

Is emotional contagion special? An fMRI study on neural systems for affective and cognitive empathy

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ABSTRACT

Empathy allows us to simulate others' affective and cognitive mental states internally, and it has been proposed that the mirroring or motor representation systems play a key role in such simulation. As emotions are related to important adaptive events linked with benefit or danger, simulating others' emotional states might constitute of a special case of empathy. In this functional magnetic resonance imaging (fMRI) study we tested if emotional versus cognitive empathy would facilitate the recruitment of brain networks involved in motor representation and imitation in healthy volunteers. Participants were presented with photographs depicting people in neutral everyday situations (cognitive empathy blocks), or suffering serious threat or harm (emotional empathy blocks). Participants were instructed to empathize with specified persons depicted in the scenes. Emotional versus cognitive empathy resulted in increased activity in limbic areas involved in emotion processing (thalamus), and also in cortical areas involved in face (fusiform gyrus) and body perception, as well as in networks associated with mirroring of others' actions (inferior parietal lobule). When brain activation resulting from viewing the scenes was controlled, emotional empathy still engaged the mirror neuron system (premotor cortex) more than cognitive empathy. Further, thalamus and primary somatosensory and motor cortices showed increased functional coupling during emotional versus cognitive empathy. The results suggest that emotional empathy is special. Emotional empathy facilitates somatic, sensory, and motor representation of other peoples' mental states, and results in more vigorous mirroring of the observed mental and bodily states than cognitive empathy.

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Introduction

Emotional processes assess the importance of sensory events to our well-being and adjust our physiological, behavioural, and cognitive responses to cope with the presented challenges. Emotions occur when we observe events that are potentially harmful or beneficial to ourselves, and they prepare us to engage in appropriate approach–avoidance behaviour. Perception of other peoples' emotional states can also result in spontaneous emotional empathy or emotional contagion, that is, elicitation of corresponding emotions and respective approach–avoidance behaviour in the observer (Hatfield et al., 1994). Empathy is, however, a broad concept that refers to our ability to mentally simulate others' – not necessarily emotional but also cognitive – mental states, which helps us to predict their experiences, intentions, and needs (Preston and de Waal, 2002). Recent studies have suggested that both emotional and cognitive

empathy may be based on so-called mirroring systems, that is, automatic activation of the motor representations of the observed actions (Carr et al., 2003; Leslie et al., 2004; Wild et al., 2003), which helps us to understand others' mental states via simulation. Given the special role of the emotion networks in automatic management of human information processing priorities, physiological states, and motivational dispositions (Lang et al., 1990), we wanted to compare whether i) emotional and cognitive empathy recruit the motor/action representation systems to similar extent and ii) whether emotional and cognitive empathy recruit different brain networks extending beyond the action representation system.

The mirror neurons found in the ventral premotor (area F5) and parietal (area PF) cortex fire both when a monkey observes or performs a goal-directed action (Rizzolatti et al., 2001) and it has thus been argued that understanding of others' behaviour is based on mapping of a motor or somatosensory representation of the observed action (Brass and Heyes, 2005). Neuroimaging studies in humans have generally supported this notion. First, both perceiving and executing an action activates the premotor cortex, providing evidence for action observation/execution matching system in humans (Hari et al., 1998).

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Further studies have shown that in addition to the premotor cortex, brain networks focused around the temporo-parietal junction (Jackson et al., 2006; Lyons et al., 2006) and inferior frontal cortex (Iacoboni et al., 2005; Iacoboni et al., 1999) are involved in action mirroring and understanding others' behaviour. This mirroring phenomenon is qualified by two findings. First, inferior frontal cortical regions show stronger activation for performing, for example, hand actions that are triggered by observing of similar (imitation) versus dissimilar hand movements or simple spatial cues, suggesting an imitation mechanism that directly matches the observed action into its motor representation (Iacoboni et al., 1999). Second, the motor representation of an action is activated more strongly when the observed action is perceived from first-person versus third-person viewpoint (Jackson et al., 2006), suggesting a viewpoint-specific representation of the actions.

Mirroring effects have been reported for observing of emotional behaviours as well. Observing and experiencing of disgust activates overlapping regions in an emotional circuit involving insula (Wicker et al., 2003), thus it can be argued that mere perception of others' emotional states may elicit corresponding empathetic reactions in the observer. Moreover, as participants' self-reported empathy skills predict insular responses to perception of others positive and negative gustatory emotions (Jabbi et al., 2007), it is likely that the insular cortex plays a key role in transforming observed emotional states into experienced states. It has also been shown that observation and imitation of facial expressions activate the same premotor areas (Carr et al., 2003; Leslie et al., 2004; Wild et al., 2003), thus providing support for the hypothesis that a common coding mechanism for observation and experience of emotions might account for the contagion of emotional responses (i.e., emotional empathy).

The above studies thus suggest that both emotional and cognitive empathy rely on the mirror neuron or action representation circuit. In general, largest overlap between brain activations resulting from action observation, simulation, and execution are manifested in the supplementary motor and dorsal premotor cortex, the supramarginal gyrus, and the superior parietal lobe (Grèzes and Decety, 2001). This can thus be considered as the “core” system for all types of empathy, as it provides elementary understanding of others' actions and behaviours via motor simulation. Nevertheless, the studies on emotional empathy (Jabbi et al., 2007; Wicker et al., 2003) also show that emotional empathy recruits various “extended” systems (such as insular cortex) for understanding others emotional states; these systems are not empathy-specific but are also involved in perceiving and generating emotional states. However, it is not known whether a similar extended system would be involved in cognitive empathy as well. Emotional reactions often occur rapidly and involuntarily (see below), whereas understanding others' nonemotional mental states often requires voluntary effort and active mentalizing. The medial prefrontal cortex (mPFC) around BA 8 has been implicated in both empathy and “theory of mind” processing (Gallagher and Frith, 2003). Thus, it is likely that the mentalizing or theory of mind systems would constitute the extended system for cognitive empathy.

Additionally, three lines of evidence suggest that emotional empathy might engage the “core” empathy system more effectively than cognitive empathy does. First, information about the emotional valence of a stimulus is rapidly forwarded to the somatosensory cortices, resulting in a bodily reaction of emotion such as freezing (Adolphs, 2002). Studies employing the startle reflex paradigm have demonstrated that emotional reactions facilitate behavioural responses that are congruent with the experienced emotion. Specifically, viewing unpleasant emotional stimuli potentiates and viewing pleasant pictures inhibits startle responses to independent probe stimuli, thus suggesting a tight coupling between the emotional and motor systems (Lang, 1995). Second, a bulk of psychophysiological experiments has suggested that emotional contagion is an automatic and rapid process. These studies have measured facial electromy-

graphic (EMG) responses to pictures of facial expressions, and have revealed that people unconsciously and rapidly (i.e. within hundreds of ms) mimic the expressions presented to them (Dimberg and Thunberg, 1998; Dimberg et al., 2000). These facial responses do not constitute of purely physical imitation, instead, it is likely that emotional contagion plays a role here. This is clearly illustrated in studies which have shown that hearing of vocal expressions (Hietanen et al., 1998) or viewing of body postures (Magnee et al., 2007) of positive/negative emotions results in corresponding facial expressions in the observer. This implies that the “emotional mirroring” may be supported by two separate pathways: one that is based purely on physical imitation (similar to any motor imitation) of the observed emotional behaviour, and another that is based on the somatosensory and motor responses triggered by the emotional content of the stimulus. Third, a recent magnetoencephalographic (MEG) study suggested that there may exist a filtering mechanism which assesses the social relevance of an observed action and modulates how the information is forwarded to the areas subserving its motor representation (Kilner et al., 2006). If such a social relevance filter exists, it will most likely be biased to forward emotional information to the action representation systems, as emotional events have high adaptive significance.

