

The influence of relationship closeness on default-mode network connectivity during social interactions

Dominic S. Fareri,¹ David V. Smith,² and Mauricio R. Delgado³

¹Gordon F. Derner School of Psychology, Adelphi University, Garden City, NY 11530, USA, ²Department of Psychology, Temple University, Philadelphia, PA 19122, USA, and ³Department of Psychology, Rutgers University, Newark, NJ 07102, USA

Correspondence should be addressed to Dominic S. Fareri, Gordon F. Derner School of Psychology, Adelphi University, Blodgett Hall, Rm. 212B, 1 South Avenue, Garden City, NY 11530, USA. E-mail: dfareri@adelphi.edu.

Abstract

Reciprocated trust plays a critical role in forming and maintaining relationships, and has consistently been shown to implicate neural circuits involved in reward-related processing and social cognition. Less is known about neural network connectivity during social interactions involving trust, however, particularly as a function of closeness between an investor and a trustee. We examined network reactivity and connectivity in participants who played an economic trust game with close friends, strangers and a computer. Network reactivity analyses showed enhanced activation of the default-mode network (DMN) to social relative to non-social outcomes. A novel network psychophysiological interaction (nPPI) analysis revealed enhanced connectivity between the DMN and the superior frontal gyrus and superior parietal lobule when experiencing reciprocated *vs* violated trust from friends relative to strangers. Such connectivity tracked with differences in self-reported social closeness with these partners. Interestingly, reactivity of the executive control network (ECN), involved in decision processes, demonstrated no social *vs* non-social preference, and ECN-ventral striatum connectivity did not track social closeness. Taken together, these novel findings suggest that DMN interacts with components of attention and control networks to signal the relative importance of positive experiences with close others *vs* strangers.

Key words: default-mode network; connectivity; trust; reciprocity; social closeness

Introduction

Trust and reciprocity are cornerstones of forming and maintaining close relationships (reviewed in Simpson, 2007; Krueger and Meyer-Lindenberg, 2019). Indeed, deciding whether to trust or reciprocate generosity depends upon our ability to integrate prior experiences and knowledge about others with future expectations of them (reviewed in Fareri, 2019). Substantial evidence suggests that regions supporting social cognition and reward circuitry (e.g. medial prefrontal cortex [mPFC], striatum) help to distinguish between close and distant others

and integrate prior expectations with future choices during social interactions (Krienen *et al.*, 2010; Tamir and Mitchell, 2012; Fareri *et al.*, 2012a, 2015). However, the way in which close relationships shape the function and connectivity of large-scale networks during social interactions is largely unknown, which is a critical point to consider given recent work demonstrating representation of social space in a network of ‘social brain’ regions (Parkinson *et al.*, 2017, 2018).

We have previously demonstrated that information about relationship closeness can shape the representation of shared

Received: 22 October 2019; Revised: 7 January 2020; Accepted: 6 March 2020

© The Author(s) 2020. Published by Oxford University Press.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

positive experiences and of reciprocity at the behavioral and neural levels. The ventral striatum (VS) shows enhanced activation when earning a shared monetary reward with a close friend relative to a stranger (Fareri et al., 2012b), and people compute an added social value when experiencing reciprocity from a friend contingent upon interpersonal aspects of the friendship (Fareri et al., 2015). These findings have built upon extant literature suggesting that neural circuits supporting reward valuation (e.g. striatum, ventral mPFC; Haber and Knutson, 2010; Bartra et al., 2013) are also sensitive to social information (for review see Fareri and Delgado, 2014; Ruff and Fehr, 2014), representing the value of experienced and anticipated social rewards (e.g. social approval, praise) (Izuma et al., 2008; Mobbs et al., 2009; Izuma et al., 2010; Smith et al., 2010; Chib et al., 2018) and the encoding of probabilistic social feedback (i.e. acceptance, rejection) (e.g. Somerville et al., 2006; Jones et al., 2011).

While relationships clearly shape neurocomputational signals of social value, much less is known about how the context of close relationships influences the response and connectivity of networks of regions—in particular, networks that respond to social information during trust-based interactions. The DMN, which is often most active at rest (Raichle et al., 2001; Buckner and Vincent, 2007; Buckner and DiNicola, 2019), is comprised of structures including the precuneus, mPFC, posterior cingulate cortex (PCC) and temporoparietal junction. While the DMN is posited to be involved in self-referential thought, it has also been theorized to generate predictions based on past experiences to inform future action (Barrett, 2017), and its subcomponents are all frequently implicated in social cognition (Adolphs, 2009; Stanley and Adolphs, 2013). Together, these findings have prompted additional hypotheses that a major function of the default state of the brain is to prime us for social cognition (Schilbach et al., 2008; Spunt et al., 2015; Meyer, 2019). Yet, how and to where such social information gets communicated during social interactions is not well-established.

A host of networks may be involved in representing and integrating information about close others during social interactions (Laurita et al., 2017). One possibility is that the DMN interacts with reward circuitry to integrate the context of a close relationship with experienced reciprocity in computing social reward value, as both activation in both mPFC and VS correlate with computational social value signals (e.g. Fareri et al., 2015). An alternative possibility is that the DMN may interact with components of control and attention-related networks (e.g. executive control network [ECN], salience network, frontoparietal network) to integrate information about the context of close relationships and inferred intentions of close others (relative to strangers) during trust-based interactions (Igelström et al., 2016; Monfardini et al., 2016; Bellucci et al., 2019). The DMN may thus draw on past experiences to aid in social prediction (Barrett, 2017). Relatedly, other networks, such as the ECN—which includes lateral PFC, anterior insula, mPFC (anterior and paracingulate cortices; Smith et al., 2009) and is broadly implicated in goal-directed behavior—may be involved with processing positive and negative outcomes more generally. This would be consistent with the idea that social processes may involve subnetworks that may be exclusive from those supporting more general cognitive function (Meyer and Lieberman, 2012).

