Full Length Article

Interactions between the default network and dorsal attention network vary across default subsystems, time, and cognitive states

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A R T I C L E   I N F O

A B S T R A C T

Anticorrelation between the default network (DN) and dorsal attention network (DAN) is thought to be an intrinsic aspect of functional brain organization reflecting competing functions. However, the effect size of functional connectivity (FC) between the DN and DAN has yet to be established. Furthermore, the stability of anticorrelations across distinct DN subsystems, different contexts, and time, remains unexplored. In study 1 we summarize effect sizes of DN-DAN FC from 20 studies, and in study 2 we probe the variability of DN-DAN interactions across six different cognitive states in a new data set. We show that: (i) the DN and DAN have an independent rather than anticorrelated relationship when global signal regression is not used (median effect size across studies: $r=-.06$; 95% CI: $-.15$ to $.08$); (ii) the DAN exhibits weak negative FC with the DN Core subsystem but is uncorrelated with the dorsomedial prefrontal and medial temporal lobe subsystems; (iii) DN-DAN interactions vary significantly across different cognitive states; (iv) DN-DAN FC fluctuates across time between periods of anticorrelation and periods of positive correlation; and (v) changes across time in the strength of DN-DAN coupling are coordinated with interactions involving the frontoparietal control network (FPCN). Overall, the observed weak effect sizes related to DN-DAN anticorrelation suggest the need to re-conceptualize the nature of interactions between these networks. Furthermore, our findings demonstrate that DN-DAN interactions are not stable, but rather, exhibit substantial variability across time and context, and are coordinated with broader network dynamics involving the FPCN.

1. Introduction

The last decade has witnessed extraordinary interest and progress in network neuroscience—the understanding of how interconnected brain regions operate in concert as large-scale networks, and how these networks relate to healthy and pathological cognitive functioning (Buckner et al., 2013; Bullmore and Sporns, 2009; Fox and Raichle, 2007; Medaglia et al., 2015; Petersen and Sporns, 2015). Resting state functional connectivity has emerged as a powerful, non-invasive tool for delineating the functional network architecture of the human brain. Correlated fluctuations in BOLD signal measured during "rest" are thought to reveal intrinsic networks that persist across time (Damoiseaux et al., 2006) and context (Cole et al., 2014; Smith et al., 2009) due to their presumed source in stimulus-independent brain

activity reflecting the underlying polysynaptic structural neuroanatomy (Fox and Raichle, 2007; Van Dijk et al., 2010).

One of the most influential findings to emerge from network neuroscience is the demonstration of anticorrelated networks, ostensibly reflecting competing functions (Fox et al., 2005; see also Fransson, 2005; Golland et al., 2008). The default network (DN) is involved in a variety of internally-directed processes, including self-reflection, autobiographical memory, future event simulation, conceptual processing, and spontaneous cognition (Andrews-Hanna et al., 2014; Buckner et al., 2008; Christoff et al., 2016; Ellamil et al., 2016; Fox et al., 2015, 2016; Raichle, 2015; Raichle et al., 2001) and exhibits decreased activation during many cognitive tasks that demand external perceptual attention (Greicius, Krasnow, Reiss, and Menon, 2003; Gusnard and Raichle, 2001; Shulman et al., 1997). In contrast a

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collection of regions, known initially as the "task-positive" network, demonstrate activity increases during cognitive tasks that require externally focused visuospatial attention (Cole and Schneider, 2007; Corbetta and Shulman, 2002; Dosenbach et al., 2006; Duncan, 2010; Fox et al., 2005; Golland et al., 2007; Miller and Buschman, 2013; Vincent et al., 2008). The idea of competitive large-scale network interactions emerged when Fox et al. (2005) reported that the DN and "task positive" network were anticorrelated during the resting state, potentially reflecting a toggling between internally-oriented and externally-oriented cognitive processing (see also Fransson (2005)). However, subsequent studies led to a refinement of this idea, demonstrating co-activation and positive functional connectivity between the DN and the frontoparietal control network (FPCN)−a component of the "task positive" network−during some task conditions, including mind wandering (Christoff, 2012; Christoff et al., 2009; Fox et al., 2015), spontaneous thought (Ellamil et al., 2016), autobiographical future planning (Gerlach et al., 2014; Spreng et al., 2010), creativity (Ellamil et al., 2012), memory recall (Fornito et al., 2012), working memory guided by information unrelated to current perceptual input (Konishi et al., 2015), social working memory (Meyer et al., 2012), and semantic decision making (Krieger-Redwood et al., 2016). Moreover, cooperative dynamics between the FPCN and DN correlate with better task performance in some cases (e.g., Fornito et al., 2012). Cooperative dynamics between these networks may occur when meta-cognitive awareness and/or deliberate control is brought to bear on internally-oriented processing (Andrews-Hanna et al., 2014; Christoff et al., 2016; Dixon et al., 2014b; Fox and Christoff, 2014; Smallwood et al., 2012). On the other hand, studies have generally found anticorrelation between the DN and other components of the "task positive" network, particularly the dorsal attention network (DAN) (Chai et al., 2012, 2009; De Havas et al. 2012; Fornito et al., 2012; Gao and Lin, 2012; Holmes et al., 2015; Josipovic et al., 2012; Kelly et al., 2008; Lee et al., 2012; Spreng et al., 2016; Van Dijk et al., 2010; Yeo et al., 2015).

The idea of competitive anticorrelated networks has been influential and used to explain the origin of attentional lapses and behavioral variability in healthy adults (Keller et al., 2015; Kelly et al., 2008; Weissman et al., 2006), cognitive immaturity in children (Chai et al., 2014), and abnormal functioning in conditions such as ADHD (Sonuga-Barke and Castellanos, 2007). Although global signal regression can induce spurious anticorrelations when included as part of data preprocessing (Murphy et al., 2009; Saad et al., 2012), negative FC between the DN and "task-positive" regions has been observed even without this step, suggesting that it is a true biological phenomenon (Chai et al., 2012; Chang and Glover, 2009; Fox et al., 2009). However, there are a number of important questions that have not been addressed. We still lack a clear understanding of the strength of negative FC between the DN and DAN; the extent to which the relationship between these networks varies across DN subsystems, different cognitive states, and time; and how DN-DAN interactions relate to broader network dynamics involving the FPCN. Here, we provide a systematic investigation of DN-DAN interactions to address these questions.

In study 1, we sought to determine the effect size of negative FC between the DN and DAN. While the notion of anticorrelation is often highlighted in papers that examine DN-DAN interactions, rarely is there discussion of the actual effect size. It is quite possible that negative FC between the DN and DAN is a statistically reliable but weak effect, rather than a true anticorrelation. This is a critical question given that initial studies of anticorrelation used global signal regression (GSR) which is known to alter the distribution of correlation coefficients, and may not provide an accurate assessment of the true effect size of negative FC between the DN and DAN (Murphy et al., 2009). By removing the global signal as part of preprocessing, this mathematically ensures that there are a roughly equal number of positive and negative correlations that are distributed around 0, which can introduce artifactual negative correlations, or inflate the strength of true

negative correlations (Murphy et al., 2009). We therefore conducted a meta-analysis of 20 studies reporting anticorrelation to examine empirical effect sizes, and the potential impact of including GSR as part of preprocessing.

In study 2, we examined the variability of DN-DAN interactions in a new data set using several different approaches. Since the discovery of DN-DAN anticorrelation, developments in understanding the DN have now revealed that it is not a unitary entity, but rather, composed of three distinct subsystems (for a review see Andrews-Hanna et al. (2014)). Our first goal was to examine whether the DAN exhibits similar or distinct functional interactions with these subsystems. Although it is too early to definitively characterize the function of each subsystem, preliminary evidence suggests: (1) a Core subsystem involved in self-referential processing, including the construction of a temporally-extended self with attributes, preferences, and autobiographical details; (2) a dorsomedial prefrontal subsystem involved in semantic processing and mentalizing (i.e., generating inferences about mental states including beliefs and desires); and (3) a medial temporal lobe subsystem involved in retrieving and binding together contextual details during the recollection of episodic memories and simulation of future events. Interestingly, studies have found coactivation of the DAN and dorsomedial prefrontal subsystem during a social working memory task (Meyer et al., 2012), and coactivation of the DAN and medial temporal lobe subsystem during a memory-guided attention task (Summerfield et al., 2006), raising the possibility that these subsystems may not be antagonistic with the DAN. Indeed, learning often requires a synergy between perceptual and memory processes (Chun and Turk-Browne, 2007; Hasselmo and McGaughy, 2004), and mental state inferences often draw upon perceptual input (e.g., facial expressions) (Baron-Cohen et al., 2001). Discerning the nature of functional interactions between the DAN and the distinct DN subsystems may provide critical information about the cognitive processes that may or may not be inherently competitive.

A second goal of study 2 was to examine the stability of anticorrelations across time and across different cognitive states. Mounting evidence suggests that the strength and topography of functional connectivity patterns reconfigure across time and different tasks (Allen et al., 2014; Braun et al., 2015; Cole et al., 2013; Davison et al., 2015; Geerligs et al., 2015; Gonzalez-Castillo et al., 2015; Hermundstad et al., 2014; Hutchison et al., 2013; Krienen et al., 2014; Kucyi et al., 2016; Mennes et al., 2013; Shine et al., 2016; Shine et al., 2016; Shirer et al., 2012; Simony et al., 2016; Zabelina and Andrews-Hanna, 2016; Zalesky et al., 2014). It is possible that anticorrelations are related to the cognitive state elicited by rest, that is, spontaneous thoughts of current concerns, past events, and future plans (Andrews-Hanna, 2012; Delamillieure et al., 2010). DN-DAN interactions may depart from anticorrelation under some cognitive states, for example, those that require a mixture of perceptual processing and internal conceptual thoughts (Dixon et al., 2014b). A recent study observed DN engagement during an externally-directed working memory task when participants leveraged prior knowledge of the stimuli to complete the task (Spreng et al., 2014), suggesting that there may be task conditions affording greater cooperation between the DN and DAN. Finally, there is some evidence that negative FC involving the DN may vary across time even during rest (Allen et al., 2014; Chang and Glover, 2010). Here, we investigated possible contextual and temporal variability of DN-DAN interactions by examining their relationship across time and different cognitive states within the same participants.

The third goal of study 2 was to examine the possibility that changes across time in DN-DAN FC strength are related to broader temporal dynamics involving the coordination of multiple large-scale networks. Recent work has demonstrated that the strength of FC between a pair of nodes (regions) can increase or decrease across time, and this tends to occur in a coordinated manner, with sets of connections evolving in concert (Bassett et al., 2014; Davison et al.,

2015; Zalesky et al., 2014). Here, we sought to extend this idea by examining the temporal co-evolution of interactions at the level of large-scale networks rather than individual regions. Based on evidence that the FPCN has extensive functional interconnections with the DN and DAN (Spreng et al., 2013) and plays a role in regulating internal and external attention (Dixon et al., 2014b; Dixon et al., in press; Gao and Lin, 2012; Smallwood et al., 2012; Spreng et al., 2010; Vincent et al., 2008), we hypothesized that there would be dynamic interactions coordinated across the FPCN, DN, and DAN. For example, we hypothesized that changes across time in the strength of DN-DAN coupling would be tightly coordinated with changes across time in the strength of FPCN-DAN coupling.

