Response inhibition in adolescents is moderated by brain connectivity and social network structure

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Abstract

The social environment an individual is embedded in influences their ability and motivation to engage self-control processes, but little is known about the neural mechanisms underlying this effect. Many individuals successfully regulate their behavior even when they do not show strong activation in canonical self-control brain regions. Thus, individuals may rely on other resources to compensate, including daily experiences navigating and managing complex social relationships that likely bolster self-control processes. Here, we employed a network neuroscience approach to investigate the role of social context and social brain systems in facilitating self-control in adolescents. We measured brain activation using functional magnetic resonance imaging (fMRI) as 62 adolescents completed a Go/No-Go response inhibition task. We found that self-referential brain systems compensate for weaker activation in executive function brain systems, especially for adolescents with more friends and more communities in their social networks. Collectively, our results indicate a critical role for self-referential brain systems during the developmental trajectory of self-control throughout adolescence.

Key words: response inhibition; social networks; cognitive control; network science; community structure

Introduction

Social interaction confers cognitive benefits across the lifespan (Hawkley and Cacioppo, 2010; Ybarra *et al.*, 2011; Hikichi *et al.*, 2017; Beadleston *et al.*, 2019). Research has shown robust benefits of social connections across different age populations (Ybarra and Winkielman, 2012; Hikichi *et al.*, 2017; Beadleston *et al.*, 2019) and species (Baarendse *et al.*, 2013; Simpson *et al.*, 2016). In particular, social connection is associated with increased performance on cognitive tasks including executive function (Ybarra *et al.*, 2011), verbal reasoning (Beadleston *et al.*, 2019) and self-control (Meldrum *et al.*, 2012; Farley and Kim-Spoon, 2014). Although research has shown benefits of social connection for cognitive performance, an open question is whether social resources can compensate when cognitive skills are underdeveloped or underutilized.

In this study, we examine whether processing in social brain regions that help us make sense of ourselves and others can compensate when an individual has weaker recruitment of cognitive brain systems to successfully regulate their behavior. Increasing evidence from network neuroscience suggests that the coordinated action of multiple brain regions as well as interactions between systems support fast and efficient information processing (Vatansever *et al.*, 2015; Shine *et al.*, 2016). Given evidence that social interactions can boost cognitive performance (2008; Ybarra *et al.*, 2011; Beadleston *et al.*, 2019), we suggest that social brain systems might facilitate better cognitive performance, especially for individuals with weaker recruitment of executive brain systems. Adolescents exhibit heightened social sensitivity, (Braams and Crone, 2017) and appraising, representing and processing information about the self-concept are a fundamentally social process for adolescents (Hart, 1988; Sebastian *et al.*, 2008; Pfeifer *et al.*, 2009). Thus, our analyses here focus on both self-referential and mentalizing brain systems within the broader social brain.

We also build on a small but growing body of evidence that suggests social context may be relevant to how people use their brains to perform cognitive tasks (Falk and Bassett, 2017). Having larger networks, having more communities, or having communities that are more separated from each other might require cognitive capacities within the social brain related to tracking and sharing information with different groups (Bickart *et al.*, 2012; O'Donnell *et al.*, 2017) and tracking one's own status relative to the group (Zerubavel *et al.*, 2015). For instance, there is variability in how actively people recruit individuals into their network, maintain existing communities within their network, and keep social sub-groups segregated for distinct functions (e.g. separate groups provide support for romantic relationships, school, or work; Rainie and Wellman, 2012). Thus, the degree to which an individual's social network is organized into many (versus few) or segregated (versus overlapping) communities could be associated with the cognitive or social resources that individuals are likely to recruit to regulate their behavior.

Here, we used functional magnetic resonance imaging (fMRI) to measure brain activation while adolescents completed a Go/No-Go response inhibition task. We focus here on adolescents, given their sensitivity to social influence (Braams and Crone, 2017; Wasylyshyn *et al.*, 2018). We also collected information about adolescents' real-life social networks in order to assess the moderating role of social network properties. We hypothesize that distributed patterns of activation across response inhibition brain regions and social brain systems (self-referential and mentalizing systems) should be associated with response inhibition performance. Additionally, we expect that the effects of social brain systems on response inhibition will be greater for individuals who have larger social networks organized into many (versus few) or segregated (versus overlapping) communities.

Method

Participants

One hundred three adolescent males (all 16-year-olds) were recruited through the Michigan state driver registry database as part of a larger study on peer influences on adolescent driving (Falk *et al.*, 2014). Participants met standard magnetic resonance imaging (MRI) safety criteria. In accordance with Institutional Review Board approval from the University of Michigan, legal guardians provided written informed consent, and adolescents provided written assent. 29 participants did not complete the social network measure and 10 participants were missing behavioral data for the Go/No-Go task. One participant had poor behavioral performance (less than 50% accuracy), and one participant had excessive head motion (greater than 3mm framewise displacement). Analyses were conducted on the 62 remaining participants.

