2006; Tomova et al., 2014; see also Christov-Moore et al., 2014, for comprehensive review). Hence, it will be important to test whether the current results also extend to the male population.

In conclusion, as proposed by the shared representations account, our study indicates that specifically tailored subsystems of the human brain seem to be engaged to share positive versus negative touch of others. The direct comparison of different emotion valences within one study has also wider implications for social cognition and neuroscience models of empathy, which apart from few exceptions so far largely focused on empathy's role in the domain of negative affect and pain. Future investigations should also expand the current approach to include different types of emotions, and test whether there is not only a specificity of shared representations across valences, but also across different types of emotions in general. Ultimately, this will bring us closer to the goal of the social neuroscience of empathy, which is to pinpoint which aspects of the emotions of others are specifically shared, and what role this sharing plays in enabling the understanding of the affective states of others.

Acknowledgments

REFERENCES

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.

Berridge, K. C., & Kringelbach, M. L. (2008). Affective neuroscience of pleasure: reward in humans and animals. *Psychopharmacology, 199*(3), 457–480. http://dx.doi.org/10.1007/s00213-008-1099-6.

Berridge, K. C., & Kringelbach, M. L. (2011). Building a neuroscience of pleasure and well-being. *Psychology of Well Being, 1*(1), 1–3. http://dx.doi.org/10.1186/2211-1522-1-3.

Berridge, K. C., & Kringelbach, M. L. (2013). Neuroscience of affect: brain mechanisms of pleasure and displeasure. *Current Opinion in Neurobiology, 23*(3), 294–303. http://dx.doi.org/10.1016/j.conb.2013.01.017.

Blakemore, S. J., Bristow, D., Bird, G., Frith, C., & Ward, J. (2005). Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. *Brain, 128*(Pt 7), 1571–1583. http://dx.doi.org/10.1093/brain/awh500. awh500.

Bolognini, N., Rossetti, A., Convento, S., & Vallar, G. (2013). Understanding others' feelings: the role of the right primary somatosensory cortex in encoding the affective valence of others' touch. *Journal of Neuroscience, 33*(9), 4201–4205. http://dx.doi.org/10.1523/JNEUROSCI.4498-12.2013.

Bradley, M. M., & Lang, P. J. (2007). The international affective picture system (IAPS) in the study of emotion and attention. In J. A. Coan, & J. J. B. Allen (Eds.), *Handbook of emotion elicitation and assessment* (pp. 29–46). Oxford: Oxford University Press.

Bufalari, I., Aprile, T., Avenanti, A., Di Russo, F., & Aglioti, S. M. (2007). Empathy for pain and touch in the human somatosensory cortex. *Cerebral Cortex, 17*(11), 2553–2561. http://dx.doi.org/10.1093/cercor/bhl161. bhl161.

Christov-Moore, L., Simpson, E. A., Coude, G., Grigaityte, K., Iacoboni, M., & Ferrari, P. F. (2014). Empathy: gender effects in brain and behavior. *Neuroscience & Biobehavioral Reviews, 46*(Pt 4), 604–627. http://dx.doi.org/10.1016/j.neubiorev.2014.09.001.

Craig, A. D. (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. nrn2555.

Decety, J. (2010). To what extent is the experience of empathy mediated by shared neural circuits? *Emotion Review, 2*(3), 204–207. http://dx.doi.org/10.1177/1754073910361981.

Decety, J. (2011). The neuroevolution of empathy. *Annals of the New York Academy of Sciences, 1231*(1), 35–45. http://dx.doi.org/10.1111/j.1749-6632.2011.06027.x.

Decety, J., Michalska, K. J., & Akitsuki, Y. (2008). Who caused the pain? A functional MRI investigation of empathy and intentionality in children. *Neuropsychologia, 46*(11), 2607–2614. http://dx.doi.org/10.1016/j.neuropsychologia.2008.05.026.

