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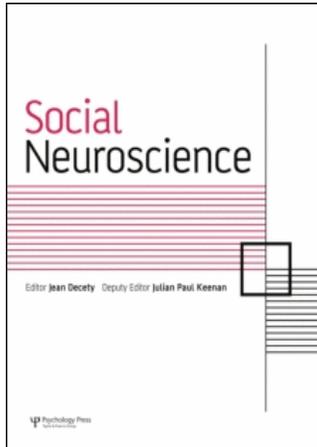
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The neural substrates of cognitive empathy

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Neuroscientific research has consistently found that the perception of an affective state in another activates the observer's own neural substrates for the corresponding state, which is likely the neural mechanism for "true empathy." However, to date there has not been a brain-imaging investigation of so-called "cognitive empathy", whereby one "actively projects oneself into the shoes of another person," imagining someone's personal, emotional experience as if it were one's own. In order to investigate this process, we conducted a combined psychophysiology and PET and study in which participants imagined: (1) a personal experience of fear or anger from their own past; (2) an equivalent experience from another person as if it were happening to them; and (3) a nonemotional experience from their own past. When participants could relate to the scenario of the other, they produced patterns of psychophysiological and neuroimaging activation equivalent to those of personal emotional imagery, but when they could not relate to the other's story, differences emerged on all measures, e.g., decreased psychophysiological

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responses and recruitment of a region between the inferior temporal and fusiform gyri. The substrates of cognitive empathy overlap with those of personal feeling states to the extent that one can relate to the state and situation of the other.

Empathy is an elusive process that has stirred centuries of debate regarding its mechanisms (e.g., Preston & de Waal, 2002). From a neuroscientific perspective, investigators have consistently found neural evidence that perception of another's emotional state, be it a basic emotion (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Decety & Chaminade, 2003; Wicker, Perrett, Baron-Cohen, & Decety, 2003) or pain (Decety & Grèzes, 2006; Jackson, Brunet, Meltzoff, & Decety, 2006; Lamm, Batson, & Decety, 2007; Singer et al., 2004), engage brain areas related to the representation of one's own feeling states such as the anterior insula and the cingulate cortices. These data generally support the application of mirror-neuron (Gallese, 2001; Iacoboni & Lenzi, 2002), simulation (Adolphs, 1999; Gallese & Goldman, 1998) or perception–action theories (Blakemore & Decety, 2001; Lipps, 1903; Merleau-Ponty, 1962/1970; Preston & de Waal, 2002; Prinz, 1987) of empathy, although brain imaging cannot be used to identify common representations for perception and action within a single cell, as was demonstrated in mirror neurons in the monkey premotor cortex (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992).

Studies comparing first- and third-person perspective taking related to emotion (Ruby & Decety, 2004) or pain (Jackson et al., 2006; Jackson, Meltzoff, & Decety, 2005; Lamm et al., 2007) also find great overlap in the feeling structures activated by the two conditions; however, there are also differences as third-person perspective taking engages to a greater extent the posterior cingulate/precuneus (Jackson et al., 2005, 2006; Ruby & Decety, 2004) and inferior parietal cortex (Decety & Chaminade, 2003; Jackson et al., 2006; Ruby & Decety, 2004).

Taken together, neural substrates have been discovered in relation to both the emotion-matching aspects of empathy as well as the cognitive, perspective-taking aspects. This supports long-standing, developmental theories of empathy that postulate a sequential development of empathic abilities in evolution and ontogeny, beginning with emotional resonance and developing into more complex forms such as cognitive empathy and perspective taking (e.g., Eisenberg, 1986; Feshbach, 1975; Hoffman, 1978,

1982). These studies further suggest that empathic processes rely heavily on regions that subservise one's own feeling states, but also recruit areas specific to the task of adopting another's perspective.

Because the empathy literature is particularly plagued by confusion and disagreement regarding the definition of terms such as empathy, cognitive empathy and perspective taking (Wispé, 1987), we provide the following working definitions to clarify our usage throughout (after Preston & de Waal, 2002). We define *empathy* broadly, comparably to Hoffman (2000), as *any process where the attended perception of the object's state generates a state in the subject that is more applicable to the object's state or situation than to the subject's own prior state or situation*. This is largely a bottom-up process that occurs directly from attending to the state of an object, magnified by the extent to which the subject is similar to or familiar with the object or the object's situation. In contrast, this study investigated *cognitive empathy*, which is a top-down process whereby *the subject effortfully tries to represent the state of the object*; also referred to as “putting oneself in the place of another” or “imaginatively projecting oneself into the situation of another” (Allport, 1937; Buchheimer, 1963; Demos, 1984; Goldie, 1999; Smith, 1989). While cognitive empathy is often used interchangeably with *perspective taking*, perspective taking is a higher-order concept that includes both emotional and nonemotional forms of transitioning into the situation of another; in this experiment we are not investigating the cognitive process of transitioning between perspectives, but rather the state of being in the shoes of the other, after the switch has taken place, which we refer to as cognitive empathy.

In everyday situations, cognitive empathy often occurs as one tries to actively imagine what it would be like to be another person in a particular, difficult situation. Existing data suggest that subjects do not engage their own feeling substrates to the same extent when imagining an event from another's perspective (Jackson et al., 2005, 2006; Ruby & Decety, 2004). According to most models of empathy, the emotional experience of subjects are expected to be quantitatively

reduced during cognitive empathy because subjects must maintain awareness of themselves as distinct individuals, lest they become personally distressed by the state of the other and confuse the object's plight with their own (e.g., Decety & Sommerville, 2003; Eisenberg et al., 1989). Additionally, because the aforementioned studies investigated perspective taking per se, comparing first- and third-person perspectives, they focused on activation related to the process of switching from first- to third-person perspectives. It is to be expected that subjects would be distracted from fully feeling the state of the other during this perspective-switching process. However, once a subject has successfully adopted another's perspective, there is no a priori reason why subjects should feel less emotion when imagining their own or another's experience. For example, according to simulation theory (Gallese & Goldman, 1998; Goldman, 1992), which provides a very useful model of cognitive empathy, one could hypothetically access all of the necessary sensory information such as sights, sounds, and even feeling states needed to construct the other's scenario in an online, top-down manner, resulting in a successful image. However, a perception-action model of empathy (Preston & de Waal, 2002) and Damasio's view on emotion (Damasio, 1994, 2003) specifically postulate that subjects commonly access existing representations from past experience when imagining emotional states; thus, the intensity of the subject's feeling, as well as the accuracy of the empathic process, depend crucially upon the extent to which the subject has existing representations for the object, state, and situation. Given this, even after successfully switching perspectives, the extent to which a subject feels the state of the other is directly correlated with the extent to which they have existing representations for the state. This study was designed to test these predictions.

We compared the feeling states of participants while imagining a personal scenario from their own past versus a nonpersonal scenario from the past of another participant, *as if it were happening to them*. Psychophysiological data and functional neuroimaging data using positron emissions tomography (PET) were obtained during emotional imagery; a nonemotional personal imagery condition was also included as a reference. We did not focus on the process of transitioning from one's own perspective to the perspective of the other; rather, we were interested in what happens in the brain and body while the participant

maximally experiences the state of the other, reliving the other's experience as if it is happening to them. Thus, data were collected only after participants indicated that they were feeling emotion from the imagined experience in the other's perspective, in the other's shoes. In this way, regions associated with perspective taking in former studies such as the inferior parietal cortex and the frontal pole (Decety & Chaminade, 2003; Decety, Chaminade, Grèzes, & Meltzoff, 2002; Ruby & Decety, 2001) were not expected to be significantly different between conditions. That is, since both the personal and nonpersonal imagery conditions were in the first person, and were measured after the subject successfully imagined the object's situation, no additional cognitive processes were expected to be necessary for the nonpersonal imagery. In contrast, we predicted that there would remain great overlap between personal and nonpersonal imagery in brain areas associated with the representation of feeling states such as the orbitofrontal, insula, anterior cingulate, somatosensory (SII), and mesial parietal cortices, brainstem autonomic areas and cerebellum (Damasio, 2003).

According to our view of empathy (cf. Damasio, 1994, 2003; Preston & de Waal, 2002), even if subjects activate the same neural regions to sustain personal and nonpersonal imagery, the success of the nonpersonal imagery and the amount of brain activation still depend on the extent to which subjects have an existing representation for the object's state. To investigate this further, Experiment 1 compared personal scenarios to nonpersonal scenarios to which participants could relate *the most* (maximizing the possibility for overlap between conditions), while Experiment 2 compared personal scenarios to nonpersonal scenarios to which subjects could relate *the least* (minimizing the possibility for overlap between conditions). We predicted that the nonpersonal scenario would create almost identical levels of psychophysiological and brain activation when the participants could relate to the scenario well in Experiment 1 but that the nonpersonal scenario would produce reduced levels of psychophysiological and brain activation when participants could not relate well to the scenario in Experiment 2, and this is where it is more likely that additional areas may be recruited to guide the imagery of an unfamiliar situation.

EXPERIMENT 1

Method

The [^{15}O]H $_2\text{O}$ PET experiment was approved by the University of Iowa's Institutional Review Board and Medical Radiation Protection Committee. The emotional imagery was induced and the PET scans were administered as in a prior investigation (Damasio et al., 2000). The major differences were that we only investigated anger and fear imagery and did not investigate sad or happy imagery; instead, we added a nonpersonal emotional episode to compare to the personal emotional episodes.

Two emotions were included to determine if the correlates of cognitive empathy generalized across emotions, as they would if there was a region associated with the process of being in the shoes of another, or if the patterns of activation were specific to the state being imagined, as they would if one simply recruits neural systems associated with imagining the respective emotion (cf. Damasio et al., 2000).