To examine these questions, we used fMRI in conjunction with functional connectivity (FC) and machine learning classification analyses. We monitored brain activation dynamics during six conditions: (i) rest; (ii) movie viewing; (iii) analysis of artwork; (iv) social preference shopping task; (v) evaluation-based introspection; and (vi) acceptance-based introspection. Because these conditions differ from traditional cognitive tasks, we refer to them as cognitive states or contexts, rather than tasks. These conditions were designed to elicit mental states that resemble those frequently experienced in everyday life, and were predicted on theoretical grounds to result in variable DN-DAN interactions (Dixon et al., 2014b). That is, we designed conditions that we believed were most likely to show a change in FC away from a negative correlation between the DN and DAN to provide a general test of whether DN-DAN interactions remain stable across different contexts. These conditions involved a combination of internal and external processing requirements, or deliberate control over internal processing. Each condition elicited a continuous mental state and did not require any responses. All data underwent the same preprocessing procedure typically used with resting state fMRI that does *not* rely upon global signal regression (Whitfield-Gabrieli and Nieto-Castanon, 2012).

2. Materials and methods

2.1. Study 1 Effect size meta-analysis

In study 1, we examined the effect size of DN-DAN FC in 20 studies. Using Google Scholar and PubMed, we performed searches containing the words: "default network", "anticorrelation", "functional connectivity", and "fMRI". We found additional studies through the reference lists of these papers. Studies were included in the analysis if they met the following criteria: (i) used fMRI; (ii) acquired data from healthy young adults; (iii) examined DN-DAN FC; and (iv) reported a relevant effect size—an r or z(r) value, or provided figures with legends that allowed for an approximation of the effect size. Because some studies did not report an effect size, our meta-analysis is not exhaustive. Where studies reported results with and without GSR, we included both results for comparison. We report 95% confidence intervals for the median effect size, generated based on bootstrapping with 1000 samples. In most cases studies provided data for a resting state condition, however, there were a few exceptions: Golland et al. (2007) reported data from a movie viewing condition; Fornito et al. (2012) reported "spontaneous" fluctuations reflecting data from a recollection task, after task-related signals had been regressed out; and Amer et al. (2016) reported data from a 1-back task. All studies acquired data from healthy adults. However, two studies had unique samples that are worth commenting on. Anderson et al. (2011) used a large sample with ages ranging from 7–35 years (mean=18.8, SD=6.1). Although DN-DAN interactions change across development, it is currently unknown when they reach adult-like patterns (Chai et al., 2014; Gao et al., 2013). Thus, it should be kept in mind that the effect size from this study (reflecting data from all participants) may potentially underestimate DN-DAN negative FC. Josipovic et al. (2012) examined DN-DAN FC in a sample of experienced meditators.

It is currently unknown whether meditation training leads to enduring changes in resting state network organization, so the finding from this study should be viewed with caution. Additionally, it should be noted that Chang and Glover (2009) only reported data for three participants, and therefore, the values we report from this study likely over-estimate the strength of negative FC. Additional details for each study are presented in Supplementary Table 1.

2.2. Study 2 Participants

Participants in study 2 were 24 healthy adults (Mean age=30.33, SD=4.80; 10 female; 22 right handed), with no history of head trauma or psychological conditions. This study was approved by the UBC clinical research ethics board, and all participants provided written informed consent, and received payment ($20/hour) for their participation. Due to a technical error, data for the movie and acceptance-based introspection conditions were not collected for one participant. At the end of scanning, another participant reported experiencing physical discomfort throughout the scan. Similar results were obtained with or without inclusion of this participant's data, so they were included in the final analysis.

2.3. Experimental conditions

Each participant performed six conditions in separate six-minute fMRI runs (see Supplementary methods for additional details): (1) *Rest*. Participants lay in the scanner with their eyes closed and were instructed to relax and stay awake, and to allow their thoughts to flow naturally. (2) *Movie watching*. Participants watched a clip from the movie "Star Wars: Return of the Jedi", during which Luke Skywalker engages in a light-saber duel with Darth Vader. (3) *Artwork analysis*. Participants viewed four pieces of pre-selected artwork, each for 90 s, and were instructed to attend to the perceptual details and the personal meaning of the art. (4) *Shopping task*. Participants viewed a pre-recorded video shot from a first-person perspective of items within several stores in a shopping mall, and were instructed to imagine that they were shopping for a birthday gift for a friend, and to think about whether each item would be a suitable gift based on their friend's preferences. *(5) Evaluation-based introspection*. Participants reflected on a mildly upsetting issue involving a specific person in their life and were asked to analyze why the situation is upsetting, who caused it, what might happen in the future, and to become fully caught up in their thoughts and emotions. *(6) Acceptance-based introspection*. Participants reflected on a mildly upsetting issue involving a specific person in their life and were asked to cultivate a present-centered awareness, grounded in the acceptance of moment-to-moment viscero-somatic sensations (i.e., to notice and experience arising thoughts, emotions, and bodily sensations with acceptance, and without any elaborative mental analysis or judgment).

Task order was held constant. The introspection conditions were placed at the end so that participants would not continue thinking about the upsetting issue, which may have otherwise influenced thought content during the remaining tasks. Furthermore, because acceptance-based introspection requires an inhibition of the default tendency to engage in evaluative/narrative processes (Farb et al., 2007), we placed this condition after evaluation-based introspection. Given that the task conditions were completely different and did not require responses, there was no concern about practice effects from one condition to another. That is, there were no specific perceptual or attentional task requirements that participants could improve upon and that could translate from one task condition to another. Additionally, before each of the six conditions we stressed to participants that they should remain as alert as possible, and they reported that they did so (this was confirmed through post-scanning questions regarding attention and the content of each condition). Furthermore, we designed our conditions to be as engaging as possible. Finally,

inspection of individual participant data did not reveal evidence of linear changes in DN-DAN FC across the six contexts (Supplementary Fig. 1). In fact, Fig. 5 reveals that changes in FC across context were brain region specific, and varied in direction (anticorrelations may increase or decrease); no global patterns emerged, suggesting that general factors do not account for our findings.

2.4. MRI data acquisition

fMRI data were collected using a 3.0-Tesla Philips Intera MRI scanner (Best, Netherlands) with an 8-channel phased array head coil with parallel imaging capability (SENSE). Head motion was minimized using a pillow, and the effect of scanner noise was minimized using earplugs. T2*-weighted functional images were acquired parallel to the anterior commissure/posterior commissure (AC/PC) line using a single shot gradient echo-planar sequence (repetition time, TR=2 s; TE=30 ms; flip angle, FA=90°; field of view, FOV=240 mm; matrix size=80 × 80; SENSE factor=1.0). Thirty-six interleaved axial slices covering the whole brain were acquired (3-mm thick with 1-mm skip). Each session was six minutes in length, during which 180 functional volumes were acquired. Data collected during the first 4 TRs were discarded to allow for T1 equilibration effects. Before functional imaging, a high resolution T1-weighted structural image was acquired (170 axial slices; TR=7.7 ms; TE=3.6 ms; FOV=256 mm; matrix size=256 × 256; voxel size=1 × 1 × 1 mm; FA=8°). Total scan time was ~ 60 min. Head motion was minimized using a pillow, and scanner noise was minimized with earplugs.

2.5. Preprocessing

Image preprocessing and analysis were conducted with Statistical Parametric Mapping (SPM 8, University College London, London, UK; http://www.fil.ion.ucl.ac.uk/spm/software/spm8). The time-series data were slice-time corrected (to the middle slice), realigned to the first volume to correct for between-scan motion (using a 6 parameter rigid body transformation), and coregistered with the T1-weighted structural image. The T1 image was bias-corrected and segmented using template (ICBM) tissue probability maps for gray/white matter and CSF. Parameters obtained from this step were subsequently applied to the functional (re-sampled to 3 mm^3 voxels) and structural (re-sampled to 1 mm^3 voxels) data during normalization to MNI space. The data were spatially-smoothed using an 8-mm^3 full-width at half-maximum Gaussian kernel to reduce the impact of inter-subject variability in brain anatomy.

To address the spurious correlations in resting-state networks caused by head motion, we identified problematic time points during the scan using Artifact Detection Tools (ART, www.nitrc.org/projects/artifact_detect/). Images were specified as outliers according to the following criteria: translational head displacement greater than .5 mm from the previous frame, or rotational displacement greater than .02 rad from the previous frame, or global signal intensity > 4 standard deviations above the mean signal for that session. The mean number of identified outliers was 4.93 (range: 0–15) and did not differ across conditions (p > .4). Each participant had at least 5.3 minutes of non-outlier time points. Outlier images were not deleted from the time series, but rather, modeled in the first level general linear model (GLM) in order to keep intact the temporal structure of the data. Each outlier was represented by a single regressor in the GLM, with a 1 for the outlier time point and 0 elsewhere.

Using the CONN software (Whitfield-Gabrieli and Nieto-Castanon, 2012), physiological and other spurious sources of noise were esti-mated and regressed out using the anatomical CompCor method (Behzadi et al., 2007). Global signal regression was not used due to fact that it mathematically introduces negative correlations, and renders the results difficult to interpret (Murphy et al., 2009). The normalized anatomical image for each participant was segmented into

white matter (WM), gray matter, and CSF masks using SPM8. To minimize partial voluming with gray matter, the WM and CSF masks were eroded by one voxel. The eroded WM and CSF masks were then used as noise ROIs. Signals from the WM and CSF noise ROIs were extracted from the unsmoothed functional volumes to avoid additional risk of contaminating WM and CSF signals with gray matter signals. The following nuisance variables were regressed out: three principal components of the signals from the WM and CSF noise ROIs; head motion parameters (three rotation and three translation parameters) along with their first-order temporal derivatives; each artifact outlier image; linear trends. A band-pass filter (0.009 Hz < f < 0.10 Hz) was simultaneously applied to the BOLD time series during this step.

2.6. ROI definition

To explore DN-DAN interactions in relation to well-established network boundaries, we used anatomical regions of interest (ROIs) created by Yeo and colleagues (Krienen et al., 2014; Yeo et al., 2015) based on their 17-network parcellation derived from the data of 1000 participants (Yeo et al., 2011) (Supplementary Fig. 2). The 17-network parcellation was split into a set of 114 cortical regions composed of roughly symmetric territories in the left and right hemispheres, and were defined in relation to network boundaries, sulcal patterns, and confidence maps. For each network, spatially connected regions were combined to form a single ROI, whereas spatially disconnected regions became separate ROIs. Vertices near between-network boundaries were peeled back. The current analysis focused on 32 ROIs spanning the DAN and three DN subsystems, and 10 ROIs spanning the FPCN. We extracted the mean activation timeseries from each of these ROIs.

