

An fMRI study of caring vs self-focus during induced compassion and pride

Emiliana R. Simon-Thomas,¹ Jakub Godzik,² Elizabeth Castle,³ Olga Antonenko,⁴ Aurelie Ponz,⁴ Aleksander Kogan,⁴ and Dacher J. Keltner⁴

¹The Center for Compassion and Altruism Research and Education, Stanford University, Stanford, California, USA, ²Department of Medicine, Washington University, St. Louis, Missouri, USA, ³Department of Psychology, University of California, Los Angeles, Los Angeles, CA, USA, and ⁴Department of Psychology, University of California, Berkeley, Berkeley, California, USA

This study examined neural activation during the experience of compassion, an emotion that orients people toward vulnerable others and prompts caregiving, and pride, a self-focused emotion that signals individual strength and heightened status. Functional magnetic resonance images (fMRI) were acquired as participants viewed 55 s continuous sequences of slides to induce either compassion or pride, presented in alternation with sequences of neutral slides. Emotion self-report data were collected after each slide condition within the fMRI scanner. Compassion induction was associated with activation in the midbrain periaqueductal gray (PAG), a region that is activated during pain and the perception of others' pain, and that has been implicated in parental nurturance behaviors. Pride induction engaged the posterior medial cortex, a region that has been associated with self-referent processing. Self-reports of compassion experience were correlated with increased activation in a region near the PAG, and in the right inferior frontal gyrus (IFG). Self-reports of pride experience, in contrast, were correlated with reduced activation in the IFG and the anterior insula. These results provide preliminary evidence towards understanding the neural correlates of important interpersonal dimensions of compassion and pride. Caring (compassion) and self-focus (pride) may represent core appraisals that differentiate the response profiles of many emotions.

Keywords: nurturing; self-focus; caregiving; midbrain periaqueductal gray; posterior medial cortex

INTRODUCTION

Compassion and pride represent new frontiers of inquiry in affective science. Compassion is an other-oriented emotional response to perceived suffering that involves wanting to care for those in need (Goetz *et al.*, 2010). Pride, in contrast, is a self-oriented state responsive to actions that elevate individual or in-group status (Tracy and Robins, 2004, 2007). Empirical studies have begun to document how these two emotions are associated with different non-verbal signals (Tracy and Robins, 2004; Hertenstein *et al.*, 2006; Simon-Thomas *et al.*, 2009) and modes of thinking about relations between the self and others (Oveis *et al.*, 2010). These different lines of inquiry suggest that compassion is defined by a caring orientation at the level of signal behavior and social cognition (an increased sense of similarity to others) whereas pride is defined by an individuating, rank-related self-focus. In the present investigation we examine whether specific neural systems support the core properties of these two states: caring *vs* self-focus.

Compassion and caring: predictions of neural correlates

In the present research, we are guided by an appraisal tendency approach to emotion, which posits that distinct emotions are defined by core appraisals (Smith and Ellsworth, 1985; Lazarus, 1991; Lerner and Keltner, 2001). For example, anger is defined by a sense of unfairness caused by others' intentional actions. Emotion-specific appraisals shape how emotions influence different kinds of cognition (Keltner and Lerner, 2010), and presumably the neural systems engaged during a particular emotion.

Within an appraisal framework, compassion is defined by two core processes: the empathic recognition of another's suffering and the motivation to care for another (Lazarus, 1991; Goetz, *et al.*, 2010). Importantly, this conceptual analysis distinguishes empathy, which involves mirroring and identifying another's state, from compassion, which also involves caregiving motivation to reduce another's suffering (Batson and Shaw, 1991). This conceptual analysis, as well as select neuroscience findings, set the stage for predictions concerning the neural correlates of compassion, distinguished by its core theme of caring.

The empathic response to another person's suffering is the first stage of compassion (Batson and Shaw, 1991). By implication, empathy-related neural processes may be activated during experiences of compassion. Within the neuroscience literature several kinds of empathy have been investigated,

Received 27 April 2011; Accepted 22 June 2011

Advance Access publication 6 September 2011

This work has been supported by The Templeton Advanced Research Program, sponsored by the Metanexus Institute on Religion, Science and the Humanities, with the generous support of the John Templeton Foundation.

Correspondence should be addressed to Emiliana Simon-Thomas, 306 Jordan Hall, The Center for Compassion and Altruism Research and Education, Stanford University, Stanford, CA 94305, USA. E-mail: simonthomas@stanford.edu

ranging from the feelings produced by automatic mirroring, simulation or embodiment of other peoples' feelings ('affective' empathy) to understanding other peoples' mental states ('cognitive' empathy), typically as the other people experience inflicted pain (Decety and Jackson, 2004; Singer, 2006; Singer and Lamm, 2009; Hooker *et al.*, 2010; Reniers *et al.*, 2011). These studies, while yielding variation in certain patterns of neural activation, do converge on what some consider an 'empathy network'. This network typically includes: the insula, midbrain regions, the cingulate cortex, the anterior temporal cortex, sensorimotor cortex, the inferior frontal gyrus (IFG), the medial prefrontal cortex (mPFC), the superior temporal sulcus and gyrus and temporal parietal cortex (TPC) areas. Interestingly, individuals' self-reported feelings of empathy, as well as the tendency to feel empathetic in daily life, predict greater activation in certain regions of the empathy network—those typically involved in representing and processing the empathizer's own internal states (Saarela *et al.*, 2007; Pfeifer *et al.*, 2008; Hooker, *et al.* 2010). From responding with feeling to understanding what other peoples' suffering expressions mean, regions of the empathy network are candidates of possible activation during compassion.

Beyond the initial empathic response, there is a second core process involved in compassion: the motivation to provide care to alleviate the other person's suffering (Batson and Shaw, 1991; Eisenberg *et al.*, 2002; Goetz *et al.*, 2010). Hypotheses about neural correlates of this caregiving motivation are informed by neuroimaging studies of empathy toward in-group *vs* out-group victims: namely, certain regions of the empathy network show more robust activation in response to in-group victims likely to receive more care from empathizers. For example, Mathur and colleagues reported greater mPFC activation in response to the pain of others with in-group *vs* out-group membership, as well as greater altruistic motivation (Mathur *et al.*, 2010). Another recent study showed heightened anterior cingulate, anterior insula and PAG activation during empathy toward the pain of a loved one as opposed to an unknown victim (Cheng *et al.*, 2010). Finally, in an examination of how perceptions of responsibility affect empathy, innocent victims (who are likely to evoke greater care) led to greater activation in cingulate, anterior insula and PAG regions of the empathy network than blameworthy (less careworthy) victims (Decety *et al.*, 2009). These studies, however, did not explicitly assess caregiving motivation, and thus do not unambiguously document a relationship between reported activation and caregiving motivation. An alternative interpretation is that the activation changes merely reflect a stronger empathic response wherein increased mirroring leads to increased engagement of social cognitive regions, i.e. more feelings and more accurate understanding. Nevertheless, a theme running across loved ones, targets of altruistic intent, and vulnerable victims, all of which known to increase activation within key regions of the empathy network, is the stronger inclination

to provide care to reduce their suffering, the core appraisal that differentiates compassion from empathy (Goetz *et al.*, 2010). If so, key regions of the empathy network may relate to a distinct process directly tied to caregiving motivation, that when engaged, produce the distinct experience of compassion.

Recent theorizing and neuroscientific inquiry into a possible caregiving system provide a second platform for making predictions about neural activation associated with compassion (Mikulincer *et al.*, 2005; Swain, 2010). Studies of non-human mammals have implicated several key regions in parental nurturance behaviors (crouching over pups, retrieval to nest, licking, prolonged nursing), which include the medial preoptic area (MPOA), the ventral bed nucleus of the stria terminalis (VBST), and areas of the midbrain including the periaqueductal gray (PAG) (Lonstein and Stern, 1997; Numan and Numan, 1997; Sturgis and Bridges, 1997; Lonstein and De Vries, 2000; Stack *et al.*, 2002). Oxytocin (OT), a neuropeptide, which is broadly implicated in the formation of attachment bonds, caregiving behavior and pro-social orientation affects functioning within these parental nurturance regions (Insel *et al.*, 2001; Baumgartner *et al.*, 2008; Carter *et al.*, 2008; Rodrigues *et al.*, 2009; Gordon *et al.*, 2010). A recent study tied OT in the MPOA to increased reinforcement valuation for caregiving/nurturance behaviors in lactating rats (Shahrokh *et al.*, 2010); another showed that infusing OT into the midbrain PAG led to decreased self-focused vigilance behavior in rat dams, presumably freeing up resources to support caregiving behaviors under conditions of threat (Figueira *et al.*, 2008). In sum, these findings highlight the midbrain-preoptic–anterior hypothalamic neural circuits that support basic parental nurturance behaviors and the formation of early attachment bonds as a candidate system for supporting the formation of attachment bonds throughout life, as well as for generating caregiving motivation toward a wide spectrum of others.

Importantly, the midbrain PAG, while implicated in caregiving, is also involved in descending pain control through the release of endogenous opioids that inhibit ascending pain signals before they reach the cortex (Heinricher *et al.*, 2009; Lovick and Adamec, 2009). Still, PAG activation has been reported during situations that do not involve pain to the self. Alongside other regions like the orbital frontal cortex and thalamus, PAG activation has been reported in several studies of mothers viewing images of their own *vs* acquainted or unknown infants, or viewing video clips of their own infants exhibiting attachment-figure soliciting behaviors like smiling and crying (Bartels and Zeki, 2004; Nitschke *et al.*, 2004; Noriuchi *et al.*, 2008; Swain, 2008). PAG activation was also observed, along with other empathy network regions, in participants instructed to generate 'unconditional love' toward images of disabled people (Beauregard *et al.*, 2009), and while participants viewed sad facial expressions with instructions to extend a

'compassionate attitude' toward them (Kim *et al.*, 2009). One study that examined neural activation during 'relieved' compassion reported activation in insula, anterior cingulate, posterior medial cortex, thalamic and midbrain areas, though not explicitly reported as the PAG (Immordino-Yang *et al.*, 2009). Finally, Harrison *et al.* reported an intriguing relationship between empathetic pupillary contagion, i.e. mirroring the pupil size of sad faces, and the magnitude of midbrain PAG activation; suggesting PAG involvement in early, automatic responding to other's sadness. Although it plays a central role in pain regulation, the PAG is also involved in empathy and caregiving motivation; as part of the human parental caregiving system (Swain, 2010), the PAG may support caregiving motivation toward victims of suffering during experiences of compassion.