Participants. Participants were recruited through advertisements in a local newsletter, a newspaper, and campus posting. Prescreening on the phone was used to exclude participants with a history of neurological or psychiatric illness or currently on medications that affect the central nervous system. The screening session in the laboratory (detailed below) was used to exclude participants who were not dominantly right-handed according to the Oldfield-Geschwind questionnaire (scores $< +85$) or were not able to recall a specific, profound, emotional memory of either fear or anger to be used as their personal imagery scenario. This latter criterion excluded abstract emotional memories like anger stories about hating a particular person, or fear stories about phobias and excluded routine emotional events such as anger caused by a typical dispute with a roommate or fear caused by a recent bad dream. Four volunteers were excluded on the basis of this criterion. Five subjects dropped out of the study after the screening session in the lab and before the PET scan. A total of sixteen participants were studied, half male and half female, mean age = 31.81 ($SD = 6.53$) ranging from 25 to 44; half of each gender was assigned before testing to one of the two emotion conditions (fear or anger) and to an order of imagery

types (personal first, or nonpersonal first; Table 1). All participants gave informed consent in compliance with federal and institutional guidelines, and they were all approved by the IRB at the University of Iowa.

Screening session. After verifying that the subject could indeed recall an appropriate personal imagery scenario and recording the event, participants selected a nonpersonal imagery scenario from a list of seven scenarios that were collected from participants in a prior investigation of emotional imagery (Damasio et al., 2000). All fourteen nonpersonal stories (seven for each emotion) are included in full in Table 2 as a reference, along with the number of subjects who selected each story by condition and experiment. To operationalize the construct of "strongly relating" to another's experience, we gave participants the complete text of all seven scenarios and asked them to select the one to which they could relate the *most*. Lastly, the experimenter collected a scenario for the neutral imagery condition by asking participants to recall a nonemotional event from a specific day (the current day unless it was emotional), from getting up in the morning and preparing breakfast to getting ready to leave for school or work.

After all scenarios were compiled, participants were instructed by the experimenter to begin each imagery scenario in turn while lying back with eyes closed in a darkened testing room. The complete verbal instructions given to subjects to induce emotional imagery are included below; no other instructions were given regarding the method of induction or imagery. Based on their assigned order, half of the participants imagined neutral, personal, neutral, nonpersonal while the other half imagined neutral, nonpersonal, neutral, personal, in that order. After participants indicated that they were successfully engaging in the imagery (with a hand signal), timing began, and

TABLE 1

Participants for Experiments 1 and 2 broken down by emotion, degree to which subjects related to their nonpersonal imagery scenario, and gender

<i>Experiment</i>	<i>Relatability</i>	<i>Emotion</i>	<i>Female</i>	<i>Male</i>
1	High	Fear	4	4
		Anger	4	4
2	Low	Fear	5	4
		Anger	4	4

TABLE 2

Scenarios used for nonpersonal imagery. All scenarios were generated as personal imagery scenarios by subjects in a prior investigation (Damasio et al., 2000). Subjects were given the complete text of all seven scenarios in their emotion condition (fear or anger) and were asked to select the scenario to which they could relate the most (Experiment 1) or the least (Experiment 2). This exact text was also read to the subjects just before imagery in the prescreening and PET imaging sessions along with the instructions presented in the methods section. The word count and number of subjects who selected each scenario is also provided

<i>Emotion</i>	<i>Story</i>	<i>Word Count</i>	<i>N, high relate</i>	<i>N, low relate</i>	<i>Full text of scenario given to subjects</i>
Fear	1	33	0	4	You are traveling in Russia when three cops stop you. Before you know it, the cops take you away and start beating you up. After a while they let you go, but they are soon chasing after you again. You are very scared and are trying to run away from them. Picture yourself in that situation and feel as scared as you can.
	2	44	2	0	You are driving on a highway in the middle lane with a lot of traffic. Your son is sitting in the front seat next to you, and your two daughters are in the back. You see a semi truck in the right lane suddenly pull in front of you. You slam on the breaks, but discover that the car has no breaks! You try to escape to the left lane, but a car appears on your left. You are cornered, approaching the semi truck at high speed. Your kids are screaming and you are scared that you are all going to die. Picture yourself in that situation and feel as scared as you can.
	3	108	0	1	You are climbing a mountain over a very high cliff with a river underneath. You are almost at the top when your foot slips, and you slide down towards the cliff. Just before you go off of the cliff, you grab onto a small tree with one hand. All of your body is hanging over the cliff and you are holding on with only one hand. Your friend is coming close to save you, but your arm is giving up and you are about to let go and fall. Your life is hanging by a thread. Picture yourself in that situation and feel as scared as you can.
	4	80	3	0	You are riding in the car with your friend, crossing over a train track. You see that a train is coming closer and closer. You are not driving and have no control over the wheel and cannot run away. Your heart is pumping and you are scared. You see the train approaching. The train actually hits the car and it is smashing in your side of the car. Picture yourself in that situation and feel as scared as you can.
	5	75	1	2	You are white water rafting in Colorado. You are knocked out of the raft. Your kids were with you and now you don't know where they are. You spouse was also with you and you realize that your spouse's leg is caught in a rock. The water is drifting you downstream and you don't know where you are all going to end up. Picture yourself in that situation and feel as scared as you can.
	6	67	1	2	You were younger and playing with fireworks with your brother. The next firecracker you shoot off hits your sister in the chest. Your sister is knocked out, unconscious. You are screaming and freaking out, fearing that your sister is dead. You are running around, trying to find some way to get her to a hospital. Picture yourself in that situation and feel as scared as you can.
	7	50	1	0	You are walking at night to a friend's house. You see two strangers approaching you, holding a knife. They come towards you and hold you at knifepoint. You are freaking out and think you are about to die. Picture yourself in that situation and feel as scared as you can.

TABLE 2 (Continued)

Emotion	Story	Word count	N, high relate	N, low relate	Full text of scenario given to subjects
Anger	1	87	5	0	You need to study for an important exam that is tomorrow. You were studying late in the library, but the library closed, so you went home to continue your studying. You arrive home and discover your roommate having a party in your room. This party was never discussed between the two of you. The exam is tomorrow and now you cannot study in your room. You are extremely angry and want to kill your roommate. Picture yourself in that situation and feel as angry as you can.
	2	88	0	2	You are sitting in the hospital next to your dad who just came out of surgery. You mom is sitting across the room. Your sister arrives and immediately starts to put you down and tell stories that make you look bad in front of your parents. Your sister always does these kinds of things, and you hate her for it. You are especially mad that she is doing it now and you feel like killing her. Picture yourself in that situation and feel as angry as you can.
	3	76	1	0	You are driving and another guy hits your car. He admitted that it was his fault, so you agreed not to call the police. Later on, he started denying that it was his fault and was avoiding you so he wouldn't have to pay the damage. You keep trying to get him to pay, but he keeps avoiding you. You are angry and frustrated. Picture yourself in that situation and feel as angry as you can.
	4	69	0	2	You are walking with your mother and she gets mugged. You see the guy getting out of the car, approaching your mother from behind, and snatching her purse. You become very mad and angry with him. Now you are running after the guy; you are so mad and you want to beat the hell out of him. Picture yourself in that situation and feel as angry as you can.
	5	57	2	3	You found out from your daughters that the babysitter was hitting them. The babysitter finds out that your daughters told you and then tries to force your kids to say that they originally lied about the hitting. This makes you very angry with the sitter. Picture yourself in that situation and feel as angry as you can.
	6	73	0	1	Your spouse always makes excuses about having to work late and you are becoming angry and suspicious. One day you decide to look into it and discover that your spouse is not working late, but instead is going to a coworker's place. You confront your spouse but s/he denies it. You get into a big argument and you are very angry. Picture yourself in that situation and feel as angry as you can.
	7	93	1	0	A woman guaranteed you a truck rental. You go to the rental place on the day of your move and there are no trucks available. She tells you to come back later, which you do, and there are still no trucks. Meanwhile, you need to move out of your apartment and there are people waiting to move in who are pressuring you. The situation is getting desperate and you become very angry and furious at the woman from the rental company. Picture yourself in that situation and feel as angry as you can.

participants imagined the scenario for 90 seconds. To verify that the participant experienced the assigned emotion in the lab during imagery, self-report ratings of the primary emotion experienced and its intensity were collected after each scenario. All subjects reported feeling the intended emotion with a minimum subjective rating of 3 (from 0–4) for the intensity of that emotion (fear or anger). On this basis, all subjects tested in prescreening were included in the PET study.

In this study, we were specifically interested in investigating the feeling states and neural correlates of cognitive empathy once subjects were already in the shoes of the other person. Thus, we did not manipulate, measure, or try to control for possible differences in the way subjects chose to achieve this emotional imagery by instructing them to use a specific method of recall. Instead, we chose to maximize the validity of the construct of emotional imagery by allowing each participant to use the recall strategy they regarded as the most effective. The possible variability in content of the personal scenarios was exchanged for the effectiveness of autobiographical memories in inducing an intense emotion. The variability in cognitive strategies used by participants was compensated by the fact that data were collected only after participants reported feeling the target emotion.

Imagery induction instructions

I want you to close your eyes and pay attention to me. When you hear me say the word “begin”, I want you to picture in your mind that time when [description of story], and you felt very [scared or angry]. I want you to focus on that image as much as you can, and feel as [scared or angry] as you can. As you are trying to re-experience that emotional event, your mind may wander sometimes, and you may lose concentration. Whenever you lose that concentration, the important thing is to return to thinking again about that experience, bring back these images again, and focus again on that emotional experience until you hear me asking you to stop. Before we start this, I want you to remember the following: Close your eyes and listen to the description of the story. Wait for me to say “begin.” After I tell you to begin, start bringing that emotional experience into focus, and as soon as you start feeling that emotion give me a hand signal [lift your hand], to indicate to me that you are starting to feel

the emotion. You may hear walking, whispering, and noise around you. Don’t pay any attention to anything that goes around you. You have only one thing to do: to focus on that emotional experience, feel it, and hold it as much as you can. Feel free to express emotion, just don’t move your head or body too much. Continue to feel the emotion until I tell you to stop, it will be a few minutes.

Self-report measures. Self-report data ratings of overall emotional intensity from 0 (*none*) to 4 (*most intense*) were collected after each trial in the screening and PET imaging sessions to verify that participants had felt the target emotion during their personal, emotional imagery, and to compare how emotional they felt during their imagery of a personal event compared to a nonpersonal or neutral event.

