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Functional connectivity of specific resting-state networks predicts trust and reciprocity in the trust game

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Abstract
Economic games are used to elicit a social, conflictual situation in which people have to make decisions weighing self-related and collective interests. Combining these games with task-based fMRI has been shown to be successful in investigating the neural underpinnings of cooperative behaviors. However, it remains elusive to which extent resting-state functional connectivity (RSFC) represents an individual's propensity to prosocial behaviors in the context of economic games. Here, we investigated whether task-free RSFC predicts individual differences in the propensity to trust and reciprocate in a one-round trust game (TG) employing a prediction-analytics framework. Our results demonstrated that individual differences in the propensity to trust and reciprocity could be predicted by individual differences in the RSFC. Different subnetworks of the default-mode network associated with mentalizing exclusively predicted trust and reciprocity. Moreover, reciprocity was further predicted by the frontoparietal and cingulo-opercular networks associated with cognitive control and saliency, respectively. Our results contribute to a better understanding of how complex social behaviors are enrooted in large-scale intrinsic brain dynamics, which may represent neuromarkers for impairment of prosocial behavior in mental health disorders.

Keywords Trust · Reciprocity · Trust game · Multivariate regression analysis · Machine learning · Resting-state functional connectivity

Introduction

Cooperation is an essential social human behavior implying costs and benefits to the cooperators. Economic games, such as the trust game (TG), can reproduce social dilemmas in which a counterpart's immediate self-interest is tempting, but all counterparts benefit from acting in the long-term collective interest (G. Emonds, Declerck, Boone, Vandervliet, & Parizel, 2012). In the TG, an investor decides to share (trust) or keep (distrust) an initial monetary endowment. If money is shared, the trustee receives the (generally) tripled amount of it and decides whether to return some money (reciprocity) or keep the whole sum (betrayal). Both investors and trustees face an inherent social dilemma that needs to be resolved for successful cooperation (Berg, Dickhaut, & McCabe, 1995; Camerer, 2003).

On the one hand, investors will be better off if they trust and their partner reciprocates. However, if the partner betrays them, they should prefer distrusting. This dilemma can be resolved by evaluating the partner's trustworthiness, which implies making inferences on their intentions (Burnham, McCabe, & Smith, 2000; A. K. J. Fett, Gromann,

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Giampietro, Shergill, & Krabbendam, 2014a; Krueger et al., 2007; McCabe, Rigdon, & Smith, 2003). Cooperation is initiated when the other is recognized to have good intentions or a good character (Acevedo & Krueger, 2005; Declerck, Boone, & Emonds, 2013; McCabe et al., 2003; Simpson, 2007). When knowledge about the partner is missing, decisions about their cooperation can be based on prior information (Aimone & Houser, 2012; Burnham et al., 2000) or accepted social norms enabling reliable estimations of the other's most likely behavior (Bicchieri, 2005; Falk, Fehr, & Fischbacher, 2008; van 't Wout & Sanfey, 2008).

On the other hand, trustees may be motivated to betray, as they would then keep all the money they received. However, a betrayal implies a violation of the reciprocity norm and a breach of cooperation. This dilemma can be resolved by suppressing selfish motives and stressing the advantages of prosocial motives (Loewenstein, Thompson, & Bazerman, 1989; Romano, Balliet, Yamagishi, & Liu, 2017). Indeed, failing to suppress self-serving motives increases the likelihood of non-cooperative behaviors, suggesting the importance of cognitive control mechanisms for cooperation maintenance (Griet Emonds, Declerck, Boone, Vandervliet, & Parizel, 2011; Fett et al., 2014a; Sutterlin, Herbert, Schmitt, Kubler, & Vogele, 2011; W. van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2011).

Overall, cooperative behaviors are shaped by individual differences in prosocial preferences (Romano et al., 2017), which depend on personality traits (Ferguson, Heckman, & Corr, 2011; Ibanez et al., 2016; Zhao & Smillie, 2015) and are reflected by neural activation patterns (W. van den Bos, van Dijk, Westenberg, Rombouts, & Crone, 2009). Recent evidence has shown that resting-state functional connectivity (RSFC) reflects an individual's neural fingerprint, given its stability across fMRI sessions (Finn et al., 2015) and its relation with personality traits, cognitive capacities, and social preferences (Alavash et al., 2017; Başar, 1998; Gordon et al., 2017; Hahn, Notebaert, Anderl, Reicherts, et al., 2015a; Kannurpatti, Rypma, & Biswal, 2012; Rosenberg et al., 2016). Therefore, RSFC as a task-free fMRI approach is an appealing alternative to the task-based fMRI approach for characterizing neurodiversity (Gabrieli, Ghosh, & Whitfield-Gabrieli, 2015). Previous work has been mainly descriptive and only a few studies have used RSFC to predict people's behavior (Rosenberg, Casey, & Holmes, 2018; Woo, Chang, Lindquist, & Wager, 2017).

Functional connectivity networks exhibiting intrinsically consistent co-activations among cortical and subcortical brain regions (Fox et al., 2005; Raichle, 2015) have been shown to relate differently to trust and reciprocity. A multivariate predictive model using electroencephalography (EEG)-based RSFC significantly predicts initial trust toward an unknown trustee in a multi-round TG (Hahn, Notebaert, Anderl, Teckentrup, et al., 2015b). EEG electrodes with the highest contribution to the prediction were located over the temporoparietal junction (TPJ) —an essential hub of the default-mode network (DMN). This finding concurs with previous fMRI studies indicating the involvement of the TPJ in inferences involved in others' intentions (A.-K. J. Fett et al., 2014a; Xiang, Ray, Lohrenz, Dayan, & Montague, 2012) and of the medial prefrontal cortex (PFC) in inferences on the others' personality traits (Derks, Van Scheppingen, Lee, & Krabbendam, 2015; Fouragnan, 2013; Krueger et al., 2007; McCabe et al., 2003; Wunderlich, Rangel, & O'Doherty, 2009).

