Reliance on functional resting-state network for stable task control predicts behavioral tendency for cooperation

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ABSTRACT

Humans display individual variability in cooperative behavior. While an ever-growing body of research has investigated the neural correlates of task-specific cooperation, the mechanisms by which situation-independent, stable differences in cooperation render behavior consistent across a wide range of situations remain elusive. Addressing this issue, we show that the individual tendency to behave in a prosocial or individualistic manner can be predicted from the functional resting-state connectome. More specifically, connections of the cinguloopercular network which supports goal-directed behavior encode cooperative tendency. Effects of virtual lesions to this network on the efficacy of information exchange throughout the brain corroborate our findings. These results shed light on the neural mechanisms underlying individualists' and prosocials' habitual social decisions by showing that reliance on the cinguloopercular task-control network predicts stable cooperative behavior. Based on this evidence, we provide a unifying framework for the interpretation of functional imaging and behavioral studies of cooperative behavior.

Introduction

The way in which we divide resources between ourselves and other individuals is central to the emergence and maintenance of cooperation. A wealth of behavioral investigations has shown that a stable individual preference for the division of resources – commonly termed Social Values Orientation (SVO; (Van Lange, 1999)) – exists, which renders cooperative behavior fairly consistent across situational contexts (Bogaert et al., 2008). In this framework, the so-called "prosocials" maximize the sum of resources for themselves and for others, while simultaneously minimizing the difference between the two. They strive for a fair share. In contrast, the so-called "individualists" maximize resources for themselves only and are not concerned with the welfare of others. The disposition of SVO can affect cooperative behavior in diverse situations, from trusting in economic games and contributing to the public good to real-life situations such as preferring public transport to taking your own car to go to work to protect the environment (Balliet et al., 2009; Bogaert et al., 2008; Kanagaretnam et al., 2009). SVO has been shown to be stable over long periods of time, enabling prediction of

behavior in early adulthood from preferences displayed as early as four years of age (Eisenberg et al., 1999).

Over the last decade, a plethora of investigations – mainly employing paradigms from behavioral economics – has investigated the neural basis of cooperation (for reviews, see Krueger et al. (2008) and Rilling and Sanfey (2011)). Depending on task context, these studies have shown differential activity in brain regions associated with the processing of social signals and extrinsic incentives to be crucial for individual differences in the tendency to cooperate (Declerck et al., 2013). However, no study has addressed the more fundamental question of how a stable behavioral disposition such as SVO can modulate cooperative behavior across a wide variety of contexts. Thus, it is unclear how individual differences might be implemented in the brain to allow for the broad and consistent effects on cooperative behavior we empirically observe in humans.

To this end, we focused not on the neural correlates of any specific economic game or behavior, but investigated the neural substrates of trait-related SVO by relating it to the brain's resting-state dynamics, i.e. its spontaneous, task-independent activation (Damoiseaux et al., 2006; Dosenbach et al., 2006, 2007, 2008; Fox et al., 2005). Specifically, we aimed to predict individual SVO from whole-brain, resting-state functional network connectivities. Then addressing the question by which mechanisms resting-state functional dynamics associated with

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SVO might affect behavior across situations, we simulated a series of virtual lesions on five functional brain networks (Dosenbach et al., 2007, 2010) and assessed changes in the efficacy of information exchange throughout the brain for prosocials and individualists (see Fig. 1 for an overview of the analysis steps).

Methods

Participants

Thirty-one healthy, right-handed subjects participated in the present study. Two subjects had to be excluded due to excessive head motion (>1.5 mm/degree in any direction). The remaining sample consisted of 16 females and 13 males with a mean age of 25.0 years (SD = 3.53). All were recruited from a German local community through advertisements. Written informed consent was obtained from all participants after a complete description of the study was provided. Our study was approved by the ethics committee of the German Society of Psychology (Deutsche Gesellschaft für Psychologie).

Psychometric assessment of Social Value Orientation

All participants completed the 15-item Social Value Orientation (SVO) measure by Murphy et al. (2011) in its German paper version. While the SVO questionnaire measures four tendencies (altruistic, prosocial, individualistic and competitive), we focus on only two of those in this study – namely the prosocial and the individualistic tendencies – as the other two categories are extremely rare (less than 4% were competitive individuals while altruistic tendencies did not occur at all in two samples totalling N = 156 participants; for details, see Murphy et al. (2011)).