Pride, self-focus and status: predictions of neural correlates

Pride is most typically experienced when an individual, or a group related to the individual's identity, rises in social status (Tracy and Robins, 2007). Pride is defined by enhancement in the individual's standing relative to other individuals and social standards. In this regard, pride is at its core an individuating, self-focused emotion (Tracy *et al.*, 2007). In light of this conceptual analysis, one would expect the experience of pride to engage regions associated with self-referential processes.

Neuroimaging studies of self-referential processes frequently report activation along the cortical midline, typically focused in medial prefrontal and posterior medial cortex (mPFC and PMC, respectively). MPFC activation has been reported in participants monitoring their own physical appearance or actions (Blakemore and Frith, 2003; Sugiura *et al.*, 2005b), making judgments about their own qualities (Kelley *et al.*, 2002; Kjaer *et al.*, 2002; Blakemore and Frith, 2003; Damasio, 2003; Fossati *et al.*, 2003; Lieberman *et al.*, 2004; Ochsner *et al.*, 2004; Mitchell *et al.*, 2005b; Heatherton *et al.*, 2006; Johnson *et al.*, 2006; Northoff *et al.*, 2006; D'Armenteau *et al.*, 2007), assessing the relevance of stimuli to their own goals (Montague *et al.*, 2006; Harris *et al.*, 2007), and in conjunction with hippocampal structures, to retrieving autobiographical information (Macrae *et al.*, 2004; Daselaar *et al.*, 2008). Activation in the PMC has been related to assessing the familiarity of stimuli, retrieving episodic emotional information and to attributing emotional quality and personal relevance to perceived stimuli (Maddock *et al.*, 2001, 2003; Sugiura *et al.*, 2005a; Immordino-Yang, *et al.*, 2009). As a result, mPFC and PMC areas are theorized to support cognitions about the self and personal goals that are characteristic of pride (D'Armenteau *et al.*, 2009).

An functional magnetic resonance imaging (fMRI) investigation aimed at measuring pride, in contrast to joy, presented participants with brief, status enhancing statements selected to elicit pride, e.g. 'I won a prize at a scientific meeting' (Takahashi *et al.*, 2008). Compared to activation

during the joy-eliciting statements, e.g. 'I ate my favorite cake,' pride led to activation in the posterior superior temporal sulcus (pSTS), an area implicated in perceiving social meaning, in theory of mind (TOM) and in interpreting motivation or intent from others' actions (Pelphrey *et al.*, 2005; Saxe and Powell, 2006; Lamm *et al.*, 2007). The authors of this study concluded that pride involves appraisals of social meaning not inherent to joy, and attributed the lack of predicted, self-referential activation in medial cortex regions to participants' failure to genuinely personalize the statements, and presumably, experience true self-focused pride (Takahashi, *et al.*, 2008).

In light of theoretical claims that self-reference is central to pride and the literature on medial cortical areas and self-referential processing, we predicted that pride stimuli would selectively engage midline cortical structures, the mPFC and PMC.

Neuroimaging compassion and pride

In the present investigation, we induced compassion and pride using sequences of pre-tested picture slides found to elicit intense and relatively pure episodes of these two emotions (Oveis *et al.*, 2010). We also collected real time subjective experience ratings for compassion, caring, pride, achievement, distress and enjoyment to validate the evocative properties of the slides and to evaluate relationships between self-reported experience and hypothesized regions of neural activation. Neural activation during compassion and pride slide conditions was contrasted with that produced by viewing sequences of neutral slides. Although the neutral slides were not expected to evoke caring or self-focus, thus providing a suitable contrast for compassion and pride slides, it is important to note that self-report data were collected in real time for all conditions. This task feature prompted ongoing self-monitoring across compassion, pride and neutral slide conditions. Thus, given the overlapping role of the mPFC in self-monitoring, social and emotional appraisal and possibly empathy-related processes (Mitchell *et al.*, 2005a; Rudebeck *et al.*, 2008), we note that predicted emotion-specific mPFC activation may not be observable from data acquired within this study design.

Given the present study's design and our caregiving analysis of compassion, we predicted that compassion induction would engage regions of the empathy network that show greater activation toward in-group or vulnerable suffering such as the anterior insula, inferior frontal gyrus and the midbrain PAG, as well as other areas that support parental nurturance behaviors. In light of the self-referential core of pride, we hypothesized that pride would selectively engage self-referential cortical midline areas.

MATERIALS AND METHODS

Participants

Twenty students (11F) were recruited from a large, urban university population to participate in this study.

Participants were screened for right-handedness, current undergraduate enrollment at UC Berkeley, no history of neurological or psychiatric disorder or drug use, and negative pregnancy status. The use of human subjects was approved by the Committee for the Protection of Human Subjects at UC Berkeley and informed consent was obtained prior to participation. Participants were paid hourly for their participation.

Study design and task

The study design and task used here were adapted from a prior study that investigated the effects of induced compassion and pride on social judgment (Oveis *et al.*, 2010). During fMRI acquisition, participants performed two repetitions of a blocked emotion induction, emotion self-report task as depicted in Figure 1. Instructions presented on-screen prior to the task included the following text ‘...after each sequence (of pictures), you will be asked to rate the intensity and the nature of any feelings that arose while you were viewing those pictures.’ The task consisted of 8, 55-s blocks of slide stimuli that alternated between emotionally evocative and neutral categories. A continuous sequence of 5, 11-s slides from a single category was presented during each block. Each slide block was preceded by the word ‘Ready...’ presented at central fixation for 11 s. Each block of slides was followed by a text display that prompted participants to rate the overall intensity of their emotional response to the preceding sequence of slides, and then a second display that prompted participants to rate the quality of their overall emotional experience as they viewed the preceding slides. The durations of both self-report pages were self-paced by each participant.

Emotion-inducing slide blocks progressed through compassion eliciting and pride eliciting categories, as well as pleasure and awe eliciting categories. Data from pleasure and awe slide blocks are not presented here. Neutral slide blocks were presented between each successive emotion-inducing slide block. The order of emotion-inducing slide blocks was randomized for each task repetition within, and between participants. Compassion slides featured depictions of vulnerable suffering and harm. Pride slides featured depictions of in-group, or untargeted (no pictured recipient, perspective directed toward the viewer) achievement and status including graduation scenes, home university victories, medals and trophies. The neutral slides depicted people in unexpressive, mundane contexts as well as ordinary objects like a filing cabinet (Figure 1).

The slide images used in the present study were drawn from a previous study, which had pre-tested over 150 slides, and validated a set of 15 compassion and 15 pride slides that successfully induced the target states, as well as distinct judgments of self-other similarity (Oveis *et al.*, 2010). To refine and adapt this paradigm for use in the fMRI environment, we substituted several slides from the original set (e.g. medals and trophies replaced patriotic symbols from the original pride set) and gathered a set of neutral slides matched for social content (number of people depicted) and perceptual features (brightness, contrast). Substitute slides were drawn from the International Affective Picture System (Lang, 1999) and static images from the internet. Slide validation data from an independent sample of 36 participants who viewed the slides and reported upon their emotional experiences in response to each slide used in the present

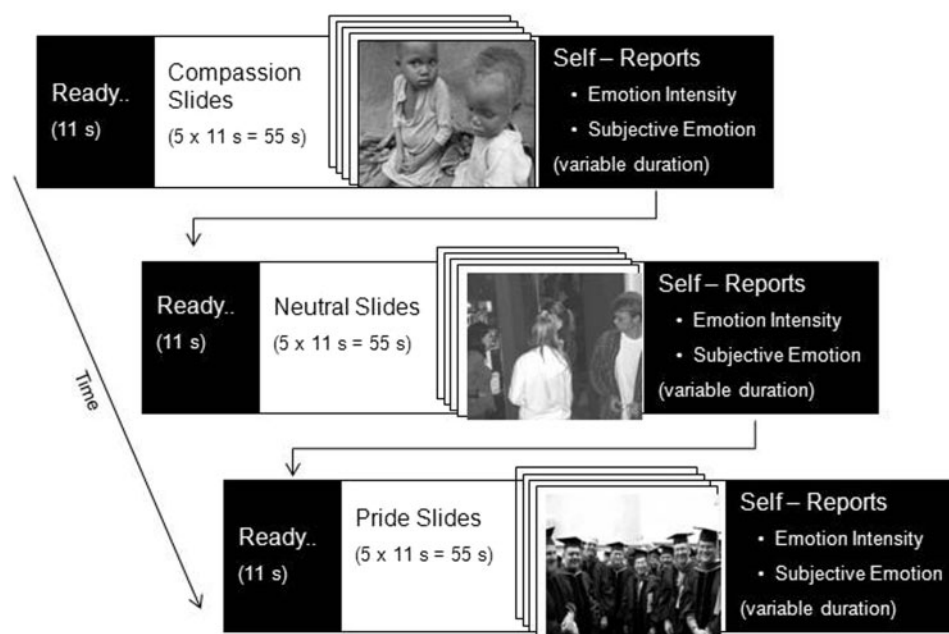


Fig. 1 A schematic representation of a partial task sequence including a compassion, a neutral and a pride slide block. A task run included one slide block for each target emotion: compassion and pride with neutral blocks interleaved. Each participant completed two task runs.

study showed that compassion, pride and neutral slides, respectively, produced reliably different self-reported levels of 'compassion' ($M=4.3$, $s.e.=0.1$, $M=1.9$, $s.e.=0.07$, $M=1.6$, $s.e.=0.06$), 'caring' ($M=3.9$, $s.e.=0.1$, $M=2.0$, $s.e.=0.07$, $M=1.7$, $s.e.=0.06$), 'pride' ($M=1.3$, $s.e.=0.04$, $M=3.2$, $s.e.=0.09$, $M=1.3$, $s.e.=0.04$) and 'achievement' ($M=1.2$, $s.e.=0.03$, $M=3.0$, $s.e.=0.09$, $M=1.4$, $s.e.=0.04$) (Figure 2a).