2.7. Subsystem analysis

To examine whether anticorrelations are present for each DN subsystem, we used the residual timeseries (following nuisance regres-sion) for each ROI to compute condition-specific correlation matrices consisting of all node-to-node connections. After Fisher r-to-z trans-forming the correlation values, we averaged the $z(r)$ values reflecting pairwise connections between the DAN and each DN subsystem. We first computed average FC separately for the left and right hemispheres, and then averaged them given the similar results; that is, there was no difference between the left and right hemispheres (paired t-tests: ps > .19). This yielded a single value reflecting the relationship between the DAN and each DN subsystem for each participant. These values were submitted to a one-way repeated measures analysis of variance (ANOVA), with subsystem as the factor.

2.8. Seed-based voxel analysis

We computed seed-based functional connectivity (FC) maps for DAN regions in order to examine the spatial topography of antic-orrelated voxels. The timeseries of all voxels within each DAN ROI were averaged, and first-level correlation maps were produced by computing the Pearson correlation between that seed timeseries and the timeseries of all other voxels. Correlation coefficients were con-verted to normally distributed Fisher transformed z-scores to allow for second-level GLM analyses. Correction for multiple comparisons was accomplished using combined height (Z > 3.1) and cluster (p < .05 FWE corrected) thresholding. Results were visualized with CARET brain mapping software (http://brainmap.wustl.edu/caret; Van Essen, 2005; Van Essen et al., 2001). We examined the location of anticorrelated voxels in relation to the network boundaries from Yeo et al.'s (2011) 17-network parcellation.

2.9. Similarity analysis

To examine potential variability of DN-DAN interactions across the six contexts, we determined the similarity of FC values across contexts. For each participant, we extracted and vectorized all between-network correlations (excluding interhemispheric connections) for each context. Many prior studies have reported stronger within-hemisphere functional connectivity, and it seems likely that interhemispheric functional connections are often indirect, mediated via other brain regions. Thus, we excluded interhemispheric connections to provide more precise results that are likely to reflect direct functional connections. After applying a Fisher's r-to-z-transform, we used the Pearson correlation as a measure of the similarity of the FC vectors for each pair of contexts. These correlation values were Fisher transformed and averaged, to arrive at a single value reflecting the similarity of FC across contexts. We contrasted across-context similarity with within-context similarity, that is, the similarity of FC values for the early period (first three minutes) and late period (last three minutes) of each condition. The difference between within- and across-context similarity provided an index of the influence of context on DN-DAN FC. Importantly, we computed similarity for each participant separately, and then determined average similarity across the group, thus accounting for individual variability.

2.10. Machine learning classification analysis

We used a support vector machine (SVM) classifier to discern whether an individual's current mental state could be correctly discriminated based solely on DN-DAN FC patterns. Accurate classification would imply a unique configuration of FC values within each context. The SVM classifier was implemented with The Spider toolbox (Weston et al., 2005). Following prior work (Dosenbach et al., 2010), we set the cost parameter, C, to 1, and used a radial basis function (RBF) kernel, with sigma set to 2 (similar results were obtained with a linear classifier; see Supplementary Fig. 3). For each individual we created a vector consisting of all DN-DAN *z*-transformed correlations (excluding interhemispheric connections) for each context. The correlation vectors served as input features (96 in total), and were assigned a value of 1 or −1 to specify the context to which they belonged. We tested the accuracy of the classifier using leave-one-out cross validation: the classifier was trained on the FC patterns for all but one participant, and then tested on that left-out participant, and this was repeated for each individual. The methods used for the main analysis were selected *a priori*. We selected parameters used in prior work (Dosenbach et al., 2010) and did not attempt any type of iterative optimization, and we did not perform any type of feature selection (i.e., all 96 FC values were used). Thus, our analysis method should minimize the chance of overfitting (Skocik et al., 2016). For statistical testing, we obtained an empirical null distribution by performing the classification analysis 1000 times with condition labels randomly permuted. The mean classification accuracy over the 1000 iterations ranged from 49.62% to 50.43% with a standard deviation that ranged from 6.03% to 6.73%, depending on the specific pair of conditions. In each case, inspection of the null distribution revealed that 95% of these models had accuracies below 60.4%. Classification accuracies larger than the 95th percentile of the null distribution were considered to be statistically significant at $p < .05$. To correct for multiple comparisons, classification accuracies larger than the 99.7th percentile of the null distribution (equivalent to 66.7% accuracy) were considered to be statistically significant at $p < .05$, bonferroni corrected. To further test the robustness of classification based on DN-DAN FC, we used 4-fold cross-validation in which data were split into 4 equal-sized groups, with 75% of the data used for training the classifier, and the left-out 25% used for testing the classifier. This process was repeated 4 times until every participant was used in the testing set once. In this case, we used a feed-forward neural network classifier that was trained using

back propagation using Rapid Miner (Hofmann and Klinkenberg, 2013). The learning rate was set to .3 and momentum was .2. Significant classification was observed with this method as well (Supplementary Fig. 4).

2.11. Logistic regression analysis

We also tested more directly if each condition was associated with distinct FC values by using a logistic mixed-effects modeling approach (Pinheiro and Bates, 2000) implemented with the *lme4* package in R (Bates et al., 2007). This approach allowed us to analyze the FC values at the item level while modeling the within-subjects variance, as opposed to using a between-subjects approach (e.g., relying on average FC values across participants). Whereas a typical logistic regression (a fixed-effects only model) does not allow for multiple instances per person (violation of the independence assumption), a mixed-effects model deals with non-independence by effectively estimating a random intercept for each individual subject. This ultimately helps to account for the extraneous differences in FC values that are inherently introduced by having multiple observations per subject (Pinheiro and Bates, 2000). The dependent variable was the presence (1) or absence (0) of each condition, yielding six total regressions where each condition was compared against all others. Participant was the random effect in all models, while FC values were fixed effects. A prediction was made for every FC value—was the value from a specific condition (1) or not (0)—while accounting for the within-subjects variance. All significance testing was done using two criteria: (1) a two-tailed α set to 0.05 and (2) a 95% confidence interval as recommended by (Nakagawa and Cuthill, 2007). CIs were determined using bootstrapping with 1000 samples. All six logistic regression models were statistically significant based on these criteria and the models were also significantly different when compared to a random intercept only model ($p < .05$). Comparisons to the random intercept only model highlight the fact that FC values explained differences in the conditions above and beyond the within-subject variability.

2.12. Dynamic FC analysis

To examine time-dependent changes in FC during rest, we examined DN-DAN FC within 60 windows, shifted by one timepoint (2 seconds) each time. Within each window, we calculated the average strength of FC between the DAN and each DN subsystem by computing the mean of the relevant pairwise (node to node) correlations (e.g., averaging the Fisher transformed correlations for each pair of DAN-Core subsystem regions). To limit the possibility of detecting spurious temporal fluctuations in FC, we bandpass filtered the data ($0.0167\,\text{Hz} < f < 0.10\,\text{Hz}$) such that frequencies lower than $1/w$ were removed, where w is the width of the window (Leonardi and Van De Ville, 2015). We then computed the percentage of windows with $z(r) < 0$ between the DAN and each DN subsystem, to provide a simple measure of time periods with positive or negative functional coupling. This was done separately for the left and right hemispheres and then averaged given that there was no difference (p's > .23). A one-way repeated measures ANOVA with subsystem as the factor and follow up paired-samples *t*-tests were used to compare dynamic FC patterns across the DN subsystems.

2.12.1. Temporal co-evolution of network interactions

To examine the temporal co-evolution of interconnected nodes, Bassett and colleagues devised a method of identifying groups of FC connections with statistically similar temporal profiles (Bassett et al., 2014; Davison et al., 2015). This approach first determines the strength of time-varying FC between each pair of nodes (regions), providing numerous time-series of edge-weights (connection strength). This approach then uses the correlation coefficient as a measure of the linear association between sets of edge-weight time series, to discern groups of functional connections that display similar changes in

strength across time. Here, we adopted this approach, but instead of focusing on node-to-node interactions, we focused on network-to-network interactions defined based on the boundaries of Yeo et al. (2011). Within each 60-second window, we computed the average strength of FC between the DAN and each DN subsystem, and between the FPCN and each DN subsystem, and between the FPCN and DAN. This provided several time-series of between-network FC values reflecting changes across time in the strength of interactions between each pair of networks. We then computed the correlation between each pair of time-series to examine the linear relationship between changes across time in the strength of interactions between each pair of networks. For example, we computed the strength of DN-DAN FC across time and the strength of FPCN-DAN FC across time, and then determined if these changes were correlated. A significant correlation would imply that time-dependent DN-DAN interactions are coordinated with time-dependent FPCN-DAN interactions, and reveal that dynamic changes in FC values across multiple large-scale networks evolve in concert. We computed correlations for the left and right hemispheres separately and then averaged them (following Fisher r-to-z transform) given that the values were highly similar in each case (that is, there was no effect of hemisphere, all $ps > .05$, corrected for multiple comparisons). To account for the number of correlations performed, we used a Bonferroni correction, such that results at $p < .004$, uncorrected, were considered statistically significant at $p < .05$, corrected for multiple comparisons.

We conducted a control analysis to rule out the possibility that temporal co-evolution of network interactions could be driven by participant motion. We examined total motion and framewise displacement. We computed the average amount of motion in each window, just as with between-network FC, and then computed the correlation between changes across time in motion and changes across time in between-network FC for each pair of networks. For each participant we then used the Fisher r-to-z transform of the correlations and determined the mean relationship between temporal variation in motion and between network FC, separately for each type of motion, and each of the six task conditions. These values were submitted to a one-sample t-test to assess statistical significance at the group level, based on $α=.05$, corrected for multiple comparisons.

3. Results

3.1. Study 1

3.1.1. Effect sizes of functional connectivity between the DN and DAN
Our first question concerned the strength of negative FC between

the DN and DAN. To examine this, we summarized effect sizes from 20 studies of DN-DAN interactions (Fig. 1; Table 1). We noted a number of variables including whether preprocessing included GSR. As illustrated in Fig. 1, studies that used GSR show the expected effect of negative FC between the DN and DAN with a median effect size of $r=−.24$ ($SD=.28$; 95% CI: −.50 to −.18). A contrasting picture emerged from studies that did not use GSR. These studies generally show a weak negative correlation or even a small positive correlation between the DN and DAN, with a median effect size of $r=−.06$ ($SD=.20$; 95% CI: −.15 to .08). These findings suggest that the DN and DAN may have an *independent* relationship. Given that GSR is known to shift the distribution of correlation coefficients, this preprocessing step inflates the magnitude of negative FC between the DN and DAN and may give a distorted picture of their associations. Notably, many studies that did not use GSR included multiple preprocessing steps to carefully minimize the effect of noise (e.g., regressing out signals related to respiratory and cardiac effects, white matter and CSF timecourses, and outlier time points) and still reported only weak negative correlations (Table 1).

