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# Functional Connectivity at Rest is Sensitive to Individual Differences in Executive Function: A Network Analysis

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**Abstract:** Graph theory provides a means to understand the nature of network characteristics and connectivity between specific brain regions. Here it was used to investigate whether the network characteristics of the brain at rest are associated with three dimensions thought to underlie individual differences in executive function (EF)—common EF, shifting-specific EF, and updating-specific EF (Miyake and Friedman [2012]). To do so, both an *a priori* analysis focused mainly on select frontoparietal regions previously linked to individual differences in EF as well as a whole-brain analysis were performed. The findings indicated that individual differences in each of the three dimensions of EF were associated with specific patterns of resting-state connectivity both in *a priori* and other brain regions. More specifically, higher common EF was associated with greater integrative (i.e., more hub-like) connectivity of cuneus and supplementary motor area but less integrative function of lateral frontal nodes and left temporal lobe nodes. Higher shifting-specific EF was associated with more hublike motor-related nodes and cingulo-opercular nodes. Higher updating-specific EF was associated with less hublike lateral and medial frontoparietal nodes. In general, these results suggested that higher ability in each of these three dimensions of EF was not solely characterized by the connectivity characteristics of frontoparietal regions. The pattern was complicated in that higher EF was associated with the connectivity profile of nodes outside of the traditional frontoparietal network, as well as with less hublike or centrality characteristics of some nodes within the frontoparietal network. *Hum Brain Mapp 37:2959–2975, 2016.* © **2016 Wiley Periodicals, Inc.**

**Key words:** executive function; resting-state fMRI; individual differences; network analysis; graph theory

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## INTRODUCTION

The goal of the present study is to examine whether differences in the connectivity profiles of brain regions at rest are associated with differences among individuals in their level of executive functions (EF). EF are a set of abilities that allow for the directed pursuit, maintenance, and modification of goals [Banich, 2009], and they are altered in a large number of psychiatric and neurological disorders [e.g., Barkley, 1997; Nieuwenstein et al, 2001]. It is generally agreed that such abilities rely preferentially on frontal cortex, based on both the results of individuals whose EFs are

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compromised as a result of localized brain damage [Alvarez and Emory, 2006; Stuss and Alexander, 2000] and on neuroimaging studies that use univariate approaches to identify those brain regions whose activation increases when EF demands are increased [e.g., Banich et al., 2000a,b]. One of the more prominent theories regarding the neural bases of EF suggests that frontal regions work to modulate the processing in remote target brain regions so as to enable task goals [Miller and Cohen, 2001]. Implicit in this theory is the notion that the successful application of executive control requires interaction between brain regions. Empirical evidence supports such an idea as meta-analyses indicate that EF tasks not only activate frontal regions, but a network of brain regions extending to parietal regions and beyond [Jurado and Rosselli, 2007; Wager et al., 2004]. Finally, computational models that can successfully mimic performance on EF tasks indicate that network dynamics are critical for such executive control [e.g., Chatham et al., 2011; Herd et al., 2006, 2014]. Given the strong evidence that EF is supported by an interaction between disparate brain networks, it is somewhat surprising that neuroimaging studies have, for the most part, not focused on network properties to better understand individual variation in EF, an issue we address in the current study.

One notable aspect of EF is that it is known to vary substantially across individuals [Miyake and Friedman, 2012]. Research on individual differences, including studies utilizing behavioral genetics techniques, has provided a theoretical framework from which to consider how individuals differ in their EF abilities. One prominent theory, the unity and diversity model, derived from intercorrelated patterns of performance across individuals on multiple measures of EF, posits that EF can be well characterized as consisting of at least three latent factors [Miyake and Friedman, 2012]. The first factor is a common EF, representing the unity aspect of the model, on which all EF tasks load. This factor is thought to represent the general capacity to actively maintain a task goal or "attentional set." The second two orthogonal factors represent the diversity aspect of the model and are more specific processes above and beyond common EF. Statistically speaking, these factors are residuals of the EF abilities once common EF has been taken into account. One factor, the shifting-specific factor (shifting), reflects abilities relating to flexibly shifting between different tasks or mental sets, while the other factor, the updating-specific factor (updating) indexes the process of rapidly adding or deleting information from the current contents of working memory.

Neuroimaging studies examining brain activation while performing a variety of EF tasks suggest that these three EF factors are likely to be supported by overlapping yet somewhat distinct brain systems. The ability to actively maintain a task goal is thought to rely on areas of lateral prefrontal cortex extending from BA 10 through mid-dorsolateral prefrontal cortex [Banich, 2009; Braver, 2012; Herd et al., 2007; Sakai, 2008], potentially including the anterior cingulate and frontal operculum as well [Dosenbach et al., 2008]. Set shifting, which requires changes in task, appears to engage more posterior regions of dorsolateral prefrontal cortex (e.g., inferior frontal junction) as well as parietal regions [e.g., intraparietal sulcus; Derrfuss et al., 2005; Wager et al., 2003]. Working memory updating has been suggested to involve fronto-striatal connections and require input from the basal ganglia [Braver et al., 1997; McNab and Klingberg, 2008; O'Reilly and Frank, 2006]. The impression that these three EF factors rely on both overlapping and distinct brain regions was supported by a positron emission tomography (PET) study performed by Collette et al. [2005], who directly investigated which brain regions consistently activate across all subjects for a variety of EF tasks similar to those typically employed by Miyake and colleagues. Collette et al [2005] observed that on average across all individuals the left superior parietal gyrus and the right intraparietal sulcus, and to a lesser degree, mid- and inferior prefrontal regions activated for all EF tasks. Moreover, left frontopolar cortex (BA 10) activity was specifically associated with tasks designed to assess updating-specific EF, while activity of the left intraparietal sulcus was associated with tasks designed to assess shifting-specific EF. Taken together, these studies demonstrate the variety of cortical and subcortical regions implicated in these different aspects of EF. Moreover, they provide information on the brain regions that are likely to act as key nodes in brain for each of these distinct EF factors, and across them more generally. Nonetheless, as these studies focus on the average pattern of activation across groups of individuals, they provide no information on how connectivity of such regions might be related to individual differences in EF, an issue we address in the current study.

To examine this issue, we investigate connectivity profiles of specific brain regions during resting-state fMRI (rs-fMRI) because rs-fMRI is purported to reflect stable aspects of brain function for a given individual. More specifically, rs-fMRI has been used to characterize and quantify low frequency fluctuations in the BOLD signal while individuals are not engaged in an experimentally-directed task [hence the name "resting" state: Fox and Raichle, 2007]. A growing number of studies have shown the pattern of this intrinsic oscillatory behavior between regions mimics patterns of co-activation during task-based fMRI studies. Specifically, regions that work in concert during the performance of tasks seem to fluctuate together during resting-state scans [Cole et al., 2014; Smith et al., 2009]. Importantly for the purposes of the present study, these patterns of co-activation across regions are consistent within an individual across multiple time points that span months to years [Choe et al., 2015; Shehzad et al., 2009], suggesting that they can serve as a sensitive measure of individual differences. Hence, the present study examines whether graph theoretic measures of such static connectivity patterns, which are intrinsic to an individual, are associated with individual differences in EF. If so, it would suggest that subtle but important individual differences in the organization of brain networks are associated with the ability to exert executive control.

In the current article we focus on analyzing such rs-fMRI data using graph theoretic measures. Graph theory is used to mathematically characterize the functional architecture of the brain as a set of interconnected nodes [Sporns et al., 2004]. Typically in a graph theoretic approach, the connections (edges) between regions (nodes) are Pearson's *r*-values for each possible pairwise relationship. Summarizing a single node's pattern of edges to the rest of the brain (or to the subset of regions to which it is most highly connected) can provide an abundance of information about the propagation of information through a complex system like the brain, and specifically, what a given region's role might be in the context of a larger system. Local graph theoretic measures can be broadly classified into several groups: measures of integration (including some measures of centrality), segregation, or other measures of centrality that do not necessarily fall into either of the previous categories [Rubinov and Sporns, 2010]. Measures of integration, such as betweenness centrality and participation coefficient, assess a region's ability to link disparate parts of the brain (i.e., act as a hub). Measures of segregation, such as clustering coefficient, assess the involvement of a particular region in specialized local processing. Other measures, such as degree centrality and eigenvector centrality, are useful for characterizing the general importance of a given region based on the number of connections to other regions or the number of connections to other important regions, respectively. In the "Methods" section we discuss all graph theoretic measures used in the current study in more detail.