For the present study, a fixed set of 40 slides (5 for each emotion and 20 neutral) was used during each task run; 8 of the 10 compassion and matched neutral slides depicted people and 5 of the 10 pride and matched neutral slides depicted people. Task runs were presented in counterbalanced order between subjects. After the final slide in each block, participants provided self-reports of their emotional response to the slides that they had just viewed guided by the following prompt: 'While I was viewing those pictures, I experienced feelings that were: 1 = completely neutral, 4 = moderate, and 7 = very intense,' above a row of boxes labeled 1 through 7. Participants clicked an enumerated box between 1 and 7, after which they then clicked on a box labeled 'Next' to continue. Participants then rated their experience of several different emotions, including 'achievement, admiration, awe, caring, compassion, distress, enjoyment, pride and savoring'. Emotion terms appeared in a vertical column on the left side of the screen, each flanked

by row of boxes enumerated 1 through 7 labeled '1 = not at all, 4 = moderately and 7 = very strongly' along the top of the grid. Self-reports of 'compassion', 'caring', 'pride' and 'achievement' served as manipulation checks for compassion and pride induction, and yielded data relevant to the question of whether the experiences of compassion and pride would correlate with activation in different neural systems. Self-reported 'distress' and 'enjoyment' provided further validation of the valence-level evocative properties of the slides.

Procedure

Prior to entering the fMRI scanning chamber, participants were debriefed about the study. Specifically, experimenters told participants that they would see pictures while lying in the scanner, and then be asked to indicate how the pictures had made them feel. Participants were told that the study aimed to measure neural activation associated with their authentic emotional responses, not with their beliefs about how they ought to respond, nor with their judgments regarding what kinds of emotions the pictures represented. Participants then completed a brief practice version of the slide-viewing, self-report task that featured one mixed-category block of slides followed by the intensity-of-feeling and quality-of-emotion self-report prompts.

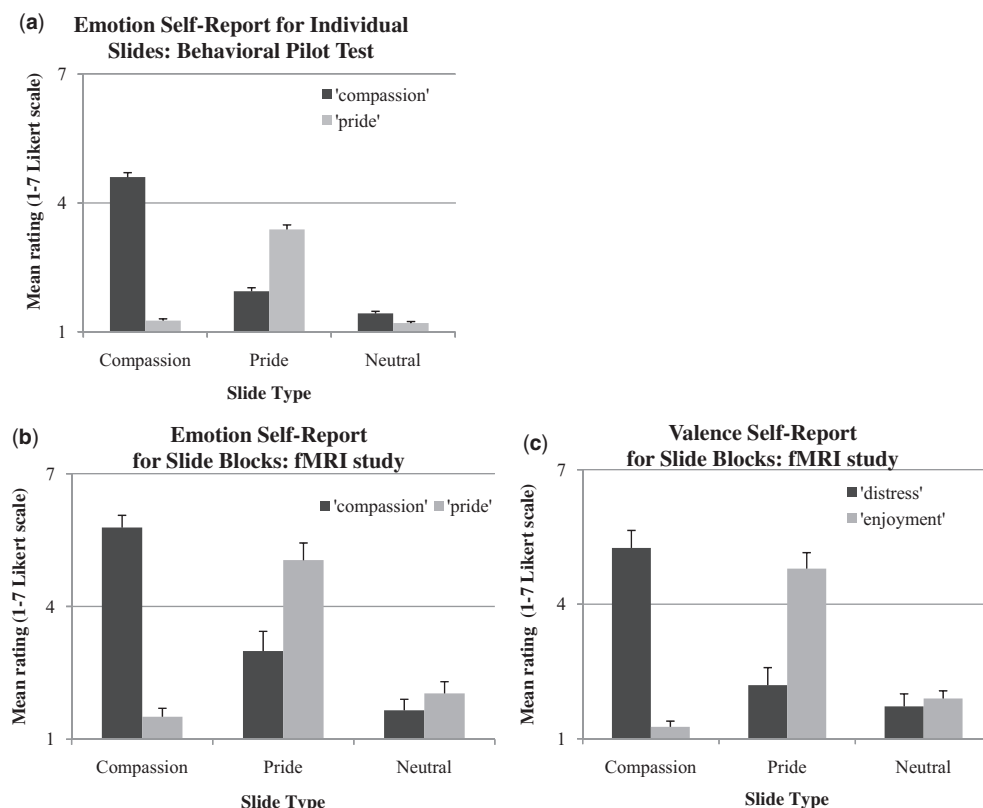


Fig. 2 Mean self-reports of 'compassion' and 'pride' in response to the compassion, pride and neutral slides for (a) the behavioral pilot sample responding to each individual slide and (b) the fMRI participants responding to slide sequences. Mean self-reports of valence, 'distress' and 'enjoyment,' for the fMRI participants responding to slide sequences are depicted in (c).

Experimenters reminded participants to respond naturally to the pictures and to be honest and forthright in their emotion self-report, and suggested that disingenuous self-report would be harmful to the study.

Once inside the fMRI scanner chamber, participants were positioned in a standard transverse electromagnetic (TEM) send-and-receive radio frequency (RF) head coil with an eye-level mirror for viewing the task presentation screen. Participants held an fMRI compatible laser mouse in their right hand resting on their right thigh for making self-report ratings after each slide sequence from within the scanner chamber.

fMRI

Functional whole-brain images (30 axial slices, anterior commissure/posterior commissure orientation) were acquired in a 4T Varian INOVA scanner with a gradient echo T2*-weighted 1-shot gradient-echo echo-planar imaging (EPI) sequence (repetition time 2 s, echo time 28 ms, flip angle 20, field of view 224 mm with a 64 x 64 matrix size resulting in an in-plane resolution of 3.5 x 3.5 mm for each 5-mm slice). High-resolution, in-plane T1-weighted anatomical images were acquired using a gradient-echo multislice sequence (GEMS) for anatomical localization and a T1-weighted 3D MPFlash sequence was acquired for data display. Preliminary image reconstruction including ghost correction, geometric distortion correction and temporal interpolation routines was performed with ReconTools, a Python-based tool developed at UC Berkeley's Brain Imaging Center (<https://cirl.berkeley.edu/view/BIC/ReconTools>).

Data analysis

Self-reports of emotion

Self-reports of compassion ('compassion', 'caring'), pride ('pride', 'achievement') and valence terms ('enjoyment', 'distress') in response to compassion, pride and neutral slide blocks were averaged across two task runs. Given high Cronbach's α coefficients between target emotion terms, we created composite measures of the experience of 'compassion' ('compassion' and 'caring', $\alpha = 0.95$) and 'pride' ('pride' and 'achievement', $\alpha = 0.94$) for the remainder of analyses. Though correlations were also high between self-reports of 'distress' and 'compassion' and between 'enjoyment' and 'pride' ($r = 0.51$ and $r = 0.79$, respectively), data for 'distress' and 'enjoyment' terms were analyzed independently to enable specific assessment of valence. Self-reports of 'compassion', 'pride', 'distress' and 'enjoyment' were submitted to a one-way ANOVA with slide type (compassion, pride or neutral) as the independent variable and self-report values for these four terms as the dependent variables. Self-report data for one task run from one participant were excluded due to outlying levels of 'distress' and 'pride' in response to the pride slides ('distress' > 2 s.d.'s from the mean, 'pride' < 2 s.d.'s from the mean). The participant's own

described feelings about these pride slides during debriefing indicated an unusual and specific personal interpretation of the slides (namely, that the images of military medals were connected to conspiratorial ideas about politics). Self-report data from the second task run for that individual, which were within 2 s.d.s of the mean, were included.

fMRI analysis

Participants' functional images were realigned to correct for head movement, smoothed (8-mm full-width at half-maximum), normalized (parameters from MPFlash to SPM2 T1 template were applied), then submitted to a whole-brain analyses using random-effects models in Statistical Parametric Mapping (SPM) (<http://www.fil.ion.ucl.ac.uk/spm>) to identify brain areas specifically activated during contrasts between each emotion and neutral slide conditions. fMRI data from three participants were excluded from all group analyses due to large head size or aberrant slice definition during acquisition, factors which produced increased frontal susceptibility artifact and caused poor image normalization results ($n = 17$). fMRI data from one participant during the pride condition were excluded from analyses due to outlying self-report values ($n = 16$ for pride fMRI analyses).

Emotion slide blocks, neutral slide blocks, self-report intervals and six-dimension movement parameters determined during the realignment process were included as covariates in each participant's SPM model. Statistical analyses were performed using a modified general linear model (Worsley and Friston, 1995) reference function that convolved the time series of covariates for each task condition and the movement parameters for each task run with a block-wise, idealized hemodynamic response function. Contrast images for each participant were created for compassion > neutral, pride > neutral, compassion and pride combined > neutrals from both conditions and direct comparisons between compassion and pride. Contrast images were submitted to a second level, group-wise ($n = 17$ for compassion > neutral, $n = 16$ for pride > neutral, $n = 16$ for across and between-emotion comparisons) t -test for each contrast ($P < 0.001$, uncorrected; extent: 15 voxels). Simulation using the 3D ClustSim function in AFNI (http://afni.nimh.nih.gov/pub/dist/doc/program_help/3dClustSim.html; 10 000 iterations, 64 64 30 dimensions, 3.5 3.5 5 voxels, BALL mask applied, 8-mm smoothness) indicated that an uncorrected $P < 0.001$ threshold and voxel cluster extent = 12.2 would provide protection against Type I error at a false discovery rate (FDR) of 0.05 (Bennett *et al.*, 2009; Lieberman and Cunningham, 2009). Contrast images were also submitted to a second level, group-wise ($n = 17$ for compassion > neutral, $n = 16$ for pride > neutral) multiple regression with constant analysis ($P < 0.001$, uncorrected; extent: 15 voxels) using individuals' emotion self-report as predictors. Specifically, multiple regression was used to examine whether 'compassion' or 'distress' self-report

values predicted activation during compassion > neutral conditions and whether 'pride', 'enjoyment' or 'compassion' self-report values predicted specific activation during pride > neutral conditions.

