Title

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Journal

Human Brain Mapping, 37(4)

ISSN

1065-9471

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Publication Date

2016-04-01

DOI

10.1002/hbm.23119

Peer reviewed

◆ **Human Brain Mapping 37:1544–1558 (2016)** ◆

Self-Other Resonance, Its Control and Prosocial Inclinations: Brain–Behavior Relationships

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Abstract: Humans seem to place a positive reward value on prosocial behavior. Evidence suggests that this prosocial inclination is driven by our reflexive tendency to share in the observed sensations, emotions and behavior of others, or "self-other resonance". In this study, we examine how neural correlates of self-other resonance relate to prosocial decision-making. Subjects performed two tasks while undergoing fMRI: observation of a human hand pierced by a needle, and observation and imitation of emotional facial expressions. Outside the scanner, subjects played the Dictator Game with players of low or high income (represented by neutral-expression headshots). Subjects' offers in the Dictator Game were correlated with activity in neural systems associated with self-other resonance and anticorrelated with activity in systems implicated in the control of pain, affect, and imitation. Functional connectivity between areas involved in self-other resonance and top-down control was negatively correlated with subjects' offers. This study suggests that the interaction between self-other resonance and top-down control processes are an important component of prosocial inclinations towards others, even when biological stimuli associated with self-other resonance are limited. These findings support a view of prosocial decision-making grounded in embodied cognition. *Hum Brain Mapp 37:1544–1558, 2016*. © 2016 Wiley Periodicals, Inc.

Key words: empathy; altruism; magnetic resonance imaging; decision-making

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INTRODUCTION

Humans' ability to "resonate" with the internal and behavioral states of others may encourage prosocial behavior towards them. When we observe someone in pain or someone expressing emotion, growing evidence suggests that we process the experience much in the same way we would our own [reviewed in Zaki and Ochsner, 2012]. Additionally, we often imitate one another's behaviors (consciously or unconsciously) as a marker of affiliation and rapport [Chartrand and Bargh, 1999; Iacoboni, 2009; Lakin and Chartrand, 2003; Pfeifer et al., 2008; Sperduti et al., 2014]. We are even able to share in the implied states of fictional characters and absent third persons [Clay and Iacoboni, 2011; Davis, 1983]. We will refer to this ability as "self-other resonance" (SR) [Batson, 1991; Eisenberg and Fabes, 1990; Masten et al., 2011; Smith, 2006]. The dominant empirical correlate of SR is "neural resonance" [Zaki and Ochsner, 2012], the phenomenon of shared neural representations for the perception and experience of disgust [Jabbi et al., 2007; Wicker et al., 2003], somatosensation [Bufalari et al., 2007; Masten et al., 2011; Singer et al., 2006], emotion [Carr et al., 2003; Pfeifer et al., 2008], and motor behavior [Keysers and Fadiga, 2008].

Additional Supporting Information may be found in the online version of this article.

Contract grant sponsor: National Institute of Health; Contract grant number: R21 MH097178

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Received for publication 1 June 2015; Revised 11 December 2015; Accepted 4 January 2016.

DOI: 10.1002/hbm.23119

Self-Other Resonance and Prosocial Inclinations

The blurring between self and other provided by SR may encourage prosocial inclinations to help and cooperate with others [Batson, 1991; Eisenberg and Fabes, 1990; Hein et al., 2010, 2011; Ma et al., 2011; Masten et al., 2011; Smith, 2006]. Indeed, individuals who show increased neural resonance in response to others' *pain* tend to give more charitable donations [Ma et al., 2011]. Hein et al. [2010, 2011] found that vicarious neural and physiological responses to the pain of in- and out-group members predicted later costly helping towards those same people. Behavioral forms of neural resonance, like spontaneous and deliberate imitation are also linked to prosocial behavior and social competence [Chartrand and Bargh, 1999; Iacoboni, 2009; Lakin and Chartrand, 2003; Pfeifer et al., 2008; Zaki and Ochsner, 2012]. However, we are not universally prosocial: individual predispositions and contextual factors like closeness, perceived need, and affiliation modulate our willingness to share with others at personal cost in economic games [Engel, 2011] and in daily life [Trivers, 1971].

Top-Down Control in SR and Prosocial Inclination

Top-down control of SR may *modulate* the extent to which we treat others' states (and outcomes) as if they were our own: We do not "resonate" with all others equally. Indeed, our closeness to others, their group affiliation and their perceived trustworthiness modulate neural resonance [Cheng et al., 2010; Gu and Han, 2007; Guo et al., 2012; Hein and Singer, 2008; Lamm et al., 2007; Loggia et al., 2008, Reynolds-Losin et al., 2012, 2014, 2015; Singer et al., 2006]. The prereflective nature of neural resonance suggests that this sensitivity to context is the result of *implicit* control. Furthermore, this control seems to be *inhibitory*. Prefrontal cortex lesions associated with compulsive imitative behavior suggest that, for normal behavior to exist, some mechanisms to control neural resonance are always at play, unless damaged [De Renzi et al., 1996; Lhermitte, 1983].

Top-down control of affective, somatosensory and motor processes in behavior and decision-making is subserved by a large set of prefrontal and temporal systems, including the medial and dorsolateral prefrontal cortex (MPFC and DLPFC) and temporoparietal junction (TPJ) [Banks et al., 2007; Brighina et al., 2010; Cho and Strafella, 2009; Decety and Lamm, 2007; Miller and Cohen, 2001; Spengler et al., 2009, 2010; Tassy et al., 2012; Volman et al., 2011; Winecoff et al., 2013]. Many of these areas (dorsolateral prefrontal cortex, dorsal, and ventral medial prefrontal cortex, among others) are also associated with economic and moral decision-making [Clark et al., 2008; Hare et al., 2010; Knoch et al., 2006; Volman et al., 2011; Tassy et al., 2012]. These disparate findings from economics, social psychology and neuroscience suggest a link between our SR, its modulation and the relative reward value we place on others' welfare.

Linking SR, Top-Down Control and Prosocial Inclinations

Despite these findings, the relationship between SR, top-down control and prosocial decision-making remains unclear. We propose that during economic interactions (allocation or exchange of resources or cooperation) with a human "other" (present or implied), we implicitly assign reward values (or utilities, to use the neuroeconomic term) to the outcomes of our possible decisions (Fehr and Camerer, 2007). In order to assign such values, we must construct an internal model of the "other", including their intentions, moral character, group affiliation, etc. as well as perceptual, affective, and motor experiences we associate with people from past experience. Indeed, a major proposed subcomponent of empathy is fantasizing [Clay and Iacoboni, 2011; Davis, 1983], our ability to take the perspective of absent or fictional characters and become correspondingly invested in their welfare (our screams to warn the hero onscreen about a monster behind them, or our sadness at their demise). This embodied model of the "other" may evoke SR and its top-down control, thus influencing the relative utility of their welfare [Bechara and Damasio, 2005]. This framework may explain why individual differences in neural and behavioral markers of SR and its top-down control have been correlated with prosocial inclinations in decision-making.