The goal of this study was to characterize how close relationships influence network function and connectivity during trust-based social interactions with friends and strangers. We employed a novel form of psychophysiological interaction analysis (Friston et al., 1997)—network PPI (nPPI) (Utevsky et al., 2017). Unlike seed-based approaches, which examine connectivity

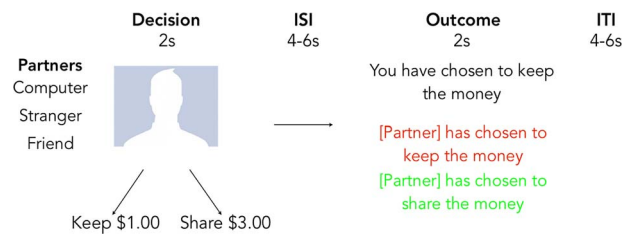


Fig. 1. Task schematic. Participants played an iterated economic trust game with three different partners: a computer, a same-sex stranger and a same-sex close friend (see Fareri et al., 2015).

between specific voxels or a specific region and the rest of the brain, nPPI capitalizes on the dynamics of entire neural networks and allows for the examination of network connectivity during task conditions. We hypothesized that the DMN would demonstrate increased reactivity to social relative to non-social (i.e. computer) conditions, and that this might be heightened as a function of the relationship one has with a partner (i.e. friend > stranger). Based on our prior work, we further hypothesized that the DMN would exhibit increased connectivity with reward-related circuitry (i.e. VS) when experiencing reciprocity from a close friend relative to a stranger, and that this pattern would vary with the degree of social closeness felt towards friends and strangers. We also tested whether the ECN, which has been shown to facilitate goal-directed processes in general as well as orientation towards socially relevant stimuli (Seeley et al., 2007; Smith et al., 2009; Utevsky et al., 2017) demonstrated differential reactivity and connectivity during social interactions for friends relative to strangers. However, we did not expect that this would vary with self-reported social closeness.

Methods

Participants

Secondary data analyses were conducted on data collected from 26 participants (14 F/12 M, mean age = 21.36, s.d. = 3.67) in a previously published study from our group (Fareri et al., 2015). Participants had no history of head trauma or psychiatric illness and all participants provided informed consent. All procedures were approved by the Rutgers University Institutional Review Board.

Experimental paradigm

All participants played an iterated economic trust game with three different partners (Figure 1)—a same-sex close friend, a same-sex stranger (laboratory confederate) and a computer (Fareri et al., 2015). Participants were asked to bring a same-sex close friend with them to the experimental session at the Rutgers University Brain Imaging Center (RUBIC, Newark, NJ). Participants and their friends met a same-sex confederate (stranger) at the imaging center who was portrayed as another participant in the study, but was actually a member of the laboratory team. Briefly, participants undergoing functional magnetic resonance imaging (fMRI) were in the role of investor in the trust game (Berg et al., 1995; King-Casas et al., 2005) and the three partners were in the role of trustee. Participants chose whether to invest money with or keep money from one of their three partners on each trial (event-related design, partner presentation was randomly presented). After submitting their decision, if they chose to invest with a partner, participants experienced a jittered interstimulus interval (ISI) during which they awaited their partner's response (i.e. reciprocity, violation of

trust). All participants were trained together on the trust game task in the scanner control room, and were under the impression they would be interacting in real time over networked computers between the scanner and control room. In reality, friends' and strangers' behavior was preprogrammed into the task script (E-Prime 2.0; Psychology Software Tools, Pittsburgh, PA), such that all partners provided 50% reinforcement rates (i.e. partners reciprocate and defect with equivalent probability) on trials in which the fMRI participant decided to invest (see Fareri et al., 2015 for complete details). Prior to the start of the task, fMRI participants filled out the inclusion of other in self scale (IOS), a self-report questionnaire assessing social closeness (Aron et al., 1992) with their three partners (friend, stranger and computer).

fMRI acquisition and preprocessing

Neuroimaging data were acquired on a 3 T Siemens Magnetom Trio whole-body scanner at the RUBIC (Newark, NJ). Structural images were collected using a standard T1-weighted MPRAGE sequence (256 × 256 matrix; Field of View (FOV) = 256 mm; 1761 mm sagittal slices). Functional images were acquired using a single shot gradient echoplanar imaging (EPI) sequence (TR = 2000 ms, TE = 30 ms, FOV = 192, flip angle = 90°, bandwidth = 2232 Hz/Px, echo spacing = 0.51), comprising 33 oblique-axial slices (3 × 3 × 3 mm voxels) parallel to the anterior-posterior commissure line, collected in an ascending-interleaved order. Data were preprocessed using a combination of custom scripts (<https://github.com/rordenlab/spmScripts>) for SPM12 and FSL (FMRIB Software Library) v5.09). Standard preprocessing steps including motion correction, brain extraction and coregistration were performed in SPM. Functional data were acquired in an ascending-interleaved fashion; slice-time correction was performed in SPM aligning to the first slice. Motion artifact was addressed through an automated independent components analysis approach employing ICA-AROMA in FSL (Pruim et al., 2015). This approach identifies noisy components in single subject functional data by computing the degree to which each component is characterized by characteristic patterns of motion artifact (i.e. high-frequency signals, correlation with standard realignment parameters, overlap with cerebrospinal fluid (CSF) and edge voxels); components that highly identify with these characteristic patterns are removed from single subject functional data at the single run level via linear regression. The resulting denoised data serve as input to first-level models. We additionally computed estimates of frame-to-frame motion using MCFLIRT in FSL to derive relative mean framewise displacement, which were subsequently used as an additional group level covariate in offline analyses of relationships between connectivity and behavior (see below); this allowed for assessment of whether observed results were not due solely to motion.

Network psychophysiological interaction analysis

We employed a novel connectivity approach, nPPI (Utevsky et al., 2017), aimed at assessing changes in task-based connectivity of canonical neural networks. nPPI improves upon seed-based connectivity approaches by leveraging the fact that the brain is organized into functional neural networks during both task and rest states (Smith et al., 2009). nPPI treats entire functional networks as 'seeds' to capture functional network dynamics and maps those to interactions with other regions of the brain at voxel level. Specifically, we captured network dynamics using a spatial regression, where the functional data were regressed onto a

four-dimensional design matrix consisting of the 10 canonical networks from prior work (Smith et al., 2009). Notably, this process is identical to the first stage of the popular dual-regression analysis (Filippini et al., 2009; Nickerson et al., 2017) and extends it by including psychophysiological interactions with specific networks of interest (Friston et al., 1997; Smith et al., 2016) while controlling for the dynamics of other networks in the analysis (McLaren et al., 2012).