Subjects were alternatingly given parallel versions of the task which contain the same items, but differ regarding item order. In the SVO measure, participants make decisions among various combinations of outcomes for themselves and another person. Specifically, they are asked to indicate their preference regarding how much money they would allocate to themselves and to another person. Self-other allocation options are paired such that SVO can be derived while transitivity as a fundamental psychometric requirement can be assessed. Generally, the Murphy SVO measure shows high reliability as well as high internal and external validity (Murphy et al., 2011). Our sample consisted of 15 prosocials and 14 individualists. The two groups did not differ significantly with regard to age (t(27) = .31; p = .758) or gender ($\chi^2(1)$ = .29; p = .588). All subjects produced completely transitive sets of social preference choices, i.e., all participants showed internally consistent responses.

Resting-state fMRI acquisition

Subjects were scanned for 5 minutes. No specific instructions were given except to close their eyes, relax and hold still. Head movements were minimized by using a cushioned head fixation device. Imaging was performed using a 1.5 T Siemens Magnetom Avanto TIM-system MRI scanner (Siemens, Erlangen, Germany) equipped with a standard 12 channel head coil. In a single session, twenty-four 4-mm-thick, interleaved axial slices (in-plane resolution: 3.28×3.28 mm) oriented at the AC-PC transverse plane were acquired with 1 mm interslice gap, using a T2*-sensitive single-shot EPI sequence with following parameters: repetition time (TR; 2000 ms), echo time (TE; 40 ms), flip angle (90°), matrix (64×64), field of view (FOV; 210×210 mm^2), and number of volumes (150).

Functional MRI resting-state preprocessing

All analyses were conducted using the REST toolbox (Song et al., 2011) with the Data Processing Assistant for Resting-State fMRI (DPARSFA; V2.3) and Matlab software (The Mathworks, Natick, Massachusetts). The first six volumes were discarded to account for
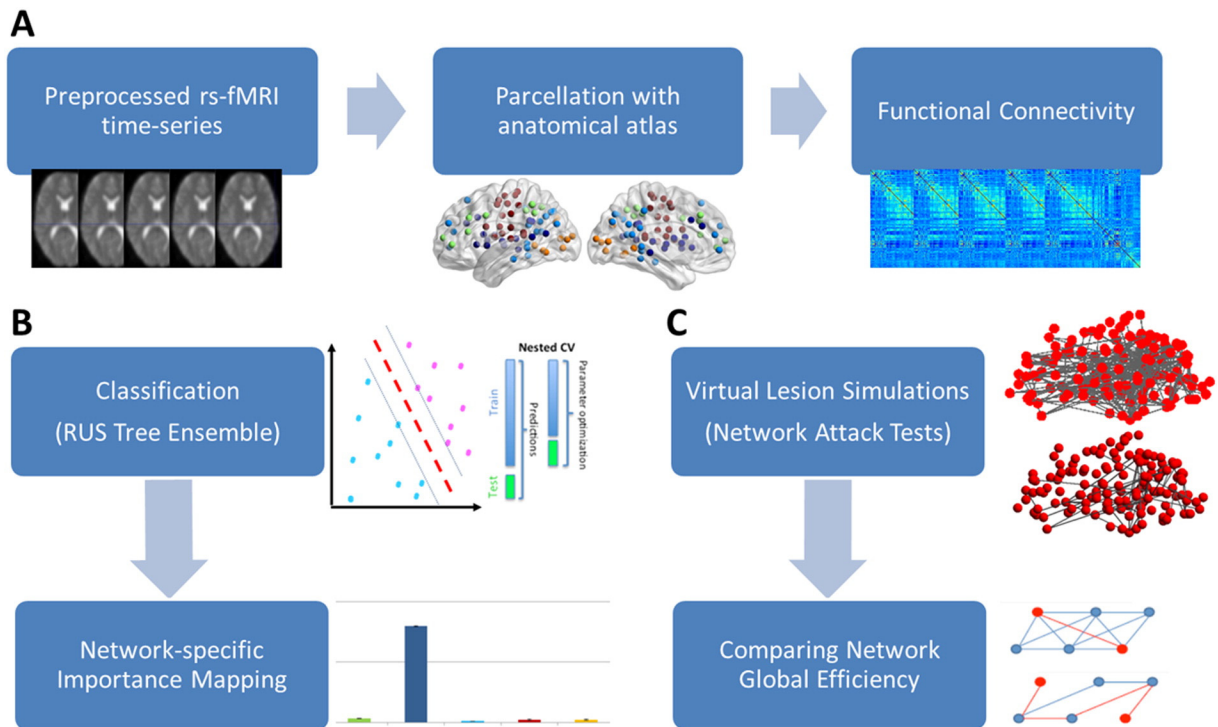
Fig. 1. Data processing and analysis strategies. A) First, resting-state fMRI data was preprocessed, time-series for each region in the Dosenbach atlas were extracted and a functional connectivity matrix was computed for each participant. B) Using a multivariate pattern classification approach, we assessed whether a participants Social Value Orientation (SVO) can be predicted from whole-brain functional connectivity. Then, we measured to what extent information from each of the five Dosenbach networks contributed to classifier performance. C) Additionally, we compared changes in Global Efficiency between Prosocials and Individualists before and after simulating virtual lesions to each of the five Dosenbach networks.