Indeed, the notion of common systems has support in extent literature. Top-down control processes are increasingly implicated in the contextual modulation of neural resonance [Cheng et al., 2010; Gu and Han, 2007; Guo et al., 2012; Hein and Singer, 2008; Lamm et al., 2007; Loggia et al., 2008; Reynolds-Losin et al., 2012, 2014, 2015; Singer et al., 2006]. Conversely, recent research suggests that motor, somatosensory, and affective processing contribute in to our evaluations of others' beliefs, internal states, and intentions [Frith and Singer, 2008; Gallese, 2007; Obhi, 2012; Schulte-Rüther et al., 2007], as well as our conscious decisions about others' welfare [Camerer, 2003; Hewig et al., 2011; Greene et al., 2001; Oullier and Basso, 2010; Van 't Wout et al., 2006].

Measuring SR

We propose that activation in and connectivity between SR and top-down control systems inform individual differences in prosocial inclination and its contextual modulation. To test this theory, we recruited subjects to perform two tasks, each examining an important component of SR, inside an MRI scanner. For the first task, subjects passively observed a human hand being prodded with a syringe or a q-tip (the Needle Test or NT). This was taken as a measure of reflexive SR in response to painful stimuli in another. For the second task, subjects either passively observed or actively imitated emotional facial expressions (Emotion imitation and observation or EOI).

Vicarious activation of motor and limbic regions during observation of emotional facial expressions has been linked to empathic concern while similar activation during imitation of facial expressions is linked to social competence [Pfeifer et al., 2008]. Indeed, imitation has been suggested as a way to *deliberately* engage vicarious emotional responses to the emotions of others [Carr et al., 2003]. The needle test should reflect vicarious sensory and affective responses to another's pain and their control. The emotion imitation task, on the other hand, should reflect vicarious emotional processing evoked via deliberate motor imitation [Carr et al., 2003], and *its* respective control. We propose that despite the different contexts of these tasks, analogs patterns of SR- and control-related neural activity should correlate with prosocial decision-making.

Measuring Prosocial Inclinations

Prosocial decisions in economic games involving sharing are often due to multiple factors, such as strategy (sharing enough that the offer will not be rejected), or social pressure (altruistic behavior enhances reputation). To control for these factors, we employed a modified Dictator game, a task thought to measure altruistic fairness, in which subjects show rich variation in response to context [Aguiar et al., 2008; Benenson et al., 2007; Eckel and Grossman, 1996; Hoffman et al., 1996; Liebe and Tutic, 2010; Weiland et al., 2012]. Subjects were tasked with dividing up a sum of money ($10/trial) between themselves and 24 players (represented with photographic profiles) representing people of *high* or *low* income (a proxy for socioeconomic status, or SES). This was done to introduce a contextual variable which could be ascribed to top-down control in the prosocial decision-making process (typically subjects share relatively less money with players of high income/low perceived need) [Engel, 2011]. In order to engage subjects in the task, they were truthfully informed that a random subset of the players represented real people in Los Angeles who would *actually receive the money they allotted to them*. To control for social pressure, subjects were truthfully informed that they would perform the task alone and unobserved, that their data was linked to an ID number devoid of identifying information, and that their responses would be scored by a research assistant that did not come into contact with any subjects. This strict maintenance of anonymity and lack of supervision was the primary impetus for having subjects perform the study outside of the scanner. This, to the best of our abilities, allowed us to observe behavioral correlates of prosocial inclination and its modulation in response to the opposing player's perceived need, in absence of other regulating factors such as strategy or concerns about one's own reputation.

Hypotheses

We propose that individual differences in SR and its top-down control reflect individual differences in prosocial decisions and their respective modulation during the Dictator Game (DG). Furthermore, we propose that top-down control in both contexts is inhibitory in nature. Accordingly, we hypothesized the following:

a. Brain activity during SR-evoking tasks is correlated with DG offers (a proxy for the relative utility of the players' welfare). The sign of the correlation should also reveal the nature of the processes implemented by the implicated areas, with a positive correlation (in sensorimotor and affective areas) implying greater SR and a negative correlation (in control areas like the MPFC, DLPFC and TPJ) implying greater top-down control. In other words, subjects who show greater correlates of SR during scanning should also behave more generously, while subjects who show greater inverse correlations with offers should behave less generously, especially to high SES players.
b. There are functional interactions between regions associated with SR and top-down control during the tasks and the strength of interaction will be correlated with subjects' offers.

METHODS

Subjects

Subjects were 20 ethnically diverse adults aged 18–35 (9 females). All subjects were recruited from the local community through fliers. Eligibility criteria included: right handed, no prior, or concurrent diagnosis of any neurological (e.g., epilepsy, Tourette's syndrome), psychiatric (e.g., schizophrenia), or developmental (e.g., ADHD; dyslexia) disorders, no history of drug or alcohol abuse. All recruitment and experimental procedures were performed under approval of UCLA's institutional review board.

Behavioral Task

The Dictator Game (DG)

Subjects were instructed to select a portion of a sum of money ($0-10 out of $10) to be given to a player (henceforth referred to as the *player*, to distinguish them from the subject throughout the manuscript), represented by a digital profile presented on a computer screen, for each of 24 trials. In each trial, subjects were presented with 1 of 24 full-color photographs (equalized for luminance) of neutral faces selected from stock photographs and the Nim Stim Face Stimulus Set [Tottenham et al., 2009] coupled with a name and a yearly income in dollars, both presented on the right portion of the screen in black letters with a white

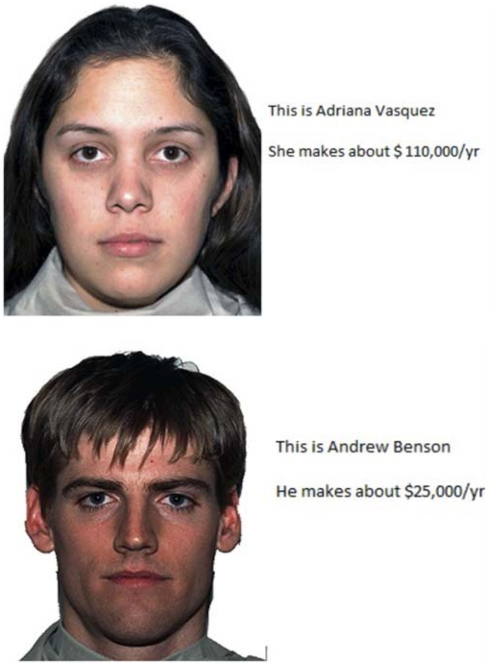

Figure 1.
Two examples of player profiles used in the Dictator Game. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

background (see Fig. 1). Player profiles had one of two levels of income: Low ($18,000–$30,000/year) or High ($70,000–$200,000/year). Income was used as a proxy for socioeconomic status (SES). Both genders were equally represented, while racial composition [(2) Caucasian: (2) Hispanic/Latino: (1) Black: (1) Asian] was derived from census data and matched between genders and income levels. Low and high SES profiles were presented in one of four different pseudorandomized orders throughout the game. Subjects encountered each player only once. Each player profile was presented for 4 s, after which the subjects were given an onscreen prompt to make their offer ("How much $would you like to offer?"), which appeared in the bottom right corner of the screen. This screen remained for 5 s, during which subjects had to make their offer.