RESULTS

Self-reports of the experience of emotion

As shown in Figure 2b, the compassion, pride and neutral slide blocks (self-report values for the two neutral slide blocks are combined) elicited the predicted patterns of emotion self-report. Compassion, pride and neutral slides, respectively, produced reliably different self-reported levels of 'compassion' ($M=5.8$, $s.e.=0.3$, $M=3.1$, $s.e.=0.4$, $M=2.0$, $s.e.=0.2$) and 'pride' ($M=1.6$, $s.e.=0.2$, $M=5.1$, $s.e.=0.4$, $M=2.1$, $s.e.=0.3$). One-way ANOVAs showed that slide type (compassion, pride or neutral) significantly affected self-reported levels of 'compassion', $F(2, 50) = 38.9$, $P < 0.001$, and 'pride', $F(2, 50) = 42.3$, $P < 0.001$. *Post hoc* comparisons between specific conditions indicated that each condition elicited: (i) higher ratings for target emotions (e.g. higher 'compassion' for the compassion slides than for the pride, or neutral slides, $P < 0.001$ for all comparisons) and (ii) low ratings for non-target emotions (e.g. low 'pride' for the compassion and neutral slides, $P < 0.001$ for all comparisons).

Though 'compassion' was significantly lower for the pride than for the compassion slide condition ($P < 0.001$), it was greater for pride than for the neutral slide condition ($P < 0.05$), suggesting that the lower than moderate self-rated level of 'compassion' in response to the pride slides was still greater than the very low 'compassion' ratings in response to neutral slides (self-reported 'compassion' is thus incorporated into regression analyses involving the pride > neutral fMRI contrast). Finally, no differences were observed between non-target 'pride' ratings for compassion and neutral slide conditions ($P < 0.001$ for all comparisons).

As evident from Figure 2c, compassion, pride and neutral slides also produced different self-report levels of affective valence measured as 'distress' ($M=5.2$, $s.e.=0.3$, $M=2.1$,

$s.e.=0.3$, $M=1.7$, $s.e.=0.19$, respectively) and 'enjoyment' ($M=1.3$, $s.e.=0.53$, $M=4.8$, $s.e.=0.36$, $M=1.9$, $s.e.=0.14$). There was a main effect of task condition on self-reported 'distress', $F(2,50) = 44.9$, $P < 0.001$; *post hoc* comparisons indicated significantly higher 'distress' for compassion than for pride or neutral slide conditions, $P < 0.001$ for both comparisons. There was also a main effect of task condition on self-reported 'enjoyment', $F(2,50) = 65.5$, $P < 0.001$; *post hoc* comparisons indicated higher 'enjoyment' for pride than for compassion or neutral conditions, $P < 0.001$ for both comparisons. No differences between 'distress' ratings for pride and neutral conditions or between 'enjoyment' ratings for compassion and neutral conditions were observed.

fMRI data

Compared with the activation produced by viewing blocks of neutral slides, viewing blocks of compassion slides was associated with activation in the midbrain PAG. No significant activation was observed in any other voxel clusters for this contrast, even in predicted 'empathy network' or parental nurturance regions, at designated thresholds. During pride compared to neutral slide blocks, the posterior medial cortex showed increased activation as predicted; no significant activation was observed in any other voxel clusters. No significant activation was observed for the combination of compassion and pride vs neutral conditions at designated thresholds ($P < 0.001$, uncorrected; extent: 15 voxels) (Figure 3 and Table 1).

In direct comparisons between the activation associated with compassion and pride conditions, no voxel clusters were observed to be significantly more active during compassion than pride. Several regions typically implicated in self-reflective processing including the PMC, parahippocampal and inferior temporal regions showed greater activation during pride in contrast with compassion (Table 1.)

We next ran multiple regression analyses to examine whether the self-reported experiences of 'compassion' and 'pride' predicted neural activation during target emotion conditions. More specifically, we ran several multiple

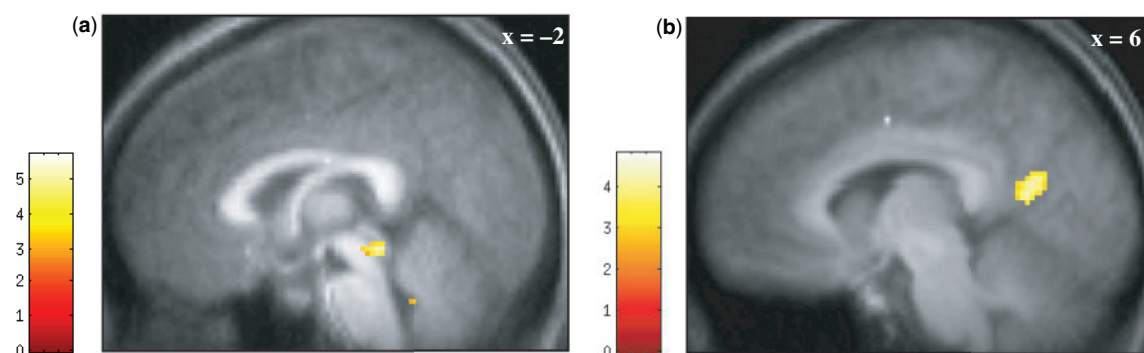


Fig. 3 (a) Activation in the midbrain PAG during the compassion > neutral condition contrast and (b) in the posterior medial cortex (PMC) during the pride > neutral condition contrast. Activation is displayed at ($P < 0.005$, uncorrected; extent: 15 voxels) to show the extent of activation and is displayed on a mean anatomical image calculated across fMRI participants.

Table 1 Brain regions that show activation during task condition contrasts, and corresponding Montreal Neurologic Institute (MNI) coordinates

Contrast	Brain region	BA	MNI coordinates			<i>t</i> -statistic	Volume
			<i>x</i>	<i>y</i>	<i>z</i>		
Compassion > neutral	Midbrain PAG		0	−32	−8	5.7	20
Pride > neutral	Posterior Medial Cortex	23/31	2	−64	16	4.17	25
Compassion and pride > neutral	Nsv		—	—	—	—	—
Compassion > pride	Nsv		—	—	—	—	—
Pride > compassion	L cerebellum		−26	−42	−28	5.75	46
			−28	−66	−26	4.94	28
	Posterior medial cortex	23/31	8	−72	10	5.35	43
			−8	−68	24	4.74	31
	L Inferior temporal gyrus	43	−54	−10	18	4.7	27
	L Parahippocampal	34	−22	4	−20	4.4	18

The MNI coordinates of the maximally active focus within each structure are reported.

BA = Brodman's Area, L = Left, R = Right, Nsv = no significant voxels.

$P < 0.001$, uncorrected; extent: 15 voxels.

regression analyses to examine whether 'compassion' and 'distress,' both characteristic responses to suffering (Eisenberg *et al.*, 1989; Goetz, *et al.*, 2010), predicted distinct activation during the compassion > neutral condition contrast. These analyses revealed that (i) 'compassion' in combination with 'distress' predicted increased activation in a near-PAG region and (ii) 'compassion' controlling for 'distress' predicted increased activation within the right inferior frontal gyrus (IFG). Though the cluster foci are distinct, the near-PAG region predicted by greater 'compassion' and 'distress' overlapped with the PAG region activated during the group-wise compassion > neutral condition contrast (Figure 4). There were no negative relationships between 'compassion' and/or 'distress' self-reports and neural activation associated with the compassion > neutral condition contrast.

Guided by a similar logic, we ran a second set of multiple regression analyses to examine whether self-reported levels of 'pride,' 'enjoyment,' and 'compassion' predicted activation associated with the pride > neutral condition contrast. No positive correlation was observed between self-report levels and pride > neutral contrast activation. Notable negative relationships, however, were observed (i) between all three predictors, 'pride,' 'enjoyment' and 'compassion,' and the right IFG (Brodmann area 47) and a closely neighboring ventral aspect of the right lateral prefrontal cortex (Brodmann area 46), (ii) between 'pride' and 'enjoyment' controlling for 'compassion' and the same right frontal regions, as well as the left anterior insula and (iii) between 'enjoyment' controlling for 'pride' and 'compassion' and the left anterior insula. In contrast to the results for 'compassion' controlling for 'distress,' participants who reported greater feelings of 'pride' and 'enjoyment' independent of 'compassion' for pride slides showed reduced activation in right IFG/prefrontal regions (Figure 5 and Table 2).

In a final set of multiple regression analyses, we examined whether self-reports of 'compassion' and 'pride' across the

compassion and pride conditions predicted specific patterns of activation in a contrast that combined compassion and pride > neutral condition contrasts. No significant positive or negative relationships were observed in this analysis at designated thresholds ($P < 0.001$, uncorrected; extent: 15 voxels).

DISCUSSION

The present research sought to document patterns of neural activation associated with compassion, an emotion defined by empathic response and caregiving motivation, and pride, a self-focused emotion focused on elevated status. Toward this end, we used validated emotionally evocative slides to elicit relatively intense and pure experiences of compassion and pride.