Similarly, a previous resting-state fMRI study on reciprocity has shown a positive relationship between reciprocal behavior in a one-round TG and RSFC of the frontoparietal network (FPN) (Caceda, James, Gutman, & Kilts, 2015), while modulation of the lateral PFC (an essential hub of the FPN) impacts prosocial and reciprocal behaviors (Knoch, Schneider, Schunk, Hohmann, & Fehr, 2009; Nihonsugi, Ihara, & Haruno, 2015). These results are consistent with the assumption that reciprocity requires suppression of self-related interests to be enacted.

Despite providing first evidence that different RSFC networks contribute to trust and reciprocity, these studies have their limitations. First, source localization using EEG-based RSFC and importance scores of multivariate models is controversial (Haufe et al., 2014; Pascual-Marqui et al., 2011). Second, the univariate analyses employed in the resting-state fMRI study on reciprocity are limited in out-of-sample generalizations and may have missed complex brain-behavior relationships (Bressler & Menon, 2010). Finally, two different game settings were used in those studies: the multi-round TG in the EEG study (in which participants repeatedly played with different players) and the one-round TG in the fMRI study (in which participants made only one, single-trust decision for each player). The different natures of the social interactions reproduced by these two TG versions have been shown to engage different cognitive processes (Bellucci, Chernyak, Goodyear, Eickhoff, & Krueger, 2017; Bellucci, Feng, Camilleri, Eickhoff, & Krueger, 2018). Therefore, the contribution of single RSFC networks in predicting trusting and reciprocal behaviors in the same TG version to date remains elusive.

Here, we combined fMRI-based RSFC with multivariate regression analyses to investigate whether different RSFC networks predict individual differences in the propensity to trust and reciprocate in a one-round TG – an economic game found to reliably induce cooperative behaviors (Peysakhovich, Nowak, & Rand, 2014). We hypothesized, on the one hand, that individual differences in trusting behavior may be predicted by RSFC of the DMN, likely involved in inferences on the partner's trustworthiness to overcome concerns related to the risk of a betrayal. On the other hand, we hypothesized that individual differences in reciprocity may be predicted by RSFC of the FPN, probably engaged in cognitive control to resolve the conflict between selfish motives (implying betrayal of trust) and selfless considerations (leading to reciprocity).

Materials and methods

Subjects

Fifty-two participants participated in the experiment, which consisted of two sessions (a behavioral and an fMRI one). One participant had to be excluded due to technical problems during RS-fMRI data acquisition, leaving a total of 51 participants (31 females) with a mean age of 22.80 years (*SD*=2.86) and mean education of 16.09 years (*SD*=2.25). Participants were recruited from the student community at the Auburn University, Alabama, USA. They were all right-handed and had no history of neurological or psychiatric disorders and as reported on a scale from 1 (low) to 10 (high) were on average from a middle social status (*M*=4.84; *SD*=1.51).

Participants gave written informed consent after a complete description of the study was provided. All the procedures involved were according to the Declaration of Helsinki and approved by the Auburn University Institutional Review Board.

Investment game

Before the scanning session (on average 19.63 days, *SD*=17.26), participants played a one-round TG on the online Qualtrics platform (https://www.qualtrics.com) (Fig. 1). Participants were randomly assigned to play either as investors (n=25) or trustees (n=26). Investors were endowed with $10 and asked to share any of their initial endowments with trustees (i.e., trust decision). Investors were told that their actual decisions would be communicated to their partner who participated in the study during the following days. Trustees were told that they were paired with another participant who previously participated in the study and made an economic decision about sharing any amount of an initial endowment received from the experimenter. Trustees were told that the amount shared by the investor was tripled by the experimenter and asked whether they wanted to share in return any monetary amount of this total amount (i.e., reciprocity decision). Decisions ranged from 0 (sharing nothing) to the total tripled amount received (sharing the entire amount of money). The proportion of money amount sent in trust and reciprocity decisions was used as a predictor variable for prediction analyses with RSFC (Berg et al., 1995).

Finally, participants completed control measures – the interpersonal reactivity index (IRI, a multi-dimensional assessment of perspective taking, fantasy, empathy, and personal distress) (Davis, 1983) and the social value orientation scale (SVO, a measure of prosocial tendencies and behavior) (Murphy, Ackermann, & Handgraaf, 2011) – to rule out differences in any socially relevant abilities between investors and trustees.

Resting-state functional connectivity acquisition and preprocessing

Image acquisition Data were collected with a Siemens MAGNETOM 7 Tesla scanner at the Auburn University MRI Research Center. While acquiring resting-state fMRI data, participants were scanned for 11 min and instructed to close their eyes, hold still, remain awake, and not think about anything systematically. The rs-fMRI scan consisted of 660 contiguous volumes acquired with a multiband EPI sequence (axial slices, 45; slice thickness, 2.0 mm; interslice gap, 0.4 mm; multiband slice acceleration factor, 3; TR, 1,000 ms; TE, 20 ms; flip angle, 70°; voxel size, 2.1 × 2.1 × 2.0 mm^3; FOV, 200 × 200 mm^2). High-resolution structural images were acquired through a 3D sagittal T1-weighted MP-RAGE (sagittal slices, 240; TR, 2020 ms; TE, 2.7 ms; slice thickness, 1.2 mm; voxel size, 1.1 × 1.1 × 1.2 mm^3; flip angle, 7°; inversion time, 1,050 ms; FOV, 215 × 215 mm^2).