Subjects were truthfully informed that a subset (n = 12) of the players in the experiment corresponded to people in Los Angeles (contacted for approval prior to the experiment) who would receive the money allotted to them by each subject. Their photograph and name was changed for confidentiality, though the photograph used was matched to their gender and race, and their actual income was displayed. Genders, races, and SES groups were equally represented among the 12 real profiles. Subjects were informed that they would be rewarded for 3 randomly selected trials out of the total 24. Thus, on any given trial, they could be playing with a real person who would actually receive the money allotted to them, and the subjects could receive what they allotted for themselves in that trial. Subjects carried out the task unobserved, in a closed room without cameras. Their responses were saved in association with an ID number, and scored by a different researcher than the experimenter, ensuring subjects' anonymity. Subjects were comprehensively informed about these controls and explicitly instructed prior to and during briefing that the paradigm included *no deception*.

The subjects' 24 offers (1 per player) were averaged and separated by player income (high or low). This resulted in 2 means per subject: low SES and high SES.

Functional MRI Tasks

Emotion Observation and Imitation (EOI)

The stimuli were 48 full-color faces comprising an ethnically diverse set of 12 individuals (6 males and 6 females taken from the Nim Stim Face Stimulus Set [Tottenham et al., 2009] expressing four different emotions (angry, fearful, happy, or sad). None of the faces used in the DG appeared in this task. Task blocks consisted of six stimuli, presented for 4.5 s each, with an interstimulus interval (ISI) of 400 ms. Prior to each block, subjects were presented for 1.5 s with a screen consisting of white letters on a black background, instructing subjects to "imitate the following facial expressions" (Imitation condition), or "look at the following faces" (Observation condition). The run consisted of 8 task blocks lasting 29 s each, interleaved with an additional 9 rest blocks consisting of a white fixation cross on a black background, lasting 15 s each. Imitation and Observation blocks were presented in alternating order for a total of four per condition.

Needle Test (NT)

The stimuli were 27 full-color videos previously used by Bufalari et al. [2007], and used with permission by their research group, depicting a human hand being pierced by a hypodermic syringe (Pain condition) and touched by a wooden q-tip (Touch condition) in varying locations, as well as a static hand without stimulation (Hand condition) for use as a control. The run consisted of 12 trial blocks lasting 26 s each, plus 8 alternating rest blocks that lasted either 5 s or 10 s. Each trial block consisted of four videos of a single condition (Pain, Touch, Hand), 5 s in duration each, with an interstimulus interval of 400 ms. Subjects were simply instructed to watch the video clips. They were assured that the hand in the video clip was a human hand and not a model, but they were not instructed to empathize with the model nor were there any audiovisual cues to indicate pain in the hand's owner.

For each task, two different block orders were used, and controlled to ensure an approximately equal proportion of male and female subjects were exposed to each block order.

The order of the fMRI and behavioral task blocks was counterbalanced across subjects, as was the order of the fMRI tasks within the fMRI task block. All tasks were coded within Presentation (created by Neurobehavioral Systems).

Behavioral Assessment

After completing the experiment, subjects were given two questionnaires, which they filled out in a closed room, unobserved.

1. Interpersonal Reactivity Index (IRI): The IRI [Davis, 1983] is widely used [Avenanti et al., 2009; Pfeifer et al., 2008] and validated [Litvack-Miller et al., 1997] questionnaire designed to measure both ''cognitive'' and ''emotional'' components of empathy. It consists of 24 statements that the subject rates on a 5-point scale ranging from 0 (Does not describe me very well) to 5 (Describes me very well). The statements are calculated to test four theorized subdimensions of empathy:

   Fantasizing Scale (FS): the tendency to take the perspective of fictional characters.

   Empathic Concern (EC): sympathetic reactions to the distress of others.

   Perspective Taking (PT): the tendency to take other's perspective

   Personal Distress (PD): aversive reactions to the distress of others

   Scores were summed for each subdimension (measured by 6 items) to make four scores per subject. Cronbach's alpha, a measure of reliability, was assessed for the IRI using SPSS (FS = 0.756, EC = 0.773, PT = 0.807, PD = 0.821).
2. Personal Altruism Level (PAL): The PAL is designed to assess the disposition to engage in prosocial behavior such as sharing, comforting and cooperating towards friends and family (subscale I), or strangers (subscale II). It consists of 18 statements that subjects rate their agreement with on a 5-point scale ranging from 0 (highly agree) to 5 (highly disagree). Scores are summed for each subscale (measured by 9 items) to make 2 scores per subject (I and II).

Demographic Information

Following all behavioral measures and questionnaires, subjects were asked their ethnicity and approximate household income. If the subject was not financially independent (as in the case of many student participants), they reported their family's household income, in order to assess their approximate socioeconomic status. Subjects' average income was $62,156 (SD = $48,824), however subject incomes were not normally distributed (Shapiro–Wilks test, $P < 0.0001$). In order to gauge whether subjects' incomes were correlated with subjects' offers, we performed nonparametric correlations (Spearman's Rho, to accommodate non-normality) between subject incomes and average offers to low and high SES players. No significant correlations were found between subject incomes and low SES ($r = 0.42$, $P = 0.065$) or high SES ($r = 0.359$, $P = 0.12$) offers.

Behavioral Analysis

Subjects' scores on each subscale of the PAL and IRI were correlated with their average offers to low SES and high SES players, separately, using SPSS.

MR Image Acquisition

fMRI data were acquired on a Siemens Trio 3 Tesla system housed in the Staglin Center for Cognitive Neuroscience at UCLA. One subject's data was collected on an identical scanner housed in the adjacent Ahmanson–Lovelace Brain Mapping Center. Functional images were collected over 36 axial slices covering the whole cerebral volume using an echo planar T2*-weighted gradient echo sequence (TR = 2500 ms; TE = 25 ms; flip angle = 90°; matrix size = 64 × 64; FOV 20 cm; in-plane resolution = 3 mm × 3 mm; slice thickness = 3 mm/1 mm gap). A high-resolution EPI structural volume was also acquired coplanar with the functional images (TR = 2500 ms, TE = 33 ms, 128 × 128 matrix size, FOV = 256 cm). Finally, a high-resolution T1-weighted volume was acquired in each subject (TR = 2300 ms, TE = 25 ms, TI = 100 ms, flip angle = 8°, matrix size = 192 × 192, FOV = 256 cm, 160 slices), with approximately 1 mm isometric voxels (1.3 × 1.3 × 1.0 mm).

Functional MRI Analysis

Analyses were performed in FEAT (FMRI Expert Analysis Tool), part of FSL (FMRIB's Software Library, http://www.fmrib.ox.ac.uk/fsl). After motion correction using MCFLIRT, images were temporally high-pass filtered with a cutoff period of 70 and 90 s for NT and EOI, respectively (approximately equal to one rest-task-rest-task period), and smoothed using a 6 mm Gaussian FHWM algorithm in three dimensions. Each subjects' functional data was coregistered to standard space (MNI 152 template) via registration of an averaged functional image to the high resolution T1-weighted volume using a six degree-of-freedom linear registration and of the high-resolution T1-weighted volume to the MNI 152 template via 12 degree-of-freedom linear affine registration, implemented in FLIRT.