There are good reasons to expect that emotional empathy would facilitate the involvement of the motor and somatosensory representation of other's bodily states via thalamocortical modulation. All incoming subcortical input to the human cortex – including somatosensory and motor cortices – is relayed via thalamus (Behrens et al., 2003), and thalamus is involved in the coordination of integrated behavioural and autonomic expression of emotions (Bard, 1928) as well as regulation of arousal (McCormick and Bal, 1997). Thalamus has also been implicated in the network of structures mediating interoceptive awareness of autonomic arousal (Pollatos et al., 2007), and interoceptive awareness of one's own (simulated) emotional reactions is likely to play a role in emotional empathy. Previous studies have demonstrated thalamic activation in the context of perceiving threatening visual material (Lane et al., 1997; Stark et al., 2004), and it has been shown that thalamus is activated by both perception and assessment of the intensity of other's pain (Jackson et al., 2006). As appraisal of others' emotional states is an essential prerequisite of accurate empathizing, these data suggest that thalamus may be directly involved in the process of emotional mirroring.

The present study

Taken together, the studies reviewed above suggest that the activity of the mirroring or core empathy systems would be enhanced if the target of empathy would be expressing an emotional state. In other words, it can be hypothesized that when compared to cognitive empathy, emotional empathy would facilitate the recruitment of brain networks involved in action observation and imitation. Further, different extended empathy networks are likely to be recruited for emotional versus cognitive empathy. To test these hypotheses, we measured brain activity with functional magnetic resonance imaging (fMRI) while the participants were empathizing persons involved in emotional and neutral activities. Our study involved two methodological advances. First, to compare brain networks for cognitive and emotional empathy in complex social situations, we presented participants with scenes – not just facial expressions – depicting interpersonal nonemotional activities (cognitive empathy blocks) or threat scenes involving an attacker and a victim (emotional empathy blocks). This enabled us to study the brain mechanisms of empathy under conditions in which the participants actually perceive the reactions of the target of the empathy (as is usually the case). As a secondary aim, we wanted to compare whether empathizing of approach and avoidance-related emotional reactions result in differential activity in the mirroring system. To that end, the participants

were asked to empathize with the attackers and the victims on separate blocks. By comparing the blood oxygenation level-dependent (BOLD) signal during the emotional and cognitive empathy blocks, and by comparing the BOLD signal during empathize aggressor and empathize victim blocks with each other, we aimed at determining i) whether emotional empathy increases activity in the core action representation and imitation networks, ii) whether emotional and cognitive empathy recruit different extended empathy networks, and iii) whether there are any differences in brain networks for approach (aggressive) and withdrawal (fearful)-related empathy. Second, to specifically test our hypothesis regarding the thalamic involvement in emotional empathy, we used anatomically unconstrained psychophysiological interactions (Friston et al., 1997) to assess the functional connectivity of the thalamus during emotional versus cognitive empathy. This enabled us to pinpoint the brain regions that show higher neuronal “coupling” with thalamus during emotional versus cognitive empathy.

Materials and methods

Participants

We scanned 10 neurologically intact, volunteer females (mean age = 26 years, SD = 5.6 years, range 21–37 years). Female participants were chosen to maximize the power of the experiment, as when compared to males, females typically experience and portray more

intensive emotional reactions, and show greater facial mimicry as indexed by EMG (Grossman and Wood, 1993). Participants with a self-reported history of neurological or psychiatric disease and those currently taking medication affecting the central nervous system were excluded from the study. Participants were screened for depression with BDI-II (Beck et al., 1988) and trait anxiety with STAI-form 2 (Spielberger, 1983). All participants had normal or corrected-to-normal vision and those who were using vision correction used contact lenses during the scanning. Prior to the scanning, pregnancy was excluded by measuring human chorionic gonadotropin (hCG) levels in the serum. The study protocol was reviewed and approved by the joint ethical committee of Turku University Hospital and the University of Turku, and all participants signed ethical committee-approved, informed consent forms. The study was performed in accordance with the Declaration of Helsinki.

Stimuli

The stimuli (see Fig. 1 for illustrations) were sixty digitized color pictures. Two categories of pictures were used: visually matched aversive (30) and neutral (30) scenes, each depicting two persons. Aversive pictures portrayed interpersonal attack scenes such as strangling or threatening with a baseball bat, while neutral pictures showed daily nonemotional activities such as having a conversation or giving instructions. Attack scenes were used because they are known to evoke reliable changes in reflex physiology (Bradley et al., 2001) as

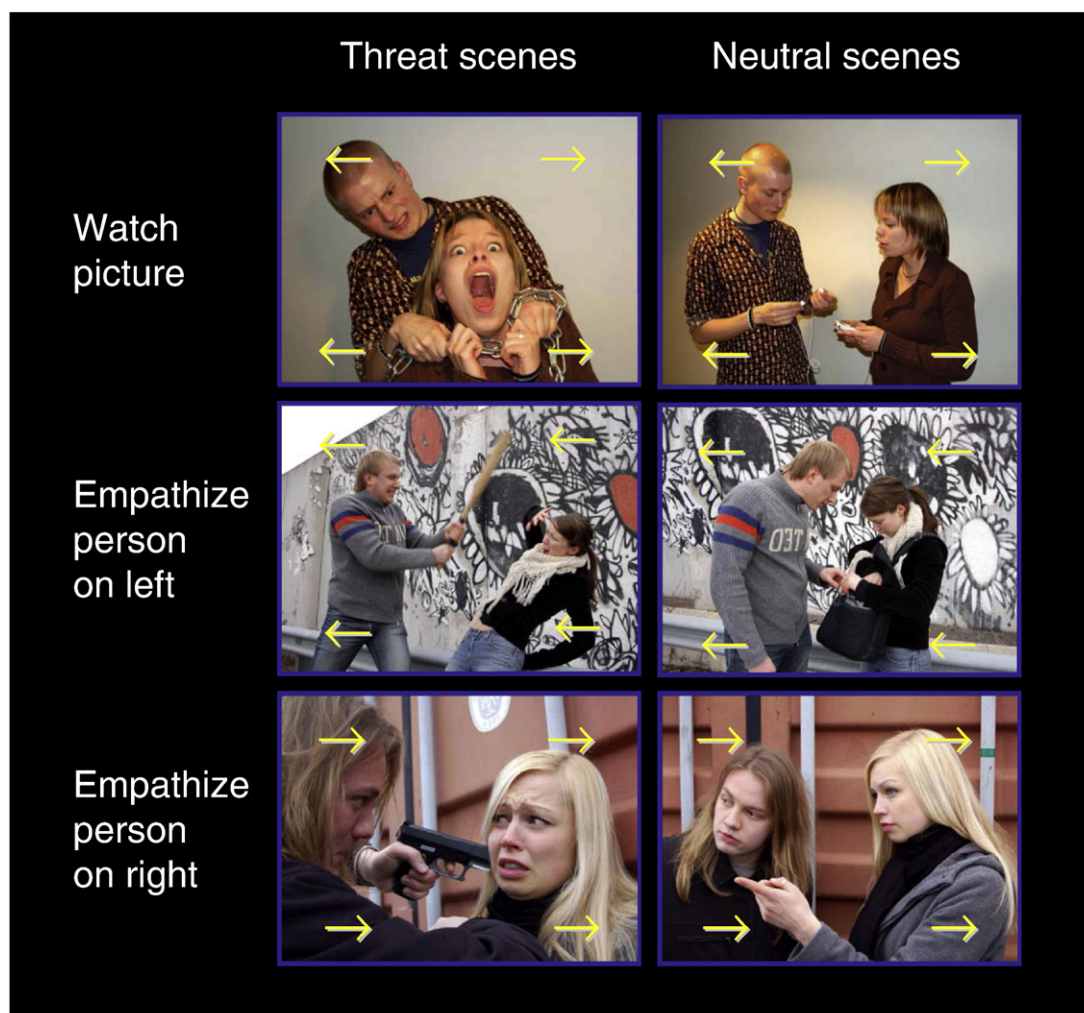


Fig. 1. Examples of emotional (left panel) and corresponding neutral control pictures (right panel) with instructions to watch pictures (upper row), empathize with person on left (attacker and neutral, middle row) and empathize with person on right (victim and neutral, bottom row).

well as in brain metabolism (Bradley et al., 2003). The attack and neutral scenes were equated in terms of luminosity, average contrast density, global energy and complexity ($Z:s<1.2$, $ps>.05$). We also measured the pixel area (%) covered by faces in each scene, as well as the frequency of the actors looking towards the camera in the pictures, and found no differences between emotional and neutral scenes, $Z:s<1.75$, $ps>.05$. Big yellow arrows at the corners of the images were used to instruct participants how to perform on each block. On “empathize” blocks all the arrows pointed to the visual field in which the target of the empathy (attacker, victim, or a person engaged in nonemotional activities, always unambiguously positioned in one visual field) was depicted in the scene. On “watch” blocks the arrows in the left visual field pointed to left and those in the right visual field to right.