Guided by appraisal analyses of the two emotions of interest, we predicted that experiences of compassion would be associated with increased activation in 'empathy network' regions (particularly regions responsive to a greater sense of care), as well as regions involved in parental nurturance behaviors. The latter prediction was supported by the data from the present study: laboratory induction of compassion relative to a neutral condition was associated with increased activation in the midbrain PAG, an area implicated across empathy and parental care-taking behaviors. Further regression analyses showed that self-reported experiences of 'compassion' and 'distress,' two core processes involved in pro-social responses to suffering (Batson and Shaw, 1991), also predicted activation in a near-PAG region.

These findings are in keeping recent studies that report PAG activation during heightened empathy for other peoples' pain and during attachment-related states, namely maternal love and unconditional love. They also dovetail with a non-human literature that has implicated the PAG, via OT connections with MPOA and VBST regions, in motivating, reinforcing and freeing up resources for parental nurturance

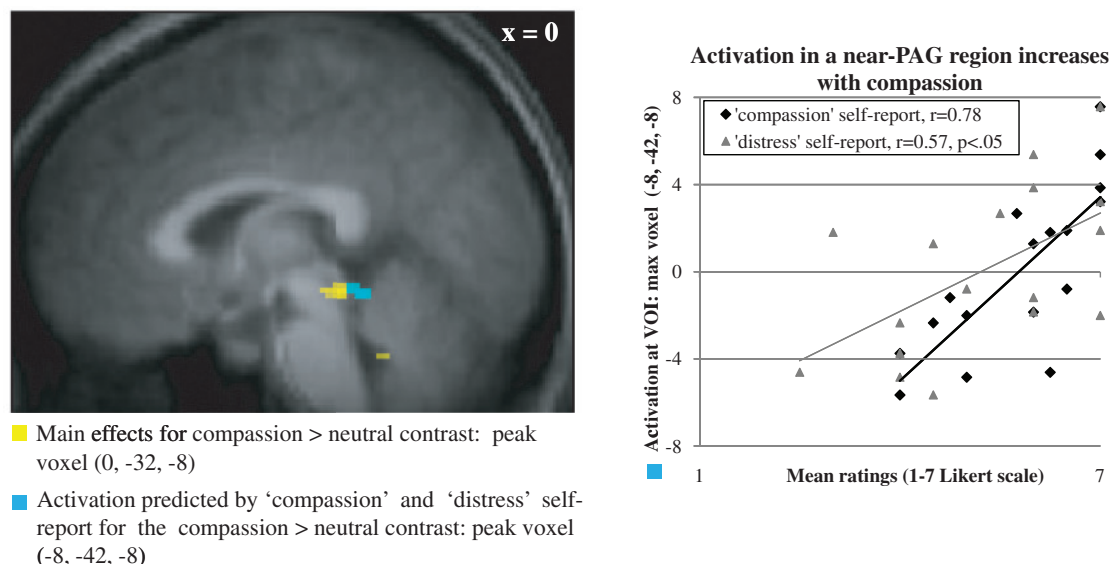


Fig. 4 Group wise main effects activation in the PAG during the compassion > neutral (yellow) condition contrast and a near-PAG cluster predicted by self-reported 'compassion' and 'distress' for the compassion > neutral contrast (cyan). Activation is displayed at ($P < 0.005$, uncorrected; extent: 15 voxels) to show the extent of activation and is displayed on a mean anatomical image calculated across fMRI participants. Self-reported 'compassion' and 'distress' for the compassion > neutral condition contrast are plotted against mean activation across voxels in the near-PAG cluster ($P < 0.001$ for correlation r values unless otherwise labeled).

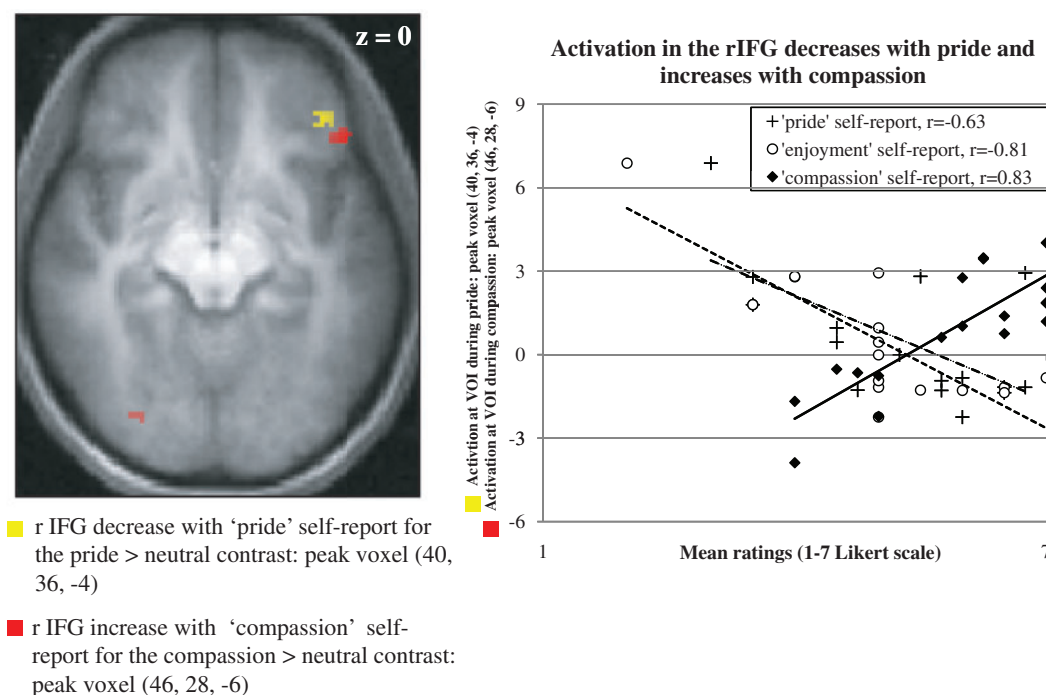


Fig. 5 Activation in the right IFG predicted by greater self-reported 'compassion' (red) for the compassion > neutral condition contrast, and by lower self-reported 'pride' and 'enjoyment' (yellow) for the pride > neutral condition contrast. Activation is displayed at ($P < 0.005$, uncorrected; extent: 15 voxels) to show the extent of activation and is displayed on a mean anatomical image calculated across fMRI participants. Self-reported 'pride' and 'enjoyment' for the pride > neutral condition contrast, and 'compassion' for the compassion > neutral condition contrast are plotted against mean activation across voxels in the right IFG regions ($P < 0.001$ for correlation r values unless otherwise labeled).

behaviors (Figueira *et al.*, 2008; Rosen *et al.*, 2008; Lovick and Adamec, 2009; Shahrokh *et al.*, 2010).

The simple conclusion that the PAG supports the care-giving tendencies that define compassion is clouded by the

PAG's well-known role in pain modulation. In the present study, it may have been that the PAG was activated due to the participant's personal, simulated experience of pain when viewing the images of suffering (Singer and Frith, 2005).

Table 2 Brain regions that show activation correlated with emotion self-report during task condition contrasts, and corresponding MNI coordinates

Multiple Regression Model	Partial regressions	Brain region: emotion > neutral	BA	MNI co-ordinates			<i>t</i> -statistic	Volume
				<i>x</i>	<i>y</i>	<i>z</i>		
POS: 'compassion' and 'distress' self-report x compassion > neutral contrast	'compassion' ^a	R Inferior frontal gyrus—triangularis	47	46	28	−6	6.45	26
	'distress' ^a	Nsv						
	'compassion' and 'distress'	PAG		−8	−42	−8	5.52	19
NEG: 'pride', 'enjoyment' and 'compassion' self-report x pride > neutral contrast	'pride' ^a	Nsv						
	'enjoyment' ^a	L Anterior insula		−36	24	2	6.46	27
	'compassion' ^a	Nsv						
	'pride' and 'enjoyment' ^a	R Lateral Prefrontal Cortex	46	48	34	12	6.74	16
		L Anterior Insula		−36	24	2	6.29	15
		R Inferior Frontal Gyrus—triangularis	47	40	36	−4	4.98	18
	'pride' and 'compassion' ^a	Cerebellum		−2	−54	−10	5.73	17
	'pride', 'enjoyment' and 'compassion'	R Lateral prefrontal cortex	46	48	34	12	6.95	20
		R Inferior frontal gyrus—triangularis	47	40	36	−4	5.8	34

Note. The MNI coordinates of the maximally active focus within each structure are reported.

^aControls for other covariate(s).

BA = Brodmann Area, L = Left, R = Right, POS = positive correlation, NEG = negative correlation, Nsv = no significant voxels.

P < 0.001, uncorrected; extent: 15 voxels.

Indeed, participants reported high levels of 'distress' alongside 'compassion' while viewing the images of suffering. Multiple regression analyses of 'compassion' and 'distress' showed activation in a cluster of voxels partially overlapping with the PAG during the group-wise compassion > neutral contrast. This combination of findings suggests that PAG activation during compassion might be related to several compassion-related processes, including the empathic mirroring of another's suffering, felt personal pain or distress in response to perceived suffering, and/or caregiving motivation. Future studies that (i) acquire additional self-report to identify appraisals related to distress, e.g. enduring personal threat or pain *vs* concern toward other person's suffering and (ii) directly contrast conditions more purely evocative of empathized personal pain or distress, i.e. induced empathy with implied threat to the self, with explicit prevention to caregiving, with no manipulation and with support for caregiving could more definitively tease apart the relative involvement of the PAG in pain, empathy, distress and caregiving processes.

The lack of observed activation in other parental nurturing regions like the MPOA and VBST in the compassion > neutral fMRI contrast analyses is noteworthy. Lack of engagement of other parental nurturing regions may relate to the complex valence properties of compassion. As elicited here, compassion was associated with self-reported 'distress', and not with 'enjoyment'. Participants did not have the opportunity to help or act on their inclination to care for the targets of compassion here, which may have attenuated any anticipated reward associated with predicted social benefits of caregiving. While OT function in the MPOA has been associated with reinforcing fundamentally neutral or mildly pleasant nurturance behaviors, OT/PAG functions may

figure more prominently in caregiving motivation particularly in response to pain and suffering, key antecedents of compassion. Direct examination of how parental nurturance systems respond to care evoking situations of different valence, and with or without the opportunity to intervene, could clarify these concerns.