magnetization saturation effects. Then the remaining data were slice time corrected, head motion correction was applied and images were normalized to the Montreal Neurological Institute (MNI) template. The resulting fMRI data were then spatially smoothed with a 6 mm FWHM Gaussian isotropic kernel. After that, the time series for each voxel was detrended and bandpass-filtered (0.01–0.08 Hz) to reduce low-frequency drift and physiological high frequency respiratory and cardiac noise before the 6 head motion parameters, the global mean signal, the white matter signal and the cerebrospinal fluid signal were regressed out. Based on the resulting data, functional whole-brain, resting-state connectivity was computed from cortical regions of interest (ROIs) previously described in Dosenbach et al. (2007, 2010) excluding the cerebellum employing Pearson correlation (see Fig. 1a). Specifically, Dosenbach et al. defined the ROIs by constructing non-overlapping spheres with a diameter of 10 mm around coordinates from a series of five meta-analyses, focused on error-processing, default-mode (task-induced deactivations), memory, language and sensorimotor functions. In this study, the Dosenbach et al. template provided with the Data Processing Assistant for Resting-State fMRI (DPARSFA; V2.3) was used for parcellation.

Assessing mean intra-network as well as inter-network connectivity reveals that intra-network connectivity is substantially higher in all cases than inter-network connectivity (Supplementary Fig. S1). This strongly suggests that the networks found previously are represented in our data. This procedure yielded 10,011 unique correlation coefficients (connectivities) between the 142 regions of interest.

Predicting Social Values Orientation (SVO)

In order to predict a participant's SVO, tree ensemble classification was performed using the Random Under Sampling Boost algorithm (Seiffert et al., 2010) as implemented in Matlab (The Mathworks, Natick, Massachusetts) with a minimum leaf size of 5 and a learning rate of 0.1 growing 1000 trees. We used this approach mainly to overcome the problem that, with a fixed number of training samples, the accuracy reduces as the dimensionality increases (Hughes effect). When attempting to generate whole-brain classification models in ultra-high-dimensional space (one dimension for each of the 10,011 connections), we also have to assume that many – if not most – dimensions add mostly noise. A prominent way to address both related problems simultaneously is to select only those features (connections in our case) during training which are known to improve the accuracy of the model. This so-called boosting process reduces dimensionality and potentially improves execution time as irrelevant features do not need to be computed. As only relevant features can receive a non-zero weight, generally weights tend to be more stable and sparse (for an introduction to boosting algorithms, see Freund and Schapire (1997)).

For this multivariate pattern recognition analysis, we performed Global Signal Regression in order to improve neuroanatomical specificity of the positive correlations (Fox et al., 2009), but only considered connectivity values larger than 0 to avoid spurious negative correlations arising when the global mean signal is regressed out (Murphy et al., 2009).

To ensure the generalizability of the classifier, we used leave-one-out cross-validation (LOO-CV) to predict a participant's SVO. In each LOO-CV run, data from all but one sample (*S*-1 of the *S* subjects) is used to train the classifier. Subsequently, the categorization of the remaining subject, which has so far been unseen by the algorithm, is calculated. This procedure is repeated *S* times, each time leaving out a different subject, yielding each subject's categorization. Accuracy is computed by dividing the number of correct classifications by the total number of subjects. To protect the algorithm against possible instability of the accuracy estimate, we repeated this procedure 10 times using the median accuracy of the 10 stability runs as an estimate of true performance. To establish whether the observed median classification accuracy is statistically significant, we ran each classifier 1000 times

with randomly permuted labels and counted the number of permutations which achieved higher median accuracy than the one observed with the true labels. The p-value was then calculated by dividing this number by 1000.