We were interested in investigating whether the default-mode network (DMN) demonstrates differential patterns of effective connectivity during social interactions involving close friends and strangers. Specifically, we focused on how DMN connectivity was altered during the processing of positive (i.e. reciprocity) vs negative (i.e. defection) trust game outcomes as experienced from these different partners. We extracted time series from 10 canonical resting state networks as identified by Smith et al. (2009). We constructed a General Linear Model (GLM) using FEAT (fMRI Expert Analysis Tool) in FSL with regressors at the first level that modeled: the decision phase (agnostic to partner and participant choice), and outcome phase (separate regressors for experienced reciprocity and defection from each partner), and nuisance regressors modeling missed trials and the outcome phase of trials in which participants defected. The first-level nPPI models also included the physiological timeseries from each network (10 total). We constructed separate first-level generalized nPPI models to examine connectivity of the DMN and the ECN, such that the PPI regressors in one model were comprised of interactions between the DMN timeseries and task regressors, while in the other we modeled interactions between the ECN timeseries and task regressors. First level GLMs were conducted at the single run level, and were combined for each subject at the second level. Group-level whole-brain analyses were corrected for multiple comparisons using permutation testing (10 000 permutations) and threshold-free cluster enhancement as implemented in FSL with variance smoothing (set to 2.13) via randomize. Group-level analyses included a mean-centered subject-level covariate representing the difference in self-reported social closeness between fMRI participants and their friends relative to strangers (i.e. IOS friend-IOS stranger).

To initially characterize the profile of the functional response of canonical networks—DMN, ECN—during the outcome phase of the task, we regressed the timeseries of each of these networks on a simpler model including only the 10 task-based regressors (decision phase: keep, share; outcome phase: reciprocate, defect for each partner, participant keep, missed trials). Parameter estimates indexing the response of each network during trust game outcomes with each partner were extracted and plotted, with differences between partner and outcome conditions tested using a repeated measure ANOVA in jamovi (jamovi.org).

Results

Enhanced DMN reactivity for social outcomes

In order to establish whether the DMN may be preferentially sensitive to social relative to non-social outcomes in comparison to the ECN, we first examined the reactivity of these networks during the outcome phase of the trust game. Regression of network timeseries from the DMN and ECN revealed divergent patterns of reactivity (Figure 2). A 2 (network) × 3 (partner) × 2 (outcome) repeated measures ANOVA revealed a significant partner × network interaction ($F_{(2,50)} = 11.88$, $P < 0.001$, Mauchly's

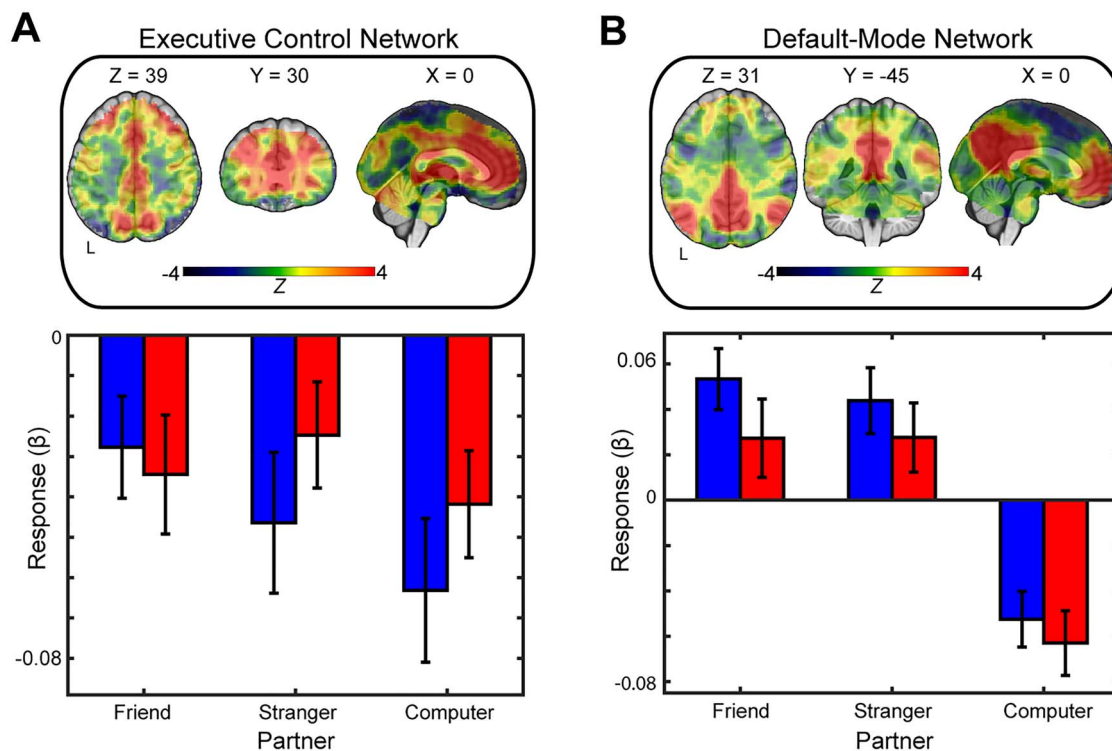


Fig. 2. Network reactivity. Regression of DMN and ECN timeseries on task conditions during social outcome processing revealed enhanced reactivity for social relative to non-social outcomes in the DMN (Panel B), but not the ECN (Panel A) (blue bars = reciprocation of trust; red bars = violation of trust). Warm colors on the brain maps represent regions that comprise the networks of interest.

test of sphericity: $W = .996$, $P = 0.95$). Participants demonstrated stronger recruitment of the DMN compared to the ECN when experiencing outcomes with a close friend ($t_{(58,2)} = 4.38$, $P < .001$) and a stranger ($t_{(58,2)} = 4.38$, $P < .001$), but not when experiencing outcomes with a computer ($t_{(58,2)} = -0.32$, $P > 0.75$). This analysis also revealed a significant outcome \times network interaction ($F_{(1,25)} = 5.14$, $P < 0.04$). Participants demonstrated stronger activation of the DMN compared to the ECN when experiencing reciprocity ($t_{(37,9)} = 4.30$, $P < .001$), but not violations ($t_{(37,9)} = 2.19$, $P = .104$), of trust. Post-hoc tests were corrected using a sequential Bonferroni correction (Holm, 1979). All other interactions were non-significant ($P_s > 0.35$). We note that the finding of enhanced DMN reactivity to social relative to non-social outcomes holds when examining the DMN in isolation using a 2 (outcome) \times 3 (partner) repeated measures ANOVA (main effect of partner: $F_{(2,50)} = 34.36$, $P < .001$, Mauchly's test of sphericity: $W = .951$, $P = .549$; friend > computer, $P < .001$; stranger > computer, $P < .001$).

