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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

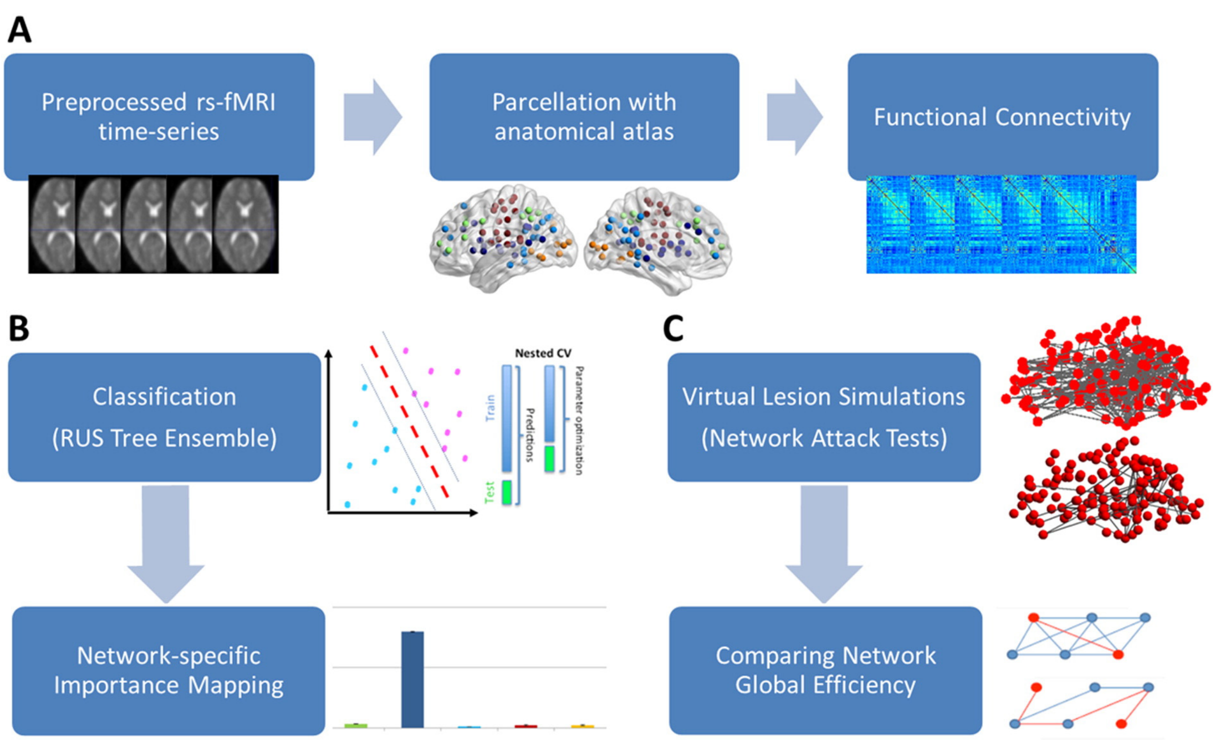

Fig. 1. Data processing and analysis strategies. A) First, resting-state fMRI data was preprocessed, time-series for each region in the Dosenbach atlas were extracted and a functional connectivity matrix was computed for each participant. B) Using a multivariate pattern classification approach, we assessed 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.