In addition to the PAG findings, multiple regression analyses showed that self-reported levels of 'compassion' controlling for self-reported 'distress' predicted activation in an anterior region of the right IFG—pars triangularis. This finding is interesting in light of findings relating right IFG activation to emotion inference, regulation, as well as empathic mirroring of facial expression (Carr *et al.*, 2003; Hooker *et al.*, 2008; Berkman and Lieberman, 2009). A recent study of patients with IFG lesions reported impaired affective empathy and emotion recognition; the authors theorized that Brodmann area 44 of the IFG, the pars opercularis, the human analog to 'mirror neuron' primate area F5 (slightly caudal to the IFG regions observed here), plays a principal role in an emotion simulation system (Shamay-Tsoory *et al.*, 2009). Increased right IFG activation predicted by self-reported 'compassion' here suggests that greater compassion experience may relate to stronger mirroring of expressions shown by the targets of compassion. The IFG is also implicated in cognitive control of memory processes (Badre and Wagner, 2007); IFG activation during compassion may also relate to controlled memory processes engaged in response to the contents of evocative slides.

Contrary to expectations generated our appraisal analysis of compassion, activation was not observed in other empathy network regions, such as the insula, mPFC or the TPC during the group-wise compassion > neutral contrast at the designated threshold (*P* < 0.001, uncorrected; extent: 15 voxels).

This could, in part, have arisen as a function of our emotion induction approach. The task required that participants report on their emotions after each block in all of the conditions, which likely prompted ongoing self-monitoring, self-evaluation and appraisal, processes which typically engage the mPFC (Hutcherson *et al.*, 2005; Northoff *et al.*, 2006). This design feature likely engaged self-evaluative and affective simulation regions like the insula and mPFC during neutral, as well as emotion slide conditions, thereby attenuating observable differences in contrasts between conditions. Similarly, use of slides that depicted people in social settings across neutral and emotion-inducing conditions likely engaged areas of TPC involved in perception of social meaning across conditions (Pelphrey *et al.*, 2005; Zahn *et al.*, 2007). With regards to other empathy network regions, particularly those that have been shown to be sensitive to caregiving orientation, at a speculative, exploratory threshold ($P < 0.005$, uncorrected; extent: 10 voxels), activation clusters in the insula (36, 6, 22; 12 voxels), anterior temporal (−32, 2, −32; 21 voxels) and left prefrontal regions (32, 50, 10; 14 voxels) were observed. Compassion may indeed engage additional empathy network areas; evidence from future studies of the compassionate response will be more definitive with respect to this possibility.

In keeping with our second set of hypotheses, activation was observed in the posterior medial cortex (PMC), an area implicated in self-reflection, during the pride > neutral contrast (Daselaar *et al.*, 2001; Maddock *et al.*, 2001; Johnson *et al.*, 2006; D'Armenbeau *et al.*, 2008). Directly compared to compassion eliciting slides, the pride slides, which included images of symbolic success like medals and trophies, also elicited activation in left inferior temporal and parahippocampal regions. The engagement of autobiographical memory processes is an important component of self-focus, was probably evoked by the pride slides (e.g. '*I remember winning a medal like this one at a swim competition...*') and likely accounts for the parahippocampal findings observed here. Future investigations of pride resulting from actual increases in personal strength or status will clarify the role of hippocampal activation and memory-related processes in the specific experience of pride.

As was the case with compassion, activation in the mPFC, a region strongly associated with self-appraisal, was not observed during pride. This finding could have been due to the self-reflective demands required of the neutral condition, as discussed earlier (Ochsner *et al.*, 2004). Overlapping, task-related self-referential processes across pride and neutral conditions may have yielded a ceiling effect for mPFC activation, minimizing emotion-specific observable differences between conditions.

Though no positive relationship was observed between self-reported 'pride', 'enjoyment' or 'compassion' in response to the pride slides and neural activation during pride (vs neutral) conditions, lower ratings on pride-related terms ('pride', 'enjoyment') predicted greater activation in the

right IFG, a closely neighboring ventral aspect of the right prefrontal cortex, and anterior insula regions. Anterior insula and IFG activation are routinely observed in emotion expression identification and empathy eliciting paradigms, are sensitive to degree of care toward a social target, and are posited to play key roles in emotion sharing, and by some accounts, empathic accuracy (Carr *et al.*, 2003; Iacoboni *et al.*, 2005; Saarela *et al.*, 2007). Less activation in the anterior insula and IFG with greater pride experience may relate to self-focus, less concern toward others, and by extension, fewer resources dedicated to processing emotional information from others. This finding is in keeping with recent studies finding that pride is associated with a reduced sense of similarity to, and in turn, caregiving sentiment toward others (Oveis *et al.*, 2010).

Examination of activation across combined compassion and pride vs neutral conditions revealed no systematic activation at designated thresholds. At a speculative, exploratory threshold ($P < 0.005$, uncorrected; extent: 10 voxels), activation was observed during this combined analysis in empathy network regions associated with perception and interpretation of social meaning or intent including the right superior temporal sulcus (STS), rIFG and fusiform gyrus (Pelphrey *et al.*, 2005; Saxe and Wexler 2005; Hooker *et al.*, 2008). This trend may reflect processing of social meaning across compassion and pride evoking vs neutral slides. Multiple regression analyses to examine whether the combination of self-reported 'compassion' and 'pride' across the compassion and pride slide conditions predicted specific activation also showed no significant result. In effect, these analyses asked whether individuals prone to the experience of compassion or pride show distinct activation in response to emotionally evocative slides. Although the present study was not designed to explore this possibility (and the low levels of 'pride' felt during the compassion slides are problematic), several recent studies have found that individual differences in emotion guide specific appraisals of broad classes of stimuli, even those unrelated to the emotion of interest (Gross *et al.*, 1998; Oveis *et al.*, 2009). This literature would suggest that individuals prone to compassion, as assessed in our self-report data, would show compassion-related patterns of activation even in response to the pride slides, and that complementary results would be observed with individuals who report high levels of pride even in response to the compassion slides. It may be more fruitful to look for 'emotion-proneness'-related patterns of neural activation by studying responses to prototypical stimuli or a broader range of emotion categories.

Inferences drawn from the present findings are constrained by certain features of the study design. First, for the purposes of gathering validation data, our emotion elicitation procedures required that participants report on their own emotional experiences, likely engaging participants in sustained monitoring of their own states. Requiring participants to monitor themselves may have interfered with

emotion-related neural activity (Northoff *et al.*, 2004; Hutcherson, *et al.*, 2005). Some brain regions hypothesized to support monitoring and self-reporting of emotions such as the mPFC, were also expected to be active during experiences of compassion and pride. Future research would be well served by studying the patterns of neural activation associated with compassion and pride in the absence of anticipated self-report procedures.

Second, our protocol featured unusually long fMRI blocks. Acquiring long blocks of fMRI data biases observations toward regions that show persistent activation over the entire interval (55 s blocks *vs* typical 15–30 s blocks). Longer induction intervals are likely to produce stronger experiences of emotion and a greater likelihood of activating core appraisals associated with the emotion, such as caregiving motivation in the case of compassion. Longer block designs also risk greater overlap low frequency artifact inherent to fMRI data (D'Esposito, 2000). Here, each participant's data was carefully inspected for quality, and high pass filtered at 220 s (4 x 55 s block length) to minimize the contribution of low frequency artifact.

Third, it is fair to raise doubts about the ecological validity of our emotion-eliciting stimuli—static slides of social situations not directly relevant to the participant's concerns (Coan and Allen, 2007). Slides are ideally suited to the environment of fMRI data acquisition, and in the case of compassion and pride, control for significant behavioral differences of the two emotions (e.g. the approach-related tendency of compassion *vs* the social disengagement associated with pride). Nevertheless, the use of slides introduced certain limitations with the present study's findings. Pride, for example, is conceptualized as a response to heightened status; our slides were limited in their ability to directly convey changes in status. Further, pride slides included images of students from the home university enthusiastically celebrating victory, which likely elicited collective, in-group pride. These concerns are mitigated, somewhat, by the self-report data gathered in the present study, and the fact that self-reports of 'compassion' and 'pride' predicted theoretically relevant regions of activation. Still, greater confidence will be gained if the present research is extended to studies using different emotion elicitation techniques. Studies of neural activation during emotional states elicited using alternative techniques, like emotional imagery, reliving and guided autobiographical recall (Damasio *et al.*, 2000; Immordino-Yang, *et al.*, 2009), point to intriguing extensions of the present work on the neural correlates of elicited emotions.

Finally, patterns of significant activation in only one voxel cluster for the compassion > neutral and pride > neutral contrasts, or none at all in the case of the combined compassion and pride analysis, confers some degree of ambiguity to interpretation of the results reported here. Generally, complex social emotions like compassion and pride are expected to engage parallel brain networks supporting concurrent affect

and appraisal processes. The lack of multiple regional activation here, may, in part be related to the long fMRI block approach used here, which may average out fluctuating engagement of multiple regions, leaving only signals from regions making the most enduring, tonic contribution to the processes. The lack of significant activation for combined compassion and pride may be related to variability in subjective experience of these complex emotions, or to variance in temporal properties of regional activation supporting fluctuating, complex affective and cognitive processes across the long emotion elicitation blocks. Further studies with different time constraints, specifically designs that independently distinctly evoke specific affect and appraisal-related component processes that factor into compassion and pride will clarify interpretation of the results reported here.

The work presented here provides a first within-subjects examination of neural activation during laboratory induction of compassion and pride. The present findings point to the possible involvement of the midbrain PAG, insula and IFG regions *vs* posterior midline structures in states characterized by other-oriented, caregiving motivation *vs* status-based self-focus, respectively. As this literature on compassion and pride grows, several opportunities await: studies of gender differences in the neural correlates of these potentially gendered emotions; trait and state-level variations in these emotions and their correlates; effects of social group status on the emergence of these emotions; and potential linkages between the central nervous system processing and possible peripheral correlates of compassion and pride. This kind of work will help delineate the physiological processes associated with compassion and pride, two emotions that serve important social functions.