Image preprocessing Neuroimaging data analyses were performed on SPM12 (http://www.fil.ion.ucl.ac.uk/spm/software/spm12/) and Artifact Detection Tools (ART, https://www.nitrc.

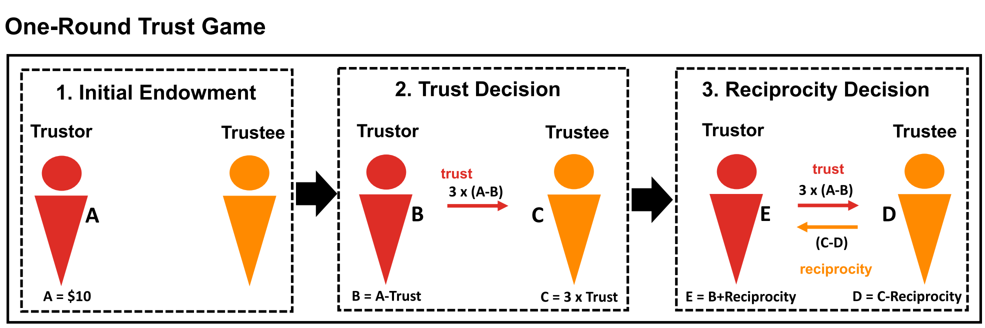

Fig. 1 *The one-round trust game.* Two anonymous players play the role of investor and trustee, and make trust and reciprocity decisions, respectively. With an initial endowment of money (e.g., $10), investors decide whether they want to share any portion of the money with their partners (trust decision) or keep it, thereby ending the exchange (non-trust decision). If the investors decide to share some of their initial endowment, the money is tripled by the experimenter and passed on to the trustees. The trustees then decide whether to share in return any portion of the received amount (reciprocity decision) or to keep this amount (defection decision). Both players are updated about their final payoffs from the transaction after the end of the game

org/projects/artifact_detect/). After discarding the first ten volumes to allow signal equilibrium, the functional images were corrected for field inhomogeneity and slice-timing and then realigned for head movement correction to the mean image. Functional images were co-registered to their structural images, and both functional and anatomical images were subsequently normalized into MNI space using deformation fields derived from anatomical segmentation (resampling voxel size was 2 × 2 × 2 mm^3). After that, functional images were spatially smoothed using a Gaussian filter (4 × 4 × 4 mm^3 full width at half maximum, FWHM) to decrease spatial noise.

In additions, the ART toolbox was employed to detect and reject artifact in the time series of functional images using the following criteria: (1) head displacement in x, y, or z-direction greater than 2 mm from the previous frame; (2) rotational displacement greater than 0.02 radians from the previous frame, or (3) global mean intensity in the image greater than 3 standard deviations from the mean image intensity for the entire resting scan. Those outliers were subsequently included as nuisance regressors within the first-level general linear model. Finally, a band-pass filter (0.01–0.1 Hz) was implemented to remove high-frequency noise and linear drift artifacts.

ROI-to-ROI connectivity RSFC was computed between 142 regions of interest (ROIs; nodes) as defined by Dosenbach's atlas (Dosenbach et al., 2010). This atlas was chosen because it represents an improvement over an anatomical atlas – since functional boundaries do not necessarily match anatomical ones – and is a good trade-off between whole-brain coverage and number of nodes to use as features in the multivariate analysis. The atlas subdivides all 142 (10-mm sphere) ROIs into five pre-defined RSFC networks: cingulo-opercular (CON), sensorimotor (SMN), default-mode (DMN), frontoparietal (FPN), and occipital (OccN) networks. Using the Functional Connectivity (CONN) toolbox (https://www.nitrc.org/projects/conn), RSFC in the form of a bivariate Pearson's correlation between the average BOLD signals of every ROI was computed. To remove potential sources of confounds, regressors of no interest were added in the first-level general linear model, including six head motion parameters (three translations and three rotations along x, y, and z-axes), outliers derived from the ART toolbox, white matter and cerebrospinal fluid signal. The Pearson's correlation coefficients obtained for each ROI-to-ROI connection (edge) were transformed into Fisher's z values to indicate the degree of ROI-to-ROI connectivity. An individual correlation matrix of 10,011 unique connections was created, which was used in the subsequent multivariate regression analyses.

Multivariate regression analyses

To predict participants' behavior in the TG, the 10,011 ROI-to-ROI RSFC values were used as features in multivariate regression analyses. A classification and regression tree (CART) algorithm (Breiman, 2001) was implemented, using for prediction the *classregtree* function in MATLAB (The Mathworks, Natick, MA, USA). CART is a non-parametric algorithm that builds a regression decision tree with binary splits for continuous labels. CART was chosen because it is well suited for estimations of multifactorial brain-behavior relationships – as previously used for prediction of social preferences and social behavior in economic games (Hahn, Notebaert, Anderl, Reicherts, et al., 2015a; Hahn, Notebaert, Anderl, Teckentrup, et al., 2015b).

A whole-brain model with selected features from all 10,011 connections was first run to investigate whether whole-brain RSFC entailed relevant information predicting trust or reciprocity decisions. Second, given the assumption in the literature about the differing cognitive mechanisms underlying trust and reciprocity, we tested whether specific within-network functional connectivity of RSFC networks – CON, SMN, DMN, FPN, and OccN – could better predict one or the other behavior.