3.2. Study 2

3.2.1. Patterns of functional connectivity between the DAN and each DN subsystem
We next examined the variability of DN-DAN interactions. First, we considered regional variability, and examined whether the DAN exhibits similar or distinct patterns of FC with the three DN subsystems during rest. To explore these interactions in relation to well-established network boundaries, we used regions of interest (ROIs) created by Yeo and colleagues (Krienen et al., 2014; Yeo et al., 2015) based on their 17-network parcellation derived from the data of 1,000 participants (Yeo et al., 2011) (Fig. 2A; Supplementary Fig. 2). We extracted the mean activation timeseries from each of 32 ROIs spanning the DAN and three DN subsystems, and calculated the timeseries correlation between pairs of regions belonging to the DN and DAN. We then computed the average strength of functional connectivity (FC) between the DAN and each DN subsystem. The results demonstrated that DN-DAN interactions significantly varied across DN subsystems [$F(2, 46)=17.78$, $p < .001$] (Fig. 2B). The DAN exhibited modest negative FC with the Core subsystem ($r=−.13$, $p < .001$), but was uncorrelated with the dorsomedial prefrontal subsystem ($r=−.01$, $p=.56$), and showed very weak but reliable negative FC with the medial temporal lobe subsystem ($r=−.04$, $p=.028$) (Fig. 2B). Negative FC was stronger for the Core subsystem relative to the dorsomedial prefrontal and medial temporal lobe subsystems [$t(23)=5.59$, $p < .001$ and $t(23)=4.02$, $p=.001$, respectively].

Supporting this, whole-brain voxel-wise analyses revealed that DAN seed regions exhibited negative FC with voxels primarily located within the borders of the Core subsystem (Fig. 2C; Supplementary Fig. 5). Similarly, FC fingerprints for DAN ROIs revealed that negative FC was mainly observed with Core subsystem regions (Fig. 2D). Thus, the strength of DN-DAN FC is spatially specific. For example, negative FC was more likely to be observed in the rostromedial prefrontal cortex than adjacent dorsomedial prefrontal cortex. Moreover, region aMT of the DAN did not exhibit anticorrelation with any DN regions. Together, these findings demonstrate regional variability in DN-DAN interactions, with little evidence of negative FC involving the dorsomedial prefrontal and medial temporal lobe subsystems.

3.2.2. Stability of DN-DAN functional connectivity across cognitive states
Next, we examined whether DN-DAN interactions exhibit stability across different cognitive states. Prior work has examined the stability of FC patterns by computing the correlation between context-specific connectivity matrices (Cole et al., 2014; Geerligs et al., 2015; Krienen et al., 2014). Strong correlations imply that FC patterns are highly
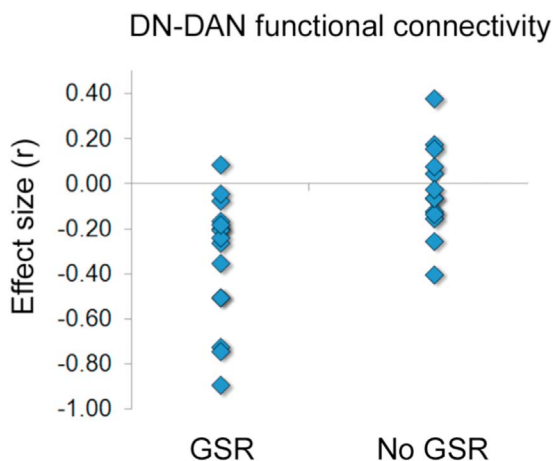
Fig. 1. Effect size of DN-DAN functional connectivity across 20 studies. Each point represents mean between-network functional connectivity from one study. Seven studies reported results with and without GSR (global signal regression).

Table 1
Effect size of DN-DAN functional connectivity across studies.

Study	N	Correlation (r)	Noise removal	Regions
Golland et al., 2007	8	0.09	GSR	Extrinsic-Intrinsic networks
Kelly et al., 2008	26	−0.89	GSR	DN-TPN
Murphy et al., 2009	12	−0.72	GSR	DN-TPN
		0.18	3	DN-TPN
Chang and Glover, 2009	15	−0.35	GSR	PCC-DAN
		−0.25	2, 3	PCC-DAN
Van Dijk et al., 2010	98	−0.24	GSR	DN-DAN
		0.16	1	DN-DAN
Anderson et al., 2011	1278	0.05	1, 2	DN-DAN
Fornito et al., 2012	16	−0.50	GSR	DN-DAN
		−0.40	1, 2	DN-DAN
Lee et al., 2012	17	−0.74	GSR	DN-DAN
Chai et al., 2012	15	−0.20	GSR	MPFC-DAN
		−0.12	1, 2	MPFC-DAN
Gao and Lin., 2012	19	−0.20	GSR	DN-DAN
De Havas et al., 2012	26	−0.26	GSR	PCC-DAN
Josipovic et al., 2012	14	−0.16	GSR	Extrinsic-Intrinsic networks
Cole et al., 2014	118	−0.07	GSR	DN-DAN
Chai et al., 2014	19	−0.15	1, 2	DN-DAN
Wotruba et al., 2014	29	−0.21	1, 2	DN-TPN
Holmes et al., 2015	1570	−0.18	GSR	DN-DAN
Yeo et al., 2015	68	−0.50	GSR	DN-DAN
		0.38	1, 2	DN-DAN
Spreng et al., 2016	54	−0.04	GSR	DN-DAN
		0.08	1, 2	DN-DAN
Amer et al., 2016	16	−0.06	1, 2	DN-DAN
Current study	24	−0.06	1, 2	DN-DAN

Note: Numbers specify preprocessing steps used in studies that did not employ global signal regression (GSR): 1 = regression of motion parameters; 2 = regression of cerebrospinal fluid and white matter timecourses; 3 = regression of respiratory- and cardiac-related signals. DN, default network; DAN, dorsal attention network; TPN, task-positive network; MPFC, medial prefrontal cortex; PCC, posterior cingulate cortex; GSR, global signal regression.

similar across contexts, thus suggesting stability. Here, we adopted this approach, but focused specifically on DN-DAN connections rather than whole-brain FC patterns (Fig. 3A). As illustrated in Fig. 3B, the similarity between DN-DAN FC patterns across different cognitive contexts was modest. Critically, across-context similarity was significantly lower than within-context similarity—that is, the similarity of DN-DAN FC from the first half to the second half of each context. This was the case when considering all DN as a whole [paired *t*-test: $t(23)$ =10.46, $p < .001$], and when breaking down the analysis by DN subsystem [Core: $t(23)$=7.84, $p < .001$; dorsomedial prefrontal: $t(23)$ =5.61, $p < .001$; medial temporal lobe: $t(23)$=9.35, $p < .001$]. The sizable difference between within- and across-context similarity reveals a substantial effect of context on DN-DAN interactions. Importantly, this was not due to the separation of contexts in time; nearly identical results were obtained when comparing FC during one context to FC during the immediately preceding context (Supplementary Fig. 6). These findings reveal that DN-DAN interactions vary considerably across different cognitive states. Notably, control analyses ruled out the possibility that the effect of context was driven by motion (see Supplementary Results).

We next sought to determine whether it is possible to accurately distinguish the cognitive state of an individual based on a classifier trained only on FC data from other participants. If possible, this would suggest that DN-DAN FC patterns flexibly reconfigure in each context in a manner that is generalizable across participants. A support vector machine (SVM) classifier was fed training data (a vector consisting of all DN-DAN correlations) and learned a model that maximized the separation of two cognitive states (e.g., rest and movie viewing) in multidimensional space, based on the pattern FC values defining each context. The SVM then used its model of the training data to predict the labels of new data. Classifier accuracy was determined using leave-one-out cross validation, and statistical significance was established using permutation testing. As depicted in Fig. 4, the SVM achieved classification accuracy that was considerably above chance-level in 12/15

comparisons ($ps < .05$, uncorrected), and 8 of those comparisons were significant when correcting for multiple comparisons ($ps < .05$, bonferroni corrected). Supporting the robustness of these results, significant classification was also obtained using 4-fold classification, with 75% of the data used for training and 25% used for testing (Supplementary Fig. 4). This suggests that the SVM classifier could distinguish pairs of cognitive states solely on the basis of DN-DAN FC patterns, thereby implying a relatively unique configuration of DN-DAN interactions within each context that was reliable across participants.

To examine more directly whether the six contexts could be discriminated based on DN-DAN FC values we used mixed-effects logistic regression. Rather than pairwise comparisons, this analysis contrasted each context against all others simultaneously. We conducted six regression analyses, and found that each context could be significantly predicted against all others (all $p's < .05$) [Rest vs others: $b=−.33$ (95% CI: −.50 to −.16); Movie vs others: $b=−1.01$ (95% CI: −1.19 to −.82); Artwork vs others: $b=−.30$ (95% CI: −.47 to −.14); Shopping vs others: $b=.28$ (95% CI: .09 to .46); evaluation-based introspection vs others: $b=.58$ (95% CI: .40 to .75); acceptance-based introspection vs others: $b=.73$ (95% CI: .54 to .92)]. This provides evidence that each context had a distinct FC pattern from the other five contexts.