Response inhibition task (Go/No-Go)

Adolescents completed a Go/No-Go task (Logan, 1994; Aron *et al.*, 2003) while their blood oxygen level dependent (BOLD) activation was measured in an MRI scanner. A total of 80% of trials were considered Go trials, and 20% of trials were considered No-Go trials. On each trial, a letter was presented on the screen for 500 ms, followed by a 1000 ms fixation interval. Participants were instructed to press a button if the letter was an A through F, and withhold their response if the letter was an X. A key component of successful response inhibition is the ability to balance responding quickly with accurately inhibiting unwanted responses on No-Go trials (Cascio *et al.*, 2015; Tomlinson *et al.*, 2020; Townsend and Ashby, 1978). To account for the tradeoff between speed and accuracy, performance was measured using Go/No-Go efficiency:

$$1 - \frac{RT_{Go}}{Acc_{NoGo}}$$

where RT_{Go} represents the average response time in seconds on Go trials, and Acc_{NoGo} represents the percentage of No-Go trials where the participants correctly withheld a response. We then subtracted this score from unity so that higher scores indicate better performance.

Real-life social network properties

Outside of the scanner, participants provided access to their Facebook network data using an online survey and the Facebook OpenGraph API (collected in 2011–2013). We anonymized the data and used the NetworkX package (Hagberg *et al.*, 2008) implemented in Python 2.7 to construct binary, undirected graphs of each participant's social network where each Facebook friend is represented as a node in the graph and each connection between friends is represented as an edge on the graph. Using NetworkX, we then computed the size, number and modularity of communities for each adolescent's social network. The size of each network was defined as the total number of friends. To determine the number of communities in each network, we used a

Louvain-like locally greedy algorithm (Blondel *et al.*, 2008) to segregate friends into nonoverlapping groups by maximizing the number of within-group connections relative to an appropriate random network null model (defined here as the configuration model; Newman and Girvan, 2004). Mathematically, the algorithm maximizes the following modularity quality function:

$$Q = \frac{1}{2m} \sum_{i,j} \left[A_{ij} - \frac{k_i k_j}{2m} \right] \delta\left(c_i, c_j\right)$$

where A_{ij} represents the strength of the connection between nodes i and j (being equal to 1 if nodes i and j share a connection, and to 0 if they do not share a connection), k_i and k_j represent the sum of the connection strengths for nodes connected to nodes i and j, respectively (equivalent to the number of first and second-degree connections for each node), $2m$ is the sum of all the connection strengths in the network (equivalent to the total number of connections in the network), δ is the Kronecker delta, and c_i and c_j represent the communities to which nodes i and j are assigned, respectively.

This process yields a partition of nodes into communities and a maximum Q value, the latter of which is often referred to as the network modularity (Newman, 2006). Network modularity ranges from 0 to 1, where a densely connected network (i.e. all of an adolescent's friends are also friends with each other) has a score closer to 0, whereas a segregated network (i.e. an adolescent has separate clusters of friends) has a score closer to 1.

fMRI data acquisition and preprocessing

Functional images were recorded using a reverse spiral sequence (repetition time = 2,000 ms, echo time = 30 ms, flip angle = 90°, 43 axial slices, field of view = 220 mm, slice thickness = 3 mm, voxel size = 3.44 × 3.44 × 3.0 mm). We also acquired in-plane T1-weighted images (43 slices, slice thickness = 3 mm, voxel size = 0.86 × 0.86 × 3.0 mm) and high-resolution T1-weighted images [spoiled gradient recall (SPGR) acquisition, 124 slices, slice thickness = 1.02 × 1.02 × 1.2 mm] for use in co-registration and normalization. Functional data were preprocessed using Statistical Parametric Mapping (SPM8, Friston *et al.*, 2007). The first four volumes were discarded before analysis. Functional images were despiked using AFNI's 3dDespike program (Cox, 1996), corrected for differences in slice timing, and spatially realigned to the first functional image. We then applied a high-pass filter (128 sec cutoff), and the subsequent volumes were weighted according to the inverse of their noise variance using the robust weighted least squares toolbox (Diedrichsen *et al.*, 2005). In-plane T1 images were registered to the mean functional image, then high-resolution T1 images were registered to the in-plane image. Structural images were then skull stripped and normalized to the skull-stripped Montreal Neurological Institute (MNI) template provided by FMRIB Software Library (FSL) (Jenkinson *et al.*, 2012).

For functional connectivity analyses, we used the nilearn package (Abraham *et al.*, 2014) in Python 2.7 to extract average timeseries from 5mm spheres defined from a whole-brain atlas (Power *et al.*, 2011). Timeseries in each region were band-pass filtered between 0.06 and 0.12 Hz, detrended and standardized. We also regressed out the average timeseries in each individual's white matter and cerebrospinal fluid, as well as six-head motion parameters. We then censored frames with framewise displacement >0.5 mm.

Putative cognitive systems

Using a whole-brain parcellation comprised of 264 regions of interest (Power *et al.*, 2011), we identified regions that were involved in response inhibition by conducting a reverse inference meta-analysis using the term 'response inhibition' in the Neurosynth database (Yarkoni *et al.*, 2011). We then conducted two additional reverse inference meta-analyses using the terms 'self-referential' and 'mentalizing'. For each meta-analysis, we identified studies that matched the key phrase (threshold = 0.001, results of database query as of October 2017; response inhibition: 176 studies; self-referential: 127 studies; mentalizing: 124 studies) and submitted the associated MNI coordinates from each set of studies to a Neurosynth meta-analysis.

