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Organization of intrinsic functional brain connectivity predicts decisions to reciprocate social behavior

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HIGHLIGHTS

- Functional connectivity predicted 20% of the variance in reciprocity behavior.
- rs fMRI, moral development and age explained 49% of reciprocity behavior variance.
- Brain imaging may be valuable to refine models of human behavior.

GRAPHICAL ABSTRACT
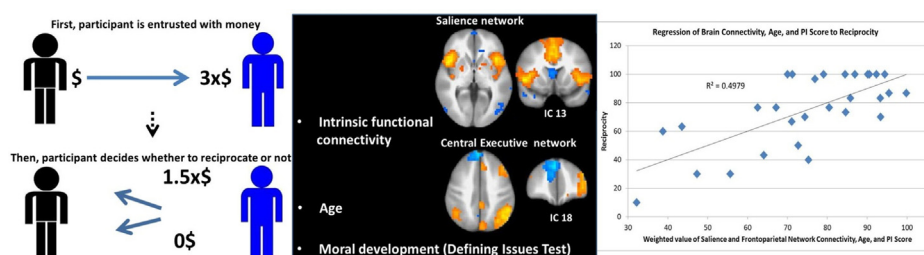
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ABSTRACT

Reciprocation of trust exchanges is central to the development of interpersonal relationships and societal well-being. Understanding how humans make pro-social and self-centered decisions in dyadic inter-actions and how to predict these choices has been an area of great interest in social neuroscience. A functional magnetic resonance imaging (fMRI) based technology with potential clinical application is the study of resting state brain connectivity. We tested if resting state connectivity may predict choice behavior in a social context. Twenty-nine healthy adults underwent resting state fMRI before performing the Trust Game, a two person monetary exchange game. We assessed the ability of patterns of resting-state functional brain organization, demographic characteristics and a measure of moral development, the Defining Issues Test (DIT-2), to predict individuals' decisions to reciprocate money during the Trust Game. Subjects reciprocated in 74.9% of the trials. Independent component analysis identified canonical resting-state networks. Increased functional connectivity between the salience (bilateral insula/anterior cingulate) and central executive (dorsolateral prefrontal cortex/ posterior parietal cortex) networks significantly predicted the choice to reciprocate pro-social behavior ($R^2 = 0.20$, $p = 0.015$). Stepwise linear regression analysis showed that functional connectivity between these two networks ($p = 0.002$), age ($p = 0.007$) and DIT-2 personal interest schema score ($p = 0.032$) significantly predicted reciprocity behavior ($R^2 = 0.498$, $p = 0.001$). Intrinsic functional connectivity between neural networks in conjunction with other individual characteristics may be a valuable tool for predicting performance during social inter-actions. Future replication and temporal extension of these findings may bolster the understanding of decision making in clinical, financial and marketing settings.

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1. Introduction

Reciprocity, defined as responding to a positive action with another positive action, is the basis for interpersonal bonds that define a society and an integral part of traditional virtues in many cultures. Human subjects have been shown to engage in reciprocity and other prosocial behaviors even at their own expense. A challenge in everyday life is to figure out in whom you can place your trust. Decisions about whom to trust are motivated by the evaluation of stable facial traits [1], similarity to kin [2], and perceived trustworthiness [3]. The brain mechanisms that underlie social decision making are less well known and have implications for diverse fields of human behavior including healthcare, economics, politics and even the legal system.

The combination of monetary exchange paradigms and neuroimaging approaches has elucidated individual differences in the cognitive and neural mechanisms underlying interactive social behaviors such as cooperation [4], trust [5], and betrayal [6]. Most of the inferences from these studies are based on behaviors elicited by tasks in which individuals engage in dyadic interactions while undergoing functional magnetic resonance imaging (fMRI). However, brain imaging has been a sought after tool for predicting human behavior, particularly at the individual level. Resting-state fMRI (rs-fMRI) is an increasingly used approach which measures the intrinsic connectivity between functional brain networks in resting, awake individuals who are not engaged in overt tasks [7]. Because resting-state does not require a task (and thus avoids the confound of study-specific task properties), rs-fMRI has been increasingly used to investigate the relationship between the functional organization of neural networks and behavior [8].