To test generalizability of the regression models, a leave-one-subject-out cross-validation (LOSOCV) approach was implemented. In every iteration, CART was trained with all, but one subject (train set) and the estimated model was used to predict the behavior of the left-out subject unseen by the algorithm (test set). This procedure was repeated n times (n=total number of subjects in each group), yielding each time a behavioral prediction for each subject. Given the high-dimensionality of the predictors (one dimension for each feature, i.e., ROI-to-ROI-connection), features selection was applied before training the regression model. In every cross-validation fold, connections of 5% of the strongest correlations (Spearman) between the train set and the targets (i.e., social behavior in the TG) were retained as the most relevant features. The algorithm was trained on those features, and the model performance was tested on the left-out subject. Importantly, feature selection was applied only on the train set and not on the whole sample. This implies that retained features for prediction changed slightly at every fold, but also guarantees independence of the train and test sets and avoids biased results on the group level (Hastie, Tibshirani, & Friedman, 2009). To determine which features and how consistently particular features were selected across folds, we estimated the survival rate of each feature across the cross-validation procedure by computing the percentage of times each feature passed the selection threshold of 5%.

Performance of a model's prediction was assessed by computing the standardized mean squared error (SMSE), i.e., the error of the algorithm's performance divided by the targets' variance. The significance of the prediction was assessed with a permutation test of 1,000 permutations. In every permutation, each cross-validated model was run with randomly permuted targets, and the number of permutations with better performance (i.e., lower SMSE) than the one with the true targets was calculated (n_{perm}). The p-value was computed dividing this number by the total number of permutations, i.e., $p = (1 + n_{perm})/(1 + 1{,}000)$.

Results

Behavioral analyses

Investors and trustees were comparable with respect to their social abilities and preferences: age ($t_{(49)}$=0.48, p=0.64), education ($t_{(49)}$=0.91, p=0.37), social status ($t_{(49)}$=-0.57, p=0.57), IRI (perspective taking: $t_{(49)}$=-0.95, p=0.35; fantasy: $t_{(49)}$=-1.08, p=0.28; empathic concern: $t_{(49)}$=-0.31, p=0.76; personal distress: $t_{(49)}$=-1.36, p=0.18), and SVO (χ^2_1 =0.21, p=0.64; prosocial participants: 21 investors vs. 23 trustees; individualistic participants: four investors vs. three trustees). None of these variables was associated with behavior in the TG of either investors or trustees (cf., Online Supplementary Materials: Associations between economic behavior and biopsychological measurements).

Analyses of trust and reciprocity revealed that our sample behaved in line with previous TG studies (see Fig. 2; Camerer, 2003; Gintis, 2000; Krueger, Grafman, & McCabe, 2008). Investors shared on average about half of their initial endowment (M=44.80%, SD=26.94) and trustees about half of the tripled amount received (M=48.21%, SD=27.46). No significant differences in the sharing behaviors (trust vs. reciprocity) were observed ($t_{(49)}$=-0.45; p=0.66).

Multivariate regression analyses

A machine-learning algorithm (i.e., CART; Fig. 3a) was applied to predict participants' behavior in the TG (i.e., targets) based on whole-brain and network-specific RSFC (i.e., features) using Dosenbach's atlas (Dosenbach et al., 2010). Performances of the cross-validated whole-brain models were significantly better than chance for both investors (SMSE=0.67, p<0.002; Fig. 3b) and trustees (SMSE=0.51, p<0.002; Fig. 3c).

Subsequently, single networks were investigated and our hypotheses were confirmed, i.e., that DMN predicted trust (SMSE=1.06, p<0.05), while FPN reciprocity (SMSE=1.05, p<0.03) (Fig. 3b). Furthermore, exploratory analyses revealed that DMN (SMSE=0.71, p<0.002) and CON (SMSE=0.96; p<0.04; Fig. 3c) predicted reciprocity as well. None of the other networks predicted either trust (CON: SMSE=1.42, p=0.27; FPN: SMSE=1.88, p=0.45; SMN: SMSE=1.32, p=0.21; OccN: SMSE=2.76, p=0.99) or reciprocity (SMN: SMSE=1.22, p=0.20; OccN, SMSE=1.53, p=0.18).