Regions of interest were considered to be involved in the process of interest if at least half of the voxels in the region were significantly activated in the False Discovery Rate (FDR) corrected ($p < 0.01$) reverse inference map for that term. We excluded regions that were identified in multiple processes to differentiate between systems involved in our three key processes, including 12 regions involved in both self-referential and mentalizing. All analyses reported in this study include 21 mentalizing regions, 8 self-referential regions and 13 response inhibition regions (Figure 1A).

Statistical analysis of imaging data

We focused on three markers of brain dynamics in our analyses: activation in each system, connectivity within each system and connectivity between systems. Activation was measured by the average BOLD activation of each system during correct No-Go versus correct Go trials. Connectivity within systems was measured by the average Pearson correlation between time series of any two nodes in the system. Connectivity between systems was measured by the average Pearson correlation coefficient between time series of any node in one system and any node in another system. All statistical analyses were conducted in R v3.4 (R Core Team, 2015).

System activation. Our first set of analyses examined mean activation for correct No-Go versus correct Go trials. Using a general linear model implemented in SPM8, the voxel activation was predicted from weighted beta coefficients for BOLD activation during correct No-Go trials, false-alarm No-Go trials and missed Go trials. We extracted the contrast weight coefficients for the correct No-Go trials versus correct Go trials from each of the 42 regions of interest, and averaged the response across regions in each system (response inhibition, self-referential and mentalizing) to calculate mean system activation.

We conducted three subsets of analyses using average activation of each system to test our planned hypotheses. First, we assessed whether average activation in the response-inhibition system, self-referential system and mentalizing system was stronger for correct No-Go versus correct Go trials using one-sample t-tests. Second, we computed the correlation between average system activation and the Go/No-Go efficiency score. Finally, we employed multiple regressions to examine the interaction between brain systems. Given multicollinearity between the self-referential and mentalizing systems, we built two models using the Go/No-Go efficiency score as the dependent variable: (i) one model used response inhibition system and self-referential system activation as independent variables, whereas
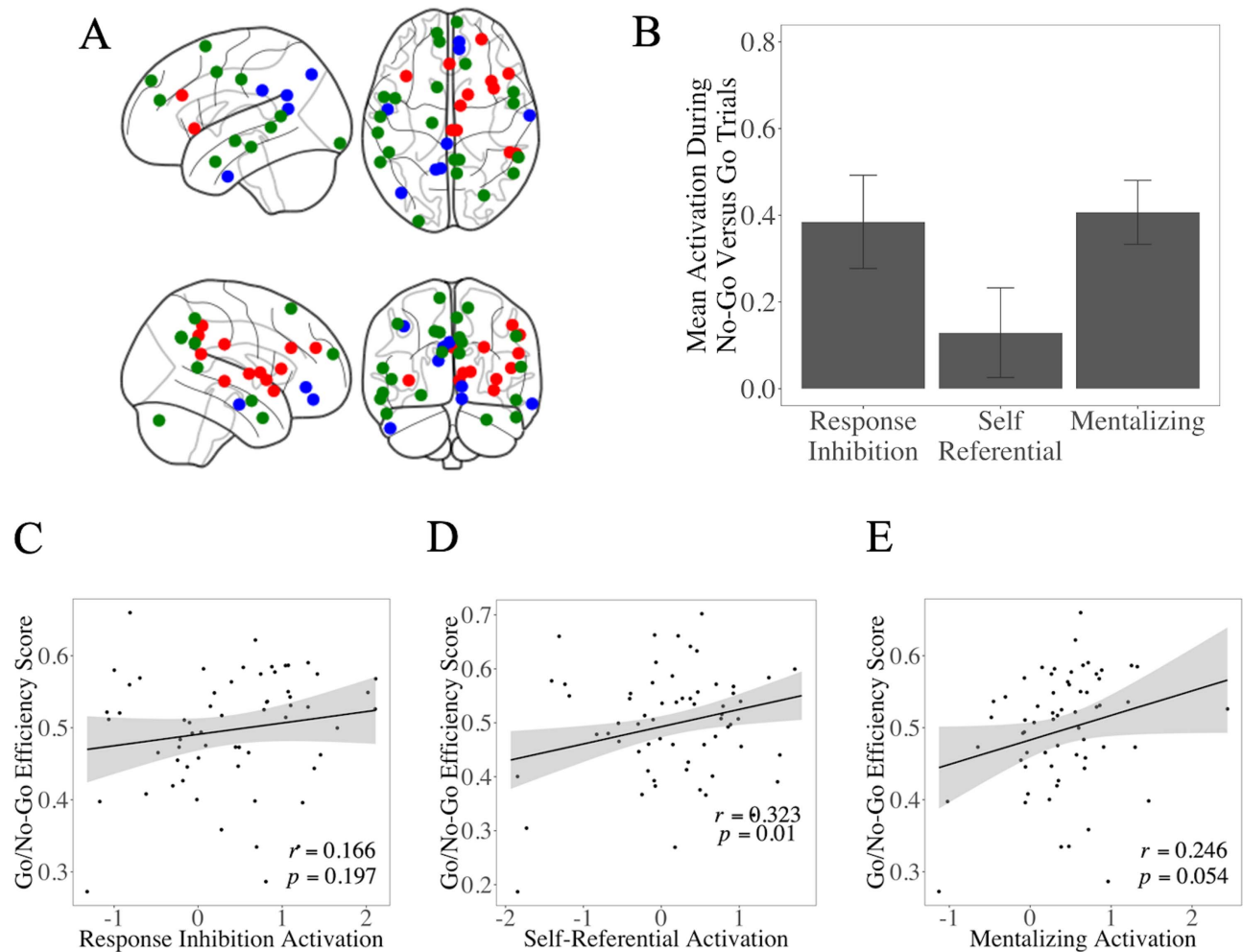
Fig. 1. Recruitment of brain systems during a task requiring response inhibition. (A) Regions in response inhibition (RI: red), self-referential (SR: blue) and mentalizing (M: green) systems identified using Neurosynth. (B) Average activation in the RI, SR and M systems for correct No-Go trials versus correct Go trials. (C) Scatterplot of Go/No-Go efficiency score versus mean activation of the RI system. (D) Scatterplot of Go/No-Go efficiency score versus mean activation of the SR system. (E) Scatterplot of Go/No-Go efficiency score versus mean activation of the M system.