REFERENCES

- Badre, D., Wagner, A.D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia*, 45(13), 2883–901.
- Bartels, A., Zeki, S. (2004). The neural correlates of maternal and romantic love. *Neuroimage*, 21(3), 1155–66.
- Batson, C.D., Shaw, L. (1991). Evidence for Altruism: toward a pluralism of prosocial motives. *Psychological Inquiry*, 2, 107–22.
- Baumgartner, T., Heinrichs, M., Vonlanthen, A., Fischbacher, U., Fehr, E. (2008). Oxytocin shapes the neural circuitry of trust and trust adaptation in humans. *Neuron*, 58(4), 639–50.
- Beauregard, M., Courtemanche, J., Paquette, V., St-Pierre, E.L. (2009). The neural basis of unconditional love. *Psychiatry Research*, 172(2), 93–8.
- Bennett, C.M., Wolford, G.L., Miller, M.B. (2009). The principled control of false positives in neuroimaging. *Social Cognitive and Affective Neuroscience*, 4(4), 417–22.
- Berkman, E.T., Lieberman, M.D. (2009). Using neuroscience to broaden emotion regulation: theoretical and methodological considerations. *Social and Personality Psychology Compass*, 3, 475–93.
- Blakemore, S.J., Frith, C. (2003). Self-awareness and action. *Current Opinion in Neurobiology*, 13(2), 219–24.
- Carr, L., Iacoboni, M., Dubeau, M.C., Mazziotta, J.C., Lenzi, G.L. (2003). Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Science*, 100(9), 5497–502.

- Carter, C.S., Grippio, A.J., Pournajafi-Nazarloo, H., Ruscio, M.G., Porges, S.W. (2008). Oxytocin, vasopressin and sociality. *Progress in Brain Research*, 170, 331–6.
- Cheng, Y., Chen, C., Lin, C.P., Chou, K.H., Decety, J. (2010). Love hurts: an fMRI study. *Neuroimage*, 51(2), 923–9.
- Coan, J.A., Allen, J.J., editors. (2007). *Handbook of Emotion Elicitation and Assessment*. New York: Oxford University Press.
- D'Argembeau, A., Feyers, D., Majerus, S., et al. (2008). Self-reflection across time: cortical midline structures differentiate between present and past selves. *Social Cognitive and Affective Neuroscience*, 3(3), 244–52.
- D'Argembeau, A., Ruby, P., Collette, F., et al. (2007). Distinct regions of the medial prefrontal cortex are associated with self-referential processing and perspective taking. *Journal of Cognitive Neuroscience*, 19(6), 935–44.
- D'Argembeau, A., Stawarczyk, D., Majerus, S., et al. (2009). The neural basis of personal goal processing when envisioning future events. *Journal of Cognitive Neuroscience*, 22(8), 1701–13.
- D'Esposito, M. (2000). Functional neuroimaging of cognition. *Seminars in Neurology*, 20(4), 487–98.
- Damasio, A. (2003). Feelings of emotion and the self. *Annual New York Academy of Science*, 1001, 253–61.
- Damasio, A., Grabowski, T., Bechara, A., et al. (2000). Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nature Neuroscience*, 3(10), 1049–56.
- Daselaar, S.M., Rice, H.J., Greenberg, D.L., Cabeza, R., LaBar, K.S., Rubin, D.C. (2008). The spatiotemporal dynamics of autobiographical memory: neural correlates of recall, emotional intensity, and reliving. *Cerebral Cortex*, 18(1), 217–29.
- Daselaar, S.M., Rombouts, S.A., Veltman, D.J., Raaijmakers, J.G., Lazeron, R.H., Jonker, C. (2001). Parahippocampal activation during successful recognition of words: a self-paced event-related fMRI study. *Neuroimage*, 13(6), 1113–20.
- Decety, J., Echols, S., Correll, J. (2009). The blame game: The effect of responsibility and social stigma on empathy for pain. *Journal of Cognitive Neuroscience*, 22(5), 985–97.
- Decety, J., Jackson, P.L. (2004). The functional architecture of human empathy. *Behavioral Cognitive Neuroscience Review*, 3(2), 71–100.
- Eisenberg, N., Fabes, R.A., Miller, P.A., Fultz, J., Shell, R., Mathy, R.M. (1989). Relation of sympathy and personal distress to prosocial behavior: a multimethod study. *Journal of Personality and Social Psychology*, 57, 55–66.
- Eisenberg, N., Guthrie, I.K., Cumberland, A., et al. (2002). Prosocial development in early adulthood: a longitudinal study. *Journal of Personality & Social Psychology*, 82, 993–1006.
- Figueira, R.J., Peabody, M.F., Lonstein, J.S. (2008). Oxytocin receptor activity in the ventrocaudal periaqueductal gray modulates anxiety-related behavior in postpartum rats. *Behavioral Neuroscience*, 122(3), 618–28.
- Fossati, P., Hevenor, S.J., Graham, S.J., et al. (2003). In search of the emotional self: an FMRI study using positive and negative emotional words. *American Journal of Psychiatry*, 160(11), 1938–45.
- Goetz, J., Keltner, D., Simon-Thomas, E.R. (2010). Is compassion a distinct emotion? An integrated review of four hypotheses. *Psychological Bulletin*, 136(3), 351–74.
- Gordon, I., Zagory-Sharon, O., Leckman, J.F., Feldman, R. (2010). Oxytocin and the development of parenting in humans. *Biological Psychiatry*, 68(4), 377–82.
- Gross, J.J., Sutton, S.K., Ketelaar, T. (1998). Relations between affect and personality: support for the affect-level and affective-reactivity views. *Personality and Social Psychology Bulletin*, 24(3), 279.
- Harris, L.T., McClure, S.M., van den Bos, W., Cohen, J.D., Fiske, S.T. (2007). Regions of the MPFC differentially tuned to social and nonsocial affective evaluation. *Cognitive Affective and Behavioral Neuroscience*, 7(4), 309–16.
- Heatherton, T.F., Wyland, C.L., Macrae, C.N., Demos, K.E., Denny, B.T., Kelley, W.M. (2006). Medial prefrontal activity differentiates self from close others. *Social Cognitive and Affective Neuroscience*, 1(1), 18–25.
- Heinricher, M.M., Tavares, I., Leith, J.L., Lumb, B.M. (2009). Descending control of nociception: specificity, recruitment and plasticity. *Brain Research Review*, 60(1), 214–25.
- Hertenstein, M., Keltner, D., App, B., Bulleit, B.A., Jaskolka, A.R. (2006). Touch communicates discrete emotions. *Emotion*, 6(3), 528–33.
- Hooker, C., Verosky, S., Germine, L., Knight, R., D'Esposito, M. (2010). Neural activity during social signal perception correlates with self-reported empathy. *Brain Research*, 1308, 100–13.
- Hooker, C.I., Verosky, S.C., Germine, L.T., Knight, R.T., D'Esposito, M. (2008). Mentalizing about emotion and its relationship to empathy. *Social Cognitive and Affective Neuroscience*, 3, 204–17.
- Hutcherson, C.A., Goldin, P.R., Ochsner, K.N., Gabrieli, J.D., Barrett, L.F., Gross, J.J. (2005). Attention and emotion: does rating emotion alter neural responses to amusing and sad films? *Neuroimage*, 27(3), 656–68.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J.C., Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *Public Library of Science: Biology*, 3(3), 529–35.
- Immordino-Yang, M.H., McColl, A., Damasio, H., Damasio, A. (2009). Neural correlates of admiration and compassion. *Proceedings of the National Academy of Science*, 106(19), 8021–6.
- Insel, T.R., Gingrich, B.S., Young, L.J. (2001). Oxytocin: who needs it? *Progress in Brain Research*, 133, 59–66.
- Johnson, M.K., Raye, C.L., Mitchell, K.J., Touryan, S.R., Greene, E.J., Nolen-Hoeksema, S. (2006). Dissociating medial frontal and posterior cingulate activity during self-reflection. *Social Cognitive and Affective Neuroscience*, 1(1), 56–64.
- Kelley, W.M., Macrae, C.N., Wyland, C.L., Caglar, S., Inati, S., Heatherton, T.F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience*, 14(5), 785–94.
- Keltner, D., Lerner, J.S. (2010). Emotion. In: Gilbert, D.T., Fiske, S.T., Lindsay, G., editors. *The Handbook of Social Psychology* 5 edn. New York: McGraw, pp. 312–47.
- Kim, J.W., Kim, S.-E., Kim, J.-J., et al. (2009). Compassionate attitude towards others' suffering activates the mesolimbic neural system. *Neuropsychologia*, 47(10), 2073–81.
- Kjaer, T.W., Nowak, M., Lou, H.C. (2002). Reflective self-awareness and conscious states: PET evidence for a common midline parietofrontal core. *Neuroimage*, 17(2), 1080–6.
- 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.
- Lang, P.J. (1999). *The International Affective Picture System*. Gainesville, FL: University of Florida.
- Lazarus, R.S. (1991). *Emotion and Adaptation*. New York: Oxford University Press.
- Lerner, J.S., Keltner, D. (2001). Fear, anger, and risk. *Journal of Personality and Social Psychology*, 81(1), 146–59.
- Lieberman, M.D., Cunningham, W.A. (2009). Type I and Type II error concerns in fMRI research: re-balancing the scale. *Social Cognitive and Affective Neuroscience*, 4(4), 423–8.
- Lieberman, M.D., Jarcho, J.M., Satpute, A.B. (2004). Evidence-based and intuition-based self-knowledge: an fMRI study. *Journal of Personality and Social Psychology*, 87(4), 421–35.
- Lonstein, J.S., De Vries, G.J. (2000). Maternal behaviour in lactating rats stimulates c-fos in glutamate decarboxylase-synthesizing neurons of the medial preoptic area, ventral bed nucleus of the stria terminalis, and ventrocaudal periaqueductal gray. *Neuroscience*, 100(3), 557–68.
- Lonstein, J.S., Stern, J.M. (1997). Role of the midbrain periaqueductal gray in maternal nurturance and aggression: c-fos and electrolytic lesion studies in lactating rats. *Journal of Neuroscience*, 17(9), 3364–78.
- Lovick, T.A., Adamec, R. (2009). The Periaqueductal Gray (PAG). *Neural Plasticity*, 2009, 360907.
- Macrae, C.N., Moran, J.M., Heatherton, T.F., Banfield, J.F., Kelley, W.M. (2004). Medial prefrontal activity predicts memory for self. *Cerebral Cortex*, 14(6), 647–54.