Our impetus for examining the relationship between graph theoretic measures of resting-state activation and individual differences in these EF dimensions is motivated by a variety of considerations. First, at least one prior study by Cole et al. [2012] has found that increased global connectivity of a left lateral prefrontal cortex region implicated in cognitive control is associated with an individual-difference measure, fluid intelligence. Those researchers speculated that global connectivity of lateral prefrontal cortex might support the ability of this region to regulate processing in many distinct and disparate brain regions, similar to the role that this region is thought to play in EF. Second, computational modeling of individual differences in EF suggest that connectivity of lateral prefrontal regions may influence both common EF and switching-specific abilities [Herd et al., 2014]. Third, at least some aspects of cognitive control may benefit from segregation rather than integration of information. For example, the basal ganglia has been suggested to play a prominent role in working memory updating [Frank et al., 2001], and segregation of Go versus No-Go circuits may support such a role [Hazy et al., 2006]. Likewise, during task switching, keeping information about specific stimulus-response mappings for each task separate might be aided by having relevant regions highly connected and irrelevant regions less connected.

In summary, the current study examines whether individual differences in dimensions of EF are related to individual differences in graph theoretic measures of brain organization as derived from resting-state data, which is known to be stable within an individual. The graph theoretic approach taken in the current study is notable for a variety of reasons. First, unlike prior studies that have examined just a single measure of EF (e.g., performance on an N-back working memory task), the current study looks at three well-validated dimensions underlying individual differences in EF. Second, the current study uses a larger-sized sample than prior studies, carefully examining individual differences in close to 100 individuals. Third, brain-EF relationships are examined in an *a priori* manner and in an unbiased manner. Prior work by our group and others provided a number of *a priori* regions of interest. For example, an earlier study from our group suggested that individual variation in brain structure—including grey matter volume, cortical thickness and cortical folding—is related to individual differences in the three EF dimensions we examine here [Smolker et al., 2015]. Moreover, in another study we observed that individual differences in brain regions contributing to or composing specific resting-state brain networks as determined by ICA (e.g., frontoparietal network, dorsal attention network) are also related to individual differences in these three EF dimensions [Reineberg et al., 2015]. While this prior study [Reineberg et al., 2015] examined the strength and composition of more large-scale resting-state networks as a function of EF dimensions in the same group of participants as the present study, the focus here is on connectivity profile of specific nodes (i.e., smaller brain regions). The current study complements these prior anatomical and network-based investigations by asking whether or not regions-of-interest in the frontoparietal network have different graph theoretic properties depending on an individual's level of function for each of these three dimensions of EF. Interestingly, our prior work also revealed that regions outside the classic network of regions commonly implicated in cognitive control, such as ventromedial prefrontal cortex, as associated with individual differences in dimensions of EF. Taking into account these findings, we also performed an unbiased analysis searching across the whole brain for regions whose connectivity is related to individual differences in each of the three dimensions of EF. By taking such a broad perspective, the current study provides important insights into how individual differences in brain connectivity may be related to individual differences in a notable aspect of cognitive function, namely EF.

## METHODS

### Overview

Behavioral and brain testing occurred over two sessions. In session one, three behavioral tasks were administered from the battery of nine tasks typically used in studies that have provided evidence for the unity and diversity model of EF [see Miyake et al., 2000; updated in Miyake and Friedman, 2012]: antisaccade, category switching, and keep track. These three tasks were chosen as they load most highly on common EF, switching-specific, and updating-specific factors, respectively [Friedman et al., 2012]. In session two, brain activation was assessed via MRI in a Siemens TIM Trio 3T scanner during a 5.5-minute resting state scan. During this time, participants were instructed to relax and close their eyes. The two sessions occurred within an average of 31.6 days of each other.

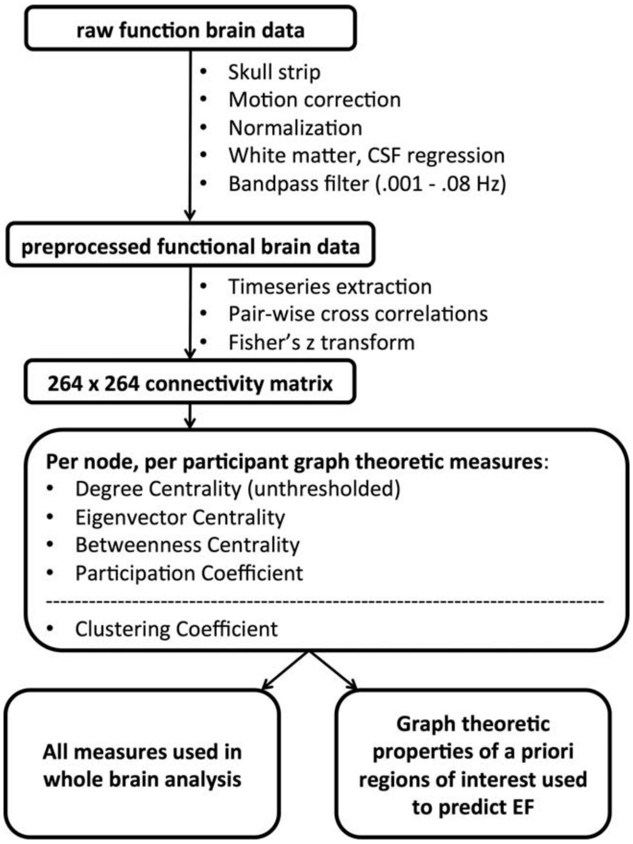

**Figure 1.**

Processing pipeline overview.

## Participants

One hundred individuals aged 18–34 years ($M = 21.31$, $SD = 2.83$) from the University of Colorado Boulder participated for payment over two sessions. Participants were paid $25.00 per hour for the fMRI session and $10.00 per hour for the behavioral session. Functional brain data from six participants were discarded due to excessive levels of movement during the scanning session (>3 mm in a single dimension). Additionally, data from three other participants were discarded due to failure to comply with rules on one of more of the behavioral tasks. All presented results are from analyses of data from the remaining 91 participants (48 females). These participants are the same group of individuals as reported in Reineberg et al. [2015].

## Behavioral Measures

We extracted three measures—common EF, shifting-specific, and updating-specific—in accordance with prior research [Miyake and Friedman, 2012]. Overall group performance and individual variation on each behavioral task were in line with prior studies [see Reineberg et al., 2015 for more detail]. Common EF was calculated by taking the average of each subject's three tasks converted to a *Z*-value (across the group of 91 participants). Shifting-specific EF was the residual variance in the category-switch task, once the contribution of common EF was regressed out. Updating-specific EF was the residual variance in the keep-track task, once the contribution of common EF was regressed out. Higher scores on three composite measures correspond to greater ability in that construct (i.e., maintain a goal, shift between task/mental sets, or update working memory).

## Brain Data

Neuroanatomical data were acquired with a T1-weighted MP RAGE sequence [acquisition parameters: repetition time (TR) = 2,530 ms, echo time (TE) = 1.64, matrix size = 256 × 256 × 192, flip angle (FA) = 7°, slice thickness = 1 mm) and resting-state data were acquired with a T2*-weighted echo-planar functional scan (acquisition parameters: number of volumes = 165, TR = 2,000 ms, TE = 29 ms, matrix size = 64 × 64 × 33, FA = 75°, slice thickness = 3.5 mm, field of view (FOV) = 240 mm]. Analysis of functional brain data was performed via a multistep process documented in Figure 1 and in detail below.

## Preprocessing

Preprocessing of brain data was performed in FSL [build 506; Jenkinson et al., 2014] and Python. To allow for signal stabilization, the first four volumes of each individual functional scan were removed, yielding 161 volumes per subject for analysis. The functional scans were corrected for head motion using MCFLIRT, FSL's motion correction tool. Brain extraction (BET) was used to remove signal associated with non-brain material (e.g., skull, sinuses, etc.). Signal was extracted from masks of the lateral ventricles and white matter and regressed out. FSL's FLIRT utility was used to perform a 6 degrees-of-freedom affine registration of each participant's functional scan to their anatomical volume and a 12 degrees-of-freedom affine registration of each participant's anatomical scan to MNI152 standard space. The transformation matrix from the latter registration was applied to each participant's functional scan. Finally, the scans were band-pass filtered (0.001–0.08 Hz band).