To quantify the contribution of each of the five functional systems, we computed network-specific importance scores by taking the mean of all feature importance scores over all cross-validation folds and stability runs. Thereafter, we summed the mean importance scores for each network separately. Generally, importance scores in this framework represent a measure of how much a feature (a functional connection between two regions in this case) contributed to classification performance while taking into account the contributions of all other features.

Network attack tests

In addition to the multivariate analysis described above, we simulated a series of virtual lesions in each of the five functional systems, respectively, and observed changes in network Global Efficiency for prosocials and individualists. Whereas the multivariate analysis of whole-brain connectivities described above shows that connections within the cinguloopercular system are highly relevant for SVO prediction, the network attack analysis builds on this result and aims to shed light on the potentially different roles the cinguloopercular system might play in individualists and prosocials. More specifically, based on the results of the multivariate analysis, we hypothesized that the cinguloopercular system might play a differential role for processing information throughout the brain. We opted for the Global Efficiency metric as it measures information transfer and provides a highly relevant characterization of whole-brain network dynamics in a single measure. Generally, Global Efficiency is used to infer the efficacy of information exchange through a network by studying its topology (Latora and Marchiori, 2001). It quantifies the extent to which nodes communicate with distant nodes, and indicates the efficacy of information exchange throughout the brain. Specifically, Global Efficiency was computed as the average of inverse shortest path length based on the undirected, weighted connection matrix (i.e. the matrix of Pearson correlations between all 142 regions) using the *Brain Connectivity Toolbox* (Rubinov and Sporns, 2010).

As the network attack test was based on the five different functional systems (frontoparietal, cinguloopercular, default mode network, sensorimotor, and occipital) described in Dosenbach et al. (2007, 2010), we used the connectivity threshold validated in these publications ($r = .20$) for further analyses. By applying this threshold, only connectivity values (i.e. Pearson correlations between all pairs of the 144 regions) of $r \geq .20$ were considered, setting all other values to 0.

The network attack analysis was conducted by first computing Global Efficiency for the entire, undamaged network (full network) for each participant. Then, we attacked each of the five networks separately by setting all those connections to 0 which connect two regions of the same network. For example, removing the cinguloopercular network was done by setting to 0 all connections between two regions belonging to this network. After each attack, we computed Global Efficiency yielding – for each participant and network attacked – one Global Efficiency value for the lesioned network.

As we were interested in potential differential effects of attacking a network in prosocials and individualists, we computed a 2×2 Analysis of Variance (ANOVA) with one between factor (individualists/prosocials) and one within (repeated measures) factor (full network/lesioned network) based on the Global Efficiency values separately for each network. If the interaction term is significant ($p < .05$, corrected for multiple comparisons as one ANOVA was computed for each network under attack), this would indicate that attacking the respective functional system has differential effects on Global Efficiency of the remaining network in prosocials compared to individualists.

In order to compute significance of the interaction term while correcting for multiple comparisons (over the five respective systems),

we ran the ANOVA with permuted data 10,000 times for each functional system. Based on the distribution of F-values for the interaction term under permutation, we obtained the maximum F-value over the five tests for each permutation. Corrected significance was then computed by counting the number of times that the true F-value for the respective test was smaller than the values of the maximum F-value distribution under permutation over all tests and dividing this number by 10,000.

Results

To test whether the resting-state functional connectome (Fig. 2) encodes SVO, we used a multivariate pattern recognition algorithm to predict individual SVO from resting-state functional connectivities of standard, previously defined cortical regions of interest grouped in five different functional systems: frontoparietal, cinguloopercular, default mode network, sensorimotor, and occipital (Dosenbach et al., 2007, 2010).

Avoiding circularity bias by using a leave-one-out cross-validation procedure, we show that the tendency to behave in a prosocial or individualistic manner can be predicted from the human functional resting-state connectome (accuracy = 75%; p < .001). Next, we investigated the role of each of the five functional systems by summing the feature importance scores from the classifier for each functional system. Surprisingly, we found that the classifier's performance was driven to a large extent by connections of a single functional system: The sum of feature importance scores within the cinguloopercular system far exceeded the sum of importance scores in all other systems (Fig. 3, bottom panel). In fact, importance scores from all other networks combined accounted for only about 11% of the importance of cinguloopercular features alone.