Duvernoy, H. M. (1991). *The human brain. Surface, three-dimensional sectional anatomy and MRI.* Wien: Springer-Verlag.

Ebisch, S. J., Ferri, F., Salone, A., Perrucci, M. G., D'Amico, L., Ferro, F. M., et al. (2011). Differential involvement of somatosensory and interoceptive cortices during the observation of affective touch. *Journal of Cognitive Neuroscience, 23*(7), 1808–1822. http://dx.doi.org/10.1162/jocn.2010.21551.

Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., et al. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage, 25*, 1325–1335.

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.

Francis, S., Rolls, E. T., Bowtell, R., McGlone, F., O'Doherty, J., Browning, A., et al. (1999). The representation of pleasant touch in the brain and its relationship with taste and olfactory areas. *NeuroReport, 10*(3), 453–459.

van der Gaag, C., Minderaa, R. B., & Keysers, C. (2007). Facial expressions: what the mirror neuron system can and cannot tell us. *Society for Neuroscience, 2*(3–4), 179–222. http://dx.doi.org/10.1080/17470910701376878, 780680218.

Gazzola, V., Spezio, M. L., Etzel, J. A., Castelli, F., Adolphs, R., & Keysers, C. (2012). Primary somatosensory cortex discriminates affective significance in social touch. *Proceedings of the National Academy of Sciences of the United States of America, 109*(25), E1657–E1666. http://dx.doi.org/10.1073/pnas.1113211109.

Grosbras, M. H., & Paus, T. (2006). Brain networks involved in viewing angry hands or faces. *Cerebral Cortex, 16*(8), 1087–1096. http://dx.doi.org/10.1093/cercor/bhj050. bhj050.

Hayes, D. J., & Northoff, G. (2011). Identifying a network of brain regions involved in aversion-related processing: a cross-species translational investigation. *Frontiers in Integrative Neuroscience, 3*(5), 49.

Hennenlotter, A., Schroeder, U., Erhard, P., Castrop, F., Haslinger, B., Stoecker, D., et al. (2005). A common neural basis for receptive and expressive communication of pleasant facial affect. *NeuroImage, 26*(2), 581–591. http://dx.doi.org/10.1016/j.neuroimage.2005.01.057. S1053-8119(05)00082-0.

Jabbi, M., Swart, M., & Keysers, C. (2007). Empathy for positive and negative emotions in the gustatory cortex. *NeuroImage, 34*(4), 1744–1753. http://dx.doi.org/10.1016/j.neuroimage.2006.10.032. S1053-8119(06)01078-0.

Janowski, V., Camerer, C., & Rangel, A. (2013). Empathic choice involves vmPFC value signals that are modulated by social processing implemented in IPL. *Social Cognitive and Affective Neuroscience, 8*(2), 201–208. http://dx.doi.org/10.1093/scan/nsr086.

Keysers, C., Kaas, J. H., & Gazzola, V. (2010). Somatosensation in social perception. *Nature Reviews Neuroscience, 11*(6), 417–428. http://dx.doi.org/10.1038/nrn2833. nrn2833.

Klimecki, O. M., Leiberg, S., Lamm, C., & Singer, T. (2013). Functional neural plasticity and associated changes in positive affect after compassion training. *Cerebral Cortex, 23*(7), 1552–1561. 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*(6), 873–879. http://dx.doi.org/10.1093/scan/nst060.

Knutson, B., Katovich, K., & Suri, G. (2014). Inferring affect from fMRI data. *Trends in Cognitive Science, 18*(8), 422–428. http://dx.doi.org/10.1016/j.tics.2014.04.006.

Koller, I., & Lamm, C. (2014). Item response model investigation of the (German) interpersonal reactivity index empathy questionnaire. Implications for analyses of group differences. *European Journal of Psychological Assessment.* http://dx.doi.org/10.1027/1015-5759/a000227.

Kringelbach, M. L., & Berridge, K. C. (2009). Towards a functional neuroanatomy of pleasure and happiness. *Trends in Cognitive Science, 13*(11), 479–487. http://dx.doi.org/10.1016/j.tics.2009.08.006. S1364-6613(09)00172-7.