The BOLD response was modeled using an explanatory variable (EV) consisting of a boxcar function describing the onset and duration of each relevant experimental condition (task conditions, rest, instruction scree) convolved with a double gamma HRF to produce an expected BOLD response. The temporal derivative of each task EV was also included in the model. In addition, each subject's 6 motion parameters were included as additional EVs of no interest, to control for head motion. Functional data were then fitted to the model using FSL's implementation of the general linear model. Higher-level analyses were implemented using DG offers to low and high SES players as separate explanatory variables. Resultant images were cluster corrected at a z-threshold of 2.3 and P value cutoff of 0.05, using FLAME 1 + 2.

Dictator Game offers were divided into two separate EVs corresponding to the mean offer for each SES group within the player profiles (low SES and high SES), per subject, and correlated with subjects' BOLD data for each functional contrast of interest, using FSLs implementation of the general linear model. Contrasts were made examining variance unique to either low SES or high SES offers (1 0 or 0 1) and shared variance (0.5 0.5). These results will be referred to throughout the manuscript as correlations with *High* or *Low SES* offers, on one hand, or *overall offers*, respectively.

Psychophysiological Interaction Analysis (PPI)

To test whether functional interactions *between* SR and top-down control regions exist and are correlated with DG offers, we examined psychophysiological interactions between EOI and NT data and DG offers. In order to remove non-neuronal sources of coherent oscillation in the relevant frequency band (0.01–0.1 Hz), preprocessed data was subjected to probabilistic independent component analysis as implemented in MELODIC (Multivariate Exploratory Linear Decomposition into Independent Components) Version 3.10, part of FSL (FMRIB's Software Library, http://www.fmrib.ox.ac.uk/fsl). Noise components corresponding to head motion, scanner noise, cardiac/respiratory signals were identified by observing their localization, time series, and spectral properties and removed using FSL's regfilt command.

To create the ROI's, time series were extracted from 6mm diameter seeds created in standard (MNI 152) space centered on voxels showing high correlations with overall DG offers in the principal contrasts reported on here (see Fig. 4). Center voxel coordinates (in voxels) and contrasts used are as follows. For the EOI gPPI analysis: right amygdala ($x = 35$, $y = 61$, $z = 25$), left amygdala ($x = 57$, $y = 58$, $z = 28$), right dorsolateral prefrontal cortex (DLPFC) ($x = 25$, $y = 75$, $z = 55$). For the NT gPPI analysis: left superior parietal lobule (SPL) ($x = 55$, $y = 39$, $z = 69$), left DLPFC ($x = 45$, $y = 68$, $z = 51$) and left precentral gyrus (PCG) ($x = 63$, $y = 67$, $z = 49$).

For each analysis, we modeled activity using the following EV's: *Psychological*, consisting of a boxcar functions modeling the onset and duration of each task condition, convolved with a canonical double-gamma HRF; *physiological*, consisting of the ROI's time series (one per analysis); and a *psychophysiological interaction* (PPI) for each task condition, modeling the interaction between the expected BOLD response to each condition and the time series of interest. These separate PPI estimates were then contrasted at the group level. This allowed us to test for voxels that display significant *changes* in correlation with the time series of the ROI for any task contrast of interest, an approach known as generalized PPI or gPPI [Mclaren et al., 2012]. gPPI analyses of EOI data employed the right amygdala and right DLPFC seeds, while NT data was analyzed with the left SPL, left PCG, and left DLPFC seeds. These sets were specifically chosen to test for functional connectivity between areas of positive correlation with DG offers (proposed primary SR areas) for NT and EOI (left SPL and right amygdala, respectively) and corresponding areas of negative correlation with DG offers (proposed control areas) (left DLPFC/left PCG and right DLPFC, respectively). First level analyses were carried out using FEAT. A higher level analysis was carried out to examine correlations between PPI parameter estimates and DG offers. Resultant images were cluster corrected at a z-threshold of 2.3 and P value cutoff of 0.05, using FLAME 1 + 2. As the two imaging tasks employed a block design rather than an event-related design, we did not perform deconvolution of fMRI data as part of our PPI model [Gitelman et al., 2003].

RESULTS

Behavior

Subjects offered, on average, \$6.18 (SD = 2.66) to low SES players, and \$2.63 (SD = 2.81) to high SES players. Subjects' offers to low and high SES players were significantly correlated ($R^2 = 0.49$, $P = 0.0004$). Subjects' scores on the Personal Distress (PD) subscale of the IRI were correlated with their offers to high SES profiles ($R^2 = 0.46$, $P = 0.0026$). Subjects' offers to low SES profiles were correlated ($R^2 = 0.2$, $P = 0.0475$) with their scores on the empathic concern (EC) subscale. Subjects' scores on the PAL did not show any significant correlation with subjects' offers or imaging data.

Needle Test

We will report here correlations between DG offers and the contrast Pain > Hand. Similar but much weaker correlations were found for the contrast Pain > Touch (see Table I). This suggests an overlap between neural resonance processes recruited during the "pain" and "touch" condition, resulting in the contrast subtracting out much of the relevant signal variance.

Overall offers were positively correlated with BOLD signal changes in a cluster encompassing primary somatosensory cortex, that previous studies have associated with the experience and observation of painful and tactile stimuli [Bufalari et al., 2007; Keysers et al., 2010], and the adjacent superior parietal lobule, an area also associated with the observation and experience of pain [Lamm et al., 2011], as well as aversive objects near one's body [Lloyd and

TABLE I. Local maxima of correlation between BOLD signal changes during needle test (NT)/emotion observation and imitation (EOI), and dictator game offers

Contrast	Correlation	Variable	Area	Coordinates (mm) x	y	z	Z	Consistent with theory
Pain > Hand	Positive	Overall offers	L Superior parietal lobe	−18	−50	66	5.59	+
			L SI	−16	−42	78	5.14	+
			L Opercular cortex	−20	−52	62	5.08	+
			L Cerebellum	−36	8	24	4.26	Unclear
			L Insular cortex	−34	42	0	3.97	+
			L Precuneus	−44	20	38	3.34	Unclear
	Negative	Overall offers	L Precentral gyrus	−42	0	34	4.1	+
			L Dorsolateral prefrontal cortex	−48	16	34	3.92	+
Imitate > Observe	Positive	LSES offers	L Temporal fusiform cortex	−34	−8	−34	4.75	+
			L Temporal pole	−34	10	−28	4.59	Unclear
			L Amygdala	−20	−6	−18	4.4	+
			L Hippocampus	−22	−10	−26	4.11	+
			L Parahippocampal gyrus	−24	−30	−20	3.88	Unclear
	Negative	HSES offers	R Angular gyrus	62	−52	16	8.06	+
			R Temporoparietal junction	50	−52	54	7.58	+
			R Precuneus	12	−64	26	6.37	Unclear
			R Dorsolateral prefrontal cortex	46	18	42	6.35	+
			L Precuneus	−12	−72	28	6.08	Unclear
			R Lateral occipital cortex	46	−60	32	6.01	+
			L Dorsolateral prefrontal cortex	28	24	52	5.31	+
			R Posterior cingulate cortex	8	−48	36	5.1	+
			Posterior cingulate cortex	0	−24	32	4.54	+
			L Parahippocampal gyrus	−20	−20	−28	3.91	Unclear

Right-most column indicates whether finding is consistent (+) or inconsistent (−) with our hypotheses.