Intrinsic functional brain connectivity is proposed to represent the product of individual inner life experience. The default mode (DMN), central executive (CEN), salience (SAL) and frontolimbic (LIM) networks have been associated with different cognitive and behavioral correlates. In the present study, we sought to test the value of rs-fMRI, in conjunction with behavioral measures to predict individual differences in human social behavior. We hypothesized that specific patterns of intrinsic connectivity between these discrete neural networks (DMN, CEN, SAL and LIM) can predict reciprocity behavior.

2. Materials and Methods

We recruited 30 healthy participants, 12 men and 18 women of diverse racial and ethnic backgrounds. Twenty-four participants were full-time students, five were employed and one participant was unemployed. One participant was excluded due to technical error (functional data was misnormalized to anatomic and could not be corrected). Inclusion criteria were: (a) age 18–30, (b) no neurological or psychiatric history, (c) ability to write and speak English, and (d) ability to provide written informed consent. Exclusion criteria were: (a) active substance use disorders, other than tobacco, by self-report; (b) ferromagnetic implants, and (c) history of claustrophobia. Following written informed consent, participants were assessed for personality trait composition using the NEO Five-Factor Inventory (NEO-FFI), moral reasoning development with the Defining Issues Test-2 (DIT-2), dysfunctional attitudes for depression (DAS), and trait impulsivity with the Barratt Impulsiveness Scale-11 (BIS-11). Lastly, participants underwent functional magnetic resonance imagining (fMRI) scanning during resting state and while playing the trustee role in the Trust Game (reported elsewhere). Participants were compensated between $20 and $100, depending on their choices within the Trust Game. All research procedures were approved by the Institutional Review Board of the University of Miami, and took place on the same day.
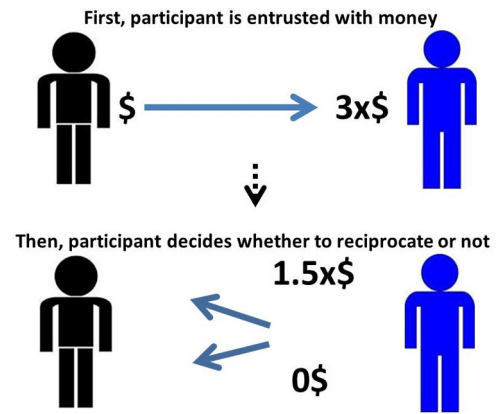
Fig. 1. Trust game. In each of the 30 single rounds the participant played the role of trustee (blue) who received a variable amount of money from the investor (3X) and needed to decide whether to give back some (1.5X) or nothing.

The Defining Issues Test (DIT-2) activates and assesses moral schemas in terms of importance judgments. Based on Kohlberg's theory of moral development, the subjects' task is to read a moral dilemma, and rate and rank corresponding statements in terms of their moral importance. Measures for the following schema are obtained: (a) Personal Interests (PI), focuses on a self-centered utilitarian approach; (b) Maintaining Norms (MN), emphasizes behavior driven by rules; and (c) Postconventional (PC), in which laws are not simply blindly accepted, but are scrutinized in order to ensure society-wide benefit [9]. Completed DIT-2 assessments were scored at the Center for Ethical Development [9].

We used a modified version of the Trust Game in which the participant plays the role of the trustee and decides whether or not to reciprocate the first player's trust. Participants played 30 rounds of the Trust game, each with a different anonymous individual [10]. Participants were informed that they would play the Trust Game with other people who have already played the game whose responses (offers) had been recorded and would be paired with those of the participants themselves. This was to convey to the participants that the investment amounts had been actually proposed by real players, so participants believe they were exposed to realistic offers. The participant (trustee) and the other anonymous individual (investor) were endowed with an initial amount of money, a portion of which ($X) the investor sent to the participant. Next, the participant received three times what the investor sent ($3X), and was asked to choose how much money he/she wanted to give back to the investor, either $1.5X or $0. In our study, reciprocity was operationally measured by the number of times participants gave money back (expressed as a percentage of the total 30 rounds). See Fig. 1.