- Maddock, R.J., Garrett, A.S., Buonocore, M.H. (2001). Remembering familiar people: the posterior cingulate cortex and autobiographical memory retrieval. *Neuroscience*, 104(3), 667–76.
- Maddock, R.J., Garrett, A.S., Buonocore, M.H. (2003). Posterior cingulate cortex activation by emotional words: fMRI evidence from a valence decision task. *Human Brain Mapping*, 18(1), 30–41.
- Mathur, V.A., Harada, T., Lipke, T., Chiao, J.Y. (2010). Neural basis of extraordinary empathy and altruistic motivation. *Neuroimage*, 51(4), 1468–75.
- Mikulincer, M., Shaver, P.R., Gillath, O., Nitzberg, R.A. (2005). Attachment, caregiving, and altruism: boosting attachment security increases compassion and helping. *Journal of Personality and Social Psychology*, 89, 817–39.
- Mitchell, J.P., Banaji, M.R., Macrae, C.N. (2005a). General and specific contributions of the medial prefrontal cortex to knowledge about mental states. *Neuroimage*, 28(4), 757–62.
- Mitchell, J.P., Banaji, M.R., Macrae, C.N. (2005b). The link between social cognition and self-referential thought in the medial prefrontal cortex. *Journal of Cognitive Neuroscience*, 17(8), 1306–15.
- Montague, P.R., King-Casas, B., Cohen, J.D. (2006). Imaging valuation models in human choice. *Annual Review of Neuroscience*, 29, 417–48.
- Nitschke, J.B., Nelson, E.E., Rusch, B.D., Fox, A.S., Oakes, T.R., Davidson, R.J. (2004). Orbitofrontal cortex tracks positive mood in mothers viewing pictures of their newborn infants. *Neuroimage*, 21(2), 583–92.
- Noriuchi, M., Kikuchi, Y., Senoo, A. (2008). The functional neuroanatomy of maternal love: mother's response to infant's attachment behaviors. *Biological Psychiatry*, 63(4), 415–23.
- Northoff, G., Heinzel, A., Bermpohl, F., et al. (2004). Reciprocal modulation and attenuation in the prefrontal cortex: an fMRI study on emotional-cognitive interaction. *Human Brain Mapping*, 21(3), 202–12.
- Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., Panksepp, J. (2006). Self-referential processing in our brain—a meta-analysis of imaging studies on the self. *Neuroimage*, 31(1), 440–57.
- Numan, M., Numan, M.J. (1997). Projection sites of medial preoptic area and ventral bed nucleus of the stria terminalis neurons that express Fos during maternal behavior in female rats. *Journal of Neuroendocrinology*, 9(5), 369–84.
- Ochsner, K.N., Knierim, K., Ludlow, D.H., et al. (2004). Reflecting upon feelings: an fMRI study of neural systems supporting the attribution of emotion to self and other. *Journal of Cognitive Neuroscience*, 16(10), 1746–72.
- Oveis, C., Cohen, A.B., Gruber, J., Shiota, L., Haidt, J., Keltner, D. (2009). Resting respiratory sinus arrhythmia is associated with tonic positive emotionality. *Emotion*, 9, 265–70.
- Oveis, C., Horberg, E.J., Keltner, D. (2010). Compassion, pride, and social intuitions of self-other similarity. *Journal of Personality and Social Psychology*, 98(4), 618–30.
- Pelphrey, K.A., Morris, J.P., Michelich, C.R., Allison, T., McCarthy, G. (2005). Functional anatomy of biological motion perception in posterior temporal cortex: an FMRI study of eye, mouth and hand movements. *Cerebral Cortex*, 15(12), 1866–76.
- Pfeifer, J.H., Iacoboni, M., Mazziotta, J.C., Dapretto, M. (2008). Mirroring others' emotions relates to empathy and interpersonal competence in children. *Neuroimage*, 39(4), 2076–85.
- Reniers, R.L., Corcoran, R., Drake, R., Shryane, N.M., Vollm, B.A. (2011). The QCAE: a Questionnaire of Cognitive and Affective Empathy. *Journal of Personality Assessment*, 93(1), 84–95.
- Rodrigues, S.M., Saslow, L.R., Garcia, N., John, O.P., Keltner, D. (2009). Oxytocin receptor genetic variation relates to empathy and stress reactivity in humans. *Proceedings of the National Academy of Science USA*, 106(50), 21437–41.
- Rosen, G.J., de Vries, G.J., Goldman, S.L., Goldman, B.D., Forger, N.G. (2008). Distribution of oxytocin in the brain of a eusocial rodent. *Neuroscience*, 155(3), 809–17.
- Rudebeck, P.H., Bannerman, D.M., Rushworth, M.F. (2008). The contribution of distinct subregions of the ventromedial frontal cortex to emotion, social behavior, and decision making. *Cognitive Affective and Behavioral Neuroscience*, 8(4), 485–97.
- Saarela, M.V., Hlushchuk, Y., Williams, A.C., Schürmann, M., Kalso, E., Hari, R. (2007). The compassionate brain: humans detect intensity of pain from another's face. *Cerebral Cortex*, 17(1), 230–7.
- Saxe, R., Powell, L.J. (2006). It's the thought that counts: specific brain regions for one component of theory of mind. *Psychological Science*, 17(8), 692–9.
- Saxe, R., Wexler, A. (2005). Making sense of another mind: the role of the right temporo-parietal junction. *Neuropsychologia*, 43(10), 1391–9.
- Shahrokh, D.K., Zhang, T.Y., Diorio, J., Gratton, A., Meaney, M.J. (2010). Oxytocin-dopamine interactions mediate variations in maternal behavior in the rat. *Endocrinology*, 151(5), 2276–86.
- Shamay-Tsoory, S.G., Aharon-Peretz, J., Perry, D. (2009). Two systems for empathy: a double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. *Brain*, 132(Pt 3), 617–27.
- Simon-Thomas, E.R., Keltner, D., Sauter, D.A., Sinicropi-Yao, L., Abramson, A. (2009). The voice conveys specific emotions: evidence from vocal burst displays. *Emotion*, 9(6), 838–46.
- Singer, T. (2006). The neuronal basis and ontogeny of empathy and mind reading: review of literature and implications for future research. *Neuroscience Biobehavioral Review*, 30(6), 855–63.
- Singer, T., Frith, C. (2005). The painful side of empathy. *Nature Neuroscience*, 8(7), 845–6.
- Singer, T., Lamm, C. (2009). The social neuroscience of empathy. *Annual New York Academy of Science*, 1156, 81–96.
- Smith, C.A., Ellsworth, P.C. (1985). Patterns of cognitive appraisal in emotion. *Journal of Personality and Social Psychology*, 48, 813–38.
- Stack, E.C., Balakrishnan, R., Numan, M.J., Numan, M. (2002). A functional neuroanatomical investigation of the role of the medial preoptic area in neural circuits regulating maternal behavior. *Behavioral Brain Research*, 131(1–2), 17–36.
- Sturgis, J.D., Bridges, R.S. (1997). N-methyl-DL-aspartic acid lesions of the medial preoptic area disrupt ongoing parental behavior in male rats. *Physiology of Behavior*, 62(2), 305–10.
- Sugiura, M., Shah, N.J., Zilles, K., Fink, G.R. (2005a). Cortical representations of personally familiar objects and places: functional organization of the human posterior cingulate cortex. *Journal of Cognitive Neuroscience*, 17(2), 183–98.
- Sugiura, M., Watanabe, J., Maeda, Y., Matsue, Y., Fukuda, H., Kawashima, R. (2005b). Cortical mechanisms of visual self-recognition. *Neuroimage*, 24(1), 143–9.
- Swain, J.E. (2008). Baby stimuli and the parent brain: functional neuroimaging of the neural substrates of parent-infant attachment. *Psychiatry*, 5(8), 28–36.
- Swain, J.E. (2010). The human parental brain: In vivo neuroimaging. *Progress in Neuropsychopharmacology Biological Psychiatry*, 35, 1242–54.
- Takahashi, H., Matsuura, M., Koeda, M., et al. (2008). Brain activations during judgments of positive self-conscious emotion and positive basic emotion: pride and joy. *Cerebral Cortex*, 18(4), 898–903.
- Tracy, J.L., Robins, R.W. (2004). Show your pride: evidence for a discrete emotion expression. *Psychological Science*, 15(3), 194–7.
- Tracy, J.L., Robins, R.W. (2007). The psychological structure of pride: a tale of two facets. *Journal of Personality and Social Psychology*, 92(3), 506–25.
- Tracy, J.L., Robins, R.W., Tangney, J.P. (2007). *The Self-Conscious Emotions: Theory and Research*. New York: Guilford Press.
- Worsley, K.J., Friston, K.J. (1995). Analysis of fMRI time-series revisited - again. *NeuroImage*, 2, 173–81.
- Zahn, R., Moll, J., Krueger, F., Huey, E.D., Garrido, G., Grafman, J. (2007). Social concepts are represented in the superior anterior temporal cortex. *Proceedings of the National Academy of Science USA*, 104(15), 6430–5.