We next conducted whole-brain seed-based analyses to provide more detail regarding the direction of changes in DN-DAN FC across different cognitive states. The results demonstrated highly variably patterns (Fig. 5). A pair of DN-DAN regions could exhibit negative FC in one context, but no correlation or even positive FC in other contexts (e.g., see aMT-pIPL in Fig. 5). Moreover, different region pairs could exhibit changes across contexts in opposite directions. For example, the frontal eye fields and dorsomedial prefrontal cortex exhibited stronger negative FC during the movie condition relative to rest, whereas the anterior intraparietal sulcus and retrosplenial cortex exhibited weaker negative FC during the movie condition relative to rest. These region-specific patterns further underscore regional heterogeneity in DN-DAN interactions.
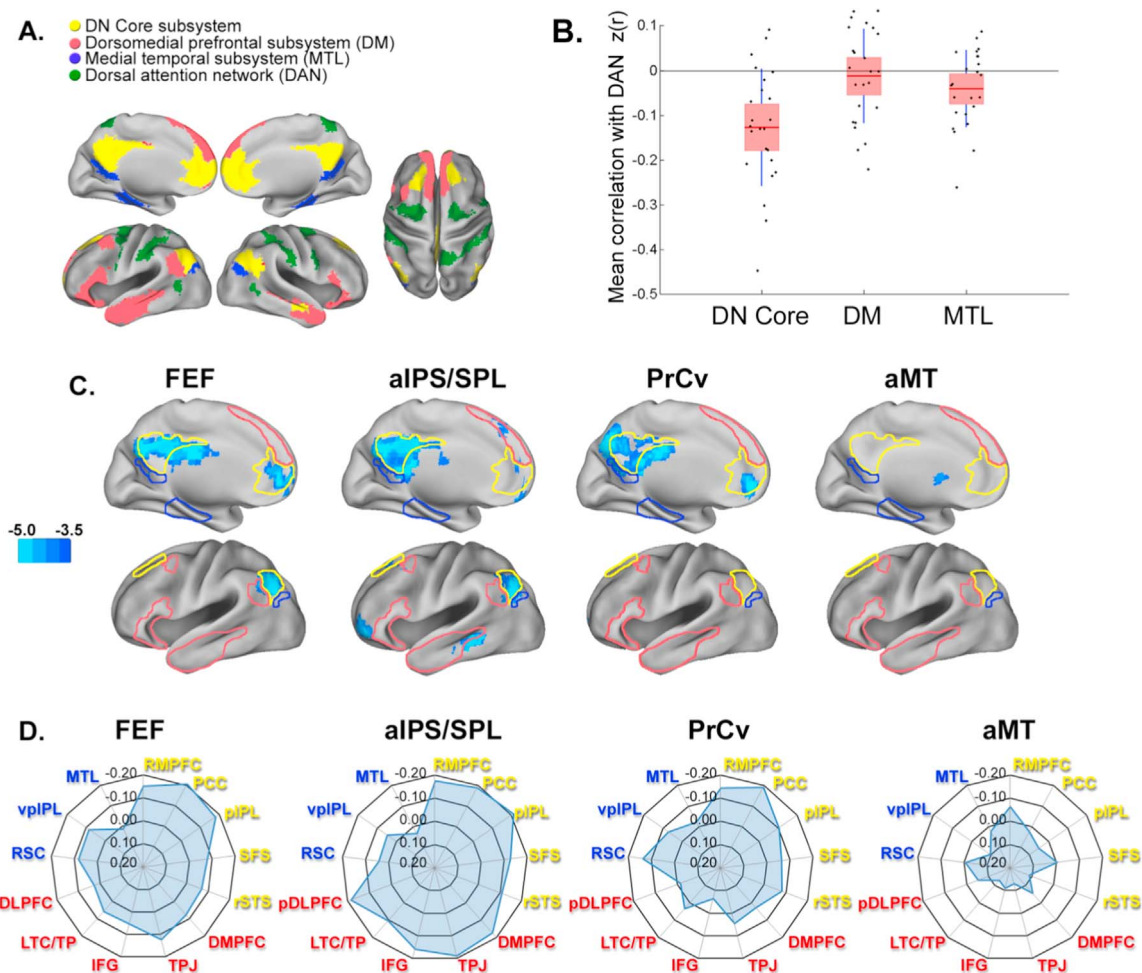
Fig. 2. Anticorrelation as a function of DN subsystem. (A) Networks from Yeo et al. (2011) used for ROIs. (B) Mean correlation between the DAN and each DN subsystem. Data for each participant (black dots), with mean (red line), 95% CI (red shaded area) and 1 SD (purple lines). (C) Seed-based connectivity analyses showing negative connectivity with DAN regions ($Z > 3.1$, $p < .05$ FWE corrected for cluster extent), with the borders of each DN subsystem highlighted. Color bar represents t-values. DAN seeds: FEF, frontal eye fields; aIPS/SPL, anterior intraparietal sulcus/superior parietal lobule; PrCv, ventral precentral cortex; aMT, anterior middle temporal region. Left hemisphere data is presented (see Supplementary Fig. 5 for right hemisphere data). (D) Functional connectivity fingerprints for each DAN region. *Core subsystem*: RMPFC, rostromedial prefrontal cortex; PCC, posterior cingulate cortex; pIPL, posterior inferior parietal lobule; SFS, superior frontal sulcus; rSTS, rostral superior temporal sulcus. *DM subsystem*: DMPFC, dorsomedial prefrontal cortex, TPJ, temporoparietal junction, TP/LTC, temporopolar cortex/lateral temporal cortex; IFG, inferior frontal gyrus, pDLPFC, posterior dorsolateral prefrontal cortex. *MTL subsystem*: MTL, medial temporal lobe; RSC, retrosplenial cortex; vpIPL, ventral posterior inferior parietal lobule. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
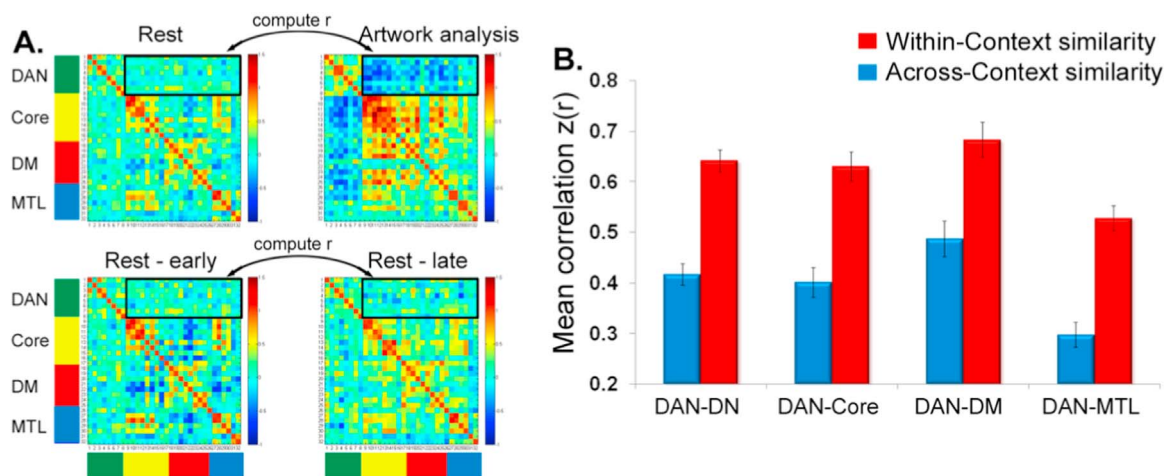

Fig. 3. Comparison of within- and across-context similarity of DN-DAN connectivity. (A) Example of the analysis approach for one participant. We extracted DN-DAN correlation values (highlighted by the black box), and then calculated the correlation between the vector of FC values for each pair of contexts, and between the vector of FC values for the early and late period within each context. (B) Mean within- and across-context similarity of anticorrelations. DAN, dorsal attention network; DN, entire default network; DM, dorsomedial prefrontal subsystem; MTL, medial temporal lobe subsystem. Error bars reflect within-subject SEM (Loftus and Masson, 1994).
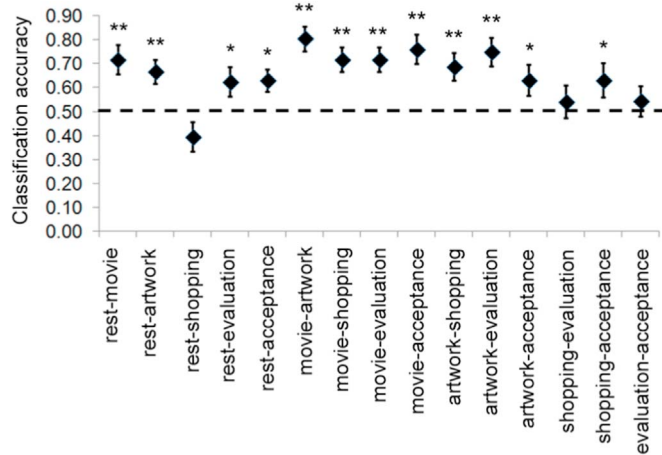
Fig. 4. Accuracy of the SVM classifier in distinguishing each pair of cognitive contexts. Classification accuracy was significantly above chance level in all cases except for the rest-shopping, shopping-evaluation, and evaluation-acceptance comparisons. Error bars reflect between-subject SEM. *$p < .05$, uncorrected. **$p < .05$, bonferroni corrected.

3.2.3. Self-reported experience

Contextual modulation of DN-DAN FC may relate to certain aspects of the task conditions we used. Although our conditions did not vary in a systematic manner, we did collect self-reports regarding several variables including the difficulty of the "tasks", level of attention, and familiarity and enjoyment with the stimuli in the movie, artwork, and shopping conditions (Table 2). Importantly, participants reported high levels of attention during the conditions with external stimuli. There was a main effect of condition on attention [$F(2, 46)=5.92, p=.005$] and enjoyment [$F(2, 46)=40.25, p < .001$], with the highest levels in both cases being reported during the artwork condition. The effect of condition on stimulus familiarity was not statistically significant [$F(2, 46)=1.94, p=.16$]. Finally, there was a main effect of condition on difficulty [$F(4, 92)=10.97, p < .001$], with the movie and artwork conditions being rated as the easiest conditions. Our sample size does not afford enough power for a proper individual differences analysis examining the correlation between these self-report variables and the strength of DN-DAN functional connectivity. However, for completeness we report this information for exploratory purposes in Supplementary Table 2. The fact that participants found the movie and artwork conditions the easiest (and there was the least amount of inter-subject variability) may have resulted in the most distinct FC patterns, and this could potentially explain why the SVM classifier was most accurate in distinguishing these conditions from the others.

3.2.4. Stability of DN-DAN functional connectivity across time

DN-DAN interactions are generally summarized as a single correlation value reflecting connection strength across a long period of time

Table 2
Self-reported experience in the current study.

Variable	Condition				
	Movie	Artwork	Shopping	Evaluation	Acceptance
Difficulty	1.06 (1.15)	1.73 (1.11)	2.42 (2.06)	3.02 (1.90)	3.88 (1.73)
Attention	5.98 (1.03)	6.40 (.071)	5.75 (1.18)		
Familiarity/ Expertise	3.81 (2.05)	3.90 (1.85)	3.08 (1.67)		
Enjoyment of task	4.27 (1.66)	6.38 (.71)	3.00 (1.59)		

Note. Participants rated each variable on a 7-point scale from 1=low to 7=high. Values reflect mean across participants with standard deviation in parentheses.