(ii) the other used response inhibition system and mentalizing system activation as independent variables.

Functional connectivity. We next examined connectivity within and between brain systems. We constructed a 42×42 functional connectivity matrix for each subject and each run where the ij^{th} element of the matrix represented the Pearson correlation coefficient between activation timeseries in region i and region j. We then averaged the functional connectivity matrices for the two runs for each participant to yield a single functional connectivity matrix for each participant. We then averaged the connectivity across all regions within each of the three cognitive systems to compute each system's within-system connectivity. Finally, we computed two between-system connectivity values between the response inhibition system and the mentalizing and self-referential systems.

We then used both within- and between-system connectivity in two subsets of hypothesis-driven analyses. First, we computed the correlation between the Go/No-Go efficiency score and connectivity. Second, we ran five separate multiple regression models using the Go/No-Go efficiency score as the dependent variable: the first three had response inhibition system activation and one of the within-system connectivity variables as the independent variables, whereas the other two had response inhibition system activation and one of the between-system connectivity variables as the independent variables.

Social network moderation analyses. Finally, we investigated the relationship between social network structure and neural and behavioral responses during a response inhibition task. Separate models were employed to avoid overfitting and multicollinearity between independent variables. We assessed whether any of the three social network properties (number, size and modularity of communities) moderated the relationship between brain activation or connectivity and task performance. Separate regression models were run with adolescents' Go/No-Go efficiency score as the dependent variable and each combination of brain measurement (mean activation of each system, connectivity within each system, and the two between-system connectivity values) and social network property (number, size and modularity of communities) as the independent variables.

Data availability

The data and code to reproduce all analyses and figures in this paper are available in Github repository [https://github.com/cnlab/Tompson_TPS_GNG_FB_SocialNet].

Results

Behavioral performance on a task requiring response inhibition

We first examined behavioral performance. Participants responded quickly ($M = 373$ ms, s.d. $= 4.36$ ms) and accurately ($M = 373$ ms, s.d. $= 4.36$ ms) on Go trials, and average accuracy on No-Go trials was 75.4% (s.d. $= 11.0$%). We observed a speed-accuracy tradeoff such that participants with greater accuracy on No-Go trials were slower on Go trials ($r(60) = 0.373$, $p = 0.003$). For all subsequent analyses, we focused on the Go/No-Go efficiency score ($M = 0.497$, s.d. $= 0.081$), where larger values indicate that participants are responding quickly but still correctly inhibiting responses on No-Go trials, and lower values indicate that a participant was either responding fast but inaccurately, or slow but accurately.

Activation of brain systems during a task requiring response inhibition

Second, we examined recruitment of the response-inhibition, self-referential and mentalizing systems during trials that required response inhibition. Average activation was significantly greater for correct No-Go trials than correct Go trials in both the response inhibition system ($t(60) = 3.58$, $p < 0.001$) and the mentalizing system ($t(60) = 5.51$, $p < 0.001$), but not for the self-referential system ($t(60) = 1.25$, $p = 0.216$; Figure 1B).

We next examined whether mean activation for No-Go trials versus Go trials in each of the three systems accounted for variability in the adolescents' Go/No-Go efficiency score. Response inhibition system activation was not correlated with individual differences in efficiency ($r(60) = 0.166$, $p = 0.197$; Figure 1C), but self-referential system activation was positively associated with efficiency ($r(60) = 0.323$, $p = 0.010$; Figure 1D). The mentalizing system showed a similar trend as the self-referential system, but its activation was marginally associated with efficiency ($r(60) = 0.246$, $p = 0.054$; Figure 1E).

Compensatory activation in social brain systems

Third, we examined our hypothesis that adolescents with less tendency to use response inhibition brain systems may instead recruit regions outside the response inhibition system to perform the task. We ran two multiple regression analyses between the response inhibition network and each of the two social brain systems, with mean system activation for No-Go versus Go trials as the independent variable and the Go/No-Go efficiency score as the dependent variable.