## Network Analyses

For each participant, we extracted the BOLD time series from each of 264, 1 cm spherical ROIs, drawn from Power et al. [2000], which serve as the nodes for the present analysis. We used these nodes as they are drawn from a meta-analysis of functional activations and have a community structure that agrees with task-based functional networks (i.e., are organized into networks such as default mode network and frontoparietal task control network). 1-cm spherical ROIs were chosen as they provide the largest possible size for a given ROI but preclude overlap with neighboring ROIs. Within each participant, all pairwise Pearson's $r$ correlations were calculated, yielding a 264 × 264 correlation matrix. All Pearson's $r$-values were subjected to the Fisher's $z$ transformation to normalize the variance in correlation values. For each node of each connectivity matrix, four graph theoretic metrics were calculated after a proportional threshold of 0.15 was applied (i.e., only the strongest 15% of positive correlations were maintained): eigenvector centrality, participation coefficient, betweenness centrality, and clustering coefficient. As there is no consensus or strong precedent on which specific sparcity threshold is best, we chose a value in the middle of a range of values commonly used in related work. We feel the selection of this value balances using very sparse graphs (e.g., <10% sparcity threshold, which has been linked to high test-retest reliability of global graph theory measures [Wang et al., 2011]) and denser graphs [e.g., >20% sparcity threshold, which could potentially reveal the cognitive-relevance of weak connections as in Santarnecchi et al., 2008]. Additionally, global connectivity was calculated in an unthresholded manner on positive edge weights within each connectivity matrix. This analysis process yielded 1,320 (264 regions × 5 graph theoretic measures) features per participant for use in further analyses. All measures were calculated using *NetworkX* package for Python [Hagberg et al., 2012].

Our selection of graph theoretic measures was based on the desire to sample a variety of connectivity characteristics. First, we chose a basic quantification of the connectedness of a region, *global connectivity*. Global connectivity is the unthresholded, weighted degree centrality, or the average of each row/column of each participant's positive connectivity matrix. Global connectivity has previously been linked to individual differences in intelligence and cognitive control [Cole et al., 2012]. Second, we chose a measure that weighs a given region's important connections more heavily than connections to less important regions, *eigenvector centrality*. Eigenvector centrality is obtained for each participant by calculating an eigenvector for that participant's connectivity matrix such that each component is greater than zero [Newman, 2010]. Third, we chose a measure that reflects how important a region is for connecting disparate parts of the brain, *betweenness centrality* (betweenness). This measure provides an index of how frequently a given region is part of the shortest path between all other pairs of regions in the brain and is one way of measuring the degree to which a region can be considered a "connector hub" [van den Heuvel and Sporns, 2013]. Mathematically, betweenness is the sum of the fraction of all other node pair's shortest paths that pass through the node of interest [Brandes, 2008; as implemented in NetworkX in the current study, the resulting value is scaled by the number of other node pairs in the graph]. Fourth, we chose a measure that reflects how diverse a given region's connections are, *participation coefficient*. For example, one region may be connected to only members of its own community (e.g., regions within the visual network), while another region may have significant connections to a variety of communities (e.g., frontoparietal network, dorsal attention network, cingulo-opercular network). Mathematically, participation coefficient measures the diversity of a regions connections to a set of *a priori* defined functional communities such as the visual and frontoparietal network [Guimerà and Amaral, 2005]. Lesions to regions with a high participation coefficient produce more severe and broad cognitive deficits than lesions to areas with a lower participation coefficient [Warren et al., 2014], suggesting that such regions play a more central role across a variety of processes. Participation coefficient is also of interest to the current study as we have recently found that the dorsal and ventral attention networks of individuals with high EF are expanded to include regions not observed in the networks of individuals with lower EF such as the frontal pole and angular gyrus [Reineberg et al., 2015]. In the current study, we measure participation coefficient using the 14 *a priori* defined functional communities provided by the authors of the reference atlas from which the nodes were obtained [Power et al., 2011]. Finally, we chose a measure thought to reflect the degree to which a given region is involved in specialized processing, *clustering coefficient*. Clustering coefficient is a measure of segregation that could reflect whether or not an area is suitably isolated from the influence of other functional communities. Mathematically, clustering coefficient quantifies the percentage of a region's neighbors that are neighbors of each other [Onnela et al., 2006].

Our *a priori* analyses only involved a select set of nodes located in close proximity to statistical clusters from our prior functional and anatomical studies of individual differences in EF [Reineberg et al., 2015; Smolker et al., 2015] as well as a set of nodes in close proximity to a lateral prefrontal cortex region described in Cole et al. [2012]. In all cases, the 1-cm spherical nodes that were selected from the reference atlas were either directly overlapping a cluster from prior research or within 1 cm of a cluster. All 18 *a priori* nodes are presented in Table I. First, we identified one node that corresponded to frontal polar cortex, two

**TABLE I.** ***A priori*** **regions of interest**

| Index | Reference atlas Index | Label | X | Y | Z |
|---|---|---|---|---|---|
| 1 | 197 | Frontal pole | −34 | 55 | 4 |
| 2 | 74 | Lateral occipital cortex | −41 | −75 | 26 |
| 3 | 87 | Precuneus | −39 | −75 | 44 |
| 4 | 243 | Cerebellum—lobule VI | −16 | −65 | −20 |
| 5 | 183 | Cerebellum—crus I/lobule VI | −18 | −76 | −24 |
| 6 | 244 | Cerebellum—lobule VI | −32 | −55 | −25 |
| 7 | 5 | vmPFC | 8 | 41 | −24 |
| 8 | 76 | vmPFC | 8 | 48 | −15 |
| 9 | 109 | Paracingulate gyrus | −3 | 44 | −9 |
| 10 | 3 | Orbitofrontal cortex | 24 | 32 | −18 |
| 11 | 180 | Orbitofrontal cortex | 24 | 45 | −15 |
| 12 | 181 | Orbitofrontal cortex | 34 | 54 | −13 |
| 13 | 200 | vlPFC | 43 | 49 | −2 |
| 14 | 188 | dlPFC | −42 | 38 | 21 |
| 15 | 220 | Frontal pole | −39 | 51 | 17 |
| 16 | 187 | Inferior frontal junction | −41 | 6 | 33 |
| 17 | 201 | dlPFC | −42 | 25 | 30 |
| 18 | 176 | Inferior frontal junction | −47 | 11 | 23 |

Table lists all *a priori* regions of interest, index number from the current study, index number from the 264 node reference atlas [Power et al., 2011], anatomical label, and MNI coordinates. Regions 1–3 were on interest due to proximity to regions taken from Reineberg et al. [2015]. Regions 4–15 were of interest due to proximity to regions from Smolker et al. [2015]. Regions 16–18 were of interest due to proximity to regions from Cole et al. [2012].

nodes that corresponded to lateral occipital cortex and precuneus, and three nodes that corresponded to cerebellum. These six nodes overlap with brain regions that previously showed a relationship between one of the three EF dimensions and functional connectivity via a complementary network analysis [Reineberg et al., 2015]. Specifically, resting state networks such as frontoparietal network were expanded to these areas (e.g., to cerebellum) in individuals who showed higher functioning on a given dimension of EF [see Fig. 4 of Reineberg et al., 2015]. Second, we identified nine regions from a variety of frontal cortical areas—ventromedial ($n = 2$), paracingulate ($n = 1$), orbitofrontal ($n = 3$), ventrolateral ($n = 1$), and dorsolateral prefrontal cortex ($n = 2$)—that were shown to vary with the level of performance on a given dimension of EF (i.e., regions presented in Figs. 1–3 of Smolker et al., [2015]). Finally, we identified three left lateral prefrontal regions in close proximity (<10 mm, average distance = 7 mm) to an area that Cole et al. [2012] showed has increased global connectivity in individuals with high fluid intelligence. One of these regions fell within middle frontal gyrus (MFG) and two fell near the inferior frontal junction [see Table I of Cole et al., 2012].

For each of these 18 *a priori* regions we calculated each of the 5 graph theoretic measures described above for a total of 90 features. In contrast, the exploratory analysis utilized all 1,320 features (264 nodes by 5 measures) to determine which graph theoretic properties of the resting brain were most strongly related to individual differences in each of the three EF dimensions.

## Statistics

### *A priori Analysis*

For the analysis of *a priori* regions of interest, we calculated the statistical relationship between each of 18 regions of interest and each of the three dimensions of EF—common EF, shifting-specific EF, and updating-specific EF. To do so, we ran linear models regressing each dimension of EF on each graph theoretic feature from the regions of interest (one model per feature) while controlling for age and possible motion-related confounds—mean translation (average motion in the x, y, and z plane during the resting-state scan) and mean rotation (average roll, pitch, and yaw movement during the resting-state scan). To account for sampling error, we performed 1,000 permutations of each regression model, sampling from the 91 participants with replacement. To determine which graph theoretic features had significant linear relationships with each dimension of EF, we calculated a $p$-value associated with the mean of each feature's bootstrapped $t$-statistics. We report graph theoretic features with bootstrap $p$-value $< 0.05$. Results of these multiple regression models are reported in section "*A Priori Analysis*" under the Section "*Results*" and Table II.