Having established that SVO can be predicted on a single-subject basis from resting-state functional connectivities – particularly driven by connections within the cinguloopercular system – we then sought to investigate by which mechanisms resting-state functional dynamics associated with SVO might affect behavior across situations. To this end, we conducted a series of virtual lesion tests assessing the changes in global network efficiency when a targeted network attack (Joyce et al., 2013) was performed on each of the five functional systems, respectively. While individualists generally display higher Global Efficiency (t(27) = 2.13; p = .033), the network attack test shows that inflicting a virtual lesion comprising the cinguloopercular network differentially affects Global Efficiency in individualists and prosocials. Specifically, if the cinguloopercular network is removed, Global Efficiency decreases more strongly in the individualists than in the prosocials (F(1,27) = 6.64; p = .022, corrected). As this effect might be driven by threshold-dependent changes in network density
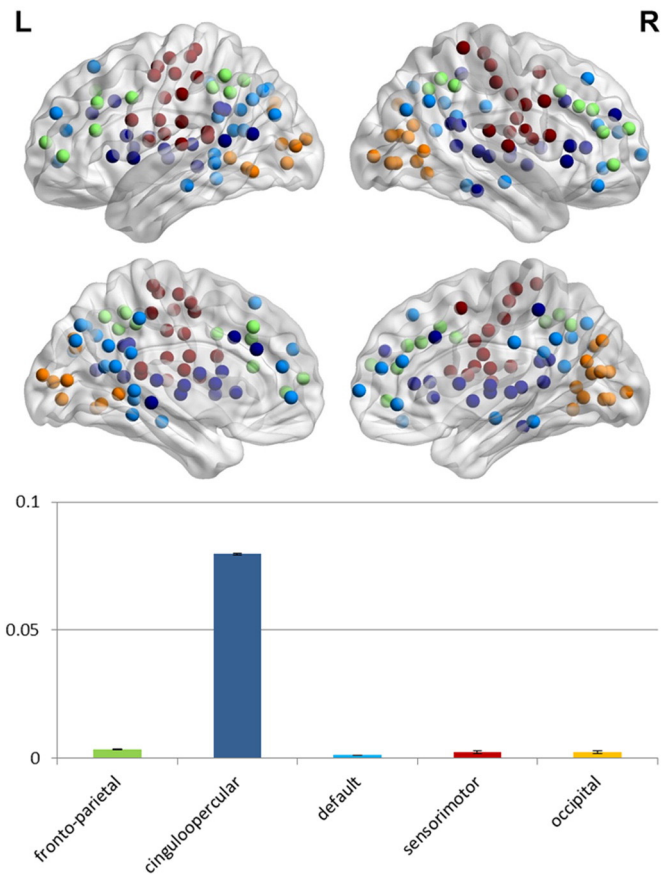
Fig. 3. *Top panel:* Visualization of the nodes for the fronto-parietal network (green), the cinguloopercular network (blue), the default network (light blue), the sensory motor network (red), and the occipital network (yellow). *Bottom panel:* Median sum of tree ensemble feature importance for each functional resting-state network (n = 29). Error bars show range of median sum of tree ensemble feature importance over 10 replication runs. Bar colors correspond to node colors in the upper panel.

(see van Wijk et al. (2010)), for details regarding the effects of network density on graph-theoretical measures), we additionally conducted the same analysis without thresholding the connectivity matrix. This approach yielded comparable results (F(1,27) = 5.19; p = .027, corrected). No such interaction effect is significant for any of the other four functional systems.
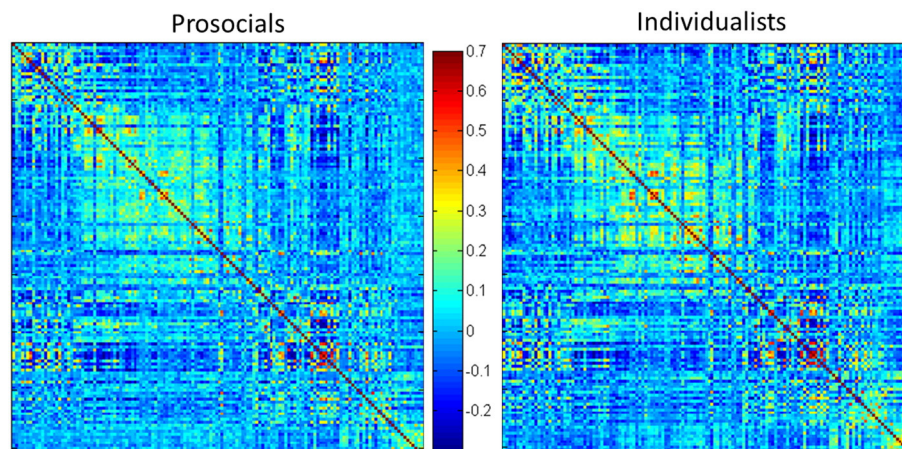
Fig. 2. Average functional connectivity matrices (142 regions of interest) for Prosocials (left) and Individualists (right).