(e.g., 5–10 min). While useful, this approach cannot reveal potential temporal variation in DN-DAN interactions. If DN-DAN FC strength is influenced by an individual's current mental state, then it may vary across time even during rest in accordance with changing mental content. We investigated dynamic changes in DN-DAN FC using a 60-second sliding window approach (Hutchison et al., 2013). Prior work has shown that functionally-relevant FC patterns can be isolated from ~ 60 seconds of data (Gonzalez-Castillo et al., 2015; Leonardi and Van De Ville, 2015; Liegeois et al., 2015; Shirer et al., 2012). For each participant, we computed average DN-DAN FC within each window during rest, and then calculated the percentage of windows during which negative FC was present. The results demonstrated considerable temporal variability, with the DN and DAN alternating between negatively and positively correlated states (Fig. 6A). On average, the DAN exhibited negative FC in 67.09% of windows with the Core subsystem, in 52.75% of windows with the dorsomedial prefrontal subsystem, and in 56.16% of windows with medial temporal lobe subsystem (Fig. 6B). The number of windows with negative FC varied by subsystem [$F(2, 46)=8.95, p =.001$], with a higher number for the Core subsystem relative to the dorsomedial prefrontal and medial temporal lobe subsystems (paired t-test: $t(23)=4.38, p < .001$ and $t(23)=3.68, p=.001$, respectively), recapitulating the distinction between the subsystems observed in the standard analysis. However, even in the case of the Core subsystem there were frequent shifts away from negative FC. Interestingly, temporal variation in FC between the DAN and each DN subsystem followed somewhat unique patterns, highlighting the importance of separating the DN into distinct subsystems rather than treating it as a homogenous network.

3.2.5. Temporal co-evolution of large-scale network interactions

Traditionally, studies have examined temporal variation in the strength of FC between a pair of regions or a pair of networks. However, it is possible that time-varying FC may involve larger coordinated dynamics involving multiple networks. Here, we assessed the possibility that interactions between the DAN and DN evolve across time in a manner that is coordinated with interactions with the frontoparietal control network (FPCN) (Supplementary Fig. 8), which has been shown to flexibly couple with these networks. We first computed the strength of FC between each pair of networks within 60-second windows. This provided a time-series of between-network FC values. We then computed pairwise correlations to measure the linear association between the time-series of FC values—our measure of the co-evolution of network interactions. That is, we examined whether sets of between-network connections exhibited statistically similar temporal profiles.

The results demonstrated that periods of time characterized by stronger *negative* FPCN-DAN coupling were associated with stronger *negative* DAN-Core coupling (Figs. 7A and 7B). This was a robust relationship, observed in every context [all $z(r) > .56$, p's < .05, Bonferroni corrected]. A similar pattern was observed for the dorsomedial prefrontal (DM) subsystem. In every context, when the FPCN became more negatively coupled with the DAN, the DAN became more negatively coupled with the DM [all $z(r) > .54$, p's < .05, Bonferroni corrected] (Figs. 7A and 7B). A different pattern was observed for the medial temporal lobe (MTL) subsystem of the DN. Changes across time in the strength of FPCN-DAN coupling were unrelated to changes across time in the strength of DAN-MTL coupling (all p's > .05, Bonferroni corrected).

Notably, with one exception, changes across time in the strength of FPCN-DN coupling were unrelated to changes across time in the strength of DAN-DN coupling, and this was true for each of the DN subsystems (all p's > .05, Bonferroni corrected). The one exception was a significant relationship between FPCN-MT coupling and DAN-MT coupling during the movie condition [$z(r)=−.21, p < .05$, Bonferroni corrected].This suggests that dynamic network co-evolution is specific to particular network interactions and cannot be attributed to a general
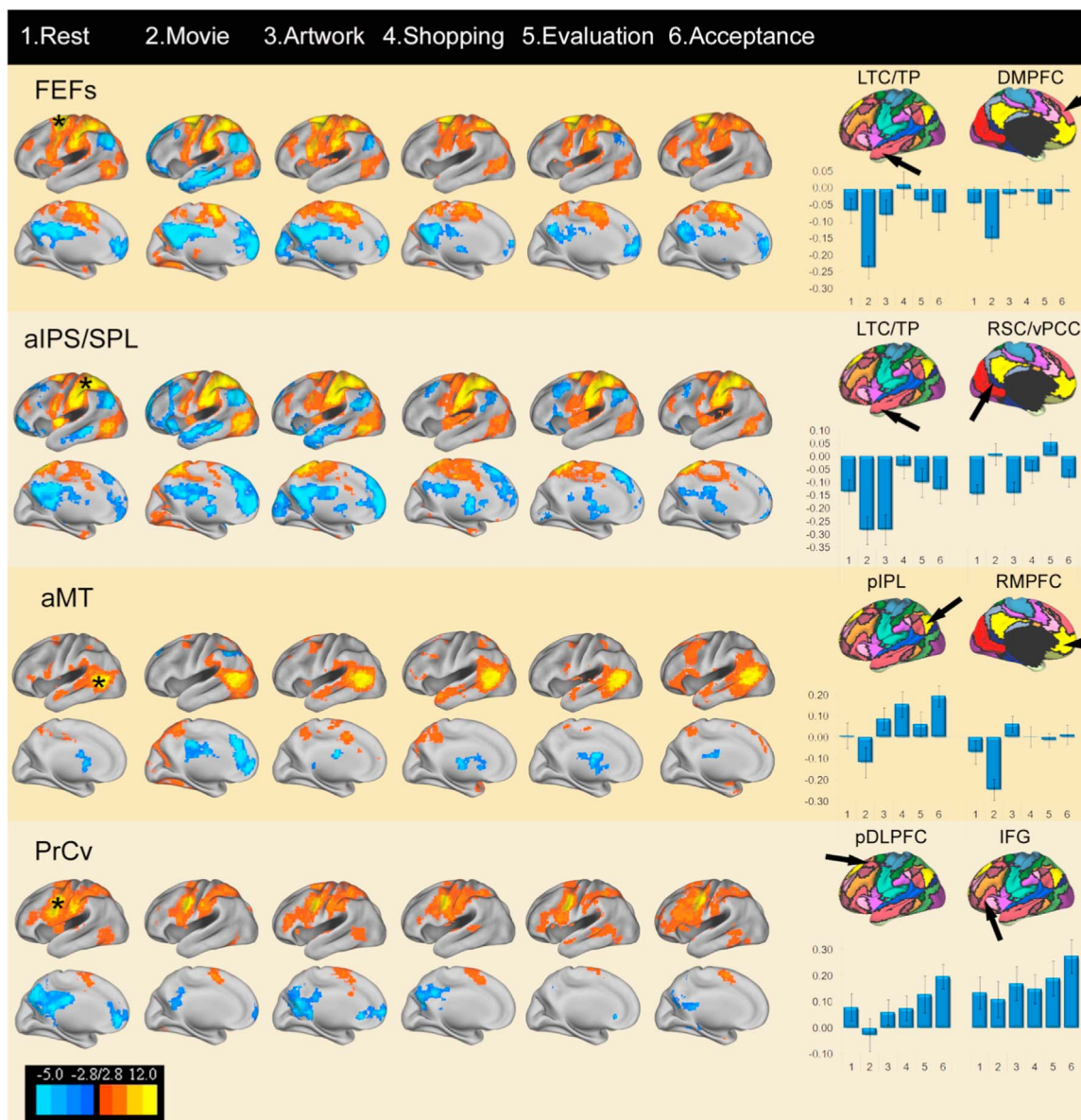
Fig. 5. Whole-brain seed-based analyses. Positive and negative functional connectivity for each DAN seed region and context. Negative FC between the DN and DAN flexibly increased and decreased in different cognitive contexts relative to rest. For illustration purposes, we use a slightly liberal threshold to show the full extent of positively and negatively correlated voxels in each context ($Z > 2.57$, $p < .05$ FDR cluster corrected). Black star denotes location of DAN seed regions. Right panel: mean FC strength, $z(r)$, for specific pairs of DN-DAN ROIs for each context. Results for the left hemisphere are presented (see Supplementary Fig. 7 for right hemisphere data). Based on visual inspection the whole-brain analysis in the left panel, we identified DN regions (indicated with black arrow) that appeared to exhibit an effect of context, and then plotted the mean FC between the DAN and DN seeds for each context in the right panel. This was intended was for illustration purposes only. Color bar shows *t*-values. Abbreviations: LTC/TP, lateral temporal cortex/temporopolar cortex; DMPFC, dorsomedial prefrontal cortex; RSC/vPCC, retrosplenial cortex/ventral posterior cingulate cortex; pIPL, posterior inferior parietal lobule; RMPFC, rostromedial prefrontal cortex; pDLPFC, posterior dorsolateral prefrontal cortex; IFG, inferior frontal gyrus. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

effect such as global fluctuations in BOLD signal. In particular, when the FPCN became more negatively coupled with the DAN, the DAN became more negatively coupled with the Core and dorsomedial prefrontal subsystems (Fig. 8).

Importantly, within each context, temporal variation in the strength of between-network FC was uncorrelated with temporal variation in the amount of participant motion. We found no significant relationships at the group level for total motion [all $|z(r)| < .07$, $p's > .22$], or framewise displacement [all $|z(r)| < .07$, $p's > .16$]. There was also no evidence of systematic relationships at the level of individual participants. We found 25 out of 284 correlations (~ 9%) were significantly positive at $p < .05$, bonferroni corrected, and 25 out of 284 correlations (~ 9%) were significantly negative at $p < .05$, bonferroni corrected. Thus, while some participants did show a significant correlation between temporal variation in the strength of between-network FC and motion in some

contexts, this was a rare occurrence, and the correlations were not systematically positive or negative. Thus, temporal co-evolution of network interactions cannot be explained by participant motion.