### *Exploratory Analysis*

For the exploratory analysis, we calculated the statistical relationship between each graph theoretic feature and each of the three EF dimensions of interest. To do so, we ran linear models regressing each EF dimension on each graph

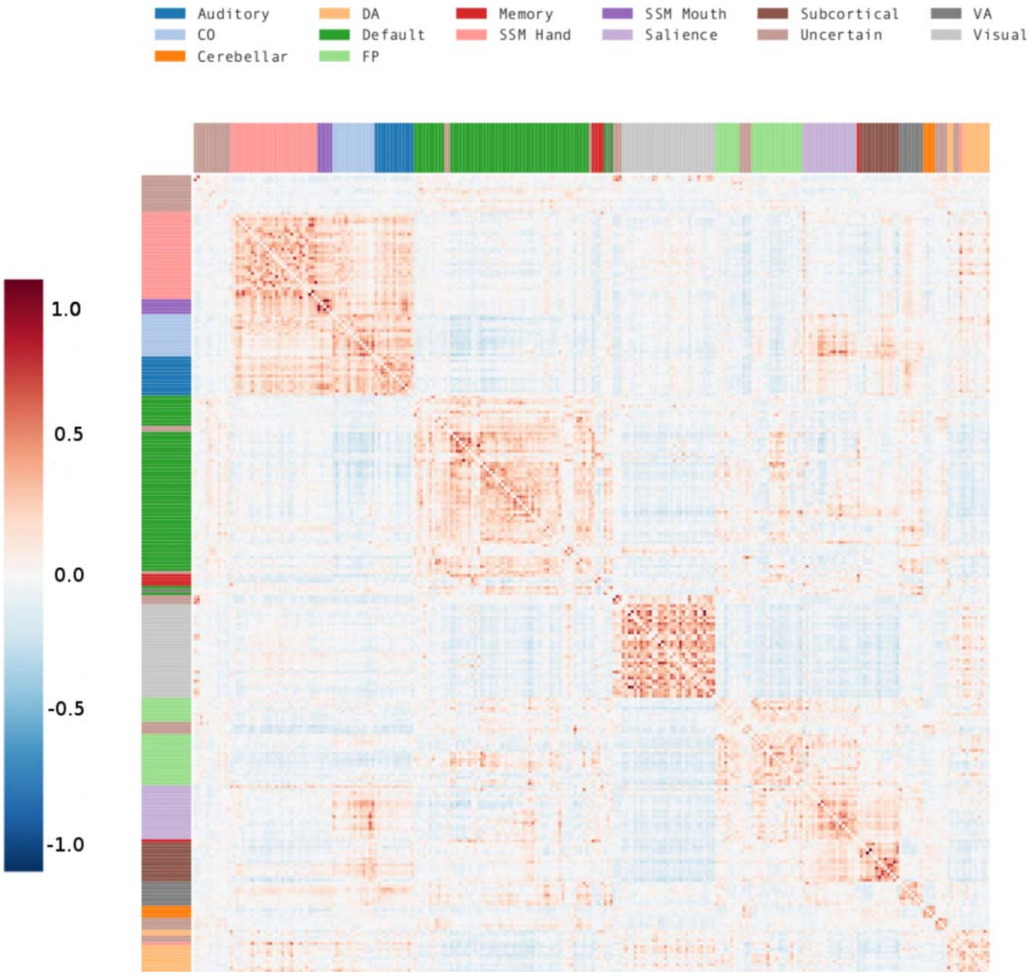

**Figure 2.**

Group average connectivity matrix. Group connectivity matrix calculated from the average of 91 participants' individual connectivity matrices. *Red* indicates positive *Pearson's r*-values and *blue* indicates negative *Pearson's r*-values. CO, cingulo-opercular; DA, dorsal attention; FP, frontoparietal; SSM, sensory/somatomotor; VA, ventral attention. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

theoretic feature while controlling for age and possible motion-related confounds—mean translation and mean rotation. To account for sampling error, we performed the same bootstrapping procedure described above. We report graph theoretic features with bootstrap $p$-value $<0.005$ ($p < 0.015/3$, or $p$ corrected for performing three sets of analyses, one for each dependent variable of interest). Results are presented in Section *"Whole Brain Analysis"* under the Section "*Results*" and Table III.

Finally, as a exploration of the amount of variance that might be potentially explained by the full set of features ($N = 1320$) identified in the exploratory analysis, we included all measures for a given EF dimension ($n = 9$ for common EF, $n = 11$ for shifting, and $n = 7$ for updating) in a multiple regression model (i.e., one model for each EF dimension). Although these models run the risk of overfitting the data, they provide a benchmark for comparison in future studies. We compared the percentage of variance explained by the combined set of appropriate features for a given EF measure to a set of graph theoretic features of the same size drawn randomly from all features. We discuss the overall amount of variance explained in each EF measure in Section *"Whole Brain Analysis"* under the Section "*Results*." All statistics were calculated using Scikit-learn [Pedregosa and Varoquaux, 2015] and statsmodels modules for the Python programming language.

## RESULTS

We first performed analyses to ensure that our sample was representative relative to prior studies. As reported

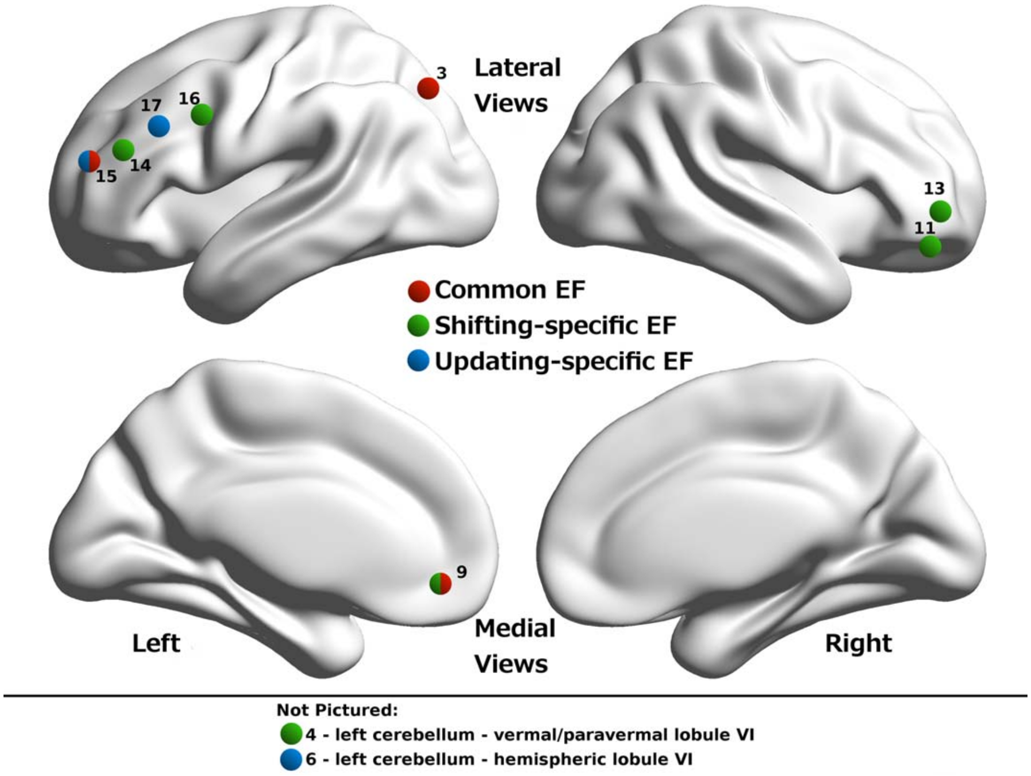

**Figure 3.**

*A priori* regions of interest with connectivity profiles related to EF. *Colored spheres* indicate the location of *a priori* regions of interest with significant relationships to one of three EF measures. *Red*, common EF; *green*, shifting-specific EF; *blue*, updating-specific EF; *multiple colors*, combination of EF measures. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

previously [Reineberg et al., 2015], behavioral performance for this group of participants on the EF tasks and pairwise correlations between the three EF tasks was in line with previous studies examining individual differences in EF using similar behavioral tasks. We then examined whether the connectivity pattern for the resting-state fMRI data