We found a significant interaction between response inhibition system activation and self-referential system activation: adolescents who had weaker response inhibition system activation showed a stronger relationship between task performance and self-referential system activation ($\beta = -0.214$, $p = 0.035$; Figure 2A). Simple slopes analyses further revealed that self-referential system activation was significantly associated with efficiency at lower levels (-1 s.d.) of response inhibition system activation ($\beta = 0.487$, $p = 0.001$), but not at higher levels ($+1$ s.d.) of response inhibition system activation ($\beta = 0.059$, $p = 0.722$).

We found a similar, albeit marginal, effect with response inhibition system activation and mentalizing system activation: adolescents who had weaker response inhibition system activation showed a stronger relationship between task performance and mentalizing system activation ($\beta = -0.176$, $p = 0.065$; Figure 2B). Simple slopes analyses further revealed that the mentalizing system activation was significantly associated with efficiency at lower levels (-1 s.d.) of response inhibition system activation ($\beta = 0.412$, $p = 0.022$), but not at higher levels ($+1$ s.d.) of response inhibition system activation ($\beta = 0.060$, $p = 0.717$).

Connectivity within and between brain systems and response inhibition

In addition to examining mean system activation, we were also interested in determining whether connectivity within and between these three systems was associated with successfully and efficiently inhibiting prepotent responses. The above analyses suggest that recruitment of social brain systems might serve a compensatory role for adolescents with less mature brain development. If self-referential and mentalizing systems are compensating for weaker recruitment of response inhibition systems, then it is possible that communication between these regions is important for efficient response inhibition.
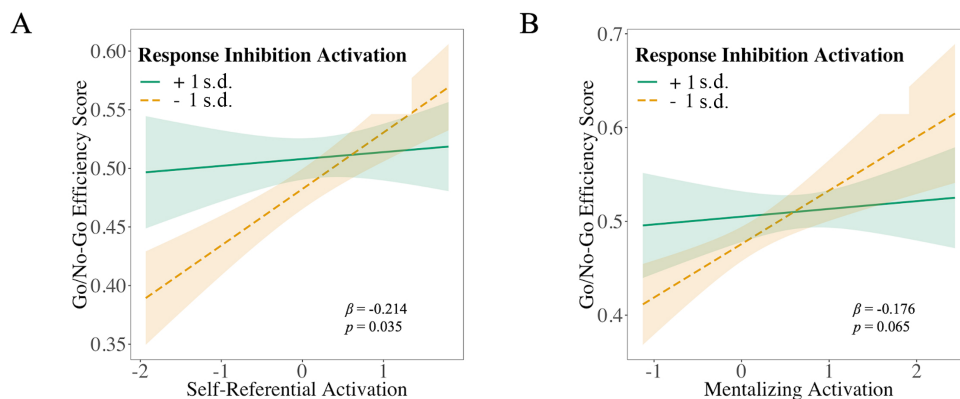

Fig. 2. Interaction between response inhibition activation and social brain systems. (A) Relationship between mean activation in the self-referential (SR) system and Go/No-Go efficiency scores for adolescents with stronger mean activation in the response inhibition (RI) system (solid line) versus adolescents with weaker mean activation in the RI system (dashed line). (B) Relationship between mean activation in the mentalizing system and Go/No-Go efficiency scores for adolescents with stronger mean activation in the RI system (solid line) versus adolescents with weaker mean activation in the RI system (dashed line).
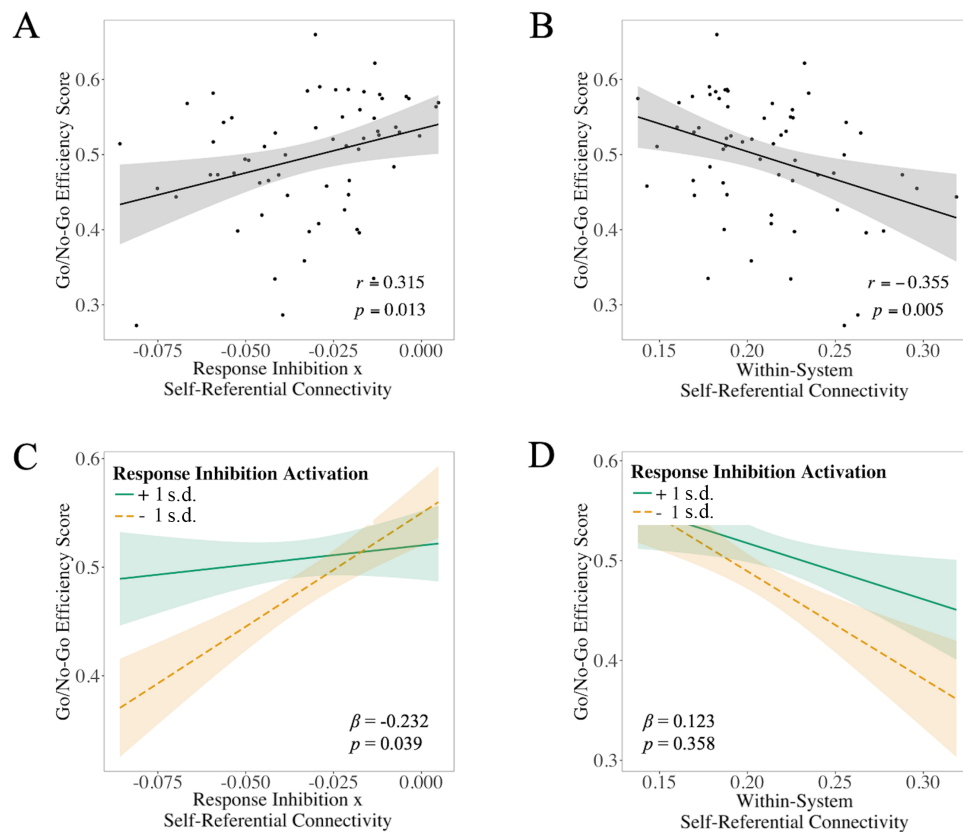
Fig. 3. Relation between inter-system connectivity and Go/No-Go efficiency score. (A) Scatterplot of Go/No-Go efficiency score versus connectivity between the response inhibition (RI) system and self-referential (SR) system. (B) Scatterplot of Go/No-Go efficiency score versus connectivity within the self-referential system. (C) Relationship between RI system x SR system connectivity and Go/No-Go efficiency scores for adolescents with stronger activation in the RI system (solid line) versus adolescents with weaker activation in the RI system (dashed line). (D) Relationship between connectivity within the SR system connectivity and Go/No-Go efficiency scores for adolescents with stronger activation in the RI system (solid line) versus adolescents with weaker activation in the RI system (dashed line).