Psychophysiology. Heart rate and skin conductance were recorded from electrodes attached to the participants at the beginning of both the screening and PET imaging sessions. Heart rate was collected using lead II EKG, with one electrode attached inferior to the costal margin, and another attached anterior to the sternocleidomastoid muscle; SCR electrodes were attached to the thenar and hypothenar areas on the palms of the left hand. Psychophysiological measures were recorded in an Astro-Med polygraph (Warwick, Rhode Island, USA) at 1000Hz and simultaneously converted from analog to digital format and transferred to a computer using an MP100WS system (Biopac systems, Santa Barbara, California, USA). The recorded data were analyzed with AcqKnowledge III software (Biopac Systems).

MR imaging. After the lab screening session, participants who qualified for inclusion in the PET study returned later to complete a T₁-weighted MR scan to plan slice orientation for use in the PET scanner, and to provide an anatomical reference for interpreting activation. For each subject, 3 MR scans were acquired on a 1.5T GE Signa scanner (SPGR 30, TR 24, TE 7, Nex 1, FOV 24cm, matrix 256 × 192). The scans consisted of 124 contiguous coronal slices (interslice distance 1.5–1.7mm, interpixel distance of 0.94) covering the whole brain. Images were co-registered using Automated Image Registration (AIR) version 3.03 (Woods, Cherry, & Mazziotta, 1992; Woods, Grafton, Watson,

Sicotte, & Mazziotta, 1998; Woods, Mazziotta, & Cherry, 1993) and averaged to produce a single data set of enhanced higher quality and higher in-plane resolution (0.7mm interpixel distance; Holmes et al., 1998) that was used to plan slice orientation for use in the PET scanner using Brainvox (Grabowski et al., 1995).

PET imaging. PET imaging was conducted in a GE 4096B tomograph (Uppsala, Sweden), yielding 15 slices covering a 10cm axial field of view, with an in-plane resolution of 10mm. Each participant received eight injections of 50mCi [^{15}O]H $_2$ O, with a minimum inter-injection interval of 15 minutes. All participants first imagined two neutral scenarios, followed by four emotional scenarios, followed by two neutral scenarios. The order of the emotional scenarios was counterbalanced, with half of the participants in each emotion condition (fear or anger) imagining two nonpersonal scenarios followed by two personal scenarios, and the other half imagining two personal scenarios followed by two nonpersonal scenarios. The same personal and nonpersonal scenarios were used for each subject's PET scan as were used in the screening session, but because the neutral scenario depicted getting ready for school or work on a particular nonemotional day, the participants would not vividly remember the day from the prescreening many weeks prior; thus, neutral scenarios were updated for the PET session to a more recent day to control for the vividness of the emotional images.

Participants were cued to recall and re-experience the appropriate scenario as described above and signaled with a right-hand movement when they felt the intended emotion. The radiotracer was then injected within five seconds into the already attached IV. Because the injection was given through an IV, subjects did not feel a needle injection at this point, but may have experienced a warm sensation as the tracer entered the arm. Dynamic image acquisition enabled reconstruction of images based on the 40 seconds of data collection following clearance of the arterial blood pool, as judged from time-activity curves in ROIs over the major vessels. Our injection technique results in arrival of the bolus of labeled water in the brain about 15 seconds after injection (Hichwa, Ponto, & Watkins, 1995). Heart rate and SCR were monitored as during the screening session, and ratings of emotional intensity (0–4) were obtained after each injection.

PET data were spatially normalized to a Talairach-compatible averaged brain through a series of co-registration steps (see Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Grabowski et al., 1995, for details). All registrations were performed using AIR 3.03 (Woods et al., 1993). First, scans from each injection were co-registered to each other and then a mean PET image was registered to the MRI scan using the PET-Brainvox fiducials (Damasio et al., 1993; Grabowski et al., 1995). Using a fifth-order nonlinear warp, the MRI data were registered to a Talairach-compatible atlas constructed by iteratively averaging 50 normal brains in Talairach space (Woods, Dapretto, Sicotte, Toga, & Mazziotta, 1999). Finally, the displacement fields from each registration step were concatenated and applied to the PET data. After spatial normalization, the PET data were smoothed with a 16mm FWHM Gaussian kernel using complex multiplication in the frequency domain. The final calculated voxel resolution was $17.9 \times 17.9 \times 17.9$ mm. Each injection was normalized to a global mean of 1000 counts per voxel.

Statistical analysis

Ancillary data. Self-report and psychophysiology data were analyzed only for the PET imagery session and are not provided from the screening session. Screening session psychophysiology data were collected only in the event that self-report or observable referents of emotion were not informative or reliable. All subjects reported feeling the intended emotion with at least moderate intensity, and the experimenter observed visible changes in respiration (from the rise and fall of the chest) and muscle tone (e.g., clenched fists) in all subjects during personal imagery; thus the prescreening psychophysiology data were not additionally analyzed here. All PET imagery measures were analyzed using separate general linear models (GLMs) in two stages. First, a GLM was used to test whether the first two neutral imagery trials differed from the last two, modeling subject identity as random factor (reduced by iterative residual maximum likelihood estimation; REML) and using a dummy code for neutral imagery trials (neutral 1 and 2 = 1, neutral 3 and 4 = 2). Assuming there were no differences between the neutral imagery trials before the emotional imagery trials and the neutral imagery trials after the emotional imagery trials, all neutral imagery trials were treated as levels of

replication (1,2,3,4) nested within the neutral imagery condition. A subsequent GLM was run using subject identity as a random factor (iterative REML) and testing for effects of imagery replication (four levels for neutral imagery, two levels each for personal and nonpersonal imagery, nested within condition), emotion (anger vs. fear), and imagery type (neutral, nonpersonal, personal). The dependent variables of interests were the PET ratings of emotional intensity (0–4), heart rate in beats per minute (BPM) and skin conductance on the left hand (area under the curve). Significant effects were followed by Tukey's honestly significant difference tests and Student's *t*-tests; these were used to interpret main effects. All GLMs were run using JMP-IN version 5.1.2 (Cary, NC, USA). The alpha level for all comparisons was set at .05.

PET contrasts. All PET data were analyzed with a pixelwise general linear model. Regression analyses were performed to test for differences between the personal and nonpersonal imagery conditions, as compared to the neutral condition. Prior to the regression analysis, data from the four neutral conditions were averaged and then subtracted from the personal and nonpersonal imagery conditions, and these difference images were used as the dependent measure. The following co-variables were included in the regression model: subject nested within emotion (fear or anger), a within-subjects factor of imagery type (personal vs. nonpersonal), a between-subjects factor of emotion (fear vs. anger), and an interaction term between condition and emotion.

Four contrasts were tested: the difference between personal and nonpersonal imagery (1), the difference between anger and fear (2), and the difference between personal and nonpersonal imagery nested within anger (3) and fear (4).

An ROI search was performed with a search volume that included regions known to be involved in emotion-feeling processes: orbitofrontal cortices, insula cortices, anterior cingulate cortices, somatosensory (SII) cortices, mesial parietal cortices, brainstem tegmentum and cerebellum (Damasio, 2003). The ROI was delineated by manual tracing on the averaged MR and measured 121.9cm³, calculated to comprise 21.3 resels. A whole brain search was also performed to look for areas of activation outside of the ROI with a higher threshold. Critical *t*-values for the planned contrasts were determined using Gaussian random field theory (Worsley, 1994). The spatial

extent statistic was used to look for especially large clusters in which the peak is less active than the critical *t*-value dictated by a magnitude threshold; the statistical images were converted to *Z*-score images and thresholded using clusters where $Z > \pm 3.0$ (Friston, Worsley, Frackowiak, Mazziotta, & Evans, 1994).

For this experiment, we expected a great amount of spatial overlap in activation across the personal and nonpersonal imagery conditions. Such overlap could produce a null result when contrasting the two conditions, thereby making interpretation of a null finding ambiguous with respect to activation of the individual conditions. We therefore performed a conjunction analysis for the personal and nonpersonal imagery conditions relative to the neutral condition using the minimum statistic compared to the conjunction null (MS/CN; Nichols, Brett, Andersson, Wager, & Poline, 2005). This conjunction approach tests for activation in both conditions as opposed to testing for activation in at least one condition (Nichols et al., 2005). The conjunction analysis was performed by individually thresholding the *t*-statistics from the personal and nonpersonal conditions (using random field theory, $p < .05$) and based on the individually significant results, determining overlapping areas of significant activation.

All imaging analyses were performed using custom software and visualized with Brainvox (Damasio & Frank, 1992; Frank, Damasio, & Grabowski, 1997). The alpha level for all comparisons was set at .05.

Results

Ancillary data. Intensity ratings were equivalent between the first two neutral imagery trials and the last two neutral imagery trials, $F(1, 41) = 0.075$, *ns*, justifying their equal treatment in a subsequent GLM testing effects across all three imagery types. In this GLM, there were no differences across replicates of the imagery types, $F(3, 92) = 0.813$, *ns*, or between fear and anger, $F(1, 92) = 0.063$, *ns*, but there was a strong main effect of imagery type, $F(2, 92) = 118.617$, $p < .0001$, due mainly to the neutral imagery trials being rated as less intense ($M = 0.670$) than the nonpersonal ($M = 2.429$) and personal ($M = 2.750$) trials; there was a trend for personal imagery to be more intense than the nonpersonal, $F(1, 92) = 3.280$, $p = .073$.

Heart rates were equivalent between the first and last two neutral imagery trials, $F(1, 33) = 0.529$, *ns*, justifying their equal treatment in a subsequent GLM testing effects across all three imagery types. In this GLM, there were no differences across replicates of the imagery types, $F(3, 80) = 0.203$, *ns*, or between fear and anger, $F(1, 80) = 2.519$, *ns*, but there were differences among the three imagery types, $F(2, 80) = 42.883$, $p < .0001$, due to lower heart rate during neutral imagery trials ($M = 66.67$ BPM) than on either nonpersonal ($M = 69.88$ BPM) or personal imagery trials ($M = 70.97$ BPM), with the personal showing a trend to being higher than the nonpersonal, $F(1, 80) = 3.623$, $p = .061$.