4. Discussion

Delineating the nature of functional interactions between the DN and DAN is critical for understanding how attention is efficiently allocated to internal conceptual thoughts and external perceptual information. While prior work suggested that DN-DAN anticorrelation is an intrinsic aspect of functional brain organization based on resting state data, our findings suggest that the DN and DAN have an independent relationship and demonstrate that interactions between these networks exhibit considerable variability: the DAN exhibited differential FC with the three DN subsystems; DN-DAN interactions
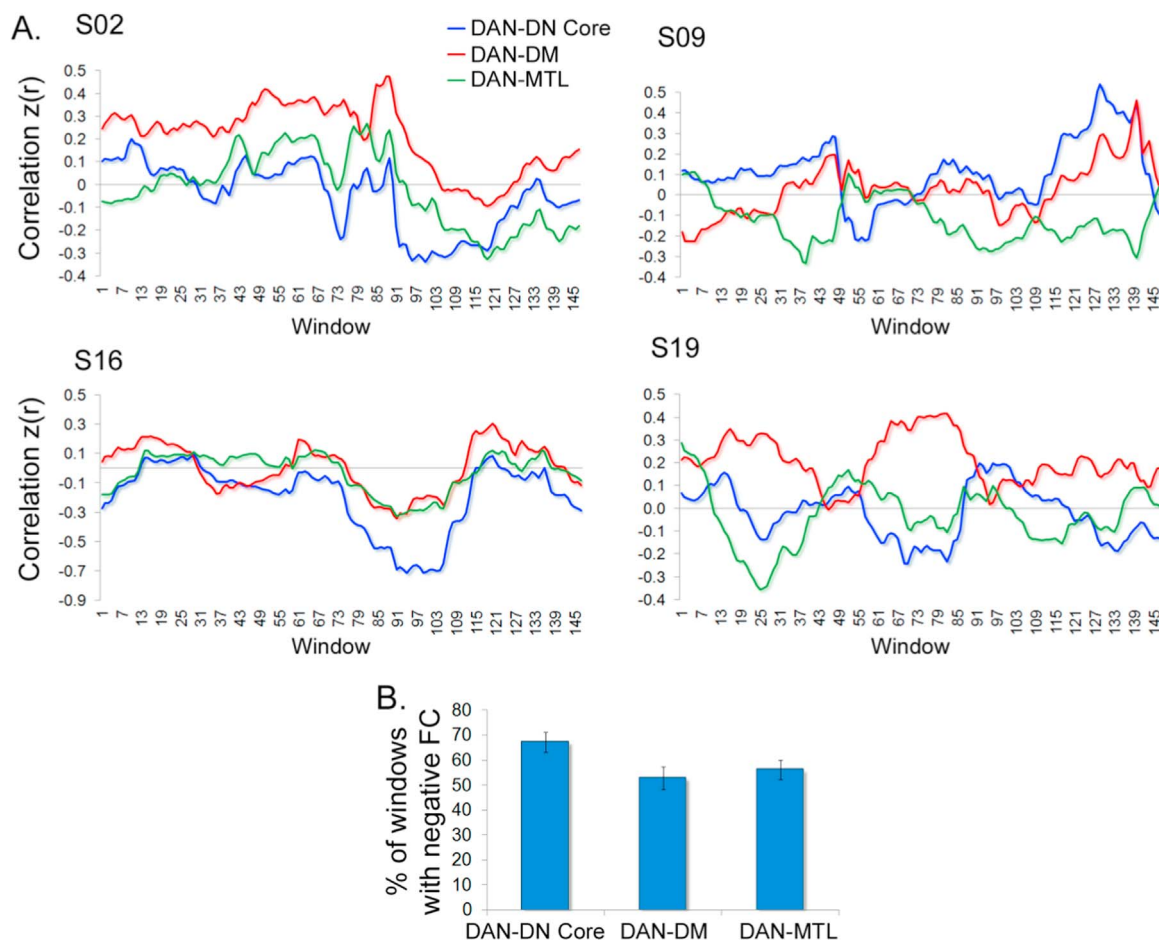
Fig. 6. Temporal variability in DN-DAN interactions during rest. (A) Data for four randomly chosen example participants demonstrating average correlation strength between the DAN and each DN subsystem within successive 60-second windows. (B) Percentage of windows with negative FC between the DN and DAN. DM, dorsomedial prefrontal subsystem; MTL, medial temporal lobe subsystem. Error bars represent between-subject SEM.

flexibly reconfigured across different cognitive states; and DN-DAN FC fluctuated across time between periods of anticorrelation and periods of positive correlation. Notably, there was one consistent relationship: temporal fluctuations in FPCN-DAN coupling were correlated with changes across time in the strength of coupling between the DAN and Core and dorsomedial prefrontal subsystems within every context, revealing evidence of temporal co-evolution of large-scale network interactions. Together, these findings suggest that the DN and DAN and the functions they support are not antagonistic, at least in the context of the six different cognitive states that we examined.

4.1. Are the DN and DAN anticorrelated?

While the notion of anticorrelation is often highlighted in papers that examine DN-DAN interactions, rarely is there discussion of the actual effect size. We therefore conducted a meta-analysis to determine the strength of FC between the DN and DAN, and to examine the influence of global signal regression (GSR) when included as part of preprocessing. Studies that did not use GSR reported weak negative correlations or even positive correlations between the DN and DAN, with a median effect size of $r=-.06$ (Amer et al., 2016; Anderson et al., 2011; Chai et al., 2012; Chai et al., 2014; Chang and Glover, 2009; Gao and Lin, 2012; Golland et al., 2007; Murphy et al., 2009; Spreng et al., 2016; Van Dijk et al., 2010; Wotruba et al., 2013; Yeo et al., 2015). The effect sizes suggest more of a weak negative coupling or an independent relationship rather than a competitive anticorrelated relationship, highlighting a disconnect between observed effect sizes and the language used to describe DN-DAN interactions. Studies that used

GSR found stronger negative FC (median effect size of $r=-.24$), however, GSR is known to distort the distribution of correlations, making them difficult to interpret (Murphy et al., 2009; Van Dijk et al., 2010). GSR inflates the magnitude of true negative correlations and shifts correlations near $r=0$ into artifactual negative correlations.

Several caveats should be taken seriously when interpreting the results of our meta-analysis: (i) we only included studies that reported an effect size and therefore did not perform an exhaustive analysis. Thus, it is quite possible that there are studies showing strong anticorrelation that were not included in this analysis; (ii) there is considerable variability in effect size across studies suggesting that the median effect size reported here should be interpreted cautiously; (iii) studies differed in network definitions; (iv) studies differed in preprocessing steps (aside from inclusion/exclusion of GSR); and (v) there may be some measurement error related to approximating some of the effect sizes from figures. While considering these limitations, this analysis clearly reveals that many studies have observed little to no negative FC between the DN and DAN. This calls into question the idea that these networks are strictly competitive.

It is possible that DN-DAN anticorrelation is a real but transient phenomenon, dependent on cognitive state. The idea that anticorrelation may be a transient rather than persistent aspect of functional network organization is supported by our dynamic FC analysis, which revealed periods of time when the DN and DAN showed strong negative FC (that is, anticorrelation), but also periods of time when these networks exhibited positive FC. Thus anticorrelation may dynamically emerge during some cognitive states, but does not appear to be an invariant feature of functional brain organization. Notably, we also
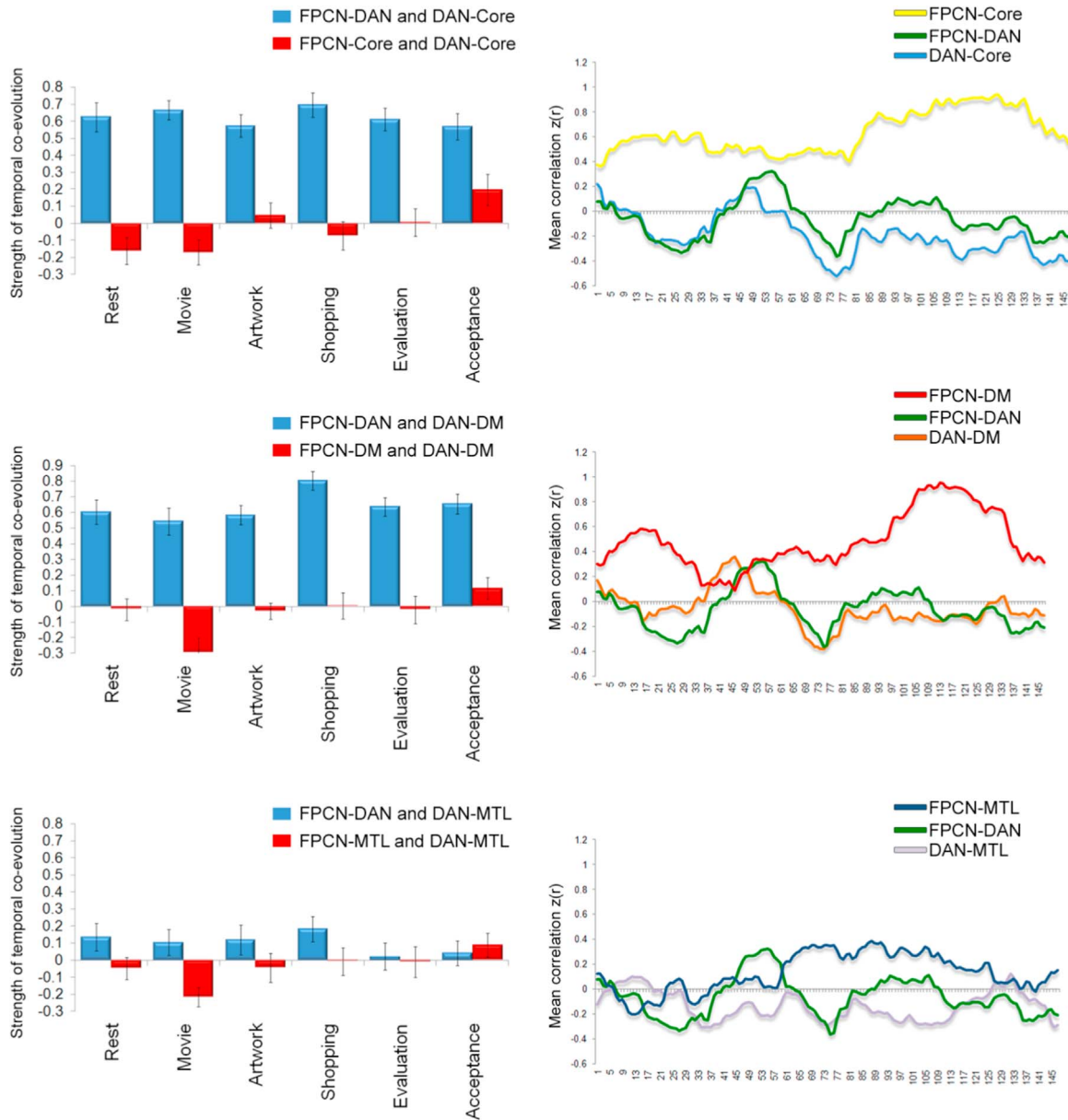
Fig. 7. Temporal co-evolution of network interactions. **(A)** Mean strength of temporal co-evolution. Error bars reflect between-subject SEM. **(B)** Data for an example participant during the movie viewing condition demonstrating changes across time in functional connectivity between each pair of networks. Top: Changes across time in FPCN-DAN coupling are positively correlated with changes across time in DAN-Core coupling. Middle: Changes across time in FPCN-DAN coupling are positively correlated with changes across time in DAN-dorsomedial prefrontal (DM) subsystem coupling. Bottom: Changes across time in FPCN-DAN coupling are unrelated to changes across time in DAN-MTL coupling.

found that region aMT of the DAN exhibited no evidence of negative FC with any DN regions during rest. In fact, during some conditions this region exhibited positive FC with DN regions including the posterior inferior parietal lobule, temporoparietal junction, inferior frontal gyrus, and temporopolar cortex. This finding suggests that aMT may provide a bridge between the DN and DAN, and underscores the fact that these networks are not strictly antagonistic. Together, these results suggest that it is *necessary to re-conceptualize the relationship between the DN and DAN*, as well as the idea of a competition between internally-oriented and externally-oriented cognitive processes. Indeed, considerable evidence suggests a more complex picture, with many cognitive states requiring a combination of internally-oriented thoughts and externally-oriented perceptual information (Dixon et al., 2014b).