Task and stimulus presentation

Upon arriving to the laboratory the participants completed a checklist for MRI exclusion factors. The purpose of the study was explained to the participants. It was emphasized to the participants that on the empathize blocks they should mentally simulate how the persons depicted in the stimuli would think and feel, and all motor responses should be avoided. Participants were also explained that on the watch blocks they should view the stimuli similarly as they were watching TV or looking at pictures in a photo album. Next, the participants were presented with ten practice blocks on a laptop computer. Finally, the participants were introduced to the scanner environment and placed in the scanner.

The stimulus presentation was controlled with Presentation computer program (Neurobehavioral Systems, Inc.). Stimuli were projected from an LCD projector onto a non-magnetic screen mounted at the foot of the bore, and an angled mirror reflected images on the screen to the participants' field of vision. The experiment was run with a blocked design. One experimental block lasted for 18 s and consisted of presentation of two pictures (9s each). Both the pictures were from the same category (attack/neutral scenes) and same empathy versus watch-condition. There were five types of blocks: 1) watch emotional scenes, 2) watch neutral scenes, 3) cognitive empathy (i.e., empathize with a person in a neutral scene), 4) emotional empathy – empathize attacker and 5) emotional empathy – empathize victim. Altogether participants saw 15 blocks of each type, with the exception of 30 cognitive empathy blocks. The number of these blocks was doubled in order to balance the design and to have an equal number of emotional and cognitive empathy blocks. Each participant performed a total of 90 blocks divided into five six-minute runs consisting of 18 blocks each. The order of the blocks was fixed (watch emotional scenes→watch neutral scenes→emotional empathy→empathize attacker→cognitive empathy→emotional empathy – empathize victim→cognitive empathy) in order to balance the presentation of emotional and neutral stimuli and to minimize carryover effects resulting from viewing the emotional pictures. The starting condition for the runs was counterbalanced across participants. There was a short break after each run.

After the experiment, participants were interviewed about complications experienced while being scanned. They were given full-color prints of all the stimulus scenes, and for each scene they were asked to evaluate i) their subjective emotional reactions while viewing the scenes, and ii) their percept of the emotional states of the persons depicted in the stimuli. The responses were given with two paper-and-pencil forms. In the form tapping subjective experience of emotions, participants rated their subjective experience of six basic emotions (fear, anger, disgust, sadness, surprise, and pleasure) resulting from watching the scenes with a scale ranging from 1 (do not feel at all) to 5 (feel very much). In the form measuring perceived emotional reactions of the actors in the scenes, the participants selected which of the six basic emotions (or neutral emotional state)

best described the emotional state of the persons depicted in the scenes. Separate ratings were acquired for attackers, victims, and people involved in daily nonemotional activities.

Eye movement recordings

We also wanted to control for the amount of overt attention the participants allocated to the expressive versus nonexpressive faces depicted in the stimuli during the passive viewing and empathy blocks, as enhanced overt attention i.e. eye fixations to the emotional scenes (Calvo et al., 2008; Nummenmaa et al., 2006) could potentially confound the imaging data. As our scanner did not have an eye tracker installed, we ran an independent eye movement study ($n=5$, mean age 31 years, $SD=1.2$ years, age range 30–33 years) outside the scanner. This was essentially a replication of the functional imaging runs with a few exceptions. Stimuli were presented on a 20 in. ViewSonic monitor (150 Hz refresh rate) with a 2-GHz Pentium IV computer. Eye movements were recorded using an EyeLink II eyetracker (SR Research, Mississauga, Ontario, Canada). The sampling rate of the eyetracker was 500 Hz, and the spatial accuracy was better than $.5^\circ$, with a $.01^\circ$ resolution in the pupil tracking mode. For data analysis, freeform ROIs were generated around the faces of the people depicted in the stimuli. We then computed the percentage of trial duration the participants spent looking at the attackers, victims, and neutral people during the passive viewing and empathy trials.

Image acquisition and analysis

Functional and anatomical volumes were collected with Philips Gyroscan Intera 1.5 T CV Nova Dual scanner. High-resolution anatomical images (1 mm^3 resolution) were acquired using a T1-weighted sequence (TR 25 ms, TE 4.6 ms, flip angle 30° , scan time 376 s). Whole-brain functional volumes were acquired using a BOLD-weighted echoplanar imaging (EPI) sequence (TR=2998 ms, TE=50 ms, 90° flip angle, 192 mm FOV, 64×64 matrix, 62.5 kHz bandwidth, 4.0 mm slice thickness, .5 mm gap between slices, 30 interleaved slices acquired in ascending order).

SPM5 software was used for the data analysis (Friston et al., 1995). First, functional images were sinc interpolated in time to correct for slice time differences and realigned to the first scan by rigid body transformations to correct for head movements. Next, the images were unwarped, and a mean functional image was generated. The mean functional images were inspected for excessive signal dropout. EPI and structural images were coregistered and normalized to the T1 standard template in MNI space (Evans et al., 1994) using linear and non-linear transformations, and smoothed with a Gaussian kernel with 8 mm FWHM. Simple t -contrast images with movement parameters as regressors of no interest were computed individually for each subject for the following contrasts: 1) watch emotional scenes–watch neutral scenes, 2) watch neutral scenes–watch emotional scenes, 3) emotional empathy (pooled across empathize attacker and empathize victim)–cognitive empathy, 4) cognitive empathy–emotional empathy (pooled across empathize attacker and empathize victim), 5) empathize attacker–empathize victim, and 6) empathize victim–empathize attacker. Low-frequency signal drift was removed using a 128-Hz high-pass filter. These images were subsequently entered into second level model, subjected to a voxel-wise contrast and t -test to assess statistical significance (Friston et al., 1995). Additionally, a 2 (Condition: empathizing versus passive viewing) \times 2 (Stimulus type: emotional versus neutral) ANOVA with subjects as random effects was used to assess the differences between brain responses during emotional and cognitive empathy. The statistical threshold was set at $p<.001$, uncorrected at the voxel level, with minimum cluster size of 20 to avoid false positives.

The right thalamus was used as a source region of interest (ROI) for the functional connectivity analyses. The anatomically defined,

spherical ROIs with an 8 mm diameter were generated individually for each participant. These ROIs were subsequently used for time series extraction in the emotional empathy versus cognitive empathy contrast. The time series for each participant was computed by using the first eigenvariate from all raw voxel time series in the ROI. This BOLD time series was deconvolved to estimate a neuronal time series for this region. The psychophysiological interaction term (PPI regressor) was calculated as the element-by-element product of the ROI neuronal time series and a vector coding for the main effect of task. This product was re-convolved by the canonical hemodynamic response function (hrf). PPI models were run separately for each participant, and contrast images generated for positive and negative PPIs. The model also included the main effects of task convolved by the hrf, and the movement regressors as effects of no interest. These models identified regions that have greater or lesser coupling with the source region according to the emotional versus cognitive empathy. The ten contrast images were entered into second level GLM analyses. The statistical significance was assessed with a threshold of $p < .001$, uncorrected at the voxel level.