MRI acquisition: Participants underwent neuroimaging using a Siemens 3T Trio MRI scanner at the University of Miami Applebaum MRI Center. The MRI scan session was as follows: a magnetization-prepared rapid gradient-echo (MPRAGE) T1 anatomic scan (5 min), a resting-state EPI fMRI scan (rs-fMRI, 5 min), an echo-planar imaging (EPI) fMRI scan during the Trust game (15 min). The MPRAGE scan had the following parameters: matrix = 248×256, 220 sagittal slices, TR/TE/FA = 2300 ms/3.08 ms/9°, final resolution=$0.86 \times 0.86 \times 1.20$ mm^3 resolution. Rs-fMRI was conducted with the following parameters: TR/TE/FA = 2000 ms/30ms/90°, FOV = 220×220 mm, matrix=64×64, 25 axial slices (acquired parallel to the AC-PC line with interleaved slice acquisition), slice thickness = 5 mm, final resolution $3.44 \times 3.44 \times 5.00$ mm^3, 150 images.

fMRI preprocessing: Image processing and analysis was conducted with AFNI, and Matlab (The MathWorks, Inc.). Functional

images underwent slice timing correction, deobliquing, motion-correction by registration to the tenth image acquired for each run using a 6-parameter transformation, spatial normalization to the Montreal Neurological Institute (MNI) template via 12-parameter affine transformation followed by nonlinear warping using basis functions, regression of nuisance signals (i.e., mean timecourses of voxels in cerebrospinal fluid and white matter), spatial smoothing with a Gaussian kernel (5 mm FWHM) to enhance signal-to-noise ratios and enable group comparisons, quadratic detrending, scaling to percent signal change, and bandpass filtering (0.01–0.10 Hz) to remove physiological noise.

2.1. Resting state ICA

After preprocessing, group-level ICA of functional image data sets was conducted using Matlab and the Group ICA of fMRI Toolbox (GIFT v1.3; http://mialab.mrn.org/software/), an approach for blind-source separation of a complex mixture of signals and noise into spatially and temporally distinct sources (components). ICA was run using Infomax algorithm to solve for 20 components. The following options were used: back-reconstruction using GICA3, subject-specific principal component analysis using expectation maximization and stacked datasets, full storage of covariance matrix to double precision, usage of selective eigenvariate solvers, two-step data reduction with 40 principal components in the first step, and scaling to z-scores. ICA was repeated 20 times using the ICASSO algorithm to identify the most reliable and stable components across all iterations. The ICASSO stability indices (all $i_Q > 0.95$) indicated a reliable solution using 20 components.

2.2. Regression analysis

The relationship between behavior and network' intrinsic functional connectivity was assessed in two steps. To reduce Type I error, we compared our networks against previously published resting-state networks to constrain our analyses to the networks with strongest replication in the literature [7]. Mean activity timecourses were extracted for these components for the rs-fMRI task. Correlation matrices of these timecourses were calculated for each subject and z-transformed to approach linearity. Linear regression then tested if resting-state connectivity between these components predicted reciprocity behavior. The resting-state correlation for each network pair was regressed against level of reciprocity; network pairs whose connectivity significantly predicted reciprocity behavior ($p < 0.05$) were then entered into a stepwise linear regression with variables age, PI, MN and PC DIT-2 scores. We report network pairs that predicted pro-social behavior in conjunction with these other variables ($p < 0.05$, Bonferroni corrected). In order to test the specificity of our findings, functional connectivity between the CEN and SAL networks was included as independent variable in separate linear regressions with impulsivity, dysfunctional attitudes, as well as neuroticism, extraversion, openness, agreeableness and conscientiousness (measured by the NEO-FFI) as dependent variables.

3. Results

The twenty nine participants included in the fMRI analysis exhibited reciprocity (Gave money back) $74.9 \pm 25.4\%$ of the time with an average amount of 598 ± 45 out of a total of $832. Nine (31%) individuals reciprocated Gives in every trial. Table 1 shows the demographics, trait impulsiveness and moral development characteristics of the participants included in the imaging analysis.

Table 1
Descriptive demographics, functional level, individual traits and trust game performance of subjects included in imaging analysis.

Demographic variables	
N	29
Age	$25.1 \pm .3$
Gender (Female/Male)	18/11
Race (African American/Caucasian/Hispanic)	4/16/9
Education (years)	16.8 ± 1.8
Handedness (R/L)	29/0
Occupation (student/work/unemployed)	19/9/1
Quantitative assessments	
Neuroticism (NEO-FFI)	19.3 ± 9.4
Extraversion (NEO-FFI)	31.3 ± 5.9
Impulsiveness (BIS-11)	60.1 ± 11.0
Dysfunctional attitudes scale (DAS)	113.2 ± 22.0
Defining issues test	
Personal interest (Stage 2/3)	24.8 ± 12.5
Maintain norms (Stage 4)	28.2 ± 14.2
Post-conventional	42.2 ± 17.6
N2 index score	39.4 ± 16.4
Trust game performance	
Reciprocity	74.9 ± 25.4

$x \pm$ s.d.
NEO-FFI: NEO five-factor inventory; BIS-11: barratt impulsiveness scale-11.