Therefore, we examined the average connectivity both *within* each of the three systems as well as the average connectivity *between* the response inhibition network and each of the social brain systems (self-referential and mentalizing). We found that adolescents who had a higher Go/No-Go efficiency score had stronger connectivity between the response inhibition and self-referential systems ($r(60) = 0.315$, $p = 0.010$; Figure 3A) and weaker connectivity within the self-referential system ($r(60) = -0.355$, $p = 0.005$; Figure 3B). There were no significant associations between mentalizing system connectivity and task performance.

Unique contribution of mean activation and average connectivity for response inhibition

Since both the mean system activation and connectivity results showed a compensatory role for the social brain systems, we included both measurements of brain activation in the same model to understand their relationship to improved performance on the response inhibition task.

We found a significant interaction between response inhibition system activation and the connectivity between the response inhibition system and the self-referential system ($\beta = -0.232$, $p = 0.039$; Figure 3C). Simple slopes analyses further revealed a significant association between response inhibition × self-referential system connectivity and efficiency at lower levels (-1 s.d.) of response inhibition system activation

($\beta = 0.559$, $p = 0.001$), but not at higher levels of response inhibition system activation ($\beta = 0.096$, $p = 0.553$). Interestingly, we observed no moderating effect for connectivity within the self-referential system ($\beta = 0.123$, $p = 0.358$; Figure 3D). Thus, activation in the self-referential system supports efficient task performance when it involves communication with response inhibition brain regions, but not when it involves communication within the self-referential system.

Real-life social networks account for compensatory role of social brain systems

Across our analyses, results demonstrated that brain systems implicated in social processes facilitate better response inhibition performance. Consequently, we examined whether social network properties (number, size and modularity of communities) moderated the observed relationship between brain activation or connectivity and adolescents' Go/No-Go efficiency score. In our study, adolescents had an average of 491 Facebook friends in their social network (s.d. = 280), which were clustered into an average of 8.42 communities (s.d. = 4.07) with a mean modularity of 0.235 (s.d. = 0.122). We tested the moderating role of each of these three social network parameters in separate models for mean activation, within-system connectivity and between-system connectivity for the response inhibition, mentalizing and self-referential systems.
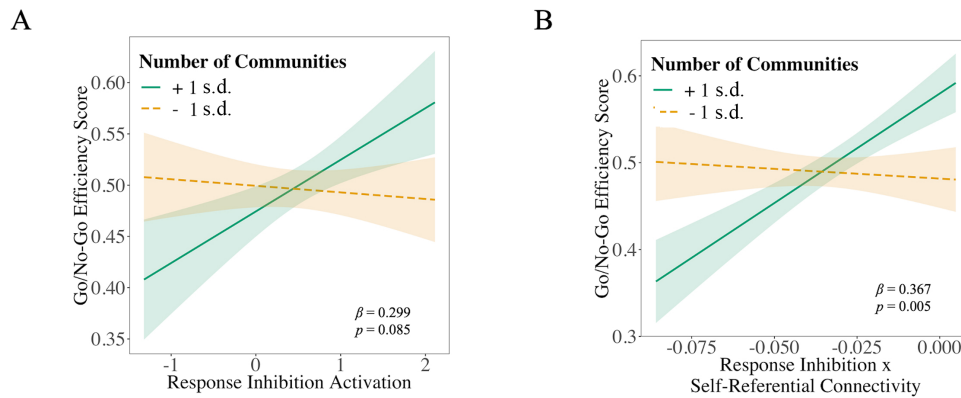
Fig. 4. Social network properties moderate the relationship between brain and behavior. (A) Relationship between activation in the response inhibition system and Go/No-Go efficiency scores for adolescents with more communities in their social network (solid line) versus adolescents with fewer communities in their social network (dashed line). (B) Relationship between response inhibition (RI) system x self-referential system (SR) connectivity and Go/No-Go efficiency scores for adolescents with more communities in their social network (solid line) versus adolescents with fewer communities in their social network (dashed line).