Kringelbach, M. L., & Rolls, E. T. (2004). The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Progress in Neurobiology, 72*(5), 341–372. http://dx.doi.org/10.1016/j.pneurobio.2004.03.006. S0301008204000395.

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., & Majdandzic, J. (2014). The role of shared neural activations, mirror neurons, and morality for empathy - a critical comment. *Neuroscience Research.* http://dx.doi.org/10.1016/j.neures.2014.10.008. EPub ahead of print.

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

Lindquist, K. A., Wager, T. D., Kober, H., Bliss-Moreau, E., & Barrett, L. F. (2012). The brain basis of emotion: a meta-analytic review. *The Behavioral and brain sciences, 35*(3), 121–143. http://dx.doi.org/10.1017/S0140525X11000446.

Lucas, M. V., Anderson, L. C., Bolling, D. Z., Pelphrey, K. A., & Kaiser, M. D. (2014). Dissociating the neural correlates of experiencing and imagining affective touch. *Cerebral Cortex.* http://dx.doi.org/10.1093/cercor/bhu061.

Marcoux, L. A., Michon, P. E., Voisin, J. I., Lemelin, S., Vachon-Presseau, E., & Jackson, P. L. (2013). The modulation of somatosensory resonance by psychopathic traits and empathy. *Frontiers in Human Neuroscience, 7*, 274. http://dx.doi.org/10.3389/fnhum.2013.00274.

McCabe, C., Rolls, E. T., Bilderbeck, A., & McGlone, F. (2008). Cognitive influences on the affective representation of touch and the sight of touch in the human brain. *Social Cognitive and Affective Neuroscience, 3*(2), 97–108. http://dx.doi.org/10.1093/scan/nsn005.

McGlone, F., Olausson, H., Boyle, J. A., Jones-Gotman, M., Dancer, C., Guest, S., et al. (2012). Touching and feeling: differences in pleasant touch processing between glabrous and hairy skin in humans. *European Journal of Neuroscience, 35*(11), 1782–1788. http://dx.doi.org/10.1111/j.1460-9568.2012.08092.x.

Medford, N., & Critchley, H. D. (2010). Conjoint activity of anterior insular and anterior cingulate cortex: awareness and response. *Brain Struct Funct, 214*(5–6), 535–549. http://dx.doi.org/10.1007/s00429-010-0265-x.

Mobbs, D., Yu, R., Meyer, M., Passamonti, L., Seymour, B., Calder, A. J., et al. (2009). A key role for similarity in vicarious reward. *Science, 324*(5929), 900. http://dx.doi.org/10.1126/science.1170539.

Morelli, S. A., Rameson, L. T., & Lieberman, M. D. (2014). The neural components of empathy: predicting daily prosocial behavior. *Social Cognitive and Affective Neuroscience, 9*(1), 39–47. http://dx.doi.org/10.1093/scan/nss088.

Nichols, T., Brett, M., Andersson, J., Wager, T., & Poline, J. B. (2005). Valid conjunction inference with the minimum statistic. *NeuroImage, 25*(3), 653–660. http://dx.doi.org/10.1016/j.neuroimage.2004.12.005. S1053-8119(04)00750-5.

Paulus, M. P., Rogalsky, C., Simmons, A., Feinstein, J. S., & Stein, M. B. (2003). Increased activation in the right insula during risk-taking decision making is related to harm avoidance and neuroticism. *NeuroImage, 19*(4), 1439–1448. S1053811903002519.

Paulus, M. P., & Stein, M. B. (2006). An insular view of anxiety. *Biological Psychiatry, 60*(4), 383–387. http://dx.doi.org/10.1016/j.biopsych.2006.03.042. S0006-3223(06)00476-8.