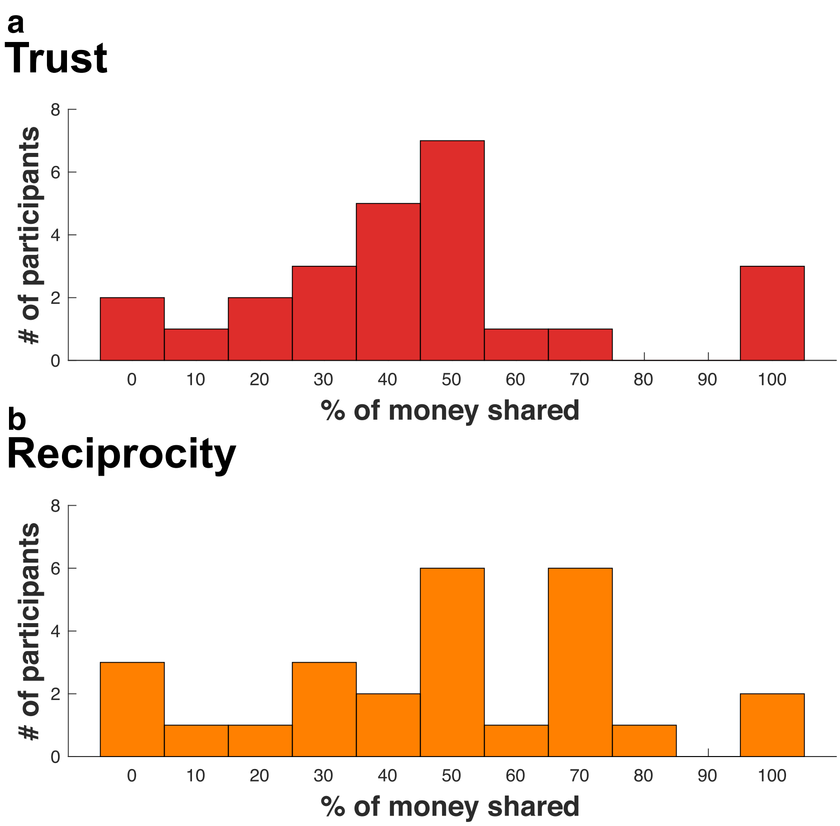

Fig. 2 *Trusting and reciprocal behaviors.* (**A**) Most of the investors decided to trust by giving around half of their initial endowments. (**B**) Most of the trustees decided to reciprocate trust by sending back around half of what they received

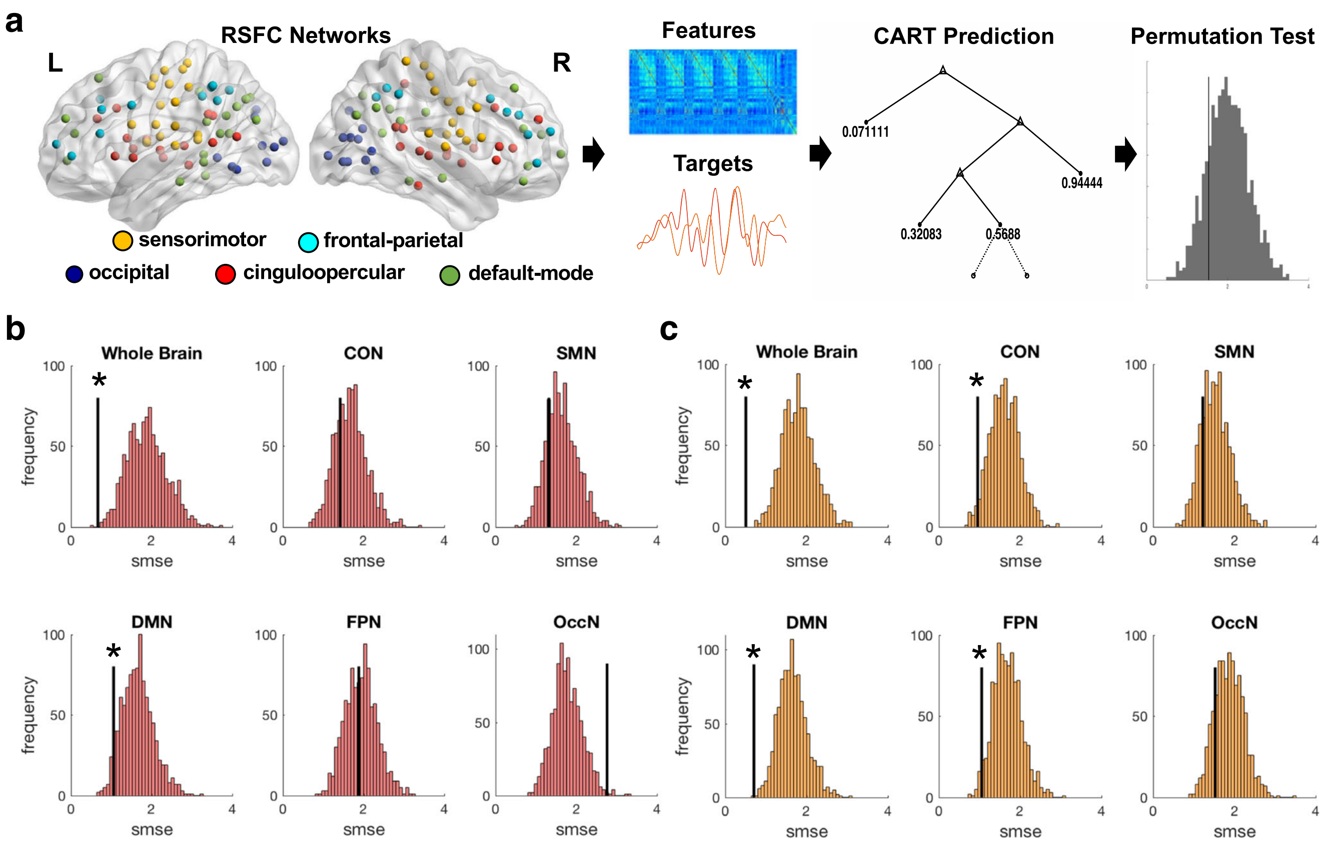

Fig. 3 *Multivariate analyses.* (**A**) Workflow of the multivariate analysis. Regions of interest (ROIs=142) were chosen and partitioned into five functional connectivity networks. Pearson correlation values representing RSFC were computed between ROIs and extracted to build network-specific correlation matrices. These correlation values were entered into multivariate regression models as features to predict participants' behaviors (trust or reciprocity) as targets. The CART algorithm was used to make out-of-sample predictions using a cross-validated approach. Prediction performance was finally tested against distribution of predictions based on CART models trained with randomly permutated targets (permutation test). (**B**) *Results for prediction of trust behavior.* Lower SMSE values indicate better performance of multivariate regression models for whole-brain and network-specific RSFC. (**C**) *Results for prediction of reciprocity behavior.* Lower SMSE values indicate better performance of multivariate regression models for whole-brain and network-specific RSFC. *L* left, *R* right, *RSFC* resting-state functional connectivity, *CART* classification and regression tree algorithm, *CON* cingulo-opercular network, *SMN* sensorimotor network, *DMN* default-mode network, *FPN* frontoparietal network, *OccN* occipital network, *SMSE* standard mean squared error