3.1. Independent component analysis (ICA)

The 10 ICA components correspond to well-documented resting-state functional networks which can be grouped into 6 cognitions / modalities (Table 2 and Fig. 1) [7]. The LIM was represented by component 4. The DMN was denoted by components 12 and 14. A CEN was reflected in activity in components 17 and 18. The SAL was represented by component 13. An occipital network (OCC) comprised by components 3, 5 and 6. Lastly, a sensorimotor network (SOM) was represented by component 15 (see Fig. 1).

3.2. Regression analysis

Stepwise linear regression demonstrated that functional connectivity between the right CEN and SAL significantly and positively predicted reciprocity behavior. Connectivity between right CEN and SAL was the first variable automatically entered into the stepwise regression, and thus singly explained the greatest (20%) variance ($F(1,28) = 6.75$, $p = .015$, $r = -.447$). At step 2, age was added into the stepwise regression; age and right CEN-SAL functional connectivity explained 39.5% of variance in reciprocity behavior ($F(1,28) = 8.27$, $p = .0015$, $r = .628$). PI score was the third variable entered into the stepwise regression, resulting in a combined model that explained 49.8% of variance in reciprocity behavior ($F(1,28) = 8.48$, $p = .0005$, $r = .706$). This model remained significant after Bonferroni correction for 45 correlational pairs (corrected $p < 0.022$). See Fig. 2G. The regressions between CEN – SAL functional connectivity with impulsivity, dysfunctional attitudes, neuroticism, extraversion, openness, agreeableness and conscientiousness showed non-significant results (all F's <4).

4. Discussion

Our main finding was that functional connectivity between salience and right frontoparietal networks predicted 20% of the variance in the decision whether to reciprocate a monetary gift in healthy subjects. When age and moral development were considered in the model, approximately 50% of the variance could be explained.

Table 2
Neural activity within components identified through independent component analysis during resting state in healthy volunteers.

| Region (Brodmann's area)	Peak voxel	t Score	Peak voxel MNI coordinates		
			x	y	z
Occipital network					
Component 5					
Lingual gyrus (r 17)	1436	16.3	3	-91	−11
Culmen (r 19)	282	−9.6	7	−52	-9
Component 6					
Insula (r 13)	1868	17.34	7	-67	5
Component 3					
Middle occipital gyrus (r 19)	1153	17.11	24	-92	8
Middle occipital gyrus (l 19)	896	14.02	−45	−74	−15
Salience network					
Component 13					
Anterior cingulate cortex (r 8)	1769	17.17	3	24	44
Middle temporal gyrus (r 39)	609	−10.84	48	−76	28
Insula (l 13)	536	18.04	-41	14	2
Insula (r 13)	388	17.11	41	18	2
Central executive network					
Component 17					
Dorsolateral prefrontal cortex (l 17)	995	15.7	−48	35	26
Precuneus (r 7)	726	−10.57	7	−58	36
Precuneus (l 19)	520	15.21	−38	−76	38
Superior temporal gyrus (r 19)	387	−10.80	53	−58	24
Cerebellum (l)	304	−9.92	−3	−69	−23
Component 18					
Dorsolateral prefrontal cortex (r 9)	614	13.20	45	30	36
Frontal pole (l 8)	560	−14.29	-3	52	45
Inferior parietal lobule (r 39)	451	13.5	41	−62	39
Middle frontal gyrus (l 47)	405	−11.77	-38	32	−1
Inferior parietal lobule (r 40)	401	−11.99	−48	−58	18
Default mode network					
Component 12					
Anterior cingulate cortex (l 32)	1816	19.81	-7	43	3
Superior temporal gyrus (r 22)	263	−10.11	56	−53	14
Component 14					
Posterior cingulate cortex (r 23)	1449	26.16	3	-47	25
Middle temporal gyrus (l 39)	281	13.68	−48	−61	21
Limbic network					
Component 4					
Parahippocampal gyrus (r 34)	178	17.20	14	1	−14
Sensorimotor network					
Component 15					
Medial frontal gyrus (l 6)	2184	18.95	0	-27	56
Inferior temporal gyrus (r 37)	810	−13.05	53	−56	−9
Inferior frontal gyrus (r 9)	413	−11.45	48	6	32
Inferior frontal gyrus (l 45)	367	−9.54	−53	13	25