Roberts, 2006]. Positive correlations were also found within a cluster encompassing the dorsal posterior insula and operculum, both of which are associated with the anticipation and experience of pain [Sawamoto et al., 2000; Segerdahl et al., 2015]. Positive correlations were also found within the cerebellum and precuneus (Fig. 2a).

As shown in Figure 2b, overall offers were negatively correlated with signal changes in areas implicated in the control of pain (left anterior precentral gyrus or PCG, left DLPFC) [Brighina et al., 2010; Garcia-Larrea and Peyron, 2007].

As in previous studies employing this paradigm [Bufalari et al., 2007], this task contrast activated a broad array of areas including cerebellum, bilateral visual cortex, MT/V5, somatosensory cortices, premotor cortex, pars opercularis, and pars orbitalis of the inferior frontal gyrus, anterolateral prefrontal cortex, anterior and posterior insula, left putamen, right thalamus, and right globus pallidus (Supporting Information Figs. 1, 3).

Emotion Observation and Imitation

We correlated DG offers with the contrast Imitate > Observe for the following two reasons: first, "rest" is difficult to control as a baseline condition, given the uncertain nature of the cognitive processes occurring therein, *particularly* with regard to prefrontal structures associated with social cognition [Amodio and Frith, 2006]. Second, imitation of emotional facial expressions typically activates structures associated with observation, but to a greater extent [Iacoboni, 2009]. Indeed, our results show significantly greater activation in all structures activated by the observation task during the imitation condition (see Supporting Information Figs. 2, 4). This contrast allows us to observe individual differences in vicarious emotional responses produced by simultaneously *executing* and *observing* emotional facial expressions [Carr et al., 2003].

Subjects' offers to low SES players were positively correlated with BOLD signal changes in areas associated with neural resonance (left amygdala) and trait empathy (left fusiform cortex) [Carr et al., 2003; Pfeifer et al., 2008]. Correlations were also found with signal changes in left hippocampus and parahippocampal gyrus (PHG), recently found to contain mirror neurons in humans during single cell recordings while subjects observed and executed facial emotional expressions [Mukamel et al., 2010] (Fig. 3a). Positive correlations were also found in the left temporal pole.

Subjects' offers to high SES profiles were negatively correlated with signal changes in areas associated with multiple forms of top-down control: control of imitation (right temporoparietal junction or TPJ) [Spengler et al., 2010] and the integration of affect into decision-making (DLPFC)

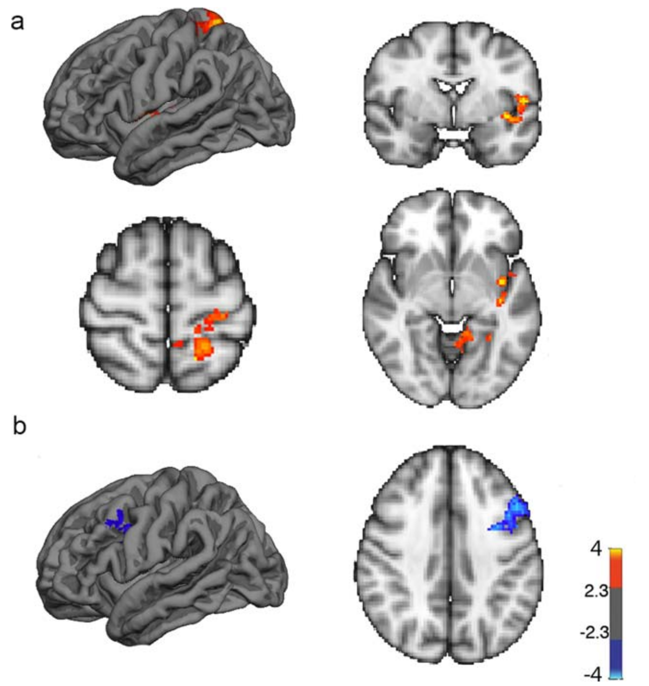

Figure 2.
Correlations between BOLD signal changes during the Needle Test and Dictator Game behavior. Areas where activation for the contrast Pain > Hand correlates positively (red yellow) and negatively (blue dark blue) with subjects' overall offers in the Dictator Game (cluster corrected at z threshold > 2.3, $P < 0.05$). Heat maps reflect z scores. Slices are displayed in radiological orientation. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

[Knoch et al., 2006; Tassy et al., 2012]. Negative correlations were also found with a cluster in the right PHG (see Table I).

Negative correlations with offers to high SES players were also found in the posterior cingulate (PCC) and precuneus (Fig. 3b). These areas have been associated with self-referential processing (Brewer et al., 2013; Cavanna and Trimble, 2006; Johnson et al., 2006; Northoff et al., 2006], perhaps suggesting that this correlation reflects self-other *distinction* rather than self-other *resonance*. Negative correlations were also found in the lateral occipital cortex.

Connectivity

We propose that neural systems supporting top-down control exert a modulatory influence on systems supporting SR during the fMRI tasks. To test this hypothesis we examined task-related changes in connectivity (psychophysiological interaction or PPI) in ROIs implicated in SR and top-down control correlated with behavior in the DG. Correlations between parameter estimates in center voxels of each ROI and DG offers are displayed in Figure 4.

PPI analyses of SPL, PCG, and left DLPFC for NT data did not yield any significant result. However, for the contrast Imitation > Observation, left amygdala showed increased connectivity with the ACC [Medford and Critchley, 2010; Miller and Cohen, 2001; Philips et al., 2003] and right paracingulate gyrus, areas implicated in affective regulation, as well as bilateral basal ganglia and posterior insula; left superior temporal gyrus and hippocampus. The right DLPFC (Fig. 5b) showed increased connectivity with a wide range of cortical and subcortical areas involved in motor behavior, affect, motivation and somatosensation (bilateral amygdala, bilateral hippocampus, left anterior insula/frontal operculum, bilateral putamen,