Follow-up analyses revealed that different edges within DMN predicted trust and reciprocity (cf., Online Supplementary Materials: Specificity of selected features for behavioral predictions). Among others, functional connectivity of the ventromedial prefrontal cortex, precuneus and TPJ were consistently selected for the prediction of trust (Fig. 4 and Table S1), while functional connectivity of the superior frontal gyrus, inferior temporal gyrus, and posterior cingulate cortex were consistently selected to predict reciprocity (Fig. 5 and Table S2). Importantly, DMN edges predicting trust failed to predict reciprocity and vice versa, indicating a functional differentiation of DMN edges predicting the two social behaviors.

Further, functional connectivity of dorsolateral PFC and parietal cortex within the FPN (Table S3) and of anterior insula, anterior/middle cingulate cortex, and precuneus within the CON (Table S4) was most consistently selected to predict reciprocity.

Finally, control analyses revealed that the time difference between the behavioral and the scanning sessions was not associated with errors in model predictions, suggesting that models' performance was not confounded by time factors (cf., Online Supplementary Materials: Relationship between-session time difference and model prediction error).

Discussion

In this study, combining the TG with a multivariate predictive framework, we investigated whether individual differences in the propensity to trust and reciprocity can be predicted by different RSFC networks. At the behavioral level, investors invested about half of their endowment and trustees reciprocated by sharing in return about half of what they received. At the neuroimaging level, RSFC of DMN predicted individual differences in the propensity to trust, whereas RSFC of FPN,

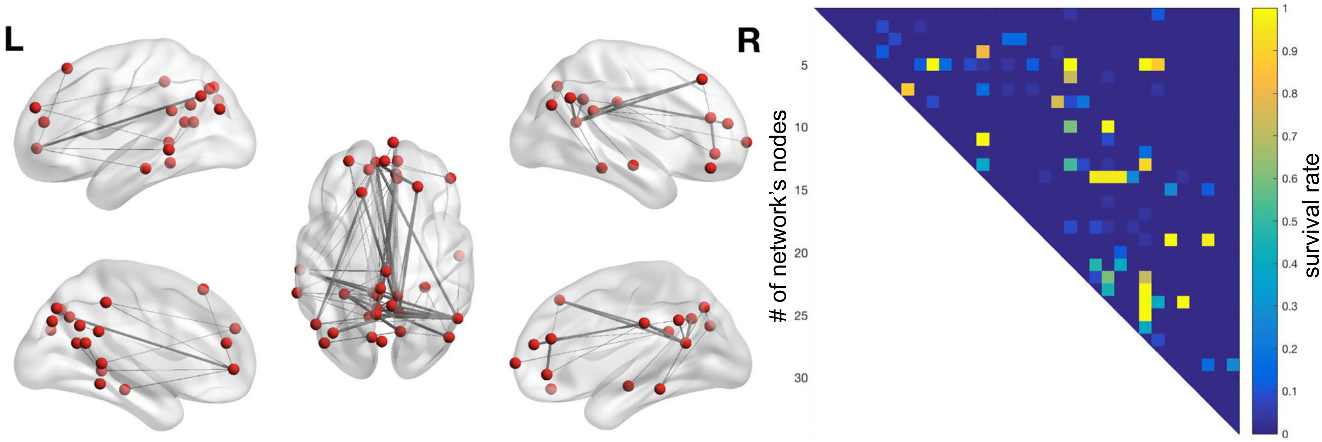

Fig. 4 *Features predicting trust behavior.* Default-mode network (DMN) regions of interest (ROIs) and edges selected across the cross-validation procedure to predict trusting behavior (on the left). Survival rates for each edge within the DMN across folds are given on the right. Survival rate values range from 0 (the edge was never selected) to 1 (the edge was selected on every fold)

DMN, and CON predicted a propensity to reciprocate, suggesting that specific resting-state dynamics are related to different social behaviors.

Previous research has shown that initial trust during single and anonymous interactions is socially risky (Fehr & Fischbacher, 2003). The dilemma of a decision to trust a stranger requires reliance on cognitive processes to infer the partner's trustworthiness, because despite the fruits of beneficial cooperation, trusting an unknown "other" entails the risk of a betrayal that is loosely disincentivized in single and anonymous interactions. Behavioral studies have demonstrated that the other's intentions (actual or inferred) shape trusting behavior, strengthening the assumption that initial trust is a norm-sensitive decision relying on an individual's ability to mentalize (Burnham et al., 2000; A. K. J. Fett et al., 2014b; Krueger et al., 2007; McCabe et al., 2003; Sutter & Kocher, 2007; Wouter van den Bos, Westenberg, van Dijk, & Crone, 2010). Mentalizing plays a pivotal role in social cognition and interactions, in which taking someone else's perspective or understanding someone else's character is often required to adopt prosocial behaviors (Frith & Frith, 2003; Greene, Sommerville, Nystrom, Darley, & Cohen, 2001; Krueger, Barbey, & Grafman, 2009).