As an additional post-hoc analysis, we tested whether the DMN timecourse was being driven by a single node of the network. We extracted the raw timecourses (i.e. task-independent) from peak seed locations within each of the mPFC (2, 56, -4), bilateral temporoparietal junction (TPJ) (left: -44, -60, 24; right: 54, -62, 28) and PCC/Precuneus (2, -58, 30). Results indicated that the timecourse of each node of the network was highly correlated with the timecourse of the entire DMN, with the PCC/Precuneus being the most strongly correlated (mPFC: $r = .62$; lTPJ: $r = .70$; rTPJ: $r = .69$; PCC/Precuneus: $r = .84$; see Supplemental Figure S1). After partialling out the contributions of other nodes within the network, however, we note that PCC/Precuneus appeared to contributing the most to the DMN timecourse (mPFC: $r = .25$; lTPJ: $r = .32$; rTPJ: $r = .17$; see Supplemental Figure S2; Utevsy et al., 2014).

DMN connectivity during social outcomes is sensitive to relative differences in social closeness

Based on both our prior work (Fareri et al., 2012a, 2015) and the above results demonstrating increased DMN reactivity to social relative to non-social trust game outcomes, we next investigated whether network connectivity during social interactions changed as a function of both partner and social outcome valence. We conducted a nPPI analysis to address this question, though we note that we interpret these results cautiously given that our sample size is less than the minimum typically suggested ($n = 40$) to assess brain-behavior relationships (Yarkoni and Braver, 2010). Specifically, we aimed to investigate whether the DMN would show increased connectivity when experiencing social reward (reciprocity) compared to social punishment (defection) from friends relative to strangers. We tested this question by conducting a double subtraction of (friend reciprocate > friend defect) > (stranger reciprocate > stranger defect). Importantly, given our prior findings showing that between subject differences in social closeness with friends and strangers plays a role in neural representations of social outcomes (Fareri et al., 2012a, 2015), we also included a between-subjects social closeness covariate (friend-stranger social closeness difference score, mean centered) for each participant. This analysis revealed significant coupling of the DMN with the superior frontal gyrus (x, y, z [MNI] = 18, 46, 40) and superior parietal lobule (x, y, z [MNI] = 10, 22, 42) ($P < .025$, whole-brain corrected with threshold-free cluster enhancement (TFCE); Figure 3). For visualization purposes, we extracted connectivity estimates from these clusters and plotted them against the difference in reported social closeness between friends and strangers; scatterplots (Figure 3) demonstrate that greater closeness exhibited towards a friend (vs a stranger) was associated with more positive coupling between the DMN

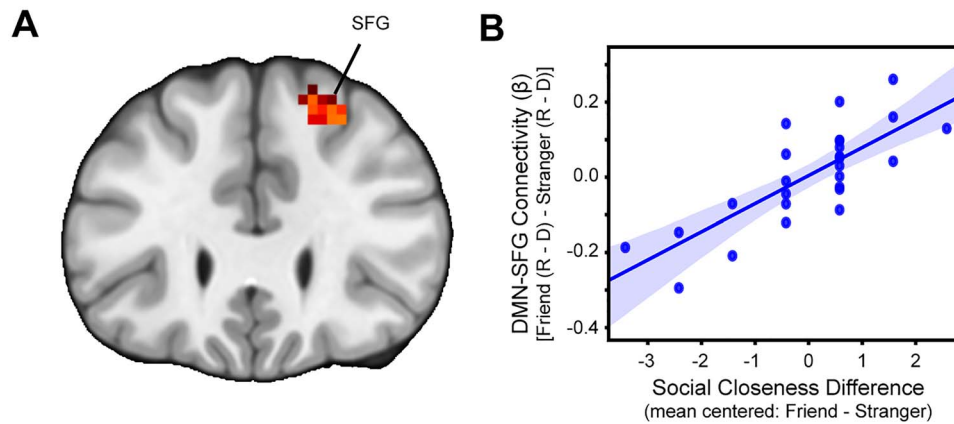


Fig. 3. nPPI: DMN connectivity. Network PPI revealed enhanced coupling of the DMN with superior frontal gyrus when participants experienced reciprocity relative to violations of trust from a friend relative to a stranger (Panel A), which correlated with differences in self-reported social closeness (IOS) with friends vs strangers (Panel B).

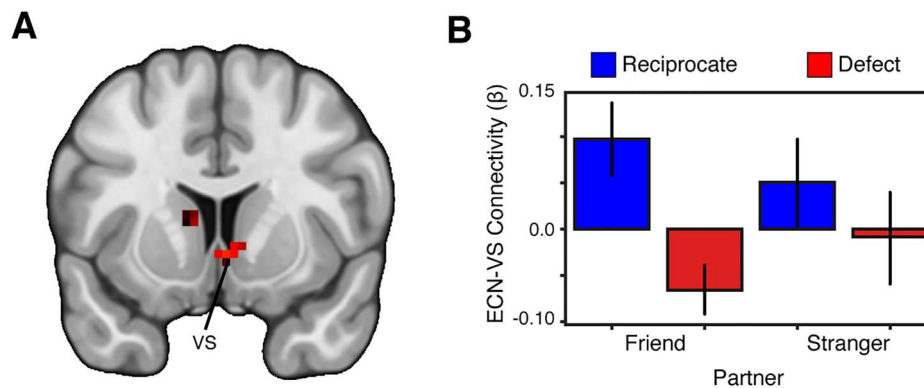


Fig. 4. nPPI: ECN connectivity. Targeted nPPI analyses during interactions with a close friend using the ECN as a seed region revealed enhanced coupling with the bilateral striatum (Panel A) during reciprocity relative to violations of trust (Panel B). Post-hoc tests indicated no significant difference in ECN connectivity with the VS during interactions with a stranger.

and these regions. Similar patterns emerged for clusters in the fusiform gyrus ($x, y, z = 17, 12, 21$) and the lingual gyrus ($x, y, z = 32, 19, 19$), but are not depicted here. Interestingly, conducting the same double subtraction using the ECN as a seed network revealed no clusters representing significant connectivity.