Skin conductance was equivalent for the first and last two neutral imagery trials, $F(1, 33) = 0.043$, *ns*, justifying their equal treatment in a subsequent GLM testing effects across all three imagery types. In this GLM, there were no differences between the first and second replicate within each imagery type, $F(3, 80) = 0.180$, *ns*, and no main effect of imagery type, $F(2, 80) = 1.322$, *ns*, but there was a significant difference between anger and fear, $F(1, 80) = 6.087$, $p = .0158$, due to higher skin conductance levels for anger ($M = 11.42$) than fear ($M = 3.57$).

PET contrasts

Anger > fear. Information about significant effects including peak locations, number of voxels and local maxima and minima are reported in Table 3. In the ROI there was more activation for anger than fear in the right anterior cingulate ($t = 6.23$, $p < .05$) and more activation for fear than anger in the right posterior cingulate ($t = -7.25$, $p < .05$).

Using a whole-brain analysis with the spatial extent statistic, there were large clusters of activation that were greater for anger than fear in the fronto-temporal region, from the left temporal pole extending forward to the frontal operculum including peaks in the superior and middle temporal gyrus, temporal pole, and lateral orbital gyrus ($Z > 3.23$, $p = .005$). Using the whole brain analysis with the spatial extent statistic, there was more activation for fear than anger in the right basal ganglia and posterior cingulate and supramarginal gyrus ($Z < -3.69$, $p < .05$).

Personal > nonpersonal. There were no brain areas in which the activation was statistically

different between the personal and nonpersonal imagery, either when the fear and anger groups were combined to increase the sample size, or when they were tested separately to reduce variance; this was true using the ROI, whole brain, and spatial extent statistic analyses ($-3.08 < t < 3.14$, *ns*). A perception–action model of empathy would predict great overlap between imagining a personal and a nonpersonal scenario, especially since participants were instructed to take the perspective of the other in the nonpersonal imagery, which greatly reduces any suspected cognitive differences in the process; however, as a null result, this could have occurred simply because of insufficient power. In order to rule out this latter hypothesis, a conjunction analysis was performed to determine whether the personal and nonpersonal imagery produced activation that was significantly different from the neutral imagery.

PET conjunction analysis—ROI. Information about significant effects including peak locations, number of voxels and local maxima and minima are reported in Table 4A and visualized in Figures 1 and 2. Within the ROI, there was significantly more activation for both personal and nonpersonal imagery compared to neutral imagery in the midbrain. There were also effects in the insula; personal imagery activated the right ventral and anterior portion of the insula more than neutral imagery, nonpersonal imagery deactivated the left, more posterior and dorsal portion of the insula. SII on the left and the posterior cingulate on the right were less active during personal imagery than neutral imagery. The orbital frontal cortex (OFC) on the left was more active during nonpersonal imagery than neutral while the amygdala was less active during nonpersonal imagery than neutral imagery.

PET conjunction analysis—whole brain. Information about significant effects including peak locations, number of voxels and local maxima and minima are reported in Table 4B and visualized in Figures 1 and 2. There were significant differences between both types of emotional imagery and the neutral imagery and there was almost complete overlap in the patterns of activation between the two, but the magnitude of the differences appeared to be greater between personal imagery and neutral imagery than between nonpersonal and neutral

TABLE 3

Significant effects in Experiment 1. There were no significant differences between the personal and nonpersonal conditions; therefore, results are reported for the contrast between imagery of fear and anger experiences using a Region of Interest (ROI) mask with a reduced threshold of $t=5.29$ and a whole brain mask using the spatial extent statistic with a threshold of $Z=3.00$. Between-subjects comparisons of fear and anger used error $df=15$, resel size = 17.9. Peak coordinates and local maxima are presented in Talairach coordinates

Comparison	Mask	Test (alpha)	Peak locations				Voxels	p	Local maxima x,y,z (t)	Side	Region
			x	y	z	t					
Anger > Fear	ROI	t (5.29)	2	12	32	5.63	74		2, 13, 33 (6.23)	R	Anterior cingulate
			3	-35	37	-5.91			131	4, -36, 37 (-7.25)	R
Anger > Fear	Whole	Z (3.00)	-41	7	-20	3.18	7648	0.005	-47, -2, -29 (3.49)	L	Superior/middle temporal gyrus
									-38, 22, -22 (3.50)	L	Temporal pole
									-33, 12, -21 (3.44)	L	Superior temporal/parahippocampal gyrus
									-40, 22, -19 (3.52)	L	Temporal pole
									-43, 22, -12 (3.28)	L	Lateral orbital gyrus
									-45, 22, -11 (3.23)	L	Lateral orbital gyrus
									-53, 13, -9 (3.36)	L	Superior temporal gyrus
									24, -32, 26 (-3.32)	R	Basal ganglia, posterior cingulate**
									22, -22, 30 (-3.84)	R	Basal ganglia, posterior cingulate**
									28, -38, 26 (-3.8)	R	Supra-marginal gyrus**

**Peak coordinates fall in white matter between three significant areas of deactivation.

TABLE 4A

Areas where there were significant differences between the neutral imagery and the emotional imagery types analyzed separately for the personal and nonpersonal imagery within the ROI (critical t value ± 3.96); fear and anger participants are combined in these analyses. Talairach coordinates listed in the same row for personal and nonpersonal imagery refer to activation in the same region in both contrasts

Side	Region	Personal					Nonpersonal				
		x	y	z	t	Voxels	x	y	z	t	Voxels
L	Orbital frontal cortex						-16	23	-15	4.89	1192
R	Anterior insula	34	9	-5	4.63	835					
L	Posterior insula						-39	-15	7	-4.29	235
L	Amygdala						-22	-2	-18	-4.05	143
L	SII	-54	-22	18	-4.37	611					
R	Posterior cingulate	4	-37	36	-4.52	628					
L	Midbrain	3	-30	-20	5.16	5065	1	-33	-20	5.16	3823

TABLE 4B

Areas with significant differences between the neutral and emotional imagery analyzed separately for personal and nonpersonal imagery in the whole brain analysis (critical t value ± 4.84); fear and anger participants are combined in these analyses. Talairach coordinates listed in the same row for personal and nonpersonal imagery refer to activation in the same region in both contrasts

Lobe	Side	Region	Personal					Impersonal				
			x	y	z	t	Voxels	x	y	z	t	Voxels
Frontal	R	Dorsolateral prefrontal cortex	44	48	2	-4.96	213					
	L	Orbital frontal cortex						-17	24	-16	5.51	733
	L	Frontal operculum						-47	24	-5	5.17	451
	L	Inferior frontal gyrus	-53	-23	17	-4.87	18					
Cingulate	L	Anterior cingulate/superior frontal gyrus	-7	48	20	5.26	1290					
	R	Posterior cingulate	4	-38	38	-5.04	178					
	L	Retrosplenial	-20	-53	5	-4.97	136					
Temporal	R	Heschel's gyrus						48	-21	9	-5.24	692
	R	Heschel's gyrus						52	-9	0	-4.92	60
	R	Medial temporal gyrus/temporal pole	42	11	-22	5.8	3708	44	14	-27	4.97	96
	L	Medial temporal gyrus/temporal pole	-47*	17	-8	5.55	5402	-47	11	-24	5.09	636
	R	Hippocampus	28	-9	-22	-5.27	834					
	R	Parahippocampal gyrus						27	-10	-25	-5.57	3236
	R	Inferior temporal gyrus	55	-44	-13	-4.86	3	55	-40	-16	-5.1	413
	L	Inferior temporal gyrus						-51	-44	-18	-5.2	1103
Parietal	R	Supra-marginal gyrus	56	-29	38	-5.26	751	55	-28	40	-5.64	732
	L	Supra-marginal gyrus						-46	-39	42	-4.97	33
	R	Precuneus	9	-63	43	-5.21	820					
	R	Superior parietal lobule						21	-62	38	-5.25	3069
	L	Superior parietal lobule						-21	-72	42	-5.05	981
Occipital	R	Lateral occipital cortex	40	-67	-1	-5.29	2436					
	R	Middle occipital gyrus	21	-77	15	-5.18	6206					
	L	Middle occipital gyrus						-29	-70	14	-5.85	26405
	L	Middle occipital gyrus						-31	-82	5	-5.22	3663
Basal ganglia	R	Globus pallidus	12	-2	3	4.94	175	17	-7	5	5.27	1036
	L	Putamen	-22	0	4	5.02	401					
Midbrain	L	Hypothalamus/colliculi	-3	-23	0	5.23	605	-3	-28	-1	4.95	87
Cerebellum	R	Cerebellum	12	-59	-26	5.93	22599	10	-54	-27	5.66	21595

*Coordinate outside brain connecting activation in temporal pole and FOp.

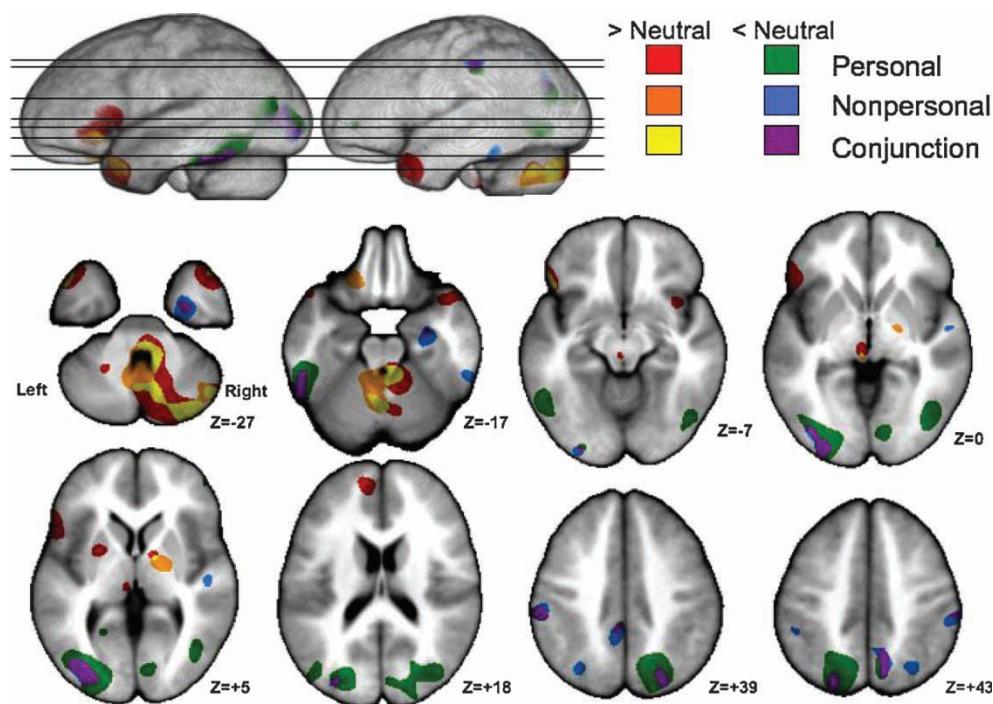


Figure 1. Experiment 1 brain activation data from conjunction analysis using a color-coded key. Areas that are significantly different in personal imagery from neutral imagery are depicted in red (>neutral) and green (<neutral); areas that are significantly different in nonpersonal imagery from neutral imagery are depicted in orange (>neutral) and blue (<neutral); areas where both personal and nonpersonal significantly overlap are depicted in yellow (>neutral) and purple (<neutral). Slices are labeled with respect to their Z-coordinate in the Talairach system.