In line with this evidence, our results revealed that RSFC of DMN (in particular RSFC of the medial PFC and TPJ) predicted an individual's initial trust. The DMN has been associated with at least three functions: autobiographic memory, envisioning the future, and mentalizing (Buckner & Carroll, 2007; Gusnard, Akbudak, Shulman, & Raichle, 2001; Schacter, Addis, & Buckner, 2008). The hypothesis of an overarching functioning of the DMN states that the defining property of this network is the ability to simulate an alternative prospective (Buckner, Andrews-Hanna, & Schacter, 2008). The DMN thus plays a pivotal role in the social domain, in which it is often required to explore and anticipate social and event scenarios before engaging in prosocial behaviors (Krueger et al., 2009) and moral decision-making (Greene et al., 2001).

Important hubs of the DMN have been observed in task-based fMRI using the TG. The medial PFC, for instance, is more engaged when investors play with a human partner than with a computerized opponent (McCabe et al., 2003) and during the initial trust-building stage (Krueger et al., 2007). Furthermore, TPJ activity increases with age during trust decisions and with social expertise (A.-K. J. Fett et al., 2014b; Xiang et al., 2012), suggesting reliance on mental models about the intentions of the other when trusting (Fletcher et al., 1995; Hahn, Notebaert, Anderl, Teckentrup, et al., 2015a; Van Overwalle, 2009). Our results confirmed that differences in RSFC of the mentalizing system (DMN) underlie individual differences in the propensity to trust a stranger and to initiate cooperation. These results suggest that individual variability in initial trust depends on differences in an individual's ability to recruit a functional network that supports inferences on how others are likely to behave.

Initial trust is socially risky because reciprocity appears to the trustee to be less appealing than a betrayal. The conflict between a selfish decision and the decision to reciprocate requires the trustee to suppress selfish motives to adopt a more prosocial behavior that enhances the likelihood of future cooperation. Research has shown that cooperative behavior is based on cognitive control of self-serving motives during economic decision-making (Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006; J. Rilling et al., 2002; J. K. Rilling, King-Casas, & Sanfey, 2008; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003; Spitzer, Fischbacher, Herrnberger, Gron, & Fehr, 2007). Our results indicated that individual differences in RSFC of FPN predict an individual's propensity to reciprocate.

The FPN has been observed to sustain control processes (Miller & Cohen, 2001) and its connectivity to increase as a function of cognitive demand (Dosenbach et al., 2007; Repovš & Barch, 2012), allowing an individual to optimize performance in situations requiring the operation and