Results

Self-report data

For the subjective emotional experience, a mean score for experience of each emotion was computed separately for the emotional and neutral pictures for each participant. The resulting scores (see Fig. 2a) were subjected to 2 (Picture type: Emotional, Neutral) \times 6 (Emotion: Fear, Anger, Disgust, Sadness, Surprise, Pleasure) repeated measures ANOVA. The results yielded significant main effects of Picture type, $F(1,9)=20.27$, $p < .01$, $\eta_p^2=.69$, Emotion, $F(5,45)=3.40$, $p=.01$, $\eta_p^2=.27$, and Picture type \times Emotion interaction, $F(5,45)=13.37$, $p < .01$, $\eta_p^2=.60$. Planned comparisons (with Bonferroni corrections) demonstrated that when compared to neutral pictures, the emotional pictures resulted in increased experience of fear, anger and disgust and decreased experience of pleasure ($ts > 3.7$, $ps < .01$). For the perceived emotional states of actors, subject-wise mean frequency for choosing each emotion was computed separately for the i) attackers and ii) victims in the emotional pictures and for iii) persons depicted in neutral pictures. The mean scores (see Fig. 2b) were subjected to a 3 (Target person: Attacker, Neutral, Victim) \times 7 (Emotional state: Fear, Anger, Disgust, Sadness, Surprise, Pleasure, NE) repeated measures ANOVA. This resulted in significant main effect of Emotional state, $F(6,54)=24.60$, $p < .01$, $\eta_p^2=.73$, and Target person \times Emotional state interaction, $F(12,108)=30.31$, $p < .01$, $\eta_p^2=.77$. Bonferroni corrected multiple comparisons demonstrated that attackers were rated as angry more often than victims or neutral persons, victims were rated as more fearful than attackers or neutral persons, and neutral persons were rated as more neutral and more pleasant than attackers or victims ($ts > 3.20$, $ps < .05$).

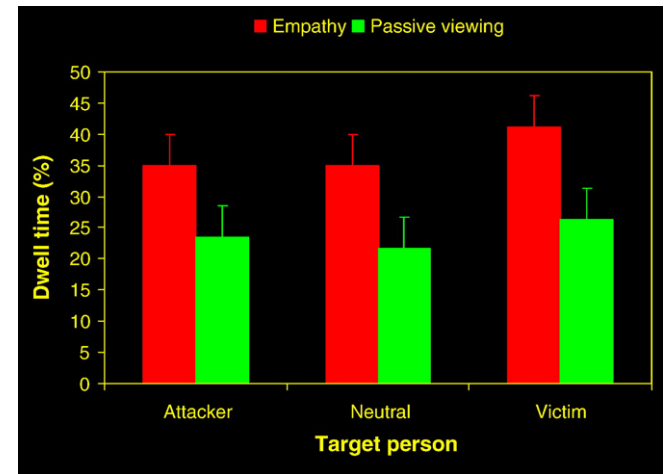


Fig. 3. The percentage of time spent looking at the attackers, neutral persons and victims during the empathy and passive viewing trials in the eye movement experiment.

Neutral) repeated measures ANOVA. This resulted in significant main effect of Emotional state, $F(6,54)=24.60$, $p < .01$, $\eta_p^2=.73$, and Target person \times Emotional state interaction, $F(12,108)=30.31$, $p < .01$, $\eta_p^2=.77$. Bonferroni corrected multiple comparisons demonstrated that attackers were rated as angry more often than victims or neutral persons, victims were rated as more fearful than attackers or neutral persons, and neutral persons were rated as more neutral and more pleasant than attackers or victims ($ts > 3.20$, $ps < .05$).

Eye movement data

The eye movement data is summarized in Fig. 3. The dwell time percentages were analyzed with a 2 (Condition: passive viewing versus empathizing) \times 3 (Target person: attacker, neutral, victim) fully within-subjects ANOVA. This analysis yielded only a significant main effect of Task, $F(1,4)=18.14$, $p=.02$, $\eta_p^2=.74$. Instruction to empathize increased the allocation of attention to the target persons' faces, but there were no reliable differences between the times spent looking at attackers, neutral persons, or victims during the passive viewing or empathy conditions.

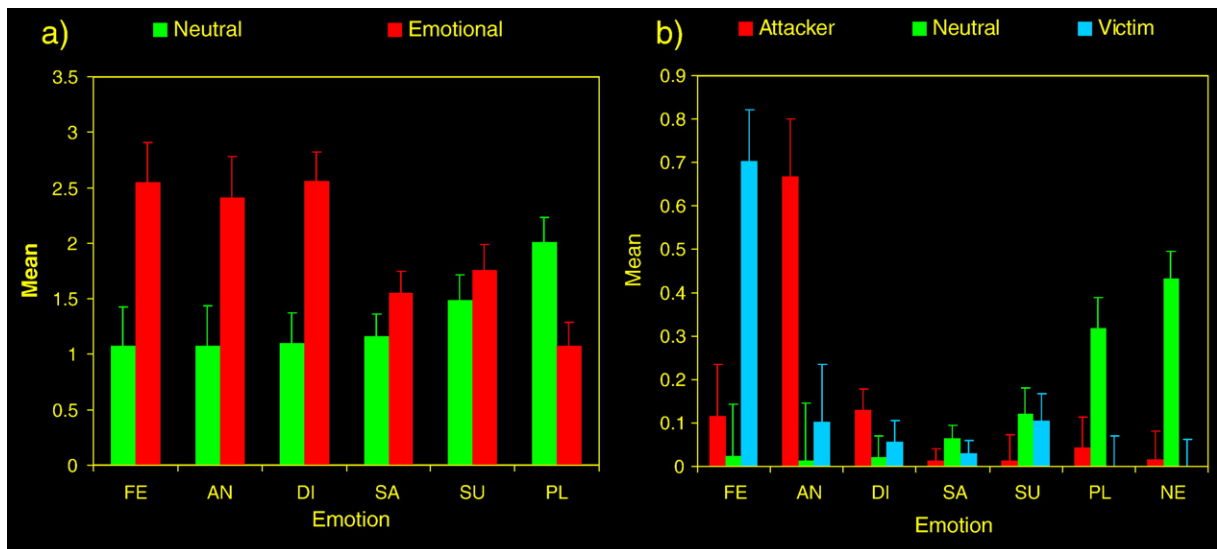


Fig. 2. Mean ratings and contrast-wise standard errors of experience of six basic emotions while watching the neutral and emotional pictures (a), and mean frequency and contrast-wise standard errors of choosing the six basic emotions and neutral emotional state for the attackers, victims, and persons engaged in neutral activities (b). FE = fear, AN = anger, DI = disgust, SA = sadness, SU = surprise, PL = pleasure, NE = neutral.

Table 1

Brain regions showing greater BOLD response ($p < .001$) to viewing emotional than neutral pictures

Region	Laterality	BA	x	y	z	T	K
PHG	R		38	-20	-18	4.61	46
PHG	L		-32	-22	-12	4.36	48
Insula/claustrum	R		30	-2	22	4.32	58
Caudate	L		-16	8	22	4.30	30
IFS	R	10	36	46	4	4.17	44
Thalamus/brainstem	R		6	-32	0	3.97	107
Caudate	R		14	6	22	3.90	37
MOG	R		36	-56	6	3.56	32

Coordinates show cluster maximas. Coordinates reflect positions relative to MNI Atlas. K = number of voxels belonging to cluster, BA = Brodmann area, IFS = inferior frontal sulcus, MOG = middle occipital gyrus, and PHG = parahippocampal gyrus.