4.1. Description of networks

The measure of intrinsic functional connectivity by signal fluctuations in rs-fMRI data is a surrogate for organized intrinsic brain activity [7]. Brain networks show strong spatial correspondence in independent analyses of resting-state and task-related activity patterns [7], suggesting that certain intrinsically coupled functional networks are also systematically engaged during cognition and behavior. Moreover, different functional repertoires can be generated by a given structural network [11,12].

The 10 ICA components generated during resting state condition (DMN, CEN, SAL, LIM, OCC and SOM networks) are consistent with previous reports of resting state neural network functional organization in healthy adults [7,13]. The DMN comprises an integrated system for self-related cognitive activity including autobiographical, self-monitoring and social cognitive functions [14]. Brain regions associated with the DMN include medial prefrontal cortex

(mPFC), medial temporal lobe, precuneus, posterior cingulate cortex, and temporoparietal junction. The DMN shows considerable overlap with two other known neural networks: a frontocingulate network involved in moral reasoning [12,15,16] and a parietocingulate network involved in theory of mind (ToM) [14]. Represented by the dorsolateral prefrontal cortex (DLPFC) and posterior parietal cortex, the CEN is theorized to process multiple demands, allowing to divide complex tasks into focused parts and to mediate the balance between externally and internally driven mental activity [17]. The SAL network, represented by the anterior insula, anterior cingulate cortex (ACC) and subcortical areas, including the amygdala, substantia nigra, ventral tegmental area and thalamus, is involved in orientation of attention to the most homeostatically relevant (salient) of ongoing stimuli [18].

Even though CEN and SAL networks are spatially independent, restricted anatomic overlap and functional correlation between these networks have been reported during resting state conditions
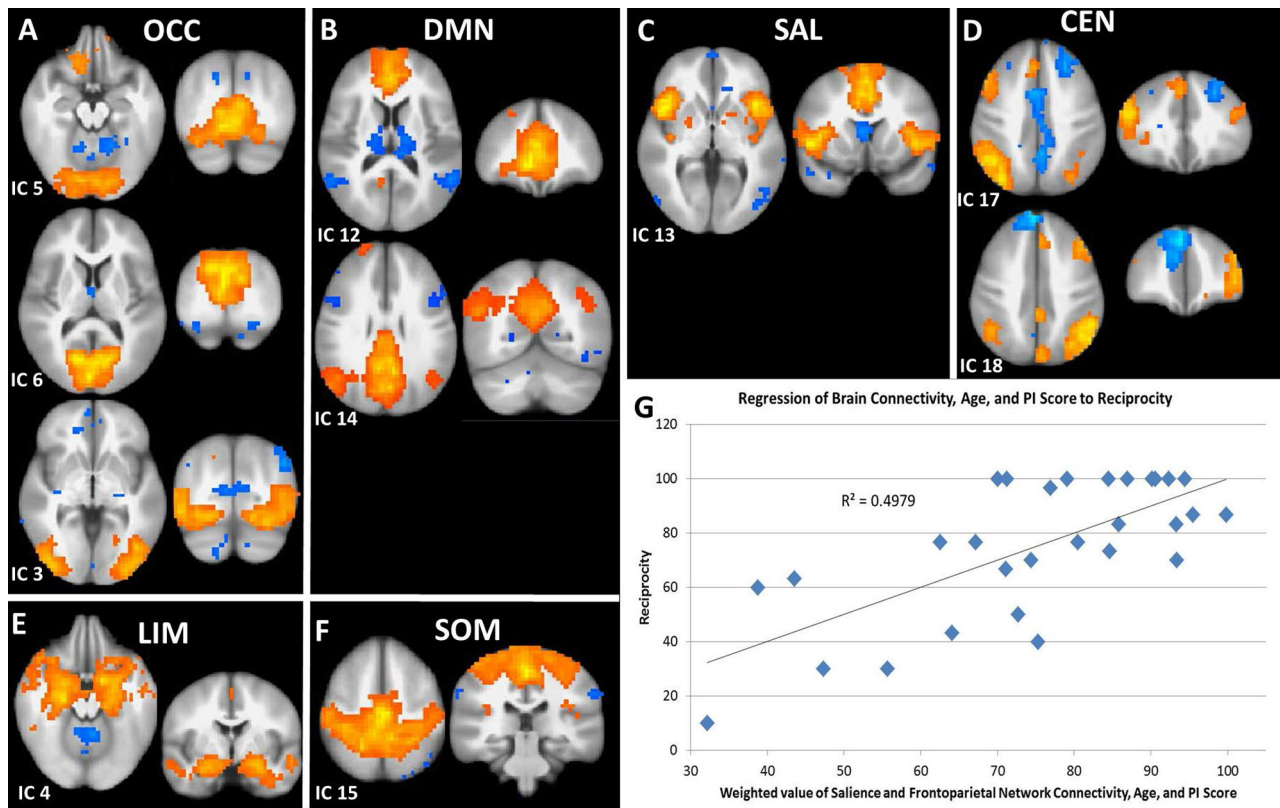
Fig. 2. Brain networks identified with Independent Component Analysis (ICA) during resting state in healthy subjects that subsequently played the Trust Game. (A), occipital network (OCC); (B) default mode network (DMN); (C) salience network (SAL); (D) central executive network; (E) limbic system network (LIM), (F) sensorimotor network (SOM), and (G) Step-wise linear regression between functional connectivity between SAL (IC 13) and right CEN (IC 18) networks, age and personal interest (PI) score with reciprocity behavior. IC (independent component).