Discussion

In this study, we investigated whether the stable, context-independent tendency to behave in a prosocial or individualistic manner is encoded in the human functional resting-state connectome. To this end, we first showed that SVO can, indeed, be decoded with high accuracy from the pattern of functional network connectivities recorded at rest. Secondly, we showed that among previously defined functional brain systems (Dosenbach et al., 2007, 2010), the cinguloopercular network provides unique information about a person's SVO classification as prosocial or individualistic compared to all other functional systems. Removing the cinguloopercular network artificially using a network lesion approach decreased the efficacy of information exchange (i.e. Global Efficiency) of the network more strongly in the individualists than in the prosocials; meaning that the cinguloopercular network is particularly relevant for cooperation-related information processing of individualists.

In summary, this evidence suggests that task-free network connectivities of the cinguloopercular network form the neural basis of SVO. This evidence sheds light on the neural mechanisms that underlie individualists' and prosocials' habitual social decisions and shows that reliance on the cinguloopercular network for task control predicts stable cooperative behavior. More broadly, individual variability in the cinguloopercular task-control network dynamics might also underlie the recently discovered 'cooperative phenotype' (Peysakhovich et al., 2014). While Peysakhovich et al. show that a domain general and temporally stable tendency to cooperate exists, our results provide a plausible neurobiological mechanism by which this is implemented in the human brain. Specifically, differential reliance on the cinguloopercular cognitive control network might render cooperative behavior consistent across tasks.

Generally, our finding that SVO can be predicted from the pattern of functional resting-state network connectivities is in agreement with a number of prior studies that found an association between resting-state dynamics and personality traits (Adelstein et al., 2011; Dawes et al., 2012; Hahn et al., 2012, 2013; Kunisato et al., 2011). Importantly, the resting-state dynamics are thought to impose constraints on the range of possible neural responses to stimulus input and task context, thereby defining personalities (Basar, 1997; Başar, 1998; Kannurpatti et al., 2012). According to our results, SVO might affect behavior in a similar fashion: Implemented in resting-state dynamics, it might determine how the network responds in social situations to the range observed in the phenotype (for a more detailed description and additional evidence supporting this notion, see Hahn et al. (2012, 2013)).

The second finding regarding the essential contribution of the cinguloopercular functional system may shed light on the question of the neural mechanisms that underlie individualists' and prosocials' stable social decisions. The cinguloopercular functional system alongside the frontoparietal system is essential for top-down control. Crucial in the context of social value orientation, however, the cinguloopercular functional system operates on a longer time scale than the frontoparietal network, providing set initiation, stable set-maintenance and error monitoring over the course of a task (Dosenbach et al., 2006, 2007, 2008). While the frontoparietal network monitors ongoing trial-by-trial processes, the cinguloopercular functional system has been shown to control goal-directed behavior over an entire task. In short, one could speculate that differences in resting-state dynamics between individualists and prosocials might entail different capabilities or preferences for strategic control behavior needed to achieve a certain goal. If one were to encode stable behavioral tendencies for cooperation by altering resting-state dynamics, constraining activation in this system thus appears most effective as virtually all cognitive processes relevant for rational, strategic decision making appear to converge here.

The same line of argument might also help to understand recent functional Magnetic Resonance Imaging (fMRI) results showing that SVO modulates neural activity in the Trust Game (van den Bos et al., 2009). Specifically, prosocials not only reciprocated more than individualists, but also showed higher activation in the insula and the right temporal-parietal-junction when they defected. On the other hand, individualists reciprocated less and showed more activation in the insula and the right temporal-parietal-junction when they reciprocated. For the anterior cingulate cortex, this pattern was reversed. If, as outlined above, resting-state dynamics impose constraints on the range of possible neural responses to stimulus input and task context, it could be assumed that the properties of resting-state dynamics in these areas affect the extent to which the insula, the temporal–parietal-junction and the anterior cingulate respond to requirements of the Trust Game. Supporting this notion, the effects found in van den Bos (2009) all lay within the cinguloopercular functional system.