Functional MRI data

Regional effects in the GLM

We first compared the BOLD responses resulting from viewing emotional versus neutral scenes. This analysis resulted in eight activation clusters (see Table 1 for coordinates, T values, and cluster sizes). The cortical activation foci were located bilaterally in parahippocampal gyri (PHG) and in right insula, inferior frontal sulcus (IFS) and middle occipital gyrus (MOG). Additionally, subcortical activations were observed in the right thalamus and brainstem as well as left caudate. However, the contrast for viewing neutral versus emotional pictures did not show any statistically significant activation clusters.

To analyze regions where emotional empathy resulted in stronger activation than cognitive empathy and vice versa, we compared these statistical maps with each other using one-way t -contrasts. Fig. 4

Table 2

Brain regions showing greater BOLD response ($p < .001$) emotional than cognitive empathy (upper) and cognitive than emotional empathy (lower)

Region	Laterality	BA	x	y	z	T	K
<i>Emotional versus cognitive empathy</i>							
FG	L	37	-46	-58	-22	5.11	251
PHG	L	28/35	-14	-22	-12	4.82	120
PG	L	1	-32	-44	72	4.79	139
Brainstem	R		10	-26	-10	4.33	54
PHG	R	28/35	20	-20	-12	4.09	60
Insula	L	13	-40	-6	-8	3.94	33
IPL	R	40	68	-30	28	3.80	65
IPL	L	40	-50	-30	26	3.78	36
MOG	L		-34	-80	-4	3.60	23
Thalamus	R		2	-24	0	3.60	38
<i>Cognitive versus emotional empathy</i>							
PHG/FG	L	37	-32	-42	-12	4.27	34
Cuneus	L/R	18	2	-94	18	3.89	38
MFS	R	8	30	30	56	3.86	45

Coordinates show cluster maximas. Coordinates reflect positions relative to MNI Atlas. K = number of voxels belonging to cluster, BA = Brodmann area, FG = fusiform gyrus, IPL = inferior parietal lobule, MFS = middle frontal sulcus, MOG = middle occipital gyrus, PHG = parahippocampal gyrus, and PG = postcentral gyrus.

displays axial sections of the brain with regions of brain showing greater BOLD responses to emotional versus cognitive empathy (red) and to cognitive versus emotional empathy (blue). Coordinates, T values, and cluster sizes of these regions are presented in Table 2. Emotional empathy increased activity in ten clusters, mainly in the left hemisphere. This involved temporo-parietal activation clusters bilaterally in inferior parietal lobules (IPL) and left fusiform gyrus (FG).

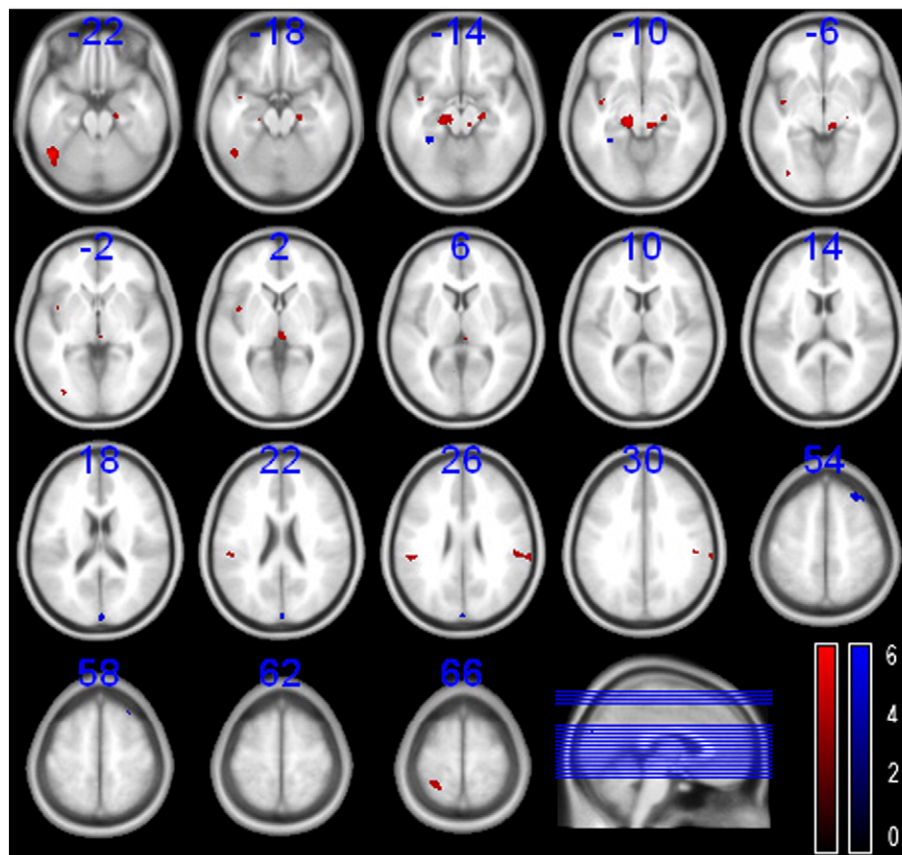


Fig. 4. Axial sections with regions of brain showing greater BOLD responses to emotional versus cognitive empathy (red) and to cognitive versus emotional empathy (blue).

Frontal activations were observed in the left postcentral gyrus (PG). Additionally, significant activation clusters were observed in left MCG and right brainstem, and bilaterally in PHG. Notably, increased activation was also observed in the left insular cortex as well as in right pulvinar thalamus. Cognitive empathy increased activation in a much less extensive network consisting of three clusters: left PHG and FG, cuneus and right middle frontal sulcus (MFS). Next, we used a 2 (Condition: empathizing versus passive viewing) $2 \times$ (Stimulus type: emotional versus neutral) ANOVA to localize the brain areas that were more active during emotional/cognitive empathy. Specifically, this contrast would exclude the activity of the emotion or cognition related brain systems that responded to mere viewing of the emotional/neutral scenes. This contrast revealed one statistically significant cluster of 40 voxels, located at right anterior premotor cortex (36, –12, 64) that showed increased activation during emotional empathy. In this contrast, no brain areas were more active during the cognitive than emotional empathy.

Finally, we compared the brain areas that were activated more by empathy towards attacker than empathy towards victim, and vice versa. Table 3 shows coordinates, *T* values, and cluster sizes of the significant activations revealed by these contrasts. When empathy towards victims was contrasted with empathy towards attacker, significant activations were revealed in left precuneus, right FG and insula, and bilaterally in IPL. No single cluster showed more activation for empathy towards aggressors than towards victims.

Functional connectivity

To test whether the thalamocortical connections play a special role in the emotional empathy, we compared the functional connectivity of right thalamus during emotional versus cognitive empathy with PPIs. This revealed increased condition-dependent coupling (see Table 4 and Fig. 5) between the thalamus and left primary motor cortex and supplementary motor area, right primary somatosensory cortex and left posterior insula.

Discussion

Our main finding was that when compared to cognitive empathy, emotional empathy increased activity in the brain networks involved in i) emotional processing, ii) perceiving faces and bodies, and iii) understanding and simulating others' actions. In general sense, this suggests that others' emotional state is a strong cue for recruiting action–observation matching systems, and prepares the approach–avoidance behaviour automatically. In the following sections, we will discuss these three findings in detail.

Passive viewing of emotional versus neutral stimuli

First of all, our emotional stimuli were successful in inducing the intended, unpleasant affective reactions. When compared to neutral pictures, the interpersonal attack scenes increased subjective experiences of fear, anger, and disgust and decreased the experience of pleasure. However, the emotional scenes did not elicit category-

Table 4

Brain regions showing greater coupling ($p < .001$) with thalamus during emotional versus cognitive empathy

Region	Laterality	BA	x	y	z	<i>T</i>	<i>K</i>
PCG/PG (SMA/PMC)	R	4/6	6	–24	62	8.55	96
PG (SSC)	L	3	–34	–36	48	6.13	69
Insula	L	13	–34	–20	18	6.06	26

Coordinates show cluster maximas. Coordinates reflect positions relative to MNI Atlas. *K* = number of voxels belonging to cluster, BA = Brodmann area, PCG = precentral gyrus, PG = postcentral gyrus, PMC = primary motor cortex, SMA = supplementary motor area, and SSC = somatosensory cortex.

specific affective reactions. Instead, participants reported experiencing multiple emotions simultaneously. Nevertheless, participants systematically rated the victims portrayed in the pictures as being afraid, and attackers as being angry. This implies that the participants did not simply passively “mirror” either attackers' or victims' emotional states, but instead integrated the emotional information represented in the scene to form a global affective representation of the picture.