imagery (Figure 1). There were large bilateral clusters that were more active for both types of emotional imagery than for neutral imagery in the cerebellum, brainstem, basal ganglia, and temporal poles. There were also large bilateral clusters that were less active during emotional imagery than neutral imagery in the left inferotemporal cortex (including the fusiform face area), right supra-marginal gyrus (SMG), right parahippocampal gyrus and left retrosplenial cortex. Personal imagery revealed an increase in activation compared to neutral imagery in the left anterior cingulate and decreased activation compared to neutral imagery in the dorsolateral prefrontal cortex (DLPFC), posterior cingulate, retrosplenial cortex, precuneus, and occipital cortex on the right. Nonpersonal imagery revealed an increase in activation compared to neutral imagery in the left orbital frontal cortex (OFC) and decreased activation compared to neutral imagery in right Heschl's gyrus, the right parahippocampal gyrus, left inferotemporal gyrus, bilateral superior parietal lobule, and the occipital cortex on the left.

Discussion

When participants were imagining, as if it were happening to them, an emotional experience from someone else's life selected to be the one they could relate to *the most*, they reported experiencing a similar level of emotional intensity as when they imagined an emotional experience from their own life. In either case, these emotional experiences were significantly more intense than those related to neutral scenarios. These findings were supported by self-report ratings of emotional intensity as well as heart rate, both of which revealed higher rates during emotional imagery than neutral imagery, without any distinction between personal imagery and nonpersonal, but "highly relatable" imagery scenarios. Skin conductance values did not differ across imagery types but were higher for anger than for fear scenarios, suggesting that anger imagery produces more sympathetic activation than fear imagery.

Anger produced more activation than fear in the anterior cingulate cortex on the right, and in a large sector of the superior temporal gyrus, extending forward to the temporal pole, and in

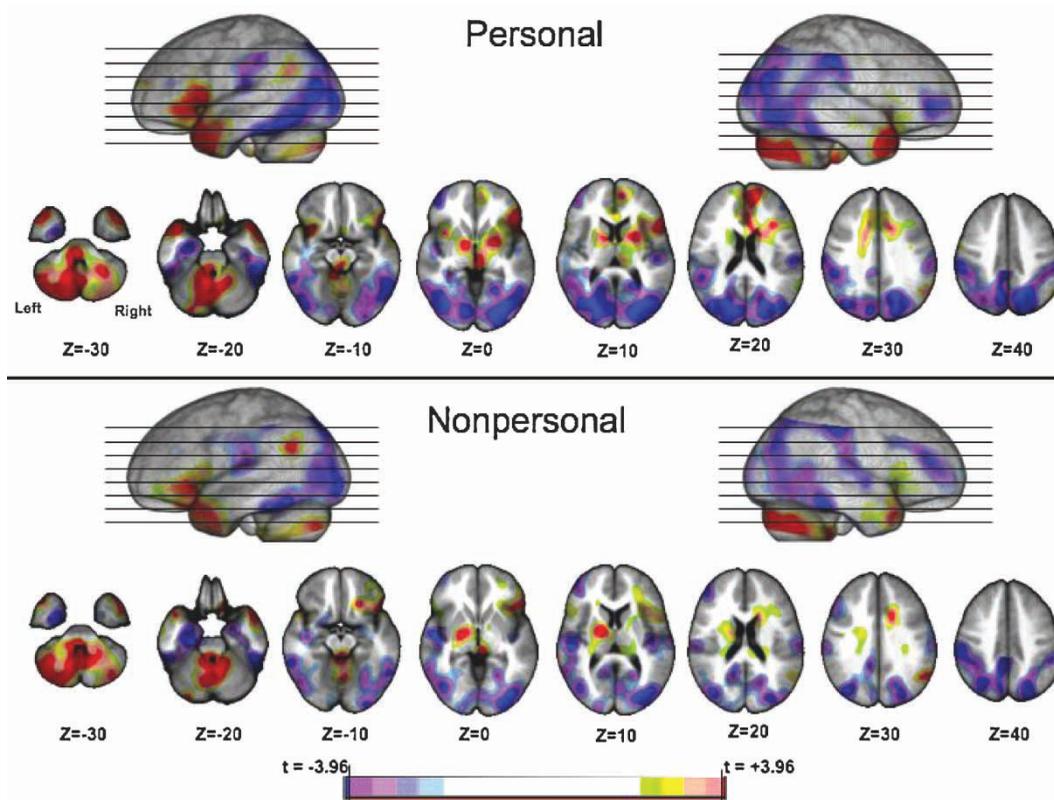


Figure 2. Experiment 1 brain activation data from the conjunction analysis showing personal imagery minus neutral imagery at the top and nonpersonal imagery minus neutral imagery at the bottom for comparison. For both conditions, significant increases in activation compared to neutral imagery are represented in red and all significant decreases in activation compared to neutral imagery are represented by royal blue as depicted in the color bar at the bottom ($t > \pm 3.96$). All images are presented in neurological convention with slices labeled with respect to their Z-coordinate in the Talairach system.

the lateral orbital cortex, which is consistent with activation related to personal imagery during anger in a prior study (Damasio et al., 2000). The predominance of anger activation on the left, especially in the frontal operculum (FOp) could reflect the nature of the task, as most of the scenarios involved heated arguments with another person, which would probably activate language-processing areas. Fear, in contrast, had had more activation compared to anger in the right hemisphere, in the posterior cingulate cortex, basal ganglia and supra-marginal gyrus, which is in keeping with the nature of fear scenarios, which usually involved physical events such as running, falling, or being attacked.

There were no significant differences in brain activation between personal and nonpersonal emotional imagery, using either the t -statistic at the level of the ROI or the whole brain, or using cluster analysis to identify large clusters of activation. Based on the results of the conjunction analysis, this null effect is not due to a lack of activation in emotional imagery trials compared

to neutral imagery, as both personal and nonpersonal imagery showed many areas that were significantly different from neutral imagery. These patterns of activation were strikingly similar with large areas of increased activation compared to neutral imagery in multiple regions including bilateral areas of the temporal pole, basal ganglia, and cerebellum and decreased activation compared to neutral imagery in bilateral areas of the inferotemporal cortex, occipital cortex and parietal lobes. There was also activation in other areas associated with the representation of feeling states, but these areas were more lateralized, with greater orbital frontal cortex (OFC), anterior cingulate, and insular activation compared to neutral imagery in the left hemisphere, all of which were more pronounced in the personal than the nonpersonal imagery contrasts with neutral imagery.

Because increases in activation were mainly found in areas that represent feeling states while decreases in activation were mainly found in areas that represent visuo-spatial processing, it

seems reasonable to suggest that emotional imagery relies importantly on reliving the feelings associated with the event and relies less on a concrete, visual image of the event. The fact that the personal and nonpersonal imagery produced such similar patterns of activation suggests that, indeed, participants do use their own substrates of processing to imagine being in the shoes of another, but this is likely to be due to the fact that they selected stories to which they could relate the most, in which case it is unclear the extent to which participants were actually imagining a related, personal scenario, akin to projection, or truly generating a new one based on the script. Based on subject comments after the nonpersonal imagery, it was clear that subjects were really trying to imagine the scenario described in the script, not simply imagining a highly similar scenario that had happened to them in the past. However, it is likely that when instructed: "Picture yourself in that situation and feel as scared/angry as you can," the subjects put great effort into trying to generate the feeling state associated with that emotion, which would necessarily activate their representations for that state based on personal experience and learning from others.

Although we found almost complete overlap between personal and nonpersonal imagery, it is still possible that there can be processing differences between personal and nonpersonal imagery in cases where subjects are less able to draw on a personal past experience in place of the other's experience. To test this, an additional experiment was conducted that was identical in design, but asked participants to select a nonpersonal experience to which they could *not* relate, or could relate to *the least*. Perhaps a more generative, creative, top-down cognitive process is needed to create an image of a novel situation or feeling, which would manifest as activation that is increased for nonpersonal imagery compared to personal. Additional self-report and psychophysiology measures were also added to aid interpretation of the data.

EXPERIMENT 2

Method

Participants. During the screening session, one participant was excluded due to ambidexterity and four participants were excluded because they

did not have a significant personal memory of fear or anger. Five participants dropped out of the study between the screening session and the PET scan. Seventeen participants were tested in total, eight male, nine female, mean age 24.65 ($SD = 5.76$) ranging from 18 to 41. Eight participants imagined experiences of anger (4 males and 4 females) and nine participants imagined experiences of fear (4 males and 5 females; see Table 1). All participant assignment was randomly determined in advance.

Procedures. Procedures were identical to those described above for Experiment 1 except that participants in this experiment were specifically instructed to select the nonpersonal story to which they could relate the *least*.

Additional self-report and psychophysiology measures were added to help address different hypotheses. Specifically, participants selected which basic emotion they felt the most during their previous imagery, in order to verify that they indeed felt the assigned emotion during the emotional but not the neutral imagery trials, and participants rated the vividness of the imagery from 0 to 4 in order to determine if differences in the effectiveness of the personal and nonpersonal imagery were related to how easy it was to imagine the scenarios or specifically to an inability to become aroused by the scenario despite equivalent quality of the imagery. Trait scales of empathy were administered at the end of the prescreening session to use as a covariate for the PET imaging data because it would be interesting to know if people who self-report as experiencing more empathy, personal distress, or perspective taking were more likely to engage, or to engage to a greater degree, a particular neural region.