Connectivity with reward circuitry during interactions with a friend

Given our prior work demonstrating a link between activation in mPFC and the VS during experienced reciprocity from a friend (Fareri et al., 2015), we conducted targeted PPI contrasts examining both DMN and ECN connectivity during reciprocity (vs defection) experienced with a close friend specifically. Interestingly, these analyses revealed no voxels exhibiting significant connectivity with the DMN. However, we did find enhanced connectivity between the ECN and bilateral striatum when experiencing reciprocity from a close friend relative to a stranger at a slightly more lenient threshold (TFCE, $P < .05$; see Figure 4). As an exploratory measure, we also extracted connectivity estimates from these same ventral striatal voxels ($x, y, z = 3, 11, -4$) during experiences with a stranger; a *post-hoc* 2 (outcome) \times 2 (partner) repeated measures ANOVA revealed no difference in ECN-VS connectivity during experiences with a friend relative to a stranger ($F_{(1,25)} = 0.02, P > 0.9$) and no interaction ($F_{(1,25)} = 1.69, P < 0.2$).

Discussion

The goal of this study was to investigate how the closeness of a social relationship shapes the connectivity of canonical neural networks during experiences of reciprocity and violations of trust. Taking a network-based approach, our findings demonstrated a preference for social relative to non-social outcomes in terms of the DMN response to experienced reciprocity relative to the ECN. Novel nPPI analyses further revealed that the DMN exhibits enhanced connectivity with later prefrontal and lateral parietal regions when experiencing reciprocity relative to violations of trust from a friend relative to a stranger, which is more positive the closer one feels to a friend. Consistent with network reactivity analyses, the ECN did not demonstrate differential connectivity as a function of outcome valence and relationship context. Interestingly, targeted analyses revealed that the ECN did show significant connectivity with the striatum bilaterally, specifically when experiencing reciprocity relative to violations of trust from a friend only, whereas this pattern of connectivity with the striatum was not observed in the DMN. Taken together, our results suggest that: (1) the DMN demonstrates a preference for socially relevant outcomes; and that (2) it may interact with components of networks involved in attention and cognitive control to differentially represent the importance of social experiences based on relationship closeness.

The role of the DMN has been classically viewed through the lens of resting-state activation and connectivity. Given

that this network demonstrates robust activation at rest in task-negative states (Raichle *et al.*, 2001; Utevsky *et al.*, 2014), it has been suggested that the DMN plays a significant role in self-referential processing (Gusnard *et al.*, 2001), memory consolidation and maintenance of intrinsic neural relationships (Buckner and Vincent, 2007). However, an alternative hypothesis built around findings that the DMN shows increased activation during self and social processes (reviewed in Buckner and DiNicola, 2019) suggests that the DMN may prime us for social function, and that social cognition may in fact be our brain's default state (Meyer, 2019). Regions comprising the DMN (i.e. mPFC, PCC/precuneus, TPJ) are broadly implicated in self-other representation, mentalizing/theory of mind, social perception, social appraisals and decision-making (Adolphs *et al.*, 1998; Amodio and Frith, 2006; Mitchell *et al.*, 2006; Adolphs, 2010; Krienen *et al.*, 2010; Koster-Hale and Saxe, 2013; Stanley and Adolphs, 2013; Deen *et al.*, 2015; Spunt *et al.*, 2015; Stanley, 2016). Activation within the DMN during rest components of a task (i.e. fixation) and when engaged in mentalizing shows significant overlap (Schilbach *et al.*, 2008; Spunt *et al.*, 2015) and is posited to form a social-affective subnetwork implicated in social cognition and emotional processes (Amft *et al.*, 2015; Eickhoff *et al.*, 2016; Alcalá-López *et al.*, 2018). Our finding that the DMN shows increased task-based reactivity (relative to the ECN) when processing social vs non-social outcomes supports the idea that the DMN preferentially engages in social cognitive processes involving self-other representation. Further, the increased reactivity of the DMN relative to the ECN during reciprocity suggests that these socially rewarding experiences may be encoded as more valued or salient than non-social rewards (Phan *et al.*, 2010; Fareri *et al.*, 2015).

We also found that the DMN exhibited enhanced connectivity with the superior frontal gyrus and superior parietal lobule—components of the frontoparietal control network—during reciprocity relative to violations of trust when interacting with close friends vs strangers. Activation within this network, involved in directing of control/attention to facilitate goal-directed behavior (Corbetta and Shulman, 2002; Vincent *et al.*, 2008), decodes tasks as a function of available performance incentives, which in turn facilitates behavior in a target detection task (Etzel *et al.*, 2016). Subnetworks within the frontoparietal system show connectivity with the DMN that appears to be specific to social and internally directed processes (Nihonsugi *et al.*, 2015; Xin and Lei, 2015; Bellucci *et al.*, 2019; Kam *et al.*, 2019). Therefore, interactions between the DMN and frontoparietal regions in our task suggest that the incentive value of reciprocity from a close friend may capture attention because of its overlap in self-other relevance based on past experience, which subsequently informs future predictions and choices (Barrett, 2017). An alternative, yet plausible account based on evidence that the DMN may represent personality information (Hassabis *et al.*, 2014), is that the DMN may be recruiting models of others' personalities when interpreting outcomes of social interactions and relaying this information to attention and control related regions to facilitate future predictions and impressions of others.

The use of a network approach to task-based connectivity—nPPI—offers novel insight into the way in which canonical networks interact with other regions during social interactions involving trust. Previous work employing seed-based PPI has highlighted connectivity between the striatum and cognitive control regions (i.e. dorsal anterior cingulate cortex (dACC), ventrolateral prefrontal cortex (vlPFC)) when deciding to trust outgroup members (Hughes *et al.*, 2016) and when experiencing violations of trust (Fouragnan *et al.*, 2013). While a seed-based

approach can be informative regarding our understanding of communication between brain regions (Smith *et al.*, 2016), it is limited in its ability to provide broader insight to network dynamics during task-based conditions (Cole *et al.*, 2010). Evidence suggests a high degree of variability in connectivity of a region (e.g. precuneus) depending on the precise location of voxels within that region chosen as the 'seed' (Cole *et al.*, 2010). Second, specific regions or nodes within a known network may demonstrate heterogeneity in function and connectivity based on the nature and difficulty of the cognitive process being investigated: activation in overlapping components of the PCC, for example, demonstrate functional connectivity with multiple neural networks (i.e. frontoparietal networks, cognitive control networks, DMN) as a function of in the moment cognitive and attentional demands (Leech *et al.*, 2011; Leech *et al.*, 2012). Related work has demonstrated that the precuneus exhibits increased connectivity with the DMN at rest, but increased connectivity with the frontoparietal network during task-states (Utevsky *et al.*, 2014). The treatment of entire networks as seeds in our approach allowed us to demonstrate that the DMN is critical for taking into account information about our social relationships when we are interacting with others and communicating that with components of frontoparietal networks possibly to indicate preferential orienting of attention. The ECN, on the other hand, appears less sensitive to the relative difference between social outcomes as a function of relationship closeness *per se*.