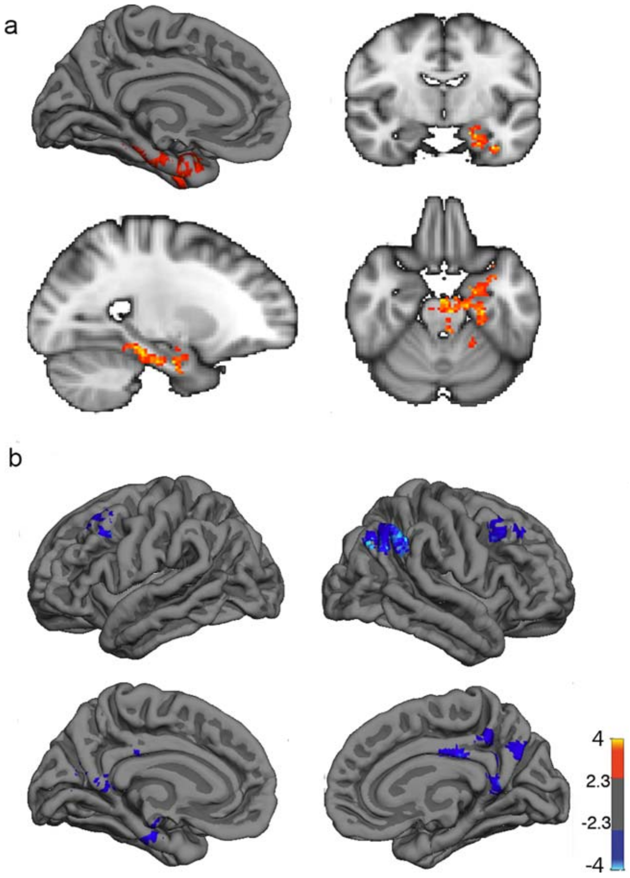

Figure 3.
Correlations between BOLD signal changes during EOI and Dictator Game behavior. (**a**) Areas where activation during Imitation > Observation correlates positively (red yellow) with offers to low SES in the Dictator Game and (b**)** areas where activation during Imitation > Observation correlates negatively (blue dark blue) with subjects' offers to high SES profiles in the Dictator Game (cluster corrected at z threshold > 2.3, $P < 0.05$). Heat maps reflect z scores. Slices are displayed in radiological orientation. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

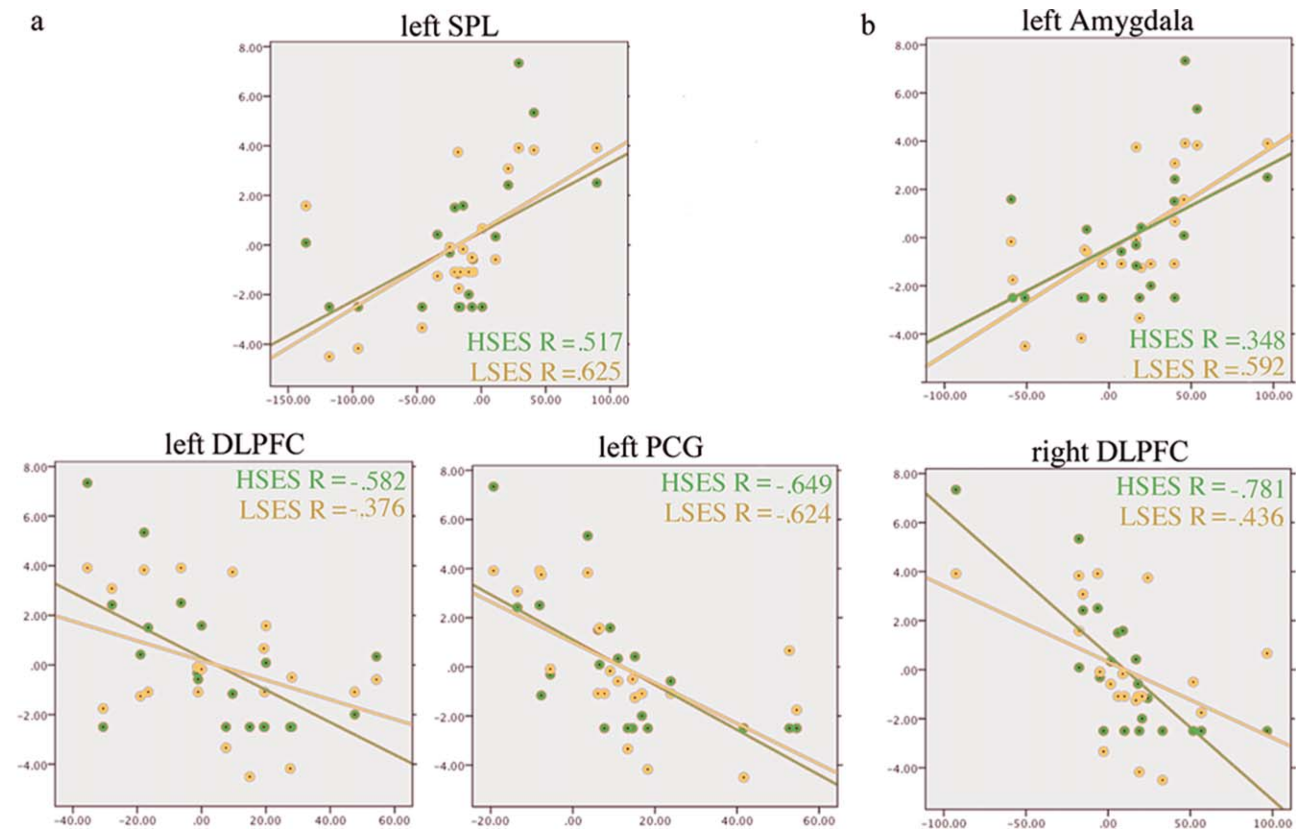

Figure 4.

Descriptive plots of correlations between DG offers and beta estimates in PPI ROI's. Areas of high correlations between demeaned DG offers (y axis, in dollars) to low (yellow) and high (green) SES players and parameter estimates (x axis) in peak voxels for the task (contrast) (**a**) NT(Pain > Hand) and (**b**) EOI (Imitate > Observe). Abbreviations and MNI voxel coordinates are as follows: SPL = superior parietal lobe (x = 55, y = 39, z = 69); left amygdala (x = 57, y = 58, z = 28); left (x = 45, y = 68, z = 51), and right (x = 25, y = 75, z = 55) DLPFC/dorsolateral prefrontal cortex; left PCG/precentral gyrus (x = 63, y = 67, z = 49). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

bilateral pallidum, bilateral post central gyrus, medial parietal lobe, SPL, and the cerebellum) (Fig. 5d).

Crucially, task-related increases in connectivity (PPI) in regions implicated in SR (left amygdala) were negatively correlated with overall offers for the contrast Imitate > Observe, i.e. higher increases in connectivity resulted in less offers. We found a negative correlation between overall DG offers and PPI between left amygdala (Fig. 6a) and bilateral ACC (Fig. 6b).

DISCUSSION

The results reported here largely fit our hypotheses:

a. Brain activity during SR-evoking tasks is correlated with DG offers (a proxy for the relative utility of the players' welfare). The sign of the correlation should also reveal the nature of the processes implemented by the implicated areas (positive for SR and negative for top-down control). In other words, subjects who show greater correlates of SR during scanning should also behave more generously, while subjects who show greater inverse correlations should behave less generously, especially to high SES players.