The functional imaging data corroborated the behavioural findings suggesting that passive viewing of the emotional stimuli elicited non-specific unpleasant affective reactions. The activation loci were similar to what is typically observed while viewing complex unpleasant scenes (Britton et al., 2006; Lane et al., 1997), and there was a clear right-hemispheric lateralization of the effects – only parahippocampal and caudate activations were bilateral. This is in line with early right-hemisphere models of emotion perception (Schwartz et al., 1975) as well as more recent variants of this hypothesis (Adolphs et al., 1996; Heller et al., 1998). The insular activity can be attributed to processing of disgusting emotional information (Calder et al., 2000) as well as experience of disgust (Wicker et al., 2003). We also observed increased activation in the left caudate, a nucleus involved in reward processing (Delgado et al., 2000) and in parahippocampal gyrus that responds to negatively valenced, complex pictorial stimuli (Lane et al., 1997). Activation was also observed in the frontal cortex around an area (BA 10) which is typically involved in executive functioning (Ramnani and Owen, 2004). However, this region has also been reported to be involved in theory of mind-processing (Vollm et al., 2006) and also in joint attention tasks (Williams et al., 2005). The observed activation thus suggests that this region may also be involved in encoding the behavioural relevance of interpersonal situations.

However, given that participants reported experiencing moderately strong unpleasant emotions (an average of 2.5 on a scale ranging from 1 to 5) it is slightly surprising that no amygdalar activation was observed neither during passive viewing of emotional scenes nor emotional empathy. Nevertheless, it has been shown that when compared to viewing of emotional facial expressions, viewing of complex unpleasant pictorial scenes elicits significantly weaker amygdalar responses (Hariri et al., 2002). Moreover, we used relatively long (18 s) blocks. As amygdala shows rapid habituation (Breiter et al., 1996), the long block duration may have attenuated the amygdalar responses.

Comparing emotional and cognitive empathy within the core system

To investigate whether emotional and cognitive empathy engage the core empathy system in a different fashion, we contrasted the brain networks involved in emotional versus cognitive empathy by an interaction (2×2 ANOVA) analysis. This was done to wipe out all emotion or cognition related effects that could arise from merely viewing the scenes. The analysis yielded three important findings. First, it showed that premotor activation was higher for emotional versus cognitive empathy. As the premotor cortex is considered as the

Table 3

Brain regions showing greater BOLD response ($p < .001$) to empathizing victim than empathizing aggressor

Region	Laterality	BA	x	y	z	<i>T</i>	<i>K</i>
FG	R	20/37	34	–42	–26	4.29	58
Insula	R	13	30	–10	18	4.18	33
IPL	R	40	40	–32	32	4.17	82
Precuneus	L	19	–8	–90	40	4.16	27
SMG/IPL	L	40	–36	–42	32	4.01	50

Coordinates show cluster maximas. Coordinates reflect positions relative to MNI Atlas. *K* = number of voxels belonging to cluster, BA = Brodmann area, FG = fusiform gyrus, IPL = inferior parietal lobule, and SMG = supramarginal gyrus.

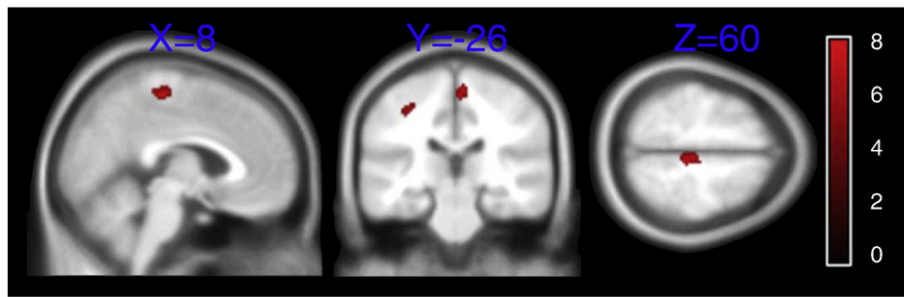


Fig. 5. Brain regions showing increased coupling with right thalamus during emotional versus cognitive empathy.

core system involved in mirroring, this finding supports our argument that emotional versus cognitive empathy results in more vigorous simulation of others' mental states, and results in enhanced activation in the core system for empathy. Second, these results showed that if emotionality and mirroring effects arising from mere perception of people in emotional/neutral contexts are controlled for, the emotional and cognitive empathy seem to share relatively similar neural architecture, as the 2×2 interaction resulted in only one significant cluster in the premotor cortex. Third, this analysis demonstrated that the emotional empathy did not result in additive effects in the emotional networks: Although brain networks involved in perception of emotional stimuli are active during emotional empathy (see below), empathy does not further increase their activation when compared to passive viewing of emotional scenes.

Comparing the extended neural systems for emotional and cognitive empathy

The second aim of the study was to compare the extended neural systems for emotional and cognitive empathy. This was done by running simple contrasts for the emotional versus cognitive empathy conditions and vice versa. The results in this respect were clear-cut. First, the emotional empathy condition increased activity in brain networks involved in processing of negative or unpleasant emotions. The thalamic activity can be attributed to increased processing of the threat depicted in the stimuli, as well as experience of unpleasant emotions (Lane et al., 1997). In line with previous studies reporting thalamic activation to visual emotional stimuli (Lane et al., 1997; Pollatos et al., 2007; Stark et al., 2004), the activation was lateralized to right. The insula is known to be involved in perception (Calder et al., 2000) as well as experience and perception of disgust (Jabbi et al., 2007; Wicker et al., 2003), thus, it is not surprising that insular activation was observed in both passive viewing and active empathizing of emotional scenes.

Second, emotional empathy increased activity in brain networks involved in processing of unemotional features of human bodies and faces. The extrastriate cluster in the MOG is reasonably close to the extrastriate body area (EBA; Downing, 2001) that has been attributed to identification of human bodies, as well as for inferring others' mental states on the basis of body posture (De Gelder, 2006; Downing, 2001). This area showed greater activation for emotional versus cognitive empathy, supporting the view that EBA is also involved in encoding of "emotional body language" (De Gelder, 2006). The increased fusiform activity could, in theory, be accounted for the active simulation of the perceived emotional states or expressions of the persons depicted in the stimuli, as increased FG activation has been reported for expression imitation versus perception (Leslie et al., 2004; Wild et al., 2003). Although FG is typically not involved in expression perception *per se* (Haxby et al., 2000; Sergent et al., 1994), it has been shown that its activity is sensitive to attentional manipulations (Vuilleumier et al., 2001). It is thus also possible that the increased fusiform activation observed in our study results from

enhanced facial encoding due to more sustained attention to the (expressive) faces in the emotional empathy condition. However, as the eye movement data (Fig. 3) do not support the latter hypothesis, we are inclined to interpret the FG activation as a facial expression imitation effect.

Third, emotional empathy increased activity in brain areas involved in perspective taking and imitation, most notably in the IPL and in the somatosensory cortices. The area PF in the macaque IPL contains mirror neurons (Lyons et al., 2006), and the IPL has been reported to be active in various imitation tasks (Iacoboni et al., 1999; Jackson et al., 2006). Accordingly, the bilateral IPL activation observed in the current study is likely to result from active mirroring of the emotional states of the persons observed in the pictures, and suggests that this area may indeed be involved in emotional contagion. The somatosensory activation confirms that when compared to cognitive, emotional empathy does indeed result in a more vigorous somatic/sensory representation of the actions of the target of empathy, most likely due to the rapid outputs from the emotional networks (Adolphs, 2002). In line with this, the results from the PPLs demonstrated that right thalamus showed increased coupling with primary and supplementary motor cortex as well as primary somatosensory cortex during emotional versus cognitive empathy. As outlined in the Introduction, because thalamus is involved in arousal regulation (McCormick and Bal, 1997) and it relays information to the somatosensory cortices, it is perfectly plausible that it can modulate the somatosensory and motor simulation of emotional states of others.