Our implementation of nPPI provides novel insight into the ways in which network connectivity is influenced by relationships during social interactions, yet the present study is not without limitations. First, while PPI analyses in general provide more in the way of characterizing neural interactions during psychological processes than connectivity analyses relying on simple correlation (Friston, 2009, 2011; Smith *et al.*, 2016), it does have multiple interpretations (Smith *et al.*, 2016). For example, clusters emerging as representing a significant PPI effect may reflect a change in connectivity due to the psychological context (e.g. reciprocity vs violation of trust changes the interaction between the DMN and superior frontal gyrus). Alternatively, a significant PPI effect may indicate a change in the response of a target region to a specific context (e.g. reciprocity vs violation) by activation in a seed (e.g. DMN). Second, these points also indicate that directionality of information flow can be ambiguous and is not directly indicated by a significant PPI result. Third, we chose to extract network time-series in this study using a 10-network parcellation as suggested by Smith *et al.* (2009); we chose this specific parcellation due to its more general anatomical definition of each network and lack of more targeted predictions about subnetworks or network nodes in our task. However, recent work (including studies cited here) has specified more fine-grained parcellations of the DMN and other networks (Dixon *et al.*, 2018; Buckner and DiNicola, 2019; Ji *et al.*, 2019). Future work looking at subnetwork connectivity during social interactions may be better able to characterize specific contributions to encoding of factors such as relationship closeness and outcome value, and may be able to identify how these processes may break down in samples with social difficulties. Fourth, we chose to keep rates of reciprocity in the trust game consistent across partners (50%), consistent with previous work from our group and to isolate any differences in neural responses to outcomes to partner context. However, it is possible that this may not best capture real-life dynamics within relationships. Additionally, while our results also appear specific to positive relative to negative social outcomes, other recent work (Park and Young, 2020) demonstrates a reduced role for one node within the DMN (rTPJ)

when experiencing trust violations from a close friend that may be associated with a lower likelihood of updating impressions of close friends. Future work could probe changes in network connectivity during social reward processing and impression updating under more naturalistic contexts when violations of trust from friends and strangers may vary at different rates. Finally, while we are encouraged and intrigued by the findings reported here given that they survive rigorous correction for multiple comparisons (i.e. permutation testing), we interpret them cautiously, given our sample size.

Close relationships provide an important social context within which many of our day to day experiences occur and are characterized by repeated instances of trust and reciprocity. Building on previous findings indicating that social relationships influence the reward value of shared social experiences and that the DMN has a specialized role in social cognition, our results demonstrate that the context of close relationships shapes functional network dynamics during social interactions as a function of the closeness people feel towards a partner. These results and our approach have important implications for clinical samples characterized by difficulties with social cognition and forming relationships (e.g. autism, borderline personality disorder, schizophrenia) (Alcalá-López et al., 2019) and individuals who may have a history of adverse social experiences (McLaughlin et al., 2019). For example, hypoconnectivity has been observed between networks implicated in cognitive control and goal-directed processes (ECN) and processing of social stimuli (face-processing network) in relation to increased levels of autistic traits (Young et al., 2015), while individuals with a history of early life caregiving adversity show hyperconnectivity at rest between the VS and mPFC that is associated with poor social regulation (Fareri et al., 2017). Taking an nPPI approach to examine how relationship context and other social factors impact connectivity during social interactions may help more precisely pinpoint links between neural function and breakdowns in social behavior, subsequently leading to targets for intervention.

Supplementary data

Supplementary data are available at SCAN online.

Conflict of interest

The authors declare no conflict of interest.

Acknowledgements

This work was supported by funding from the National Institutes of Health (MH084081 to M.R.D. and DA046733 to D.V.S.) and the McKnight Foundation (to M.R.D.).

References

- Adolphs, R. (2009). The social brain: neural basis of social knowledge. *Annual Review of Psychology*, **60**, 693–716.
- Adolphs, R. (2010). What does the amygdala contribute to social cognition? *Annals of the New York Academy of Sciences*, **1191**, 42–61.
- Adolphs, R., Tranel, D., Damasio, A. (1998). The human amygdala in social judgment. *Nature*, **393**, 470–4.
- Alcalá-López, D., Smallwood, J., Jefferies, E., et al. (2018). Computing the social brain connectome across systems and states. *Cerebral Cortex*, **28**, 2207–32.
- Alcalá-López, D., Vogeley, K., Binkofski, F., et al. (2019). Building blocks of social cognition: mirror, mentalize, share? *Cortex*, **118**, 4–18.
- Amft, M., Bzdok, D., Laird, A.R., et al. (2015). Definition and characterization of an extended social-affective default network. *Brain Structure and Function*, **220**, 1031–49.
- Amodio, D.M., Frith, C.D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, **7**, 268–77.
- Aron, A., Aron, E.N., Smollan, D. (1992). Inclusion of other in the self scale and the structure of interpersonal closeness. *Journal of Personality and Social Psychology*, **63**, 596–612.
- Barrett, L.F. (2017). The theory of constructed emotion: an active inference account of interoception and categorization. *Social Cognitive and Affective Neuroscience*, **12**, 1–23.
- Bartra, O., McGuire, J.T., Kable, J.W. (2013). The valuation system: a coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. *NeuroImage*, **76**, 412–27.
- Bellucci, G., Hahn, T., Deshpande, G., et al. (2019). Functional connectivity of specific resting-state networks predicts trust and reciprocity in the trust game. *Cognitive, Affective, & Behavioral Neuroscience*, **19**(3), 1–12.
- Berg, J., Dickhaut, J., McCabe, K. (1995). Trust, reciprocity, and social history. *Games and Economic Behavior*, **10**(1), 122–42.
- Buckner, R.L., DiNicola, L.M. (2019). The brain's default network: updated anatomy, physiology and evolving insights. *Nature Reviews Neuroscience*, **20**(10), 593–608.
- Buckner, R.L., Vincent, J.L. (2007). Unrest at rest: default activity and spontaneous network correlations. *NeuroImage*, **37**, 1091–6; discussion 1097–9.
- Chib, V.S., Adachi, R., O'Doherty, J.P. (2018). Neural substrates of social facilitation effects on incentive-based performance. *Social Cognitive and Affective Neuroscience*, **13**, 391–403.
- Cole, D.M., Smith, S.M., Beckmann, C.F. (2010). Advances and pitfalls in the analysis and interpretation of resting-state FMRI data. *Frontiers in Systems Neuroscience*, **4**, 8.
- Corbetta, M., Shulman, G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, **3**, 201–15.
- Deen, B., Koldewyn, K., Kanwisher, N., et al. (2015). Functional organization of social perception and cognition in the superior temporal sulcus. *Cerebral Cortex*, **25**, 4596–609.
- Dixon, M.L., Vega, A.D.L., Mills, C., et al. (2018). Heterogeneity within the frontoparietal control network and its relationship to the default and dorsal attention networks. *Proceedings of the National Academy of Sciences*, **115**, E1598–607.
- Eickhoff, S.B., Laird, A.R., Fox, P.T., et al. (2016). Functional segregation of the human dorsomedial prefrontal cortex. *Cerebral Cortex*, **26**, 304–21.
- Etzel, J.A., Cole, M.W., Zacks, J.M., et al. (2016). Reward motivation enhances task coding in frontoparietal cortex. *Cerebral Cortex*, **26**, 1647–59.
- Fareri, D.S. (2019). Neurobehavioral mechanisms supporting trust and reciprocity. *Frontiers in Human Neuroscience*, **13**:271.
- Fareri, D.S., Delgado, M.R. (2014). The importance of social rewards and social networks in the human brain. *The Neuroscientist* **20**(4), 387–402.
- Fareri, D.S., Chang, L.J., Delgado, M.R. (2012a). Effects of direct social experience on trust decisions and neural reward circuitry. *Frontiers in Neuroscience*, **6**, 148–17.
- Fareri, D.S., Niznikiewicz, M.A., Lee, V.K., et al. (2012b). Social network modulation of reward-related signals. *Journal of Neuroscience*, **32**, 9045–52.