**TABLE II. Results from analysis of *a priori* regions of interest**

| Index | EF | Measure | *t*-value | *P*-value | X | Y | Z | Label |
|---|---|---|---|---|---|---|---|---|
| 3 | Common EF | Eigenvector centrality | −2.3256 | 0.0223 | −39 | −75 | 44 | Precuneus |
| 3 | Common EF | Clustering coefficient | −2.5386 | 0.0128 | −39 | −75 | 44 | Precuneus |
| 9 | Common EF | Global connectivity | −2.3074 | 0.0233 | −3 | 44 | −9 | Paracingulate gyrus |
| 9 | Common EF | Eigenvector centrality | −2.1353 | 0.0355 | −3 | 44 | −9 | Paracingulate gyrus |
| 15 | Common EF | Betweenness centrality | −2.0344 | 0.0449 | −39 | 51 | 17 | Frontal pole |
| 4 | Shifting | Global connectivity | −2.6478 | 0.0096 | −16 | −65 | −20 | Cerebellum—lobule VI |
| 9 | Shifting | Clustering coefficient | −2.5633 | 0.0120 | −3 | 44 | −9 | Paracingulate gyrus |
| 11 | Shifting | Global connectivity | −2.3837 | 0.0192 | 24 | 45 | −15 | Orbitofrontal cortex |
| 11 | Shifting | Eigenvector centrality | −2.7150 | 0.0079 | 24 | 45 | −15 | Orbitofrontal cortex |
| 13 | Shifting | Clustering coefficient | −2.0620 | 0.0421 | 43 | 49 | −2 | vlPFC |
| 14 | Shifting | Clustering coefficient | 2.2049 | 0.0300 | −42 | 38 | 21 | dlPFC |
| 14 | Shifting | Participation coefficient | −2.3971 | 0.0186 | −42 | 38 | 21 | dlPFC |
| 16 | Shifting | Global connectivity | 2.0810 | 0.0403 | −41 | 6 | 33 | Inferior frontal junction |
| 6 | Updating | Global connectivity | −2.0289 | 0.0454 | −32 | −55 | −25 | Cerebellum—lobule VI |
| 15 | Updating | Betweenness centrality | −2.0176 | 0.0466 | −39 | 51 | 17 | Frontal pole |
| 17 | Updating | Participation coefficient | −2.5777 | 0.0116 | −42 | 25 | 30 | dlPFC |

**TABLE III. Exploratory relationships between EF and graph metrics**

| Index | Reference index | EF | Measure | *t*-value | *P*-value | X | Y | Z | Label |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 166 | Common EF | Betweenness centrality | 2.9155 | 0.0045 | −16 | −77 | 34 | Cuneal cortex |
| 2 | 114 | Common EF | Clustering coefficient | −3.2420 | 0.0017 | −20 | 64 | 19 | Frontal pole |
| 3 | 250 | Common EF | Clustering coefficient | −3.0780 | 0.0028 | −50 | −7 | −39 | Inferior temporal gyrus |
| 4 | 252 | Common EF | Eigenvector centrality | 4.1500 | 0.0001 | −52 | −63 | 5 | Lateral occipital cortex |
| 5 | 175 | Common EF | Eigenvector centrality | −2.9309 | 0.0043 | 48 | 25 | 27 | Middle frontal gyrus |
| 5 | 175 | Common EF | Global connectivity | −3.3353 | 0.0012 | 48 | 25 | 27 | Middle frontal gyrus |
| 6 | 83 | Common EF | Global connectivity | −2.9351 | 0.0042 | −68 | −23 | −16 | Middle temporal gyrus |
| 7 | 47 | Common EF | Betweenness centrality | 2.9690 | 0.0038 | −3 | 2 | 53 | Supplementary motor area |
| 8 | 248 | Common EF | Global connectivity | −3.0872 | 0.0027 | −31 | −10 | −36 | Temporal fusiform cortex |
| 9 | 133 | Shifting | Clustering coefficient | −3.2772 | 0.0015 | −2 | −35 | 31 | Cingulate gyrus |
| 9 | 133 | Shifting | Participation coefficient | 2.9554 | 0.0040 | −2 | −35 | 31 | Cingulate gyrus |
| 10 | 212 | Shifting | Betweenness centrality | −3.4529 | 0.0008 | −11 | 26 | 25 | Cingulate gyrus |
| 11 | 217 | Shifting | Betweenness centrality | −2.9106 | 0.0045 | 10 | 22 | 27 | Cingulate gyrus |
| 12 | 242 | Shifting | Betweenness centrality | 3.1189 | 0.0024 | −49 | 25 | −1 | Frontal operculum cortex |
| 13 | 209 | Shifting | Betweenness centrality | −2.8984 | 0.0047 | 36 | 22 | 3 | Insular cortex |
| 14 | 86 | Shifting | Betweenness centrality | 3.5551 | 0.0006 | −44 | −65 | 35 | Lateral occipital cortex |
| 15 | 9 | Shifting | Global connectivity | −2.8956 | 0.0047 | 65 | −24 | −19 | Middle temporal gyrus |
| 16 | 165 | Shifting | Clustering coefficient | −3.1289 | 0.0024 | 26 | −79 | −16 | Occipital fusiform gyrus |
| 17 | 20 | Shifting | Participation coefficient | 3.9972 | 0.0001 | −54 | −23 | 43 | Postcentral gyrus |
| 18 | 36 | Shifting | Participation coefficient | 4.9259 | < 0.0001 | 42 | −20 | 55 | Postcentral gyrus |
| 19 | 113 | Updating | Betweenness centrality | −2.9548 | 0.0040 | −3 | 42 | 16 | Cingulate gyrus |
| 20 | 218 | Updating | Betweenness centrality | −2.8861 | 0.0049 | 31 | 56 | 14 | Frontal pole |
| 3 | 250 | Updating | Clustering coefficient | −3.0971 | 0.0026 | −50 | −7 | −39 | Inferior temporal gyrus |
| 21 | 164 | Updating | Clustering coefficient | −3.2544 | 0.0016 | −42 | −74 | 0 | Lateral occipital cortex |
| 22 | 46 | Updating | Eigenvector centrality | −3.0854 | 0.0027 | 66 | −8 | 25 | Postcentral gyrus |
| 23 | 35 | Updating | Betweenness centrality | −3.1441 | 0.0023 | −13 | −17 | 75 | Precentral gyrus |
| 7 | 47 | Updating | Clustering coefficient | −3.1843 | 0.0020 | −3 | 2 | 53 | Supplementary motor area |

Table lists regions with strongest relationships to each of three EF dimensions, index from current study, anatomical label from a query of the Harvard–Oxford atlas, index from reference atlas [Power et al., 2011], relationship with EF measures, and specific graph theoretic measure.

between areas for these 91 participants is in line with prior reports [e.g., Power et al., 2011]. Figure 2 shows the community structure of the group average connectivity matrix across all 91 participants. The modules, positioned along the diagonal of the matrix are qualitatively similar to those found in group connectivity matrices from prior research using the same reference atlas (e.g., when compared with the connectivity matrix provided in Fig. 3 of Cole et al. [2014]).

## A Priori Analysis

Individual differences in the three EF dimensions were associated with differences in the graph theoretic properties of 10 of 18 *a priori* regions-of-interest (see Fig. 3 for location of all regions). For relationships between EF dimension and graph theoretic measures, all *t*-statistics are presented in Table II and are the mean *t*-statistic from 1,000 permuted multiple regression models controlling for age and movement during the resting-state scan.

a. Higher *common EF* was associated with decreased eigenvector centrality and decreased clustering coefficient of a portion of the precuneus (*a priori* Region 3), decreased global connectivity and decreased eigenvector centrality of a pregenual region of the paracingulate gyrus region (*a priori* Region 9), and decreased betweenness centrality of a dorsolateral frontal pole region (*a priori* Region 15). In sum, higher common EF is associated with less hublike and less central regions involved in cognitive control (precuneus, dorsolateral frontal polar regions), and emotion-related prefrontal areas (pregenual cortex).

b. Higher *shifting* was associated with decreased global connectivity of a region of Lobule VI of the cerebellum (*a priori* Region 4), decreased clustering coefficient of a pregenual region of the paracingulate gyrus region (*a priori* Region 9), decreased global connectivity and decreased eigenvector centrality of an orbitofrontal region of the frontal pole (BA 10/47) (*a priori* Region 11), decreased clustering coefficient of a ventrolateral (i.e. inferior frontal gyrus) frontal pole region (*a priori* Region 13), increased clustering coefficient and decreased participation coefficient of a mid-dorsolateral region (i.e., middle frontal gyrus, MFG;