Cognitive empathy increased activation in only three areas, most notably in the MFG/MFS (BA 8). The medial prefrontal cortex (mPFC) has been associated in both theory of mind and empathy processing (Gallagher and Frith, 2003) and a recent study (Vollm et al., 2006) directly comparing brain networks for theory of mind and empathy found that activation in a medial part of the BA 8 was activated by both types of tasks. Our data fit with this account and further elaborate it by showing that the mediolateral PFC is more involved in cognitive than in emotional empathy. This implies that different regions of the PFC may be involved in cognitive versus emotional empathy. Actually, a recent meta-analysis (Steele and Lawrie, 2004) has shown that it is possible to distinguish between the cognitive and emotional functions of the PFC. The cognitive functions are localized to more dorsolateral, and emotional to more medial foci. Although this meta-analysis was not specifically focused on empathy, it nevertheless provides support for the separate frontocortical basis of emotional and cognitive empathy.

We did not, however, observe any differential activation for emotional versus cognitive empathy in the premotor cortex in the simple *t*-contrasts (although activation of this region was observed in the interaction analysis). This is not totally unexpected for two reasons. First, both the emotional and neutral stimuli portrayed goal-directed actions, thus, both emotional and cognitive empathy conditions could have activated the premotor areas to similar extent. Second, the studies that have found neurons with mirroring

properties in monkeys and humans have typically employed dynamic stimulus displays of goal-directed actions (Rizzolatti et al., 2001), instead of static images such as those employed in our study.

Contrasting aggressive and fearful empathy

Overall, there were no large differences between brain networks recruited for aggressive versus fearful empathy. Most notably, no single brain area was more active during aggressive than fearful empathy. On the contrary, fearful empathy increased activity in both areas involved in emotional and face processing (Insula, FG), as well as imitation (bilateral IPL). Of these, the IPL activation is probably most interesting. As the area around the IPL is involved in action representation, this activation cluster thus suggests that fear or avoidance-related empathy indeed results in more robust representation of others' bodily states than the approach (or aggression) related empathy. Of course, it may be argued that people simply spontaneously empathize with the victims instead of with the attackers (i.e. they may have difficulties in empathizing the attackers according to the instructions), and this bias could explain our findings.

However, our behavioural and eye tracking data do not support this view. Namely, the self-report data of emotional experiences while watching the threat scenes (see Fig. 2a) did not show any differences between the experience of anger (i.e. the emotional state of the attacker) and fear (i.e. the emotional state of the victim). What is more, the eye tracking data did not show increased allocation of attention towards victims versus attackers during the free viewing or empathizing blocks. Thus, we argue that the observed effects probably cannot be attributed to spontaneous biases in choosing the target of empathizing. Nevertheless, it can be hypothesized that the asymmetric mirroring of fear versus anger may serve an important adaptive function. Reacting to others' displays of aggression does not always benefit from mirroring similar aggressive behaviour, especially if the aggressor is physically stronger or higher in social rank. On the contrary, others' displays of fear usually signal the presence of a potential threat in the environment, and rapid copying others' avoidance behaviour can in many occasions promote well-being and survival.

We had deliberately selected a female sample in order to maximize the power of the experiment, as females typically show more intense affective/empathetic responses than males (Grossman and Wood, 1993). However, a recent study has suggested that at least spontaneous empathetic responses towards disliked versus liked persons are also qualitatively different in males and females (Singer et al., 2006). When compared to females, males show reduced fronto-insular and cingulate responses while viewing disliked individuals who receive electric shocks. Although our study involved an active (voluntary) empathy task and we did not manipulate the likeability of the persons depicted in the stimuli, some caution may still be warranted when generalizing our results to males.

Conclusions

Together our data suggest that target persons' emotional state influences empathetic responses. This occurs at two different levels. First, emotional empathy increases the activity of the core empathy network, specifically in the premotor mirror neuron system. Second, emotional and cognitive empathy activate distinct extended empathy networks. The emotional empathy recruits areas that are typically involved in emotional processing, such as insula and thalamus. Moreover, emotional empathy also results in enhanced activation in the FG and EBA representing target persons' face and body posture, respectively. This enhanced visual representation of the faces and bodies of the target of the empathy, thus, enables more finer-grained motor representations of their bodily states. Accordingly, emotional empathy effectively recruits the brain networks involved in perspec-

tive taking and "mirroring" (IPL, PG), and results in more holistic representation of the actions of the targets of empathy. Cognitive empathy, in turn, is more contingent on the frontocortical systems involved in theory of mind and mentalizing. We conclude that emotion has a special role in empathy, due to the contagious nature of emotional expressions and the reciprocal links between emotion and action preparation systems.

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References

- Adolphs, R., 2002. Recognizing emotion from facial expressions: psychological and neurological mechanisms. *Behav. Cogn. Neurosci. Rev.* 1, 21–62.
- Adolphs, R., Damasio, H., Tranel, D., Damasio, A.R., 1996. Cortical systems for the recognition of emotion in facial expressions. *J. Neurosci.* 16, 7678–7687.
- Bard, P., 1928. A diencephalic mechanism for the expression of rage with special reference to the sympathetic nervous system. *Am. J. Physiol.* 84, 490–515.
- Beck, A.T., Steer, R.A., Garbin, M.G., 1988. Psychometric properties of the Beck depression inventory: twenty-five years of evaluation. *Clin. Psychol. Rev.* 8, 77–100.
- Behrens, T.E.J., Johansen-Berg, H., Woolrich, M.W., Smith, S.M., Wheeler-Kingshott, C.A.M., Boulby, P.A., Barker, G.J., Sillery, E.L., Sheehan, K., Ciccarelli, O., Thompson, A.J., Brady, J.M., Matthews, P.M., 2003. Non-invasive mapping of connections between human thalamus and cortex using diffusion imaging. *Nat. Neurosci.* 6, 750–757.
- Bradley, M.M., Codispoti, M., Cuthbert, B.N., Lang, P.J., 2001. Emotion and motivation I: defensive and appetitive reactions in picture processing. *Emotion (Washington, D.C.)* 1, 276–298.
- Bradley, M.M., Sabatinelli, D., Lang, P.J., Fitzsimmons, J.R., King, W., Desai, P., 2003. Activation of the visual cortex in motivated attention. *Behav. Neurosci.* 117, 369–380.
- Brass, M., Heyes, C., 2005. Imitation: Is cognitive neuroscience solving the correspondence problem. *Trends Cogn. Sci.* 9, 489–495.
- Breiter, H.C., Etcoff, N.L., Whalen, P.J., Kennedy, W.A., Rauch, S.L., Buckner, R.L., Strauss, M.M., Hyman, S.E., Rosen, B.R., 1996. Response and habituation of the human amygdala during visual processing of facial expression. *Neuron* 17, 875–887.
- Britton, J.C., Taylor, S.F., Sudheimer, K.D., Liberzon, I., 2006. Facial expressions and complex IAPS pictures: common and differential networks. *Neuroimage* 31, 906–919.
- Calder, A.J., Keane, J., Manes, F., Antoun, N., Young, A.W., 2000. Impaired recognition and experience of disgust following brain injury. *Nat. Neurosci.* 3, 1077–1078.
- Calvo, M.G., Nummenmaa, L., Hyönä, J., 2008. Emotional scenes in peripheral vision: selective orienting and gist processing, but not content identification. *Emotion* 8, 68–80.
- 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. *Proc. Natl. Acad. Sci. U. S. A.* 100, 5497–5502.
- De Gelder, B., 2006. Towards the neurobiology of emotional body language. *Nat. Rev. Neurosci.* 7, 242–249.
- Delgado, M.R., Nystrom, L.E., Fissell, C., Noll, D.C., Fiez, J.A., 2000. Tracking the hemodynamic responses to reward and punishment in the striatum. *J. Neurophysiol.* 84, 3072–3077.
- Dimberg, U., Thunberg, M., 1998. Rapid facial reactions to emotional facial expressions. *Scand. J. Psychol.* 39, 39–45.
- Dimberg, U., Thunberg, M., Elmehed, K., 2000. Unconscious facial reactions to emotional facial expressions. *Psychol. Sci.* 11, 86–89.
- Downing, P.E., Jiang, Y., Shuman, M., Kanwisher, N., 2001. A cortical area selective for visual processing of the human body. *Science* 293, 2470–2473.
- Evans, A.C., Collins, D.L., Mills, S.R., Brown, E.D., Kelly, R.L., Peters, T.M., 1994. 3D statistical neuroanatomical models from 305 MRI volumes. *IEEE Nucl. Sci. Symp. Med. Imaging Conf.* 1813–1817.
- Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.-B., Frith, C.D., Frackowiak, R.S.J., 1995. Statistical parametric maps in functional imaging: a general linear approach. *Hum. Brain Mapp.* 2, 189–210.
- Friston, K.J., Buechel, C., Fink, G.R., Morris, J., Rolls, E., Dolan, R.J., 1997. Psychophysiological and modulatory interactions in neuroimaging. *Neuroimage* 6, 218–229.
- Gallagher, H.L., Frith, C.D., 2003. Functional imaging of 'theory of mind'. *Trends Cogn. Sci.* 7, 77–83.
- Grèzes, J., Decety, J., 2001. Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Hum. Brain Mapp.* 12, 1–19.