Additional psychophysiology measures were collected in order to specify the reactions of the participants during the emotional imagery periods. Respiration was measured with a belt attached around the torso and generalized motor activity was measured using an EMG electrode attached to the dorsum of the right hand.

Statistical analysis

Ancillary data. All measures were analyzed using the same series of two GLMs, the first to test whether the first two neutral imagery trials differed from the last two, modeling subject identity as random factor (reduced by iterative REML) and using a dummy-code for neutral

imagery trials (neutral 1 and 2 = 1, neutral 3 and 4 = 2), the second testing for differences among the imagery types using subject identity as a random factor (iterative REML) and testing for effects of imagery replication (four levels for neutral, two levels each for personal and nonpersonal imagery, nested within condition), emotion (anger vs. fear), and imagery type (neutral, nonpersonal, personal). The dependent variables of interests were the ratings of emotional intensity (0–4), vividness, heart rate in beats per minute (BPM), and skin conductance on the left hand (area under the curve), respiration (number of peaks per unit time) and EMG (microvolts per second). Significant effects were followed by Tukey's honestly significant difference tests and Student's *t*-tests; these were used to interpret main effects. The alpha level for all comparisons was set at .05.

Descriptive statistics were calculated for the Interpersonal Reactivity Index (IRI) subscales (Empathic Concern, Fantasy, Perspective Taking, Personal Distress; Davis, 1994) and the Mehrabian and Epstein Emotional Empathic Concern Scale (EECS; Mehrabian & Epstein, 1972), which were used as covariates in the final PET analysis.

PET contrasts. Identical analyses were performed on the PET imaging data as in Experiment 1, using the regression model that included a variable for subject nested within emotion (fear or anger), a within-subjects factor of imagery type (personal vs. nonpersonal), a between-subjects factor of emotion (fear vs. anger), and an interaction term between condition and emotion. Four contrasts were again tested: personal versus nonpersonal (1), anger versus fear (2), and personal versus nonpersonal nested within anger (3) and fear (4). Again searches were performed using the ROI and the whole brain and the spatial extent statistic was calculated with statistical images converted to *Z*-images and thresholded using clusters where $Z > 3.0$ ($-3.0 < Z < 3.0$) and a corrected, cluster significance of $p < .05$ (Friston et al., 1994).

In addition to the analyses from Experiment 1, ANCOVAs were performed to determine if blood flow in the first, nonpersonal injection varied as a function of the trait empathy covariables. Due to the correlation among the trait covariables, each trait covariable was used in a separate regression analysis. In addition to the appropriate mean-centered trait covariate, each regression model contained the between-subjects factor of emotion (fear or anger). Each trait covariable was

analyzed using a *t*-statistic with thresholds determined by random field theory using $p < .05$, corrected (Worsley, 1994).

Results

Ancillary data. Overall emotional intensity ratings were equivalent between the first two neutral imagery trials and last two neutral imagery trials, $F(1, 41) = 0.782$, *ns*, justifying their equal treatment in a subsequent GLM testing effects across all three imagery types. In this GLM, there were no differences in replicates within each imagery type, $F(3, 92) = 0.906$, *ns*, or between fear and anger, $F(1, 92) = 0.462$, *ns*, but there was a main effect of imagery type, $F(2, 92) = 58.686$, $p < .0001$, due to a linear scaling of ratings with personal imagery most intense ($M = 3.220$), nonpersonal imagery significantly less intense than personal ($M = 1.881$) and neutral imagery significantly less intense than nonpersonal ($M = 1.372$). The results were identical using subject's ratings for the intensity of the specific emotion they were imagining (fear or anger), $F(2, 92) = 181.009$, $p < .0001$.

Vividness ratings were equivalent between the first and last two neutral imagery trials, $F(1, 41) = 2.545$, *ns*, justifying their equal treatment in a subsequent GLM testing effects across all three imagery types. In this GLM, there were no differences in replicates within each imagery type, $F(3, 92) = 0.333$, *ns*, or between fear and anger, $F(1, 92) = 0.494$, *ns*, but there was a main effect of imagery type, $F(2, 92) = 15.005$, $p < .0001$, due to greater reported vividness for personal ($M = 3.020$) and neutral imagery ($M = 3.020$) than nonpersonal imagery ($M = 2.270$); personal and neutral were equivalent.

Heart rate was equivalent between the first and last two neutral imagery trials, $F(1, 48) = 1.75$, *ns*, justifying their equal treatment in a subsequent GLM testing effects across all three imagery types. In this GLM, there were no differences between the first and second replicate within each imagery type, $F(3, 110) = 0.222$, *ns*, but there was a main effect of condition, $F(2, 110) = 13.055$, $p < .0001$, due to higher heart rates in personal trials ($M = 65.684$) than in nonpersonal ($M = 62.634$) and neutral imagery trials ($M = 61.055$), which were equivalent. There was also a main effect of emotion, $F(1, 110) = 6.763$, $p = .011$, due to a higher heart rate in fear participants ($M = 69.075$) than anger ($M = 57.173$).

Skin conductance was lower on the first two ($M = 4.517$) than the last two ($M = 10.367$) neutral imagery trials, $F(1, 48) = 5.803$, $p = .0199$. Thus a subsequent GLM was used that kept the first two neutral imagery trials separate from the last two, yielding four conditions: neutral before, personal, nonpersonal, and neutral after. This GLM found no differences in replicates within each imagery type, $F(4, 108) = 0.079$, *ns*, or between fear and anger, $F(1, 108) = 0.251$, *ns*, but there was a main effect of condition, $F(3, 108) = 4.408$, $p = .0058$, due to lower skin conductance in the first two neutral imagery trials ($M = 4.358$) than in personal trials ($M = 16.667$).

Respiration was equivalent between the first and last two neutral imagery trials, $F(1, 45) = 0.015$, *ns*, justifying their equal treatment in a subsequent GLM testing effects across all three imagery types. In this GLM, there were no differences in replicates within each imagery type, $F(3, 103) = 0.094$, *ns*, or between fear and anger, $F(1, 103) = 0.056$, *ns*, but there was a main effect of imagery type, $F(2, 103) = 202.859$, $p < .0001$, due to higher respiration during personal ($M = 9.09$) than nonpersonal ($M = 6.66$) and neutral imagery ($M = 6.02$), which were equivalent.

The EMG data from the hand found less motor activity in the first two neutral imagery trials ($M = 62.127$) than in the last two ($M = 191.223$), suggesting some residual change in state after the emotional scenarios or an order effect due to fatigue, as was the case with SCR. Thus, the GLM was used that kept the first two neutral imagery trials separate from the last two, yielding four conditions: neutral before, personal, nonpersonal, and neutral after. There were no main effects of replicate, $F(4, 101) = 0.374$, *ns*, emotion, $F(1, 101) = 0.139$, *ns*, or imagery type, $F(3, 101) = 1.367$, *ns*.

Among the IRI subscales, the Empathic Concern scale had a mean of 20.82 ($SD = 4.83$, range 6–28), the Fantasy Scale had a mean of 18.06 ($SD = 4.38$, range 11–28) the Perspective Taking scale had a mean of 16.53 ($SD = 5.44$, range 9–26) and the Personal Distress scale had a mean of 9.19 ($SD = 4.92$), consistent with the published means (Davis, 1980). The Mehrabian and Epstein Scale of Emotional Empathy had a mean of 36.77 ($SD = 25.53$, range –18–90), consistent with the published mean of 33 ($SD = 24$).

PET contrasts

Anger > fear. Comparing the basic emotions of anger and fear, the results were similar to those of Experiment 1, with greater activation for fear in the left inferior frontal gyrus, anterior cingulate, and the posterior sector of the superior temporal gyrus, but these results were not significant in Experiment 2 using the ROI, whole brain, or spatial extent statistic analyses ($t > -5.44$, *ns*).

Personal > nonpersonal. Information about significant effects including peak locations, number of voxels and local maxima and minima are reported in Table 5. There were no differences between personal and nonpersonal imagery in the ROI ($t < 3.22$, *ns*), but using the spatial extent statistic there were large clusters that were more active in nonpersonal than personal imagery (neutral intermediate), in the left inferotemporal/fusiform gyrus ($Z = -4.28$, $p < .05$) and lateral cerebellum ($Z = -3.63$, $p < .05$; Figure 3). Within the two emotions, fear participants did not show any significant differences between personal and nonpersonal imagery ($-3.39 < t < 3.03$, *ns*); anger participants did not have any significant differences within the ROI ($t < \pm 3.94$) but in the whole brain analysis there was increased activation in the personal imagery, compared to the nonpersonal, in the left superior temporal gyrus ($t = 5.02$, $p < .05$).

Discussion

In Experiment 1, the nonpersonal emotional scenario was selected to permit participants to relate to them easily. This produced equivalent levels of emotionality to the personal emotional scenario across multiple measures. In contrast, in Experiment 2, in which the nonpersonal emotional scenarios were selected to be hard to relate to, personal imagery produced greater emotionality than nonpersonal imagery. Participants reported higher levels of emotional intensity (overall and for the specific emotion), vividness of the imagery, had higher heart rates and greater respiration when imagining the personal than the nonpersonal scenarios.

Skin conductance no longer showed a difference between fear and anger. One possibility is that this effect was not reliable. Another possibility is that the strengths of the emotional experiences

TABLE 5

Significant effects in Experiment 2. Peak areas of activation and local maxima are presented using Talairach coordinates with inferential statistics. Results are reported for the contrast of personal and nonpersonal imagery at a whole brain level using cluster analyses with a critical Z of 3.00 and for the contrast of personal and nonpersonal imagery specifically in the emotion condition of anger using a whole brain analysis with a critical t of 4.29

Comparison	Mask	Test (α)	Peak						Local maximum (t)	Side	Region
			x	y	z	t	Voxels	p			
Personal > Impersonal	Whole	Z (3.00)	-45	-34	-18	-3.42	4511	0.029	-43, -28, -17 (-4.28)	L	ITG/fusiform
Anger Personal > Impersonal	Whole	T (4.79)	-34	-34	13	4.89	36		-50, -41, -31 (-3.63)	L	Lateral cerebellum
									-35 -35 14 (5.02)	L	STG/transverse

of anger and fear evoked during imagery in this sample were almost equivalent.