- Fareri, D.S., Chang, L.J., Delgado, M.R. (2015). Computational substrates of social value in interpersonal collaboration. *Journal of Neuroscience*, **35**, 8170–80.
- Fareri, D.S., Gabard-Durnam, L., Goff, B., et al. (2017). Altered ventral striatal–medial prefrontal cortex resting-state connectivity mediates adolescent social problems after early institutional care. *Development and Psychopathology*, **29**(5), 1865–76.
- Fouragnan, E., Chierchia, G., Greiner, S., Neveu, R., Avesani, P., Coricelli, G. (2013). Reputational priors magnify striatal responses to violations of trust. *Journal of Neuroscience*, **33**(8), 3602–11.
- Filippini, N., MacIntosh, B.J., Hough, M.G., et al. (2009). Distinct patterns of brain activity in young carriers of the APOE- ϵ 4 allele. *Proceedings of the National Academy of Sciences*, **106**, 7209–14.
- Friston, K. (2009). Causal modelling and brain connectivity in functional magnetic resonance imaging. *PLoS Biology*.
- Friston, K.J., Buechel, C., Fink, G.R., et al. (1997). Psychophysiological and modulatory interactions in neuroimaging. *NeuroImage*, **6**, 218–29.
- Friston, K.J. (2011). Functional and effective connectivity: a review. *Brain Connectivity*, **1**(1), 13–36.
- Gusnard, D.A., Akbudak, E., Shulman, G.L., et al. (2001). Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 4259–64.
- Haber, S.N., Knutson, B. (2010). The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology*, **35**(1), 4–26.
- Hassabis, D., Spreng, R.N., Rusu, A.A., Robbins, C.A., Mar, R.A., Schacter, D.L. (2014). Imagine all the people: how the brain creates and uses personality models to predict behavior. *Cerebral Cortex*, **24**(8), 1979–87.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 65–70.
- Hughes, B.L., Ambady, N., Zaki, J. (2017). Trusting outgroup, but not ingroup members, requires control: neural and behavioral evidence. *Social Cognitive and Affective Neuroscience*, **12**(3), 372–81.
- Igelström, K.M., Webb, T.W., Kelly, Y.T., et al. (2016). Topographical Organization of Attentional, social, and memory processes in the human temporoparietal cortex. *eNeuro*, **32**. ENEURO.0060-16.2016.
- Izuma, K., Saito, D.N., Sadato, N. (2008). Processing of social and monetary rewards in the human striatum. *Neuron*, **58**, 284–94.
- Izuma, K., Saito, D., Sadato, N. (2010). The roles of the medial prefrontal cortex and striatum in reputation processing. *Social Neuroscience*, **5**, 133–47.
- Ji, J.L., Spronk, M., Kulkarni, K., et al. (2019). Mapping the human brain's cortical-subcortical functional network organization. *NeuroImage*, **185**, 35–57.
- Jones, R.M., Somerville, L.H., Li, J., et al. (2011). Behavioral and neural properties of social reinforcement learning. *Journal of Neuroscience*, **31**, 13039–45.
- Kam, J.W.Y., Lin, J.J., Solbakk, A.-K., et al. (2019). Default network and frontoparietal control network theta connectivity supports internal attention. *Nature Human Behaviour*, **3**, 1263–70.
- King-Casas, B., Tomlin, D., Anen, C., Camerer, C.F., Quartz, S.R., Montague, P.R. (2005). Getting to know you: reputation and trust in a two-person economic exchange. *Science*, **308**(5718), 78–83.
- Koster-Hale, J., Saxe, R. (2013). Theory of mind: a neural prediction problem. *Neuron*, **79**, 836–48.
- Krienen, F.M., Tu, P.C., Buckner, R.L. (2010). Clan mentality: evidence that the medial prefrontal cortex responds to close others. *Journal of Neuroscience*, **30**, 13906–15.
- Krueger, F., Meyer-Lindenberg, A. (2019). Toward a model of interpersonal trust drawn from neuroscience, psychology, and economics. *Trends in Neurosciences*, **42**, 92–101.
- Laurita, A. C., Hazan, C., & Spreng, R. N. (2017). Dissociable patterns of brain activity for mentalizing about known others: A role for attachment. *Social cognitive and affective neuroscience*, **12**(7), 1072–1082
- Leech, R., Kamourieh, S., Beckmann, C.F., et al. (2011). Fractionating the default mode network: distinct contributions of the ventral and dorsal posterior cingulate cortex to cognitive control. *Journal of Neuroscience*, **31**, 3217–24.
- Leech, R., Braga, R., Sharp, D.J. (2012). Echoes of the brain within the posterior cingulate cortex. *Journal of Neuroscience*, **32**, 215–22.
- McLaughlin, K.A., DeCross, S.N., Jovanovic, T., et al. (2019). Mechanisms linking childhood adversity with psychopathology: learning as an intervention target. *Behaviour Research and Therapy*, **118**, 101–9.
- McLaren, D.G., Ries, M.L., Xu, G., Johnson, S.C. (2012). A generalized form of context-dependent psychophysiological interactions (gPPI): a comparison to standard approaches. *NeuroImage*, **61**(4), 1277–86.
- Meyer, M. (2019). Social by default: characterizing the social functions of the resting brain. *Current Directions in Psychological Science* **28**, 380–386.
- Meyer, M.L., Lieberman, M.D. (2012). Social working memory: neurocognitive networks and directions for future research. *Frontiers in Psychology*, **3**.
- Mitchell, J.P., Macrae, C.N., Banaji, M.R. (2006). Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron*, **50**(4), 655–63.
- Mobbs, D., Yu, R., Meyer, M., et al. (2009). A key role for similarity in vicarious reward. *Science (New York, NY)*, **324**, 900.
- Monfardini, E., Redouté, J., Hadj-Bouziane, F., et al. (2016). Others' sheer presence boosts brain activity in the attention (but not the motivation) network. *Cerebral Cortex*, **26**, 2427–39.
- Nickerson, L.D., Smith, S.M., Öngür, D., et al. (2017). Using dual regression to investigate network shape and amplitude in functional connectivity analyses. *Frontiers in Neuroscience*, **11**, 4141–18.
- Nihonsugi, T., Ihara, A., Haruno, M. (2015). Selective increase of intention-based economic decisions by noninvasive brain stimulation to the dorsolateral prefrontal cortex. *Journal of Neuroscience*, **35**, 3412–9.
- Park, B., Young, L. (2020). An association between biased impression updating and relationship facilitation: a behavioral and fMRI investigation. *Journal of Experimental Social Psychology*, **87**, 103916.
- Parkinson C, Kleinbaum AM, Wheatley T (2017). Spontaneous neural encoding of social network position. *Nature Human Behavior* **1**, 0072
- Parkinson, C., Liu, S., Wheatley, T. (2014). A common cortical metric for spatial, temporal, and social distance. *Journal of Neuroscience*, **34**, 1979–87.
- Parkinson, C., Kleinbaum, A.M., Wheatley, T. (2018). Similar neural responses predict friendship. *Nature Communications*, 1–14.
- Phan, K.L., Sripada, C.S., Angstadt, M., et al. (2010). Reputation for reciprocity engages the brain reward center. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 13099–104.