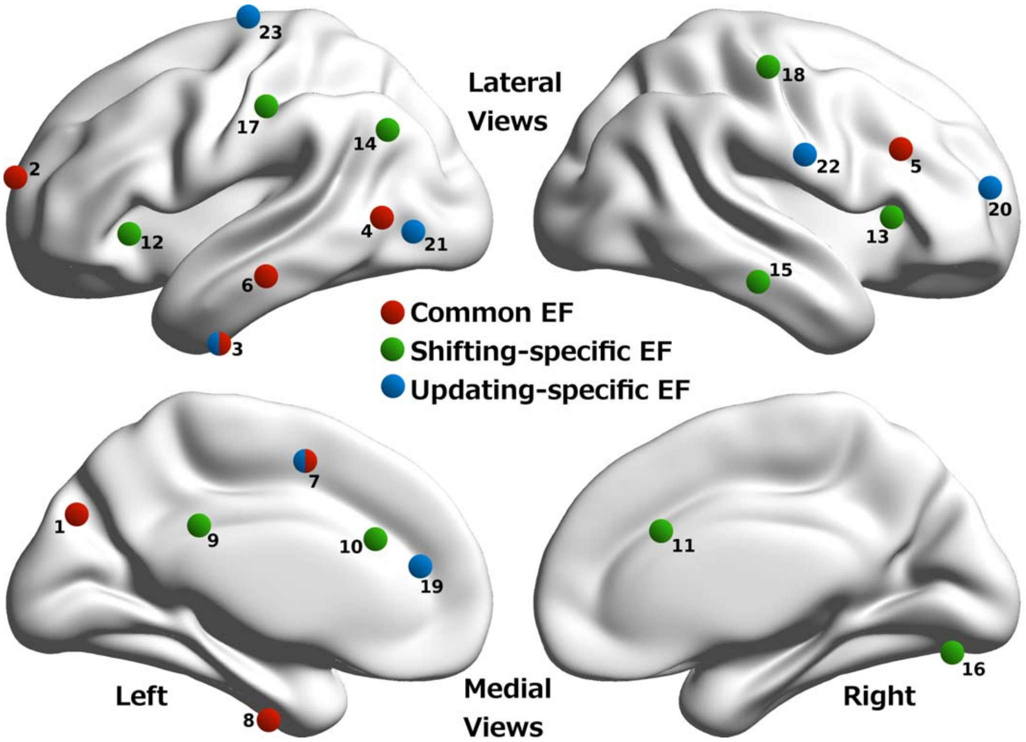

**Figure 4.**

Regions from the exploratory analysis with connectivity profiles related to EF. *Colored spheres* indicate the location of regions with most significant relationships to each of three EF measures. *Red*, common EF; *green*, shifting-specific EF; *blue*, updating-specific EF; *multiple colors*, combination of EF measures. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

*a priori* Region 14), and increased global connectivity of a posterior MFG region near the inferior frontal junction (*a priori* Region 16). In sum, higher shifting EF is associated with less locally focused connectivity (as represented by a decreased clustering coefficient) in pregenual and ventrolateral regions, but increased locally focused connectivity in midlateral frontal polar regions. It is also associated with less central attributes of orbitofrontal regions, decreased global connectivity of the cerebellum and orbitofrontal regions, and increased global connectivity of the inferior frontal junction.

c. Higher *updating* was associated with decreased global connectivity of a region of Lobule VI of the cerebellum (*a priori* Region 6), decreased betweenness centrality of dorsolateral frontal pole region (*a priori* Region 15), and decreased participation coefficient of a dorsolateral (MFG) region of prefrontal cortex (*a priori* Region 17). In summary, higher updating is associated with less hublike frontopolar and dorsolateral prefrontal regions, and less global connectivity of the cerebellum.

No relationships were found for *a priori* nodes 1, 2, 5, 7, 8, 10, 12, and 18.

### Whole Brain Analysis

All statistics are presented in Table III and are the mean *t*-statistic from 1,000 permuted multiple regression models controlling for age and movement during the resting-state scan. See Figure 4 for location of all regions.

a. The regions associated with higher *common EF* generally fell into two broad categories: frontoparietal regions, and regions of the left temporal lobe. With regards to the frontoparietal network, results revealed that higher EF was associated with decreased clustering coefficient of a dorsal frontal pole region (Region 2), decreased global connectivity and decreased eigenvector centrality of a dorsolateral prefrontal cortex region (i.e., MFG; Region 5) and increased betweenness centrality of a region of the supplementary motor area (BA 6) (Region 7). In sum, higher common EF was associated with decreased centrality of lateral prefrontal regions and more hublike medial aspects of the frontoparietal network and cuneus. With regards to temporal regions, higher common EF was associated with decreased clustering coefficient of a lateral (Region 3) and decreased global connectivity of a medial (Region 8) portion of the anterior inferior temporal gyrus, decreased global connectivity of a middle temporal gyrus region (Region 6), and increased eigenvector centrality of the posterior temporal cortex at its junction with lateral occipital cortex (Region 4). In sum, higher common EF is associated with less globally connected left anterior temporal regions and a more hublike left posterior temporal cortex. Additionally, higher common EF was associated with increased betweenness centrality of a portion of the cuneus (Region 1).

b. Higher *shifting specific EF* was associated with the connectivity characteristics of sets of bilateral nodes within the cingulo-opercular network as well as some somatomotor areas. In particular, higher shifting specific EF was associated with increased betweenness centrality of cingulo-opercular cortex in the left hemisphere (Region 12), and decreased betweenness centrality of an analogous region in the right hemisphere (Region 13); decreased betweenness centrality of a rostral anterior cingulate gyrus region both in the left hemisphere (Region 10), and the right (Region 11); and an increased participation coefficient in both the left postcentral gyrus region (Region 17) and the right postcentral gyrus region (Region 18). In sum, higher shifting-specific EF was associated with differential "hubness" of right and left fronto-opercular-insular regions, a less hublike rostral anterior cingulate cortex and a more hublike postcentral gyrus. In addition, higher shifting specific EF was associated with greater participation coefficient and decreased clustering coefficient of a posterior cingulate gyrus region (Region 9), increased betweenness centrality of a lateral occipital cortex region (Region 14), decreased global connectivity of a middle temporal gyrus region (Region 15), and decreased clustering coefficient of a region of the occipital fusiform gyrus (Region 16).

c. Higher *updating specific EF* was associated with graph theoretic properties of some frontal and parietal nodes, including decreased betweenness centrality of a frontal pole region (Region 20), decreased eigenvector centrality of a ventral postcentral gyrus region (Region 22), decreased betweenness centrality of a dorsal precentral gyrus region (Region 23), decreased clustering coefficient of a supplementary motor area region (Region 7), and decreased betweenness centrality of a supragenual region of the anterior cingulate gyrus (Region 19). In sum, higher updating specific EF was associated with less hublike lateral and medial prefrontal nodes as well as a precentral gyrus region. Higher shifting-specific EF was also associated with decreased clustering coefficient of a lateral occipital cortex region (Region 21) and an inferior temporal gyrus region (Region 3).

To explore the combined ability of each set of exploratory features to explain variance in each of the three EF dimensions, we conducted a multiple regression analysis regressing each of the three EF dimensions on the sets of regressors discussed in the three paragraphs above. For common EF, the nine exploratory features explained 42.9% of the variance in EF ability ($F_{(9,\ 81)} = 6.77$, $P < 0.001$). We permuted 1000 null models regressing common EF on randomly selected sets of 9 graph theoretic features. On average, these models explained 20.7% of variance in common EF. For shifting-specific EF, the 11 exploratory features explained 54.8% of the variance in EF ability ($F_{(11,\ 79)} = 8.72$, $P < 0.001$). We permuted 1,000 null models regressing shifting-specific EF on randomly selected sets of nine graph theoretic features. On average, these models explained 22.8% of variance in shifting-specific EF. For updating-specific EF, the seven exploratory features explained 34.1% of the variance in EF ability ($F_{(7,\ 83)} = 6.14$, $P < 0.001$). We permuted 1,000 null models regressing updating-specific EF on randomly selected sets of seven graph theoretic features. On average, these models explained 14.4% of variance in updating-specific EF. Even considering the likely overfitting of these models, the graph theoretic measures of brain systems accounted for a non-trivial amount of variance related to individual differences in each of these aspects of EF.

## DISCUSSION

The main finding of the current study is that individual differences in three different dimensions of EF—common EF, shifting-specific EF, and updating specific EF—are associated with distinct aspects of regional functional connectivity, both with regards to regions involved and the nature of their connectivity as assessed by different graph theoretic measures. While some of the identified regions fall within the frontoparietal network, which is typically conceptualized as a brain network that is critical for EF, other regions fall within networks less typically associated with EF. Importantly, exploratory analyses suggest that the graph theoretic measures identified could account for a significant amount of the variance across individuals in each of the different aspects of EF. Below we discuss the implications of these finding for each of the three EF dimensions.