The central role of the cinguloopercular network is further substantiated by the results of our virtual lesion tests which show that Global Efficiency of the brain is decreased more in individualists than in prosocials when this network was removed. Apparently, individualists depend more on the cinguloopercular system relevant for goal-directed behavior than prosocials to ensure optimal efficacy of information exchange throughout the resting brain. These results elucidate a possible neural mechanism which might explain not only why most people's first response is to cooperate and that reflecting on one's behavior can hamper this impulse (Rand et al., 2012), but also why – for a considerable number of individuals – the first impulse is non-cooperative (Bogaert et al., 2008): The fact that individualists depend more on the cinguloopercular system to ensure Global Efficiency might prevent them from readily abandoning strong control processes, making it more difficult for them to display prosocial instead of economically rational behavior—a phenomenon commonly observed in individualists (Bogaert et al., 2008). Presumably, the individualists adopt the economically more rational strategy by default as their cinguloopercular control network is more engaged. This suggests that the behavior of prosocials and individualists converges under time pressure (as shown in (Rand et al., 2012)) as the higher control processes implemented through the cinguloopercular control system cannot be provided fast enough. Since the individualists more heavily rely on the cinguloopercular functional system, time pressure ought to affect their behavior more strongly than the behavior of the prosocials.

Another line of work has viewed the cinguloopercular system not as a control network, but as a "salience network" which integrates highly processed sensory information with visceral, autonomic, and hedonic markers (Seeley et al., 2007). From this point of view, one might speculate that individualists – whom we found to rely more strongly on the cinguloopercular system to ensure efficient communication throughout the brain – integrate said markers more than the prosocials. Intuitively, one might argue that this should lead to economically less rational strategies as autonomic markers might interfere with high-level control processes. While this would contradict the view that individualists rely more strongly on rational strategy, another interpretation might be that the cinguloopercular network not only receives those markers, but actively processes them. From this point of view, individualists might adopt more rational behavior precisely because they engage their "salience network" which aids in filtering and controlling bottom-up signals.

In addition to its explanatory value, our framework also allows for the formulation of testable predictions: Based on our data, impairing neural processing within the cinguloopercular network – using for example Transcranial Magnetic Stimulation or paradigms involving specific cognitive load – will have little or no effect on the behavior of prosocials (for whom network efficiency does not depend as strongly on this system), but ought to enhance cooperative behavior in individualists as cinguloopercular control processes ought to be impaired. Furthermore, we predict that decreasing cooperative behavior in the prosocials cannot be achieved by interfering with cognitive control, but – presumably – by altering a complex network relevant for the processing of incentives and emotions as described in Declerck et al. (2013). Based on our evidence, we propose to refine the general notion

that a person's first impulse is cooperative (Rand et al., 2012) arguing that it is, in fact, a lack of neural capacity for the control of goal-directed behavior which drives prosocial acts.

Recent suggestions that individualists will recruit brain systems associated with cognitive control while prosocials will rely more on their social cognition systems (Declerck et al., 2013) are also at least partially consistent with our findings. Indeed we found that individualists depend more on the cinguloopercular system relevant for goal-directed behavior compared to prosocials to ensure optimal network efficiency, but our results do not speak to the inverse claim that prosocials rely more on social cognition systems. One possibility is that "disengaging" the cinguloopercular control system is sufficient to foster cooperative behavior in the group of prosocials.

In summary, we show that context-independent functional connectivity of the cinguloopercular network serves as the large-scale neural substrate of stable preferences for social outcomes. More generally, our results are in line with the notion that stable differences of the resting-state functional connectome are at the heart of individual differences in human behavior, specifically cooperation. Our results are in accordance with recent models of rest-task interaction (Hahn et al., 2012, 2013) and provide a unifying framework for the interpretation of recent functional imaging (van den Bos et al., 2009) and behavioral studies (Bogaert et al., 2008; Rand et al., 2012). Future investigations will have to provide models directly linking stable behavioral tendencies, resting-state dynamics, task-related activation and overt behavior.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2015.05.093.

Acknowledgments

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