Penny, W. D., & Holmes, A. (2004). Random-effects analysis. In W. Penny, A. Holmes, & K. J. Friston (Eds.), *Human brain function* (pp. 843–850). San Diego: Elsevier.

Perry, D., Hendler, T., & Shamay-Tsoory, S. G. (2011). Projecting memories: the role of the hippocampus in emotional mentalizing. *NeuroImage, 54*(2), 1669–1676. http://dx.doi.org/10.1016/j.neuroimage.2010.08.057.

Perry, D., Hendler, T., & Shamay-Tsoory, S. G. (2012). Can we share the joy of others? Empathic neural responses to distress vs joy. *Social Cognitive and Affective Neuroscience, 7*(8), 909–916. http://dx.doi.org/10.1093/scan/nsr073.

Poldrack, R. A. (2007). Region of interest analysis for fMRI. *Social Cognitive and Affective Neuroscience, 2*, 67–70.

Riecansky, I., Paul, N., Kolble, S., Stieger, S., & Lamm, C. (2014). Beta oscillations reveal ethnicity ingroup bias in sensorimotor resonance to pain of others. *Social Cognitive and Affective Neuroscience.* http://dx.doi.org/10.1093/scan/nsu139.

Rolls, E. T., O'Doherty, J., Kringelbach, M. L., Francis, S., Bowtell, R., & McGlone, F. (2003). Representations of pleasant and painful touch in the human orbitofrontal and cingulate cortices. *Cerebral Cortex, 13*(3), 308–317.

Ruff, C. C., & Fehr, E. (2014). The neurobiology of rewards and values in social decision making. *Nature Reviews Neuroscience.* http://dx.doi.org/10.1038/nrn3776.

Sergerie, K., Chochol, C., & Armony, J. L. (2008). The role of the amygdala in emotional processing: a quantitative meta-analysis of functional neuroimaging studies. *Neuroscience & Biobehavioral Reviews, 32*(4), 811–830. http://dx.doi.org/10.1016/j.neubiorev.2007.12.002. S0149-7634(08)00007-9.

Shamay-Tsoory, S. G. (2011). The neural bases for empathy. *The Neuroscientist, 17*(1), 18–24. http://dx.doi.org/10.1177/1073858410379268.

Silani, G., Lamm, C., Ruff, C. C., & Singer, T. (2013). Right supramarginal gyrus is crucial to overcome emotional egocentricity bias in social judgments. *The Journal of Neuroscience, 33*(39), 15466–15476. http://dx.doi.org/10.1523/JNEUROSCI.1488-13.2013.

Singer, T. (2006). The neuronal basis and ontogeny of empathy and mind reading: review of literature and implications for future research. *Neuroscience & Biobehavioral Reviews, 30*(6), 855–863. http://dx.doi.org/10.1016/j.neubiorev.2006.06.011. S0149-7634(06)00052-2.

Singer, T., Critchley, H. D., & Preuschoff, K. (2009). A common role of insula in feelings, empathy and uncertainty. *Trends in Cognitive Science, 13*(8), 334–340. http://dx.doi.org/10.1016/j.tics.2009.05.001. S1364-6613(09)00135-1.

Singer, T., & Lamm, C. (2009). The social neuroscience of empathy. *Annals of the New York Academy of Sciences, 1156*, 81–96. http://dx.doi.org/10.1111/j.1749-6632.2009.04418.x. NYAS04418.

Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not the sensory components of pain. *Science, 303*, 1157–1161.

Singer, T., Seymour, B., O'Doherty, J. P., Stephan, K. E., Dolan, R. D., & Frith, C. D. (2006). Empathic neural responses are modulated by the perceived fairness of others. *Nature, 439*, 466–469.

Tomova, L., von Dawans, B., Heinrichs, M., Silani, G., & Lamm, C. (2014). Is stress affecting our ability to tune into others? Evidence for gender differences in the effects of stress on self-other distinction. *Psychoneuroendocrinology, 43*, 95–104. http://dx.doi.org/10.1016/j.psyneuen.2014.02.006.