- Grossman, M., Wood, W., 1993. Sex differences in intensity of emotional experience: a social role interpretation. *J. Pers. Soc. Psychol.* 65, 1010–1022.
- Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., Rizzolatti, G., 1998. Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proc. Natl. Acad. Sci. U. S. A.* 95, 15061–15065.
- Hariri, A.R., Tessitore, A., Mattay, V.S., Fera, F., Weinberger, D.R., 2002. The amygdala response to emotional stimuli: a comparison of faces and scenes. *Neuroimage* 17, 317–323.
- Hatfield, E., Cacioppo, J., Rapson, R.L., 1994. *Emotional Contagion*. Cambridge University Press, New York.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. *Trends Cogn. Sci.* 4, 223–233.
- Heller, W., Nitschke, J.B., Miller, G.A., 1998. Lateralization in emotion and emotional disorders. *Curr. Dir. Psychol. Sci.* 7, 26–32.
- Hietanen, J.K., Surakka, V., Linnankoski, I., 1998. Facial electromyographic responses to vocal affect expressions. *Psychophysiology* 35, 530–536.
- Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. *Science* 286, 2526–2528.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J.C., 2005. Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol.* 3, 0529–0535.
- Jabbi, M., Swart, M., Keysers, C., 2007. Empathy for positive and negative emotions in the gustatory cortex. *Neuroimage* 34, 1744–1753.
- Jackson, P.L., Meltzoff, A.N., Decety, J., 2006. Neural circuits involved in imitation and perspective-taking. *Neuroimage* 31, 429–439.
- Kilner, J.M., Marchant, J.L., Frith, C.D., 2006. Modulation of the mirror system by social relevance. *Soc. Cogn. Affect. Neurosci.* 1, 143–148.
- Lane, R.D., Reiman, E.M., Bradley, M.M., Lang, P.J., Ahern, G.L., Davidson, R.J., Schwartz, G.E., 1997. Neuroanatomical correlates of pleasant and unpleasant emotion. *Neuropsychologia* 35, 1437–1444.
- Lang, P.J., 1995. The emotion probe – studies of motivation and attention. *Am. Psychol.* 50, 372–385.
- Lang, P.J., Bradley, M.M., Cuthbert, B.N., 1990. Emotion, attention, and the startle reflex. *Psychol. Rev.* 97, 377–395.
- Leslie, K.R., Johnson-Frey, S.H., Grafton, S.T., 2004. Functional imaging of face and hand imitation: Towards a motor theory of empathy. *Neuroimage* 21, 601–607.
- Lyons, D.E., Santos, L.R., Keil, F.C., 2006. Reflections of other minds: how primate social cognition can inform the function of mirror neurons. *Curr. Opin. Neurobiol.* 16, 230–234.
- Magnee, M.J.C.M., Stekelenburg, J.J., Kemner, C., De Gelder, B., 2007. Similar facial electromyographic responses to faces, voices, and body expressions. *Neuroreport* 18, 369–372.
- McCormick, D.A., Bal, T., 1997. Sleep and arousal: thalamocortical mechanisms. *Annu. Rev. Neurosci.* 20, 185–215.
- Nummenmaa, L., Hyönä, J., Calvo, M.G., 2006. Eye movement assessment of selective attentional capture by emotional pictures. *Emotion* 6, 257–268.
- Pollatos, O., Schandry, R., Auer, D.P., Kaufmann, C., 2007. Brain structures mediating cardiovascular arousal and interoceptive awareness. *Brain Res.* 1141, 178–187.
- Preston, S.D., de Waal, F.B.M., 2002. Empathy: Its ultimate and proximate bases. *Behav. Brain Sci.* 25, 1–20.
- Ramnani, N., Owen, A.M., 2004. Anterior prefrontal cortex: Insights into function from anatomy and neuroimaging. *Nat. Rev. Neurosci.* 5, 184–194.
- Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2, 661–670.
- Schwartz, G.E., Davidson, R.J., Maer, F., 1975. Right hemisphere lateralization for emotion in the human brain: interactions with cognition. *Science* 190, 286–288.
- Sergent, J., Ohta, S., MacDonald, B., Zuck, E., 1994. Segregated processing of identity and emotion in the human brain: a PET study. *Vis. Cogn.* 1, 349–369.
- Singer, T., Seymour, B., O'Doherty, J.P., Stephan, K.E., Dolan, R.J., Frith, C.D., 2006. Empathic neural responses are modulated by the perceived fairness of others. *Nature* 439, 466–469.
- Spielberger, C.D., 1983. *Manual for the State-Trait Anxiety Inventory (STAI)*. Consulting Psychologists Press, Palo Alto, CA.
- Stark, R., Schienle, A., Walter, B., Kirsch, P., Blecker, C., Ott, U., Schäfer, A., Sammer, G., Zimmermann, M., Vaitl, D., 2004. Hemodynamic effects of negative emotional pictures—a test–retest analysis. *Neuropsychobiology* 50, 108–118.
- Steele, J.D., Lawrie, S.M., 2004. Segregation of cognitive and emotional function in the prefrontal cortex: a stereotactic meta-analysis. *Neuroimage* 21, 868–875.
- 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, 655–664.
- Wild, B., Erb, M., Eyb, M., Bartels, M., Grodd, W., 2003. Why are smiles contagious? An fMRI study of the interaction between perception of facial affect and facial movements. *Psychiatr. Res.-Neuroimaging* 123, 17–36.
- Williams, J.H.G., Waiter, G.D., Perra, O., Perrett, D.I., Whiten, A., 2005. An fMRI study of joint attention experience. *Neuroimage* 25, 133–140.
- Vollm, B.A., Taylor, A.N.W., Richardson, P., Corcoran, R., Stirling, J., McKie, S., Deakin, J.F.W., Elliott, R., 2006. Neuronal correlates of theory of mind and empathy: A functional magnetic resonance imaging study in a nonverbal task. *Neuroimage* 29, 90–98.
- Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001. Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron* 30, 829–841.