Positive Correlations

Positive correlations between DG offers and brain activity during observation of pain were found in the SPL, somatosensory cortex, posterior insula, and operculum. The SPL is associated with processing aversive stimuli in peripersonal space [Lloyd and Roberts, 2006] and the somatic perception of interactions between external objects and one's own body [Naito et al., 2008]. Further, the SPL has been proposed as part of the extended human mirror

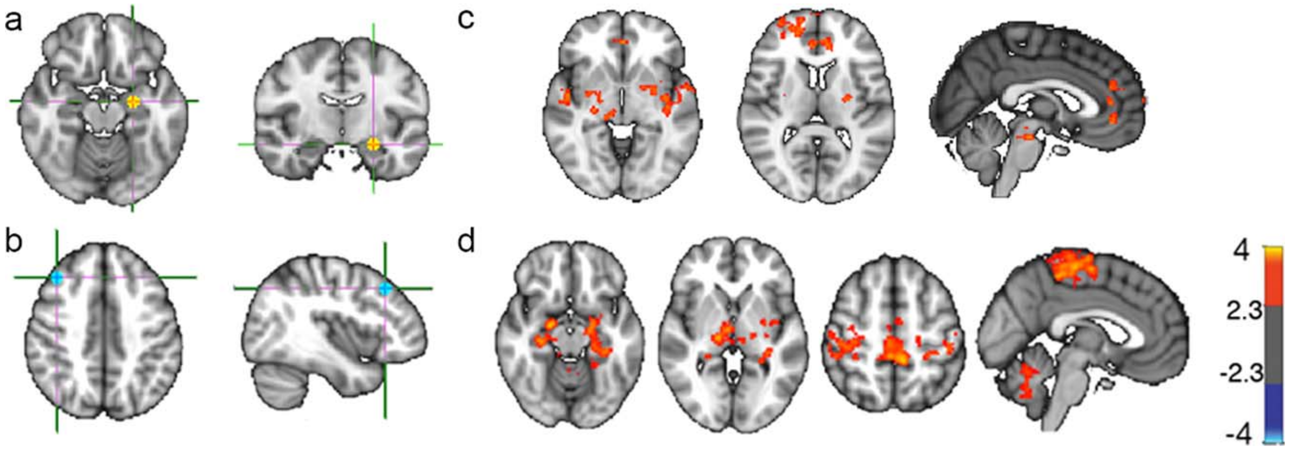

Figure 5.

Areas showing psychophysiological interaction with seed ROIs. (**a**, **b**) Locations of the seed ROI's in (a) left amygdala ($x = 57$, $y = 58$, $z = 28$) and (b) dorsolateral prefrontal cortex ($x = 25$, $y = 75$, $z = 55$). (**c**, **d**) Areas of increased connectivity during Imitation vs. Observation with (c) left amygdala and (d) right dorsolateral prefrontal cortex (cluster corrected at z threshold > 2.3, $P < 0.05$). Heat maps reflect z scores. All coordinates reported in voxels in MNI space. All slices are displayed in radiological orientation. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

neuron system [Molenberghs et al., 2009]. All of these regions have been implicated in the experience of pain [Lamm et al., 2007; Sawamoto et al., 2000; Segerdahl et al., 2015]. Positive correlations between DG offers and brain activity during imitation were found in the amygdala, two regions associated with SR for emotions [Carr et al., 2003; Pfeifer et al., 2008; Volman et al., 2011]. Correlations were also observed with fusiform gyrus, a face processing area whose activation during imitation and observation of emotional facial expressions has been correlated with trait empathy [Pfeifer et al., 2008]. These activations are consistent with proposed neural correlates of SR, i.e., the vicarious activation of similar structures for the perception and experience of internal states and behavior.

A complementary pattern emerges within areas whose activation during NT and EOI is negatively correlated with DG offers.

Inverse Correlations

For the Pain > Hand contrast, we observed negative correlations between DG offers and activation in the left DLPFC, which is directly relevant to the control of pain processing. Indeed, excitatory repetitive TMS to the left DLPFC has been shown to cause analgesia [Brighina et al., 2010]. Also, the DLPFC has been shown to have strong reciprocal connections with the ACC [Cho and Strafella, 2009], an area, i.e. also associated with processing painful stimuli in the self and others [Bufalari et al., 2007; Singer et al., 2006]. Negative correlations were also found between offers and activation in left motor cortex (PCG). Stimulation of motor cortex is effective in treating central and peripheral neuropathic pain, suggesting that it may help regulate the sensory and/or affective aspects of pain [Garcia-Larrea and Peyron, 2007; Khedr et al., 2005; Tsubokawa et al., 1993; Velasco et al., 2009].

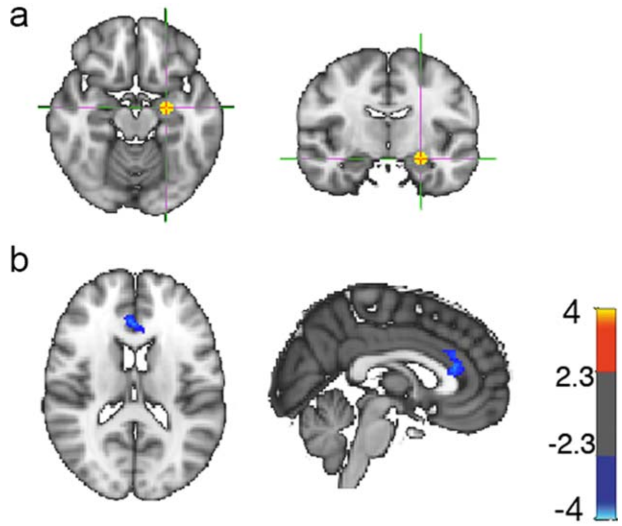

Figure 6.

Correlation between PPI variable and offers in the Dictator Game. (a) Location of the seed ROI in left amygdala ($x = 57$, $y = 58$, $z = 28$). (b) Areas where increased functional connectivity with left amygdala during Imitate > Observe correlates negatively with subjects' overall offers in the Dictator Game (cluster corrected at z threshold > 2.3, $P < 0.05$). Heat maps reflect z scores. All coordinates reported in voxels in MNI space. All slices are displayed in radiological orientation. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE II. Local maxima of correlation between psychophysiological interaction (PPI) term and DG offers

ROI	Correlation	Variable	Area	Coordinates (mm) *x*	*y*	*z*	*Z*	Consistent with theory
L Amygdala	Negative	Overall offers	L Anterior cingulate cortex	−2	28	26	3	+
			R Anterior cingulate cortex	4	34	14	3.28	+

Right-most column indicates whether finding is consistent (+) or inconsistent (−) with our hypotheses.

An analogous set of areas showed inverse correlations between activation during EOI and DG offers: The TPJ is associated with implicit control of imitation [Spengler et al., 2010]. In addition, the right DLPFC has been implicated as an executive control system during decision-making, particularly in the control of prepotent emotional reactions and the incorporation of moral rules into decision-making [Knoch et al., 2006; Tassy et al., 2012; Volman et al., 2011].

b. There are functional interactions between regions associated with SR and top-down control during the tasks and the strength of interaction will be correlated with subjects' offers.

Areas showing direct correlations with DG offers (indexing SR) and areas showing inverse correlations with DG offers (indexing top-down control), were functionally correlated (Table II). In addition, we found that increased functional connectivity between left amygdala and ACC was negatively correlated with DG offers (see Figs. (5 and 6), and Table II).