### Common EF

Our results indicated that individual differences in common EF are associated with differential patterns of connectivity for numerous nodes in our analysis. In general, the pattern observed is that individuals with higher common EF have nodes with less central attributes (i.e., lower eigenvector centrality or other measures of relative "importance") than individuals with lower common EF. Higher common EF was associated with lower eigenvector centrality, which reflects how much a node connects to other important nodes within the brain, in *a priori* regions 3 and 9 as well as exploratory region 5—precuneus, paracingulate gyrus, and MFG, respectively. Higher common

EF was associated with lower global connectivity, which measures connectivity of any strength across the whole brain, in *a priori* region 9 as well as exploratory regions 8, 6, and 8. Hence, individuals with higher common EF do not appear to have a brain organization in which a portion of the frontoparietal network acts as a highly centralized hub of brain activity. Rather variation in common EF seems to be associated with the connectivity characterizes of a widely distributed set of brain regions.

This general pattern, and more specifically lower global connectivity in a node within right lateral prefrontal cortex (exploratory region 5) situated squarely within dorsolateral prefrontal cortex (DLPFC), appears to directly conflict with the suggestion of Cole et al. [2012] that high global connectivity of the homologous region in the left hemisphere allows it to flexibly modulate activity across the whole brain. The reason for the discrepancy in these findings is not clear. It may be that these differences reflect aspects of hemispheric asymmetries that are associated with individual differences in common EF. Additionally, the reversal in the direction of this particular relationship could either highlight the utility of our multidimensional approach to EF (i.e., less susceptibility to measurement error) or perhaps suggests that the finding of Cole et al. [2012] is driven by some aspect of intelligence and working memory (the primary measure of their study) that is not captured by our common EF measure.

Regarding how well hubs integrate information across disparate brain regions, as assessed by betweenness centrality, there were some notable findings. In particular, two midline nodes in the frontoparietal network, one in the supplementary motor area and another in the cuneus, showed increased betweenness centrality with higher common EF. In addition, higher common EF was associated with increased eigenvector centrality of a region at the juncture of the occipital and temporal lobes. Notable is the identified cuneus region because this node is only slightly posterior and inferior to a superior parietal region (−18, −69, 51) that emerged in a task-based PET conjunction analysis of eight EF tasks [Collette et al., 2005] chosen for their correspondence to the three facets of EF used in the current study. Based on the location of this node in superior cuneal cortex and caudal precuneus, this region is likely involved in higher-level attentional processing, which may play a role in supporting common EF.

Regarding measures of segregation, we found higher common EF was associated with decreased clustering coefficient for nodes in the precuneus, frontal pole, and inferior temporal gyrus. This finding suggests that the functioning of these nodes is not as isolated from that of other brain regions for individuals with higher compared with lower common EF. This effect for one of the frontopolar nodes identified in our whole brain analysis (exploratory Node 2) is notable as it is close to the frontal pole region) that emerged in our prior ICA-based analysis as associated with common EF ability ($x = -26$, $y = 55$, $z = 4$) [Reineberg et al., 2015]. In particular, in that study we found that individuals with higher common EF had dorsal attention networks that extended to this region. This node falls within regions that have been suggested to enable control at the highest level of abstraction [Badre, 2008; Koechlin et al., 2003], Hence, we would speculate that decreased local processing at this node may enhance the reach or influence of such abstract control in individuals with higher common EF. According to a recent parcellation of the frontal pole performed by our lab [Orr et al., 2015], such frontopolar regions have connections that are mainly limited to prefrontal areas. In addition, our parcellation suggests a gradient of function from monitoring/regulation in more medial aspects to cognitive representations in more lateral aspects. Connectivity also suggests a second gradient representing actions and plans in more dorsal aspects and stimuli/emotions in more ventral aspects. Based on the anatomical connectivity of the frontal pole region identified in the current study, the region we have identified as associated with common EF appears to be involved in cognitive representations of actions and plans.

## Shifting-Specific EF

Connectivity patterns of several somatomotor regions were among the most related to individual differences in shifting-specific EF. Specifically, we found higher shifting-specific EF was associated with increased participation coefficient in left and right primary sensory cortices (exploratory regions 17 and 18). Shifting-specific EF is described as the ability to fluidly transition between different representations of task set. This ability involves both the mechanism of transitioning between task sets and maintaining representations of task sets that are often multimodal in nature (i.e., may contain a variety of sensory information and also mappings between the sensory stimuli and appropriate motor responses). While parietal regions are often thought of as being involved in shifts of attention, somatosensory regions are more likely to be involved in the stimulus-response mappings that vary among tasks, a more concrete and less abstract level of planning. It may be that increased connectivity in regions associated with stimulus-response mapping allows individual with higher switching-specific EF to link stimuli and responses for a given task more easily or allow for more robust or distinct stimulus-response representations for each task set. Future work is necessary to determine the specific role of somatomotor connectivity in shifting-specific EF.

Another node related to motoric function that was associated with shifting-specific EF was observed in the cerebellum (*a priori* region 4), which resides within lobule VI. As demonstrated by Bernard et al. [2012], this region has strong connectivity to motoric regions (dorsal premotor cortex) as well as regions within the frontoparietal network including the dorsolateral prefrontal cortex, the inferior frontal gyrus and the inferior parietal lobule [see

Bernard et al., 2012; Fig. 3]. Greater shifting-specific EF was associated with less global connectivity of this node, perhaps indicating greater specific connectivity to these frontoparietal regions.

In addition, shifting-specific EF was also associated with the connectivity of nodes within the cingulo-opercular network, a characteristic also not observed for common EF. Higher shifting-specific EF was associated with decreased betweenness centrality of nodes in the rostral portion of the dorsal anterior cingulate cortex (exploratory regions 10 and 11). A recent meta-analysis of functional terms significantly associated with this region [as found within Neurosynth database; Yarkoni et al., 2011] by our group [De La Vega et al., 2016] includes "shifting" (as well as inhibition and conflict). Associations between shifting-specific EF and betweenness centrality were also observed for anterior opercular regions (exploratory regions 12 and 13), but with the direction varying by hemisphere (higher shifting-specific EF associated with increased betweenness centrality in the left hemisphere, but decreased betweenness centrality in the right hemisphere). At least some research suggests that the cingulo-opercular network is associated with task sets (e.g., Petersen and Posner [2011]) although it remains unclear whether its role is to maintain task sets or to implement the selection process associated with motoric aspects of task sets (e.g., see Banich et al. [2000a,b] for a discussion of the role of lateral prefrontal cortex in maintaining task sets and Milham and Banich [2005] for discussion of the role of cingulate regions in late-stage response selection). Hence, variations in betweenness centrality, which reflects the degree to which a node connects disparate brain regions, may influence the ability to impose the task sets required to shift between tasks.

Finally, a number of lateral prefrontal nodes from our *a priori* analysis and exploratory whole-brain analysis were associated with shifting-specific EF. The location of these nodes ranged from frontopolar regions to ventrolateral regions to mid-dorsolateral regions. One *a priori* region of interest (*a priori* Region 11) for shifting-specific EF came from Smolker et al. [2015] who found decreased volume and gyrification of an orbitofrontal/ventrolateral prefrontal cortex region in individuals with high shifting-specific EF. We found an association for a ventral orbitofrontal node (BA 10/47) within that region such that decreased global connectivity and eigenvector centrality was associated with increased shifting-specific EF. Traditionally, this region has been associated with reward processing and valuation [Sescousse et al., 2010], however, some task-based studies of task-set shifting have found involvement of lateral orbitofrontal regions as well [Hampshire and Owen, 2006]. In addition, we found individuals with high shifting-specific EF had a decreased clustering coefficient in a node within the vlPFC portion of this *a priori* right hemisphere region. This region has been clearly implicated in set shifting in functional neuroimaging studies [Goel and Vartanian, 2005; Hampshire and Owen, 2006; Konishi et al., 1998; Monchi et al., 2001], with a suggested specific role in the dimensional change aspect of shifting rather than stimulus-response mapping or other shifting-related processes [Hampshire and Owen, 2006]. Our study suggests that shifting-specific EF is supported by a less encapsulated role of this region; however, we did not find complementary evidence of high integration of this area being associated with high shifting-specific. Future work is required to clarify the potential link between decreased clustering coefficient in vlPFC and dimensional change ability.