- Pruim, R.H., Mennes, M., van Rooij, D., Llera, A., Buitelaar, J.K., Beckmann, C.F. (2015). ICA-AROMA: a robust ICA-based strategy for removing motion artifacts from fMRI data. *NeuroImage*, **112**, 267–77.
- Raichle, M.E., MacLeod, A.M., Snyder, A.Z., et al. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 676–82.
- Ruff, C.C., Fehr, E. (2014). The neurobiology of rewards and values in social decision making. *Nature Reviews Neuroscience*.
- Schilbach, L., Eickhoff, S.B., Rotarska-Jagiela, A., et al. (2008). Minds at rest? Social cognition as the default mode of cognizing and its putative relationship to the 'default system' of the brain. *Consciousness and Cognition*, **17**, 457–67.
- Seeley, W.W., Menon, V., Schatzberg, A.F., et al. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. *Journal of Neuroscience*, **27**(9), 2349–56.
- Simpson, J.A. (2007). Psychological foundations of trust. *Current Directions in Psychological Science*, **16**, 264–8.
- Smith, S.M., Fox, P.T., Miller, K.L., et al. (2009). Correspondence of the brain's functional architecture during activation and rest. *Proceedings of the National Academy of Sciences*, **106**, 13040–5.
- Smith, D.V., Hayden, B.Y., Truong, T.-K., et al. (2010). Distinct value signals in anterior and posterior ventromedial prefrontal cortex. *Journal of Neuroscience*, **30**, 2490–5.
- Smith, D.V., Gseir, M., Speer, M.E., et al. (2016). Toward a cumulative science of functional integration: a meta-analysis of psychophysiological interactions. *Human Brain Mapping*, **37**, 2904–17.
- Somerville, L.H., Heatherton, T.F., Kelley, W.M. (2006). Anterior cingulate cortex responds differentially to expectancy violation and social rejection. *Nature Neuroscience*, **9**, 1007–8.
- Spunt, R.P., Meyer, M.L., Lieberman, M.D. (2015). The default mode of human brain function primes the intentional stance. *Journal of Cognitive Neuroscience*, **27**, 1116–24.
- Stanley, D.A. (2016). Getting to know you: general and specific neural computations for learning about people. *Social Cognitive and Affective Neuroscience*, **11**, 525–36.
- Stanley, D.A., Adolphs, R. (2013). Toward a neural basis for social behavior. *Neuron*, **80**, 816–26.
- Tamir, D.I., Mitchell, J.P. (2012). Disclosing information about the self is intrinsically rewarding. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 8038–43.
- Utevsky, A.V., Smith, D.V., Huettel, S.A. (2014). Precuneus is a functional core of the default-mode network. *Journal of Neuroscience*, **34**, 932–40.
- Utevsky, A.V., Smith, D.V., Young, J.S., et al. (2017). Large-scale network coupling with the fusiform cortex facilitates future social motivation. *eNeuro*, **4**. ENEURO.0084-17.2017.
- Vincent, J.L., Kahn, I., Snyder, A.Z., et al. (2008). Evidence for a Frontoparietal control system revealed by intrinsic functional connectivity. *Journal of Neurophysiology*, **100**, 3328–42.
- Xin, F., Lei, X. (2015). Competition between frontoparietal control and default networks supports social working memory and empathy. *Social Cognitive and Affective Neuroscience*, **10**, 1144–52.
- Yarkoni, T., Braver, T.S. (2010). Cognitive neuroscience approaches to individual differences in working memory and executive control: conceptual and methodological issues. In: Gruszka, A., Matthews, G., Szymura, B., editors. *Handbook of Individual Differences in Cognition Attention, Memory, and Executive Control*, New York, Springer Science + Business Media, pp. 87–107.
- Young, J.S., Smith, D.V., Coutlee, C.G., et al. (2015). Synchrony between sensory and cognitive networks is associated with subclinical variation in autistic traits. *Frontiers in Human Neuroscience*, **9**:146.