Interpretational Limitations

While we cannot be certain what neural processes were active during the Dictator Game without direct fMRI evidence (which we did not collect to preserve subjects' anonymity and lack of supervision), activation and connectivity of brain areas active in the SR task was correlated with multiple aspects of prosocial decisions in the DG, suggesting an intricate relationship between the two. This leaves us with two possibilities:

a. Brain networks active during the SR tasks and associated control systems are also employed when making conscious decisions about the welfare of others. Individual differences in the way they interact are consistent across different task demands.
b. There are intervening variables responsible for the correlation, such as subjects' engagement in the tasks, as opposed to an actual employment of these networks during the DG. Neural activity during SR in this context is hence informative but some other factor other than SR drives prosocial decisions in the DG.

Let us explore (b). One could postulate that increased attention during the NR tasks might result in increased vicarious affective and somatosensory processing, though it is unclear why this would result in decreased engagement of areas involved in top-down control. Next, it is unclear why *increased* attention to the dictator game would result in higher overall offers. One could theorize that increased attention to the Dictator Game results in increased perspective-taking, which could explain increased offers, though it is unclear why this would increase offers towards subjects of high SES (low need). In fact, there is data to suggest the very opposite: a 2014 study by Schulz et al. found that subjects with high cognitive load (intended to *disrupt* high-level cognitive processes) tended to behave *more* generously in the Dictator Game. Hence, making this assumption leaves us with a missing variable, some factor correlated with attention that would drive prosocial inclinations other than SR. This explanation is not entirely implausible, but it does lack parsimony.

As such, we favor (a), for a number of reasons. First, subjects were given ample time (5 s) in which to make their offers and showed evidence of having evaluated socioeconomic information about the player in their decisions, making it unlikely that their offers were based simply on quick, reflexive processes like those evoked during the SR tasks. Second, we hypothesized that (a) SR drives prosocial inclinations and that (b) top-down control of SR is *inhibitory* (at least under the conditions explored here) and *that it occurs in response to context*. In the context of the DG, this follows: the condition in which subjects give less money on average (high SES) [Engel, 2011] show the highest effect of inhibitory control, and vice versa. Hence, we would expect that individual differences in neural correlates of SR would dominate variance in offers to low SES, while individual differences in putative neural correlates of top-down control would dominate variance in offers to high SES. The empirical data fit these predictions: for the EOI task at least, activation in SR areas was most strongly correlated with low SES offers, while activation in areas typically associated with control was most strongly correlated with high SES offers. Additionally, we found that areas showing negative correlations with offers are also implicated in executive control. Third, affective processing and its regulation have already been implicated in decision-making, particularly when subjects are aware that other people are involved [Camerer, 2003; Hewig et al., 2011; Van 't Wout et al., 2006]. Last, one could argue that the presence of neutral faces in the DG might somewhat trigger SR, thus biasing behavioral results. Indeed, biological stimuli as sparse as a photograph have been found to increase charitable donations [Genevsky et al., 2013]. However, correlations have also been found between SR for pain and charitable donations [Ma et al., 2011] towards anonymous third persons. This suggests that while biological cues may bias us towards SR and enhance prosocial inclinations, they may not be strictly necessary for the engagement of SR processes.

Activation/offer correlations in some areas were not immediately consistent with our hypotheses, such as extrastriate visual cortex. However, there were none that invalidated it—positive correlations were not found in any area typically associated with top-down control (such as the DLPFC, DMPFC, or TPJ), nor were negative correlations found in areas typically associated with SR (such as the amygdala or somatosensory cortex). One area, the parahippocampal gyrus (PHG), showed both positive correlations with overall DG offers and negative correlations with DG offers to high SES players, though the two clusters were in different sides of the brain (see Table I). Further studies are necessary to clarify whether there are laterality effects on PHG that could explain these results.

As mentioned in "Connectivity in Results", gPPI analyses of SPL, PCG, and left DLPFC for NT data did not yield any significant results. This may be an issue of statistical power: PPI analyses examine significant changes in correlations between conditions of interest, over and above those accounted for by co-activation, thus requiring robust results to reach significance [Friston, 2011]. While the EOI and NT are of equivalent durations and TR values, the NT has three conditions compared to the EOI's two, resulting in roughly 2/3 as many data points per condition.

CONCLUSIONS

As predicted, we found that subjects who displayed greater neural markers of SR tended to behave more generously, while subjects who displayed greater inverse brain–behavior correlations tended to behave less generously. Additionally, we found that for the EOI, task-related increases in *functional connectivity* between areas associated with vicarious affect and its control were negatively correlated with subjects' costly sharing.

How would neural processes implicated during SR be involved in prosocial decision-making under conditions with impoverished SR cues (a neutral face)? We suggest that areas associated with SR and its control are employed in different capacities in different contexts: during the SR tasks we use here, somatosensory and limbic systems are vicariously activated, feeding information in a bottom-up fashion and receiving top-down, albeit implicit, modulation. During prosocial decision-making, such as in the Dictator Game, similar activity is implicitly triggered when subjects are thinking about the people represented by the player profiles, thus modulating the perceived utility of their welfare. But why would thinking about the people represented by the player profiles trigger activity associated with SR and its control? We favor the possibility that thinking about people is grounded on the perceptual and motor experiences we have when interacting with people, as suggested by the framework of embodied cognition [Barsalou, 2008; Gallese and Lakoff, 2005].

These findings have implications for neuropsychological theory and mental health. While it is intuitive to think of psychological processes as discrete and separate, it is much harder to think of neural systems in the same way. Indeed, neural systems tend to operate much more like connected clusters in a network than separate entities [Mcintosh, 2000]. Many studies have reported concurrent activation of and connectivity between areas associated with SR and top-down control, such as during reciprocal imitation [Sperduti et al., 2014], tests of empathic accuracy [Zaki and Ochsner, 2012], and comprehension of others' emotions [Spunt and Lieberman, 2012]. In cognitive neuroscience the dominant tendency is to theorize about psychological processes and then investigate the neural correlates of such processes. Perhaps it may be more useful to investigate how psychological processes emerge from brain organization [Fox and Friston, 2012].

With regard to mental health, there is wide consensus that empathy is a fundamental construct for mental health, and yet there is little consensus on how to operationalize such a complex construct [Hasler, 2012]. Having metrics that are stable across task demands and predictive of behavior is of great importance for the future of psychiatric research. This study provides a relatively tractable approach to this problem. It also suggests a potential avenue for interventions on deficits and abnormalities in different behavioral and cognitive components of empathy. Perhaps using interventions targeting the interaction between SR and its cognitive control, an approach which has been implemented successfully to enhance social cognition in autism spectrum disorder (ASD) [Ingersoll, 2012] and schizophrenia [Mazza et al., 2012], we can better understand how these processes can positively influence overall social cognition and mental health.

ACKNOWLEDGMENTS

We wish to thank Scott Huettel for his help in designing the modified Dictator Game used here, and for his generous feedback on the experimental design and final manuscript. For generous support the authors also wish to thank The Staglin Center for Cognitive Neuroscience, the Brain Mapping Medical Research Organization, Brain Mapping Support Foundation, Pierson-Lovelace Foundation, The Ahmanson Foundation, William M. and Linda R. Dietel Philanthropic Fund at the Northern Piedmont Community Foundation, Tamkin Foundation, Jennifer Jones-Simon Foundation, Capital Group Companies Charitable Foundation, Robson Family and Northstar Fund.

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