Both the skin conductance and EMG data showed differences between early and late neutral imagery trials, suggesting either that subjects are more aroused after experiencing emotional imagery, or simply move more towards the end of a long experiment (in the final two neutral imagery trials). However, this order effect does not impact the comparison of interest between the personal and nonpersonal imagery (which were counterbalanced) and only served to add noise to the imaging subtractions that averaged the neutral imagery trials together before subtracting them from the emotional imagery trials.

Interestingly, the self-reports of vividness followed a unique pattern, with neutral imagery and personal imagery being rated as significantly more vivid than the nonpersonal. Neutral imagery should not be intense or emotional, but because it was drawn from the participant's own life and had occurred recently, it was remembered as well as a highly salient memory from the subject's past. This is in contrast to a nonpersonal memory that could not be vivid because it had not been directly experienced by the subject and was, thus, harder to visualize.

In conclusion, across multiple measures, there was a difference between personal and nonpersonal imagery when participants could not relate easily to the other person's scenario, a difference that was not present when the participants could relate to the scenario, even though it was drawn from another person's life. This was also true of the brain activation data, which revealed significant differences between the personal and nonpersonal imagery under these conditions. With both emotions combined there was a large region in the inferior part of the left hemisphere including the inferior temporal and the fusiform gyri and the lateral cerebellum that was less active than neutral imagery during personal imagery (as it was in Experiment 1 for both the personal and the nonpersonal conditions) and more active than neutral imagery during nonpersonal imagery, something that did not occur in Experiment 1. It is possible that the left, lateral cerebellar activation is a spillover from the left IT/Fusiform activation, especially since the cerebellar activation is no longer present when the data are analyzed at a smaller smoothing kernel (6 FWHM). There were no significant differences between personal and nonpersonal imagery

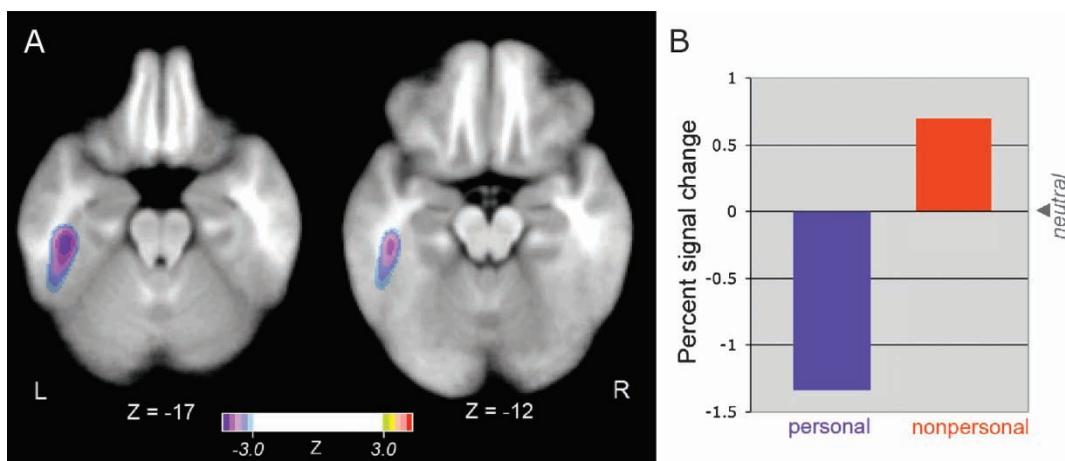


Figure 3. Experiment 2 brain activation data from the contrast of personal minus nonpersonal imagery, without respect to emotion. Part (a) depicts the extent of the cluster in the inferotemporal cortex, which was significantly more active for nonpersonal than personal imagery in two slices. The images have been masked to only show regions that were significantly different ($Z > -3.00$). All images are presented in neurological convention with slices labeled with respect to their Z-coordinate in the Talairach system. Part (b) depicts the mean activation levels for personal minus neutral imagery compared to nonpersonal minus neutral imagery.

within fear participants alone, which may be due in part to the low sample size within emotion conditions and to the manifest difficulty of inducing fear in laboratory conditions, which is consistent with lower accuracy ratings for fear in emotion recognition studies and with decreased SCR for fear in Experiment 1. However, subjective ratings were equivalent and heart rate was actually higher for fear in Experiment 2. Within anger participants, there was a significantly greater recruitment of the left superior temporal and transverse gyri for personal than for nonpersonal imagery.

GENERAL DISCUSSION

This study investigated the neural substrates of cognitive empathy, defined as the deliberate attempt to effortfully imagine what it is like to be in the emotional situation of another person as if it is happening to you. The results suggest that the substrates of cognitive empathy depend in large part on how well the participant can relate to the situation of the other. When participants selected the nonpersonal story that they could relate to the most, there were no statistically significant differences between areas recruited for personal and nonpersonal imagery. This is in keeping with all theories that propose that people activate their own emotion-producing substrates when observing the emotional state of another, including mirror neuron theories (Gallese, 2001;

Iacoboni & Lenzi, 2002), perception–action theories (Preston & de Waal, 2002), neural versions of simulation theory (Adolphs, 1999; Gallese & Goldman, 1998) and Damasio’s conceptualization of emotion (Damasio, 2003). This overlap also confirms multiple previous studies that found overlap in areas recruited for experiencing and observing basic emotions and pain in another (Carr et al., 2003; Decety & Chaminade, 2003; Singer et al., 2004; Wicker et al., 2003). However, when participants selected the nonpersonal story that they could relate to *the least*, there were differences between personal and nonpersonal imagery, suggesting that cognitive perspective-taking theories of empathy may be especially applicable when participants do not already possess representations that can encapsulate the experience of the other.

When the participants could relate less to the other person’s scenario, in both fear and anger conditions, there was more activation for the nonpersonal than personal imagery in left inferior temporal and fusiform gyri and higher-order visual association areas, including regions often associated with face processing (Kanwisher, McDermott, & Chun, 1997). As for the greater activation in the left hemisphere, this has been noted with actual and imagined self-action as well as imitation (Decety et al., 2002; Goldenberg, 1999; Grafton, Arbib, Fadiga, & Rizzolatti, 1996) and it is, thus, possible that participants recruited the left hemisphere because they were actively imagining themselves in the situation. In contrast,

in Experiment 1 there was a significant decrease compared to neutral imagery in the nonpersonal condition in Heschel's gyrus on the right, further suggesting that the nonpersonal imagery was less dependent on auditory than visual information.

There were strong differences in activation between personal and nonpersonal imagery in the cerebellum. Both fear and anger participants had greater activation for nonpersonal imagery in the ventro-lateral part of the cerebellum. This region may correspond to the posterior, lateral portion of the cerebellum, which has been associated with imagined movement (Allen, Buxton, Wong, & Courchesne, 1997; Grafton et al., 1996; Hanakawa et al., 2003).

Mental imagery is usually associated with activation in the hippocampus, amygdala, entorhinal cortex, and parahippocampal gyrus (Kreiman, Koch, & Fried, 2000). These areas were not differentially activated by the conditions in our studies, because participants were engaged in imagery in all three conditions (neutral, personal, and nonpersonal).

In conclusion, empathy depends on the degree to which we can relate to the experience of another. When we can relate to the experience of the other, we activate our own records of a comparable situation and produce an emotional experience, characteristic of "true empathy" (cf. Ungerer, 1990). It should be noted that when we activate personal representations of emotional situations in relation to the states of others, we may be predisposed to "project" our own feelings onto the other rather than truly "trying on" the state of the other, as presupposed by more cognitive accounts of empathy such as philosophical versions of simulation theory (Goldman, 1992) and perspective taking (Goldie, 1999; Smith, 1989). Thus, the fact that we access our own representations means that the difference between projection and empathy depends on the extent to which our representations are applicable to the experience of the other (Preston & de Waal, 2002). When we cannot relate to the experience of the other, presumably because we do not have records of comparable feelings and situations from our own past experience, we can achieve empathy by literally trying to imagine what it is like to be the other person, in keeping with traditional perspective-taking theories of empathy, which describe empathy as "putting oneself in the place of another" or "imaginatively projecting oneself into the situation of another"

(Allport, 1937; Buchheimer, 1963; Demos, 1984; Goldie, 1999; Smith, 1989).

Our model is not in contradistinction to mirror neuron or simulation theories of empathy, which also propose that subjects use their own representations to internally simulate the states of others (Adolphs, 1999; Gallese & Goldman, 1998; Jacoboni & Lenzi, 2002), but an important difference of emphasis and practical application is apparent from our results. Perhaps because mirror neurons were discovered with respect to grasping actions that are virtually ubiquitous across individuals and even primate species, other models implicitly assume that subjects possess the representations needed to simulate or "try on" any conceivable object experience. In contrast, nonscientific use of the term "empathy" reserves its use for a minority of cases where there is serious emotional distress and the observer has had an almost identical experience. Thus, the child cannot be said to *empathize* with the parent nor the husband with the laboring wife. This distinction likely exists because, in an important way, subjects can only really feel states that they have experienced, creating an increasingly widening intersubjective gap for states of increasing distress, less and less likely to have been experienced by others. Our model puts a high explicit demand on the need for representations developed from past experience to successfully simulate how another feels. As our data show, without similar past experience, one *can* imagine being in another's shoes, but the result is much less vivid, less emotional and even of a different quality, which likely diminishes the accuracy of the empathy, the motivation to help and the likelihood that the object will receive comfort. From a phenomenological perspective, these differences in the quality of the empathic experience are of critical importance and should not be overlooked or underestimated.