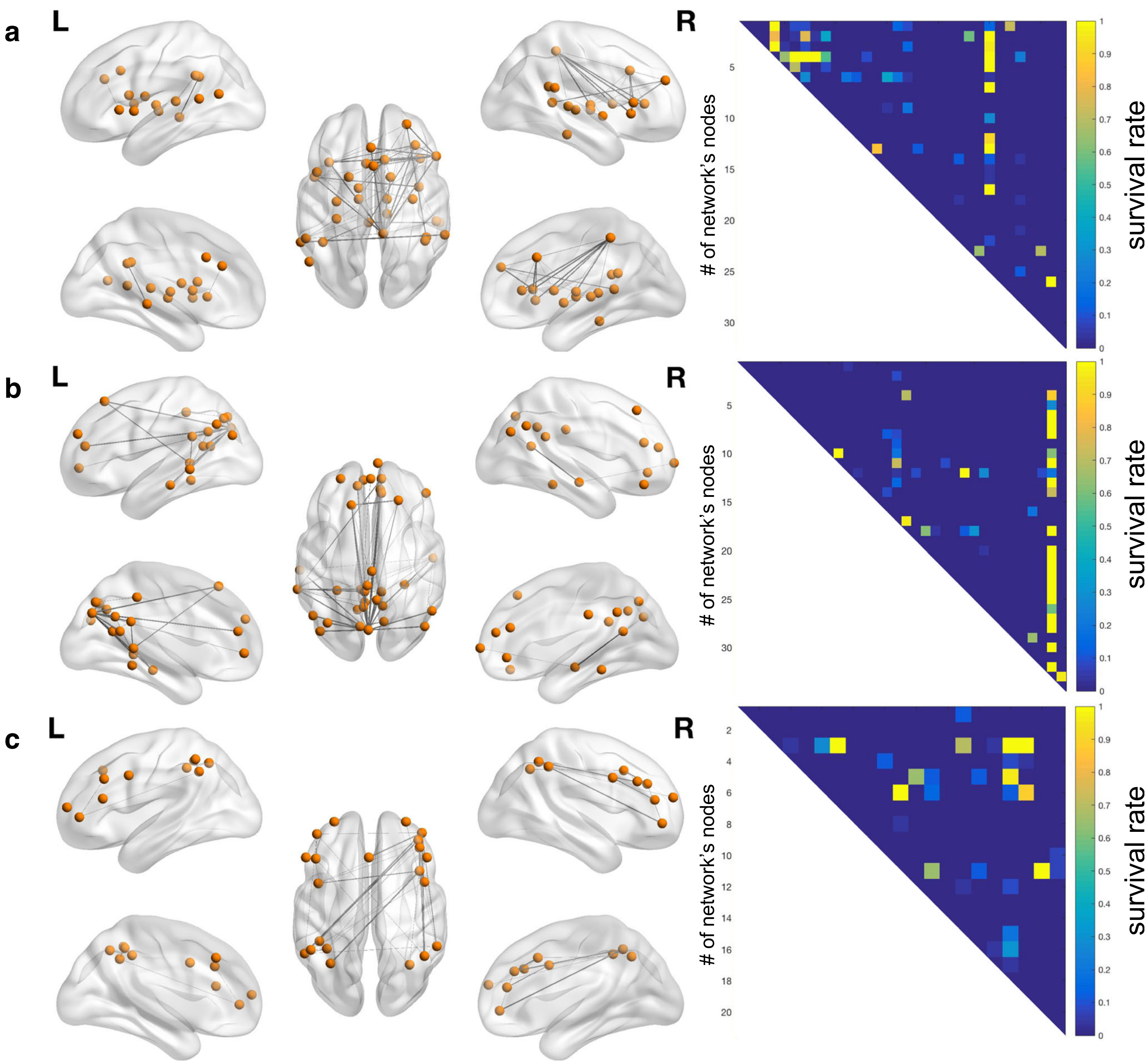

Fig. 5 *Features predicting reciprocity behavior.* Cingulo-opercular network (CON) (**A**), default-mode network (DMN) (**B**), and frontoparietal network (FPN) (**C**) regions of interest (ROIs) and edges selected across the cross-validation procedure to predict reciprocal behavior (on the left). Survival rates for each edge within each resting-state network across folds are given on the right. Survival rate values range from 0 (the edge was never selected) to 1 (the edge was selected on every fold)

coordination of different cognitive processes. Previous task-based fMRI studies have revealed the involvement of important FPN brain regions such as the dorsolateral PFC in reciprocity (W. van den Bos et al., 2009). Moreover, noninvasive transcranial direct current stimulation of the DLPFC enhances reciprocity (Nihonsugi et al., 2015), whereas inhibition of the lateral PFC using transcranial magnetic stimulation reduces behaviors enforcing reciprocal fairness even when participants knew that selfish decisions had detrimental effects on their future reputation (Knoch et al., 2009).

Our results concurred with a previous fMRI study showing a linear relationship between reciprocity in trustees and intra-network connectivity between two RSFC networks – namely FPN and CON (Caceda et al., 2015). In line with this research, we also observed that RSFC of CON predicted reciprocity – a network previously linked to cognitive control and saliency (Dosenbach et al., 2006, 2007; Seeley et al., 2007). In the social domain, the CON has been shown to support control processes for strategic behavior (Hahn, Notebaert, Anderl, Reicherts, et al., 2015b). Moreover, task-based fMRI studies reveal that CON regions – such as the anterior insula and anterior cingulate cortex – are recruited during reciprocity decisions in the TG (Bellucci et al., 2017, 2018; Chang, Smith, Dufwenberg, & Sanfey, 2011; W. van den Bos et al., 2009). Thus, in line with this research, our results suggest that stronger reliance on the FPN and CON is associated with stronger preferences for prosocial behaviors, likely enabling people to adopt social strategies that may not be particularly advantageous to them in the short term, but may turn out to be optimal in the long term.

Finally, as for trust, RSFC of DMN predicted participants' reciprocity. Similar to trust, reciprocity is conditional on the intentions of others (Fischbacher & Gächter, 2010; Gächter, Kolle, & Quercia, 2017). For example, reciprocity is less likely when a trust decision is not intentional (McCabe et al., 2003) and increases in cooperative settings as a function of received trust (Fehr & Fischbacher, 2003; Fehr, Kirchsteiger, & Riedl, 1993; Hayashi, Ostrom, Walker, & Yamagishi, 1999). However, we observed different DMN edges involved in the prediction of reciprocity as opposed to trust. In particular, edges predicting reciprocity involved regions that have been previously observed to be activated in particular stages of a reciprocity decision. For instance, the superior frontal gyrus is significantly more active when the trustee does not match the other's expectations (Chang et al., 2011) and its activity decreases linearly with increasing cooperation (Li, Xiao, Houser, & Montague, 2009). On the contrary, the posterior cingulate cortex and inferior temporal gyrus are more engaged when the trustee matches the other's expectations (Chang et al., 2011) or repays trust in the absence of sanctioning intentions from the investor (Li et al., 2009). Thus, the importance of the DMN in reciprocity might be related to the ability to infer the expectations of the other based on the observed behavior (Bellucci et al., 2018), which in turn determines whether and to which extent a kind gesture is repaid.

Our findings advance our understanding of the neural networks underlying social behaviors. However, some limitations have to be acknowledged to better understand the generalizability of our findings. First, although we employed multivariate analyses, which have higher reliability than univariate analyses (Noble, Spann, et al., 2017a), and acquired data from more than 10 minutes to improve the reliability of the functional connectivity estimates (Gordon et al., 2017; Noble, Scheinost, et al., 2017b), future studies are needed to test the relationships between RSFC and social behaviors in larger samples. Second, in this study, we opted for a between-subjects design to avoid role effects altering participants' behaviors (Burks, Carpenter, & Verhoogen, 2003; Johnson & Mislin, 2011). However, as social behaviors are sensitive to subjective preferences, group results may be subject to such individual differences if the groups entail individuals with significantly different social preferences. We tried to control for such differences acquiring a series of measurements related to social behaviors and running control analyses to test any relevant group differences. However, future studies should attempt to employ within-subject designs and acquire further psychological measures that may explain interindividual differences in social behaviors (McCarthy, Wood, & Holmes, 2017; Rempel, Holmes, & Zanna, 1985; Thielmann & Hilbig, 2015). Finally, we investigated whether RSFC predicts trust and reciprocity at one time-point. Future studies should also explore whether RSFC is a temporally stable index for those prosocial behaviors, representing a neural fingerprint of an individual's cooperative phenotype (Peysakhovich et al., 2014).

Overall, combining the TG with a multivariate analysis of RSFC to capture complex brain-behavior relationships, our findings revealed specific functional connectivity patterns underlying individual tendencies to prosocial behaviors. Our study advances the understanding of how single RSFC networks represent specific neuromarkers for an individual's propensity to social behaviors.

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest, financial or otherwise.

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