We found that the relationship between response inhibition system activation and an adolescent's Go/No-Go efficiency score was moderated by social network properties. Specifically, there was a significant interaction between response inhibition system activation and network modularity ($\beta = 0.344$, $p = 0.026$). Additionally, there were two marginally significant interactions: one occurred between activation in the response inhibition system and the number of communities ($\beta = 0.299$, $p = 0.085$; Figure 4A), whereas the other occurred between activation in the response inhibition system and the network size ($\beta = 0.211$, $p = 0.084$). We further probed these interactions using simple slopes analysis. We found that adolescents high (+1 s.d.) in network size, number of communities and modularity had a significant positive relationship between response inhibition system activation and the Go/No-Go efficiency score ($\beta = 0.390$, $p = 0.027$; $\beta = 0.530$, $p = 0.034$; $\beta = 0.625$, $p = 0.009$; respectively), whereas the relationship was not significant for adolescents low (−1 s.d.) in network size, number of communities and modularity ($\beta = -0.033$, $p = 0.853$; $\beta = -0.068$, $p = 0.713$; $\beta = -0.062$, $p = 0.703$; respectively). Interestingly, no significant interactions were found between these three social network properties and social brain system activation.

In contrast, the connectivity results revealed that an adolescent's real-life social network accounted for the compensatory role that social brain systems served for better task performance. The association between brain connectivity and task performance was significantly moderated by the number of social network communities, but not by social network size or modularity. The number of communities significantly moderated the relationship between the Go/No-Go efficiency score and the between-system connectivity of the response inhibition and self-referential systems ($\beta = 0.367$, $p = 0.005$; Figure 4B). Compared with adolescents with fewer communities in their social networks (−1 s.d.; $\beta = -0.068$, $p = 0.713$), adolescents with more communities (+1 s.d.) showed a stronger positive association between their Go/No-Go efficiency score and the between-system connectivity of the response inhibition and self-referential systems ($\beta = 0.530$, $p = 0.034$).

We also observed a marginally significant moderating effect of number of communities on the relationship between the Go/No-Go efficiency score and within-system mentalizing connectivity ($\beta = -0.250$, $p = 0.058$). Adolescents with a large number of communities exhibited a negative relationship between task performance and within-system mentalizing connectivity,

whereas adolescents with few communities showed a positive relationship between their Go/No-Go efficiency score and within-system mentalizing connectivity; however, the simple slopes were not significant in either case ($\beta = -0.277$, $p = 0.134$; $\beta = 0.224$, $p = 0.224$; respectively).

Discussion

Self-control processes predict many important outcomes in adolescence, including school success (Blair and Diamond, 2008), risky behaviors (Behan *et al.*, 2014) and psychiatric outcomes (Liddle *et al.*, 2011). Social context also predicts how adolescents engage self-control processes, such that family and peer relationships can facilitate better self-control or buffer against potential negative effects of weaker self-control (Meldrum *et al.*, 2012; Farley and Kim-Spoon, 2014). Yet, the neurophysiological drivers of successful response inhibition in adolescents remain unclear. We argue that progress in understanding has been hampered in part by a focus on activation in single brain regions as well as a lack of focus on the social context surrounding the adolescent.

Employing a network neuroscience approach (Bassett and Sporns, 2017), we found that brain regions outside the canonical response inhibition system compensated for weaker activation in the response inhibition system; adolescents who had weaker response inhibition activation still performed well on the Go/No-Go task if they had stronger activation in self-referential brain regions and greater connectivity between self-referential brain regions and the response inhibition system. Moreover, adolescents with larger social networks broken into more communities showed stronger relationships between brain systems and response inhibition. Collectively, our results provide insight into how brain systems facilitate response inhibition in adolescents, and how these brain responses are moderated by an adolescents' real-life social network.

Activation in social brain systems

This study extends previous work that finds more distributed patterns of brain activation in adolescents during response inhibition (Fair *et al.*, 2007; Rubia *et al.*, 2013). We found that activation in both the response inhibition system and mentalizing system was significantly greater during No-Go than Go trials.

Although the relationship between response inhibition system activation and response inhibition efficiency was not significant, this relationship was moderated by network dynamics in social brain systems including self-referential and mentalizing systems. Adolescents with weaker response inhibition activation still perform well on the Go/No-Go task if they have stronger activation in self-referential and mentalizing systems, and if they have greater connectivity between the self-referential and response inhibition system during the task.

The version of the Go/No-Go task used in the current study has no explicit social components, and so one might wonder how or why social brain systems are recruited during a non-social task. Since most brain regions serve multiple functions, one possibility is that the cortical regions implicated in social processing are being co-opted for response inhibition to compensate for weaker activation in other brain regions. It is also possible that, because adolescents are highly sensitive to social information, they are recruiting additional motivational or cognitive strategies from their daily social experiences to facilitate effective task performance (e.g. to perform well in front of the experimenter, feel proud of their performance or implicitly compete against others in the study). Another possibility is that self-control processes may first develop specifically for social situations in social brain systems, and then self-control becomes more domain-general once the canonical response inhibition system observed in adults develops over the course of adolescence.