[18]. It is noteworthy that weaker SAL connectivity was observed in participants who fail to display prosocial behavior during a novel virtual reality task [19]. Moreover, DLPFC is associated with altruistic behavior following compassion training [20]. Furthermore, inverse effective connectivity between right DLPFC and left insula has been reported while reading about victimized people that were responsible for their misfortunes [21]. It would be reasonable to speculate SAL engagement in response to perceived danger with a resultant behavioral outcome of focus on the self and self-preservation to the detriment of others. Therefore, the observed relationship between CEN and SAL connectivity and reciprocity converges upon a network which task-based studies suggest is involved in risk assessment.

4.2. Effect of moral development on reciprocity behavior

Overall, the range of moral development scores in our sample is comparable to those found in college students and the general population [9]. The correlation of reciprocity behavior with moral development supports the ecological validity of observed variation in behavior related to the Trust Game employed in this experiment. The lack of a correlation between CEN-SAL functional connectivity with other measures as impulsivity, personality traits or dysfunctional attitudes for depression support the case that our findings are specific to reciprocity behavior.

4.3. Practical application

fMRI has been used to identify neural signatures that predict behavior in economics, marketing and legal transactions. For instance, Demos et al. predicted weight variation and sexual behav-

ior based on nucleus accumbens response during exposure to appetitive cues six months previously [22]. Neural activity in the mPFC during persuasive messages predicted 23% of the variance in sunscreen use in the subsequent week, beyond the variance predicted by self-reported attitudes and intentions [23]. Error-related ACC activity during a go/no-go task prospectively predicted subsequent re-arrest among adult offenders within 4 years of release [24]. Moreover, Smith el al. using a data-driven approach were able to predict subjects' choice of snack based on fMRI data acquired during the contemplation phase 68% of the time [25]. The novel element of this study is the ability to predict individual behavior using a combination of a data-driven fMRI task-free approach such as rs-fMRI, age and individual moral development within the timeframe of minutes between the rs-fMRI scan and the predicted behavior.

4.4. Limitations

Even though we used a popular behavioral economic tool, it remains a simplified model of human social interaction. We did not record the income of participants, which is known to influence charitable contributions. We also did not measure biomarkers such as oxytocin or sexual hormones levels known to modulate prosocial behavior. It also remains unknown as to whether the observed patterns of intrinsic functional connectivity predict long-term social reciprocity. Lastly, given the limited sample size we were not able to stratify by sex.

5. Conclusions

Resting state functional connectivity between the right CEN and SAL neural processing networks in conjunction with other individ-

ual characteristics may be a valuable tool to predict performance in social interactions. The use of rs-fMRI, moral development and age of the individual was able to explain 49% of the variance in reciprocated behavior. The further incorporation of other markers related to brain imaging, and cognitive and personality variables holds promise to refine more accurate models of human social behavior tendencies. Further replication and temporal extension of these findings may be valuable in clinical, financial and marketing arenas.

Acknowledgment

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