We also observed a relationship for regions of left dorsolateral prefrontal cortex. One node falls within a mid-dorsolateral prefrontal region (i.e., BA 46), which is classically considered to be associated with working memory [Petrides, 2000]. Higher shifting specific EF was associated with an increased clustering coefficient, indicating enhanced local processing, and reduced participation, which is associated with connections to a wider diversity of modules. As such, it appears that this region has a more focal organization in individuals with higher shifting-specific EF. We speculate that such an organization may allow for less interference of task-sets and responses. This was an *priori* region of interest due to a study that found lateral prefrontal cortex was more globally connected in individuals with high fluid intelligence [Cole et al., 2012]. We were especially interested in this finding for two reasons. First, there is strong co-linearity between general intelligence and common EF, updating-specific EF, and to a lesser extent, shifting-specific EF [Friedman et al., 2008]. Second, the 3-back task used in that study, like all EF tasks, suffers from a task impurity limitation in that both common EF and updating-specific EF explain some of the variability in performance on the task [Miyake and Friedman, 2012]. Using our multi-component approach, however, we were able to disentangle the relationships between connectivity of lateral prefrontal cortex and each of these EF dimensions separately. We found an association with updating specific EF but not with common EF.

We also found associations with a node within a more posterior section of the left dorsolateral prefrontal cortex that is situated near the inferior frontal junction. This region has been implicated in meta-analyses as being involved in switching [Derrfuss et al., 2005]. While there are a variety of theories with regards to the function of this region, at least one prominent idea is that it is involved in linking goal-related information to action-related information [De Baene et al., 2012]. For this node greater shifting-specific EF was associated with increased global connectivity, which may allow for better integration of these two types of information (i.e., goal-related, action-related).

## Updating-Specific EF

As in our previous work [Reineberg et al., 2015], we found fewer significant relationships between measures of functional connectivity and updating-specific EF than for common EF or shifting-specific EF. One might have expected that connectivity of the DLPFC would be important for updating-specific EF as this region has also been implicated as important for the manipulation of information in working memory by a number of task-based fMRI studies and meta-analyses of working memory processes [Barbey et al., 2013; Wager and Smith, 2003]. In fact, we found higher updating-specific EF ability was associated with decreased participation coefficient in DLPFC (*a priori* region 17). This result could indicate that the cognitive functions of DLPFC depend, in part, on a more circumscribed connectivity pattern rather than broad connectivity to many functional communities in the brain. In fact, both empirical research and computational modeling [Frank et al., 2001; Hazy et al., 2007], suggest that the updating of working memory relies heavily on the specific functional, connectivity between the DLPFC and the basal ganglia. If so, higher updating-specific EF may be associated with less broad-based connectivity of the DLPFC.

The remaining set of results for updating-specific EF was fairly complex. In general, updating-specific EF was associated with less hublike and less central properties in a variety of nodes spanning laterally from frontopolar to dorsolateral to premotor cortex, and medially from sub- to supragenual portions of anterior cingulate cortex. Better updating-specific EF was associated with reduced betweenness centrality, which reflects how much a node connects disparate parts of the graph, in dorsolateral frontal pole (*a priori* region 15) as well as supragenual anterior cingulate cortex, frontal pole, and premotor cortex (exploratory regions 19, 20, and 23). In addition, higher updating-specific EF was associated with reduced eigenvector centrality of primary sensory cortex (exploratory region 22). Higher updating-specific EF was also associated with lower global connectivity in a left cerebellar lobule VI region (*a priori* region 6).

Individual differences in updating-specific EF also seem to rely on reduced segregated connectivity in some areas, as we found an association between reduced clustering coefficient in the inferior temporal gyrus, supplementary motor area, and lateral occipital gyrus (exploratory regions 3, 7, and 21). This decreased segregation was not accompanied by increased centrality or more hublike connectivity in these regions. Take together, higher updating-specific EF seems to rely on the connectivity of a diverse set of regions spanning those responsible for both higher-level and lower-level cognitive functions.

## General Discussion

One of the more perplexing aspects of EF is that it seems to rely rather generally on the frontoparietal network across many tasks and individuals, with little or no specificity to the regions involved. Explorations using an individual differences approach, such as in the present study, begin to provide insight into how variations in brain function within the regions of this critical network might be associated with both the nature and the level of executive control. In our prior work, we have demonstrated that individual differences in each of the aspects of EF explored here—common EF, shifting-specific EF, and updating-specific EF—are associated with unique patterns of gray matter volume and white matter characteristics [Smolker et al., 2015] as well as with the strength and spatial composition of resting-state networks as determined by ICA [Reineberg et al., 2015]. Here we expand that picture by showing that, in addition to variation in the size or composition of resting-state networks, EF ability may be linked to complex measures of the connectivity profile of a number of brain regions.

As mentioned above, the frontoparietal network appears to modulate processing in other brain regions so as to exert control [Miller and Cohen, 2001]. Hence, how connected these frontoparietal regions are to the rest of the brain may modulate how accessible different regions are to control by frontal regions, and such accessibility may in turn influence individual differences in dimensions of EF. Nonetheless, an important aspect of the current results is the finding that it is not just connectivity of nodes within the frontoparietal network, but also nodes outside of it that influences individual differences in EF. For example, connectivity of temporal lobe regions as well as sensorimotor regions also appears to influence dimensions of EF. These findings require a reconceptualization of the neural systems underlying EF and suggest that they may be more broad-based than is typically conceptualized.

Finally, our results provide an interesting perspective on the unity and diversity model of individual differences in EF, providing converging evidence for its validity. For the most part, the nodes whose connectedness is related to individual differences in EF were distinct for the three major facets of EF: common EF, switching-specific EF, and updating-specific EF. Such anatomical specificity suggests that indeed these constructs are tapping into distinct networks, which support each of these three dimensions of EF.

## Limitations

The current study is not without limitations. Limitations of the current study are similar to those of other investigations of individual differences in cognitive abilities as a function of rs-fMRI. Notably, we cannot disentangle whether differences in rs-fMRI are due to sculpted history of neural activity or differences in the quality of cognition or unconstrained thoughts between high and low ability individuals. On the one hand, a dominant theme emerging from prior literature is that fluctuations in rs-MRI reflect the intrinsic functional organization of the brain [Fox and Raichle, 2007], sculpted by a history of coherent neuronal firing and anatomical wiring between distributed brain regions [Wig et al., 2011]. Lending support to this hypothesis is observed stability across multiple time points within individuals [Guo et al., 2012; Shehzad et al., 2009] and under various stages of consciousness and anesthesia [Boly et al., 2008; Greicius et al., 2008]. On the other hand, an individual's state at the time of scanning may influence the patterns we observed. Several recent findings suggest that patterns of functional connectivity may be partially influenced by the participant's mental/task state [Andrews-Hanna et al., 2010; Doucet et al., 2012; Shirer et al., 2012], and can be modified on a rapid time scale [Lewis et al., 2009; Stevens et al., 2010; Tambini et al., 2010].

Our studies to date have been limited to relatively static aspects of brain organization—white matter integrity and connectivity, grey matter volume, thickness and gyrification [Smolker et al., 2015], and patterns of organization and connectivity during resting state [Reineberg et al., 2015; the current study]. Whether the same regions implicated in these studies as associated with individual differences in EF are also implicated in more dynamic aspects of brain function (such as variations in connectivity during different EF tasks) remains an open question.

Although we believe our findings establish a strong groundwork for further exploration of neuropsychological correlates of EF as assessed during resting state, it will be important for future studies to replicate our findings. For example, while in our exploratory analysis we found that the strongest associations between graph theory metrics for a given brain region and a particular EF dimension accounted for approximately 35%–55% of the variance in that EF, there is always the likelihood of such regression models overfitting the data. Nonetheless, the amount of variance accounted for is still likely to be relatively robust given the statistical approaches (e.g., bootstrapping) that were taken. It will also be important to determine the possible implications of the current findings for reduced EF in psychiatric and neurological disorders, that is, whether the relationships we have identified are reduced or altered in such populations. In addition to replication and extension, future studies might want to consider genetic and/or behavioral variation that might account for differences in resting-state functional connectivity between high and low EF individuals.

## CONCLUSION

Here we have provided evidence that the connectivity pattern of the intrinsic fluctuations in the BOLD signal explains a substantial portion of variance in individual differences in dimensions of EF. We have built upon an existing theoretical model of EF by showing separable patterns of brain connectivity influence individual differences in each of three dimensions of EF—common EF, shifting-specific EF, and updating-specific EF. The results are notable for providing a fine-grained picture of both the regions involved and their connectivity, as assessed by different graph theoretic measures. While prior work has established how a given region contributes to online EF in the form of group mean effects in typical task-based fMRI, we have shown that variability in the degree to which specific regions (or nodes) are integrated or segregated, as assessed by their resting-state connectivity profile, underlies individual variability in dimensions of EF. The current study significantly expands our knowledge of neural influences on individual difference in EF and can serve an important hypothesis-generating role for future large-scale studies of inter-individual variability in EF as it related to patterns of brain activation either at rest, or during task, as we are currently exploring.

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