Connectivity between response inhibition and self-referential brain systems

If self-referential and mentalizing brain systems within the default mode network compensate for weaker recruitment of the response inhibition system, then communication between default mode and response inhibition regions may facilitate efficient response inhibition. We found that connectivity between the response inhibition and self-referential systems was positively associated with Go/No-Go efficiency, whereas connectivity within the self-referential system was negatively associated with Go/No-Go efficiency. Thus, the self-referential brain system may compensate for weaker recruitment of the response inhibition system, but only when the self-referential system is communicating directly with canonical response inhibition brain regions. It is important to note that there were no significant effects of mentalizing system connectivity, and thus, our connectivity findings provide evidence for self-referential in promoting response inhibition, but do not provide evidence for social brain systems more broadly.

The role of brain systems linked to self-referential in contributing to effective response inhibition can also be seen as bridging the divide between 'self-appraisal' and 'self-control'. Recent work on self-referential in adolescents suggests that key regions in the self-referential brain system, including ventromedial prefrontal cortex (vmPFC), integrate self and identity-related values with other inputs to drive motivated behavior (Pfeifer and Berkman, 2018). Thus, self-referential in adolescents may be contributing to response inhibition by integrating task-relevant information with identity-related information and directing engagement of canonical response inhibition regions. As noted above, it is also possible that cortical regions implicated in self-related processing are being co-opted for response inhibition to compensate for weaker activation in other brain regions, which would explain why connectivity between self

-referential and response inhibition systems is linked to better performance, but connectivity within the self-referential system is linked to worse performance. Recent work in network neuroscience also suggests that successful performance on many cognitive tasks requires coordinated action across multiple brain regions and brain systems (Shine et al., 2016; Chai et al., 2017). This role for distributed connectivity extends to regions not typically considered important for a specific cognitive process. For example, regions in the default mode network facilitate faster response times in a motor task (Vatansever et al., 2015) and better working memory performance (Čeko et al., 2015), but are not canonically thought of as part of motor or memory circuitry. Similarly, brain systems implicated in social processes may facilitate better response inhibition performance.

Social network structure and response inhibition

The current work also contributes to a growing body of evidence linking social network structure and neural processes (Powell et al., 2012; Von Der Heide et al., 2014; O'Donnell et al., 2017; Schmälzle et al., 2017). For example, social network structure is associated with activation in mentalizing regions when thinking about others' opinions (O'Donnell et al., 2017), as well as with connectivity within the mentalizing system during a social exclusion task (Schmälzle et al., 2017).

Here, we showed for the first time that social network structure also moderated brain systems involved in a nonsocial task. Adolescents with larger social networks and more communities in their networks showed a stronger relationship between brain activation and task performance. Adolescents with more communities in their social network also had a stronger relationship between task performance and connectivity between the response inhibition and self-referential systems. Larger social network structures that have more communities or communities that are more segregated (higher in modularity) require individuals to actively maintain multiple groups of friends (Hampton and Wellman, 2003; Rainie and Wellman, 2012). The ability to actively maintain these groups may in turn be facilitated by (or require) more diverse brain systems being recruited for behavioral self-regulation.

This pattern of results is consistent with recent work showing that peer relationships and social context can strongly influence self-control. Children's self-control is influenced by group norms (Doebel and Munakata, 2018), and adolescents who are surrounded by peers with better self-control are more likely to show improved self-control over the course of adolescence (Meldrum et al., 2012). We found that social network structure was also associated with which brain systems help an adolescent regulate their behavior. It is possible that adolescents' daily experiences navigating and managing complex social relationships with multiple distinct communities influence how they use different cognitive strategies or motivational resources to complete cognitive tasks such as response inhibition. Alternatively, adolescents who recruit more diverse brain systems may be more capable of managing larger and more complex social networks.

Limitations

All of the participants in the current work were 16-year-old males, and we are therefore limited in our ability to generalize these findings to adolescent females. The original study for which these data were collected was primarily concerned with neural correlates of adolescent risky driving and was restricted

to adolescent males who had recently received their driver's license since this group has the highest statistical risk for accidents on modern roadways. Importantly, because this study only included adolescents, we are unable to draw any conclusions about the generalizability to other age groups. Because adolescents also differ from adults in neural development and performance on response inhibition tasks, it is therefore unclear whether the compensatory role of social brain regions identified in this study is unique to adolescents or may also be present in adults.

Moreover, we only measured adolescent's social networks based on their Facebook relationships, and this is only one method to identify social relationships. Future work using multiple approaches to collect information about social networks (c.f., Vettel *et al.*, 2018) might yield further insights into the link between brain networks and social networks and their importance for adolescent development.

Conclusions

In the current work, we employed a network approach to analyze brain data and examined the moderating role of social networks. This work suggests that adolescents with larger social networks with more communities recruit more diverse brain systems to successfully inhibit prepotent responses. Our results demonstrate that the relationship between behavior and brain activation, as well as connectivity between brain systems, is dependent on individual differences in social networks. These results motivate future work to examine how elements of the social networks and interpersonal dynamics influence adolescent brains.

Conflict of interest

The authors declare no competing financial interests.

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