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REFERENCES

- Adolphs, R. (1999). Social cognition and the human brain. *Trends in Cognitive Sciences*, 3(12), 469–479.
- Allen, G., Buxton, R. B., Wong, E. C., & Courchesne, E. (1997). Attentional activation of the cerebellum

- independent of motor involvement. *Science*, 275(5308), 1940–1943.
- Allport, G. W. (1937). *Personality: A psychological interpretation*. New York: Henry Holt.
- Blakemore, S.-J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature Reviews*, 2, 561–567.
- Buchheimer, A. (1963). The development of ideas about empathy. *Journal of Counseling Psychology*, 10(1), 61–70.
- Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C., & Lenzi, G. L. (2003). Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proceedings from the National Academy of Sciences*, 100(9), 5497–5502.
- Damasio, A. (1994). *Descartes's error: Emotion, reason, and the human brain*. New York: G. P. Putman's Sons.
- Damasio, A. R. (2003). *Looking for Spinoza: Joy, sorrow, and the feeling brain* (1st ed). Orlando, FL: Harcourt Books.
- Damasio, A. R., Grabowski, T. J., Bechara, A., Damasio, H., Ponto, L. L. B., Parvizi, J., et al. (2000). Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nature Neuroscience*, 3(10), 1049–1056.
- Damasio, H., & Frank, R. (1992). Three-dimensional in vivo mapping of brain lesions in humans. *Archives of Neurology*, 49(2), 137–143.
- Damasio, H., Grabowski, T. J., Frank, R. J., Knosp, B., Hichwa, R. D., Watkins, G. L., et al. (1993). PET-Brainvox, a technique for neuroanatomical analysis of positron emission tomography images. In K. Uemura, N. A. Lassen, T. Jones, & I. Kanno (Eds.), *Quantification of brain function. Tracer kinetics and image analysis in brain PET* (pp. 465–473). Amsterdam: Elsevier.
- Damasio, H., Tranel, D., Grabowski, T., Adolphs, R., & Damasio, A. (2004). Neural systems behind word and concept retrieval. *Cognition*, 92(1–2), 179–229.
- Davis, M. H. (1980). Individual differences in empathy: A multidimensional approach. *Dissertation Abstracts International*, 40(7-B), 3480.
- Davis, M. H. (1994). *Empathy: A social psychological approach*. Boulder, CO: Westview Press.
- Decety, J., & Chaminade, T. (2003). Neural correlates of feeling sympathy. *Neuropsychologia*, 41(2), 127–138.
- Decety, J., Chaminade, T., Grèzes, J., & Meltzoff, A. N. (2002). A PET exploration of the neural mechanisms involved in reciprocal imitation. *NeuroImage*, 15, 265–272.
- Decety, J., & Grèzes, J. (2006). The power of simulation: Imagining one's own and other's behavior. *Brain Research*, 1079(1), 4–14.
- Decety, J., & Sommerville, J. A. (2003). Shared representations between self and other: A social cognitive neuroscience view. *Trends in Cognitive Science*, 7(12), 527–533.
- Demos, V. (1984). Empathy and affect: Reflections on infant experience. In J. Lichtenberg, M. Bornstein, & D. Silver (Eds.), *Empathy II* (Vol. 3, pp. 9–34). Hillsdale, NJ: Analytic Press.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91, 176–180.
- Eisenberg, N. (1986). *Altruistic emotion, cognition, and behavior*. Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
- Eisenberg, N., Fabes, R. A., Miller, P. A., Fultz, J., Shell, R., Mathy, R. M., et al. (1989). Relation of sympathy and personal distress to prosocial behavior: A multimethod study. *Journal of Personality and Social Psychology*, 57(1), 55–66.
- Feshbach, N. D. (1975). Empathy in children: Some theoretical and empirical considerations. *The Counseling Psychologist*, 5, 25–30.
- Frank, R. J., Damasio, H., & Grabowski, T. J. (1997). Brainvox: An interactive, multimodal visualization and analysis system for neuroanatomical imaging. *NeuroImage*, 5(1), 13–30.
- Friston, K. J., Worsley, K. J., Frackowiak, R. S. J., Mazziotta, J. C., & Evans, A. C. (1994). Assessing the significance of focal activations using their spatial extent. *Human Brain Mapping*, 1, 214–220.
- Gallese, V. (2001). The “shared manifold” hypothesis: From mirror neurons to empathy. In E. Thompson (Ed.), *Between ourselves: Second-person issues in the study of consciousness* (pp. 33–50). Thorverton, UK: Imprint Academic.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, 2(12), 493–501.
- Goldenberg, G. (1999). Matching and imitation of hand and finger postures in patients with damage in the left or right hemispheres. *Neuropsychologia*, 37(5), 559–566.
- Goldie, P. (1999). How we think of others' emotions. *Mind & Language*, 14(4), 394–423.
- Goldman, A. I. (1992). In defense of the simulation theory. *Mind & Language*, 7(1–2), 104–119.
- Grabowski, T. J., Damasio, H., Frank, R., Hichwa, R. D., Boles Ponto, L. L., & Watkins, G. L. (1995). A new technique for PET slice orientation and MRI-PET coregistration. *Human Brain Mapping*, 2, 123–133.
- Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography: Observation compared with imagination. *Experimental Brain Research*, 112(1), 103–111.
- Hanakawa, T., Immisch, I., Toma, K., Dimyan, M. A., Gelderen, P. V., & Hallett, M. (2003). Functional properties of brain areas associated with motor execution and imagery. *Journal of Neurophysiology*, 89, 989–1002.
- Hichwa, R. D., Ponto, L. B., & Watkins, G. L. (1995). *Chemists views of imaging centers*. New York: Plenum Press.
- Hoffman, M. L. (1978). Empathy: Its development and prosocial implications. In J. H. E. Howe & C. B. Keasey (Eds.), *Nebraska symposium on motivation: Social cognitive development* (Vol. 25, pp. 169–217). Lincoln, NE: University of Nebraska Press.
- Hoffman, M. L. (1982). Affect and moral development. *New Directions for Child Development*, 16, 83–103.

- Hoffman, M. L. (2000). *Empathy and moral development: Implications for caring and justice*. Cambridge, UK: Cambridge University press.
- Holmes, C. J., Hoge, R., Collins, L., Woods, R. P., Evans, A. C., & Toga, A. W. (1998). Enhancement of MR images using registration for signal averaging. *Journal of Computer Assisted Tomography*, 22, 324–333.
- Iacoboni, M., & Lenzi, G. L. (2002). Mirror neurons, the insula, and empathy (commentary). *Behavioral and Brain Sciences*, 25(1), 39–40.
- Jackson, P. L., Brunet, E., Meltzoff, A. N., & Decety, J. (2006). Empathy examined through the neural mechanisms involved in imagining how I feel versus how you feel pain. *Neuropsychologia*, 44(5), 752–761.
- Jackson, P. L., Meltzoff, A. N., & Decety, J. (2005). How do we perceive the pain of others? A window into the neural processes involved in empathy. *NeuroImage*, 24(3), 771–779.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 17(11), 4302–4311.
- Kreiman, G., Koch, C., & Fried, I. (2000). Imagery neurons in the human brain. *Nature*, 408, 357–361.
- Lamm, C., Batson, C. D., & Decety, J. (2007). The neural substrate of human empathy: Effects of perspective-taking and cognitive appraisal. *Journal of Cognitive Neuroscience*, 19(1), 42–58.
- Lipps, T. (1903). Einfühlung, innere Nachahmung und Organempfindung. *Archiv für die gesamte Psychologie*, 1, 465–519.
- Mehrabian, A., & Epstein, N. (1972). A measure of emotional empathy. *Journal of Personality*, 40(4), 525–543.
- Merleau-Ponty, M. (1970). *Phenomenology of perception* (5th ed.). London: Routledge & Kegan Paul. (Originally published 1962)
- Nichols, T., Brett, M., Andersson, J., Wager, T., & Poline, J. B. (2005). Valid conjunction inference with the minimum statistic. *NeuroImage*, 25(3), 653–660.
- Preston, S. D., & de Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences*, 25(1), 1–71.
- Prinz, W. (1987). Ideo-motor action. In H. Heuer & A. F. Sanders (Eds.), *Perspectives on perception and action* (pp. 47–76). Hillsdale, NJ: Lawrence Erlbaum Associates, Inc.
- Ruby, P., & Decety, J. (2001). Effect of subjective perspective taking during simulation of action: A PET investigation of agency. *Nature Neuroscience*, 4(5), 546–550.
- Ruby, P., & Decety, J. (2004). How would you feel versus how do you think she would feel? A neuroimaging study of perspective-taking with social emotions. *Journal of Cognitive Neuroscience*, 16(6), 988–999.
- Singer, T., Seymour, B., O’Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science*, 303, 1157–1162.
- Smith, D. W. (1989). *The circle of acquaintance: Perception, consciousness and empathy*. Dordrecht, The Netherlands: Kluwer.
- Ungerer, J. A. (1990). The early development of empathy: Self-regulation and individual differences in the first year. *Motivation and Emotion*, 14(2), 93–106.
- Wicker, B., Perrett, D. I., Baron-Cohen, S., & Decety, J. (2003). Being the target of another’s emotion: A PET study. *Neuropsychologia*, 41(2), 139–146.
- Wispé, L. (1987). History of the concept of empathy. In N. Eisenberg & J. Strayer (Eds.), *Empathy and its development* (pp. 17–37). New York: Cambridge University Press.
- Woods, R. P., Cherry, S. R., & Mazziotta, J. C. (1992). A rapid automated algorithm for accurately aligning and reslicing PET images. *Journal of Computer Assisted Tomography*, 16, 620–633.
- Woods, R. P., Dapretto, M., Sicotte, N. L., Toga, A. W., & Mazziotta, J. C. (1999). Creation and use of a Talairach-compatible atlas for accurate, automated, nonlinear intersubject registration, and analysis of functional imaging data. *Human Brain Mapping*, 8, 73–79.
- Woods, R. P., Grafton, S. T., Watson, J. D., Sicotte, N. L., & Mazziotta, J. C. (1998). Automated image registration: II. Intersubject validation of linear and nonlinear models. *Journal of Computer Assisted Tomography*, 22, 153–156.
- Woods, R. P., Mazziotta, J. C., & Cherry, S. R. (1993). PET-MRI registration with automated algorithm. *Journal of Computer Assisted Tomography*, 17, 536–546.
- Worsley, K. J. (1994). Local maxima and the expected Euler characteristic of excursion sets of Chi(2), F, and t fields. *Advances in Applied Probability*, 26, 13–42.