Although the DN and DAN often show differences in overall activation levels in tasks that require perceptual attention versus introspective processing, this does not imply that they must exhibit anticorrelated signal fluctuations. Indeed, evidence suggests that overall activation levels may be orthogonal to functional coupling patterns (Murphy et al., 2016). For example, a recent study found that the posterior cingulate cortex exhibited diminished activation levels during a demanding semantic task, yet simultaneously exhibited increased functional coupling with "task-positive" regions (Krieger-Redwood et al., 2016). Thus, ongoing inter-regional interactions may support information processing that is, to some extent, independent from task-related activation levels. It is important to note that this re-conceptualization of DN-DAN interactions does not take away from the significance of previously reported age-related and group differences in DN-DAN interactions (Chai et al., 2014; Gao et al., 2013; Keller et al., 2015; Spreng et al., 2016). These differences likely contribute to age- and group-related differences in cognitive abilities. The findings reported here have implications for *interpreting* DN-DAN interactions and the meaning of changes in certain groups of participants, but do not question the differences themselves.
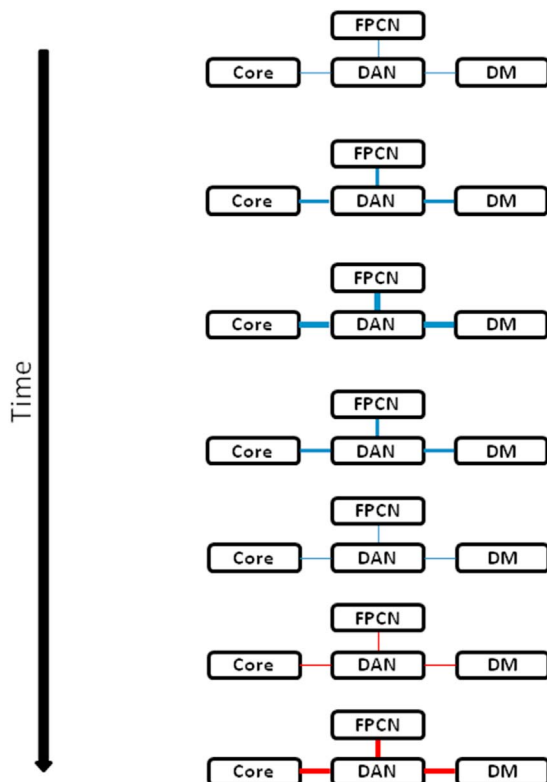
Fig. 8. Schematic illustration of temporal co-evolution of network interactions. As the FPCN becomes more anticorrelated with the DAN, the DAN becomes more anticorrelated with the Core and dorsomedial prefrontal subsystems of the DN. As the FPCN becomes more positively correlated with the DAN, the DAN becomes more positively correlated with the Core and dorsomedial prefrontal subsystems. Functional connections between the FPCN and DN Core and dorsomedial prefrontal subsystems are generally positive, and are not shown because they fluctuate across time independently of DN-DAN interactions.

4.2. Variable interactions between the DAN and DN subsystems

A previous study noted spatial heterogeneity in FC between the DN and DAN, with some connections exhibiting positive correlation and other connections exhibiting negative correlation (Anderson et al., 2011). Here, we extend this work by examining interactions in relation to the well-established division of the DN into three subsystems (Andrews-Hanna et al., 2010). The DAN exhibited modest negative FC with the Core subsystem, but was uncorrelated with the dorsomedial prefrontal and medial temporal lobe subsystems. These findings are to some extent consistent with Fox et al.'s (2005) original report of DN-DAN anticorrelation, which was based on seed regions located within the Core subsystem, but further emphasize that the DN is not a homogenous network (Andrews-Hanna et al., 2010; Andrews-Hanna et al., 2014). Even beyond the finding that the DAN exhibited distinct interactions with the three DN subsystems, we found that specific node-to-node connections between the DN and DAN exhibited different patterns of change in correlation strength across contexts. For example, the frontal eye fields and dorsomedial prefrontal cortex exhibited stronger negative FC during the movie condition relative to rest, whereas the anterior intraparietal sulcus and retrosplenial cortex exhibited weaker negative FC during the movie condition relative to rest. Together, these results suggest that a single correlation value reflecting DN-DAN interactions may overlook the variability present at a finer spatial scale, and potentially give a misleading impression of network dynamics.

The DN Core is recruited during a variety of tasks involving self-referential processing (Denny et al., 2012), value-based decision making (Bartra et al., 2013), mind wandering (Fox et al., 2015),

autobiographical memory (Andrews-Hanna et al., 2014), and reflection on personal goals (D'Argembeau et al., 2010). This subsystem may therefore play a role in thinking about the self as an object of awareness with particular goals, attributes, and a linear narrative that connects past, present, and future experience—that is, an autobiographical mode of self processing (Araujo et al., 2015; Christoff et al., 2011; Denny et al., 2012; Farb et al., 2007; Gallagher, 2000; Murray et al., 2012; Schmitz and Johnson, 2007; Wagner et al., 2012). One possibility is that periods of time characterized by negative FC between the DAN and DN Core subsystem reflects the focusing of attention towards abstract self-related information and away from more concrete perceptual information, whereas periods of positive FC may allow perception to inform self-referential thinking or vice versa. However, there is much still to be learned about the functions of the DN Core (e.g., Konishi et al., 2015; Leech, Braga, and Sharp, 2012) and the implications of these dynamics for understanding cognitive functioning.

In agreement with our results, numerous lines of evidence suggest that mentalizing and mnemonic processes that may be associated with the dorsomedial prefrontal and medial temporal lobe subsystems are not inherently antagonistic with perceptual processes associated with the DAN (Dixon et al., 2014b). For example, memory can facilitate the deployment of attention to the external environment (e.g., remembering where one last put the car keys) and this is subserved by co-activation of medial temporal and DAN regions (Summerfield et al., 2006). Similarly, another study found that working memory performance was facilitated for famous relative to unfamiliar faces, and this was accompanied by medial temporal lobe subsystem activation, consistent with the idea that mnemonic representations can facilitate perceptual encoding when it is congruent with task demands (Spreng et al., 2014). Furthermore, during the encoding of new information, medial temporal regions decouple from other DN regions (Huijbers et al., 2011), and become more sensitive to afferent sensory input, as a result of acetylcholine's modulatory influence on medial temporal lobe circuit dynamics (Hasselmo and McGaughy, 2004). Finally, during rest, the spontaneous reactivation of information stored in memory may in some cases lead to an autobiographical stream of thought that becomes elaborated upon by the Core subsystem, but in other cases may trigger a sensorimotor stream of thought (e.g., an imagined interaction with the environment) that may elicit cooperative medial temporal lobe subsystem-DAN dynamics. Accordingly, one hypothesis is that the medial temporal lobe subsystem may go in and out of phase with the DAN depending on whether mnemonic and perceptual processes pertain to the same or different goals, thus resulting in uncorrelated activation on average.

Similarly, mentalizing and perceptual processing may sometimes operate in concert, as perception of body language, facial expression, and eye-gaze often inform the inferences we make about others' thoughts, and vice versa (Baron-Cohen et al., 2001). Supporting this idea, coactivation of the DAN and dorsomedial subsystem is observed when individuals view dynamic animations and attend to the social intentional meaning of the movements (Tavares et al., 2008). Thus, mentalizing and memory processes are sometimes, but not always associated with perceptual decoupling (Schooler et al., 2011; Smallwood et al., 2012). The brain has limited attentional resources, and consequently, has difficulty performing more than one goal at a time (Marois and Ivanoff, 2005). When mentalizing and mnemonic processes can be linked to perceptual processing in service of a unified goal, there may be little to no interference, but when they pertain to different goals (e.g., during task-unrelated thought) they are likely to compete (Dixon et al., 2014b). Alternating anticorrelation and positive correlation between the DAN and these subsystems during rest may reflect the exploration of frequently occurring network states.

4.3. Contextual variability of DN-DAN interactions

A burgeoning literature has revealed context-dependent FC pat-

terns, with an emerging picture of the brain as a dynamic system that flexibly adapts to changes in internal and external states (Allen et al., 2014; Braun et al., 2015; Cole et al., 2013; Davison et al., 2015; Fornito et al., 2012; Geerligs et al., 2015; Gonzalez-Castillo et al., 2015; Krienen et al., 2014; Kucyi et al., 2016; Mennes et al., 2013; Milazzo et al., 2014; Shine et al., 2016; Shirer et al., 2012; Simony et al., 2016; Spreng et al., 2010). FC patterns have been linked to individuals' mental states (Andrews-Hanna, Reidler, Huang, and Buckner, 2010; Doucet et al., 2012; Kucyi et al., 2016), and flexibility of FC patterns appears to be adaptive, given that it correlates with task performance (Braun et al., 2015; Fornito et al., 2012; Hermundstad et al., 2014). Building upon this work, we report convergent findings revealing that DN-DAN interactions vary across different cognitive states.

Our similarity analysis revealed little stability in DAN-DN FC across different cognitive contexts. Consistent with this, a prior study found that anticorrelations were more similar from the early period to the late period of a flanker task (r=.61) than between rest and the flanker task (r=.34) (Kelly et al., 2008). This is comparable to the values that we observed, and suggests that DN-DAN interactions are dynamically tailored to one's current context. This complements other work showing context-dependent DN-FPCN interactions (Fornito et al., 2012; Spreng et al., 2010). Furthermore, we found that a machine learning classifier was able to distinguish each pair of contexts solely on the basis of DN-DAN FC patterns. While the classifier's ability to distinguish cognitive states in the current study was noticeably less accurate than results obtained in other studies using whole-brain FC patterns (Gonzalez-Castillo et al., 2015; Milazzo et al., 2014; Shirer et al., 2012), it is quite remarkable that patterns of DN-DAN FC are sufficiently distinct in each context to allow for above chance-level classification. These findings emphasize flexibility rather than stability in the DN-DAN relationship. Accordingly, DN-DAN interactions during rest do not necessarily reflect the nature of interactions between these networks in general, because other network configurations could occur in other contexts that may be consistent with, or distinct from, the pattern observed during rest. Individual and group differences in DN-DAN FC during rest could potentially reflect differences in mental state rather than fundamental differences in brain function, although parallel age-related reductions in anticorrelation during task and rest have been observed (Spreng et al., 2016).

Throughout the manuscript we have not emphasized the nature of the task conditions used in the present study because our goal was not to describe the way in which the DN and DAN interact during particular mental states. Rather, our goal was to test a fundamental hypothesis about the relationship between these networks, and to look for evidence of contextual variability, which we did observe. Our results have broad implications as they robustly demonstrate that DN-DAN interactions are not a stable, fixed feature of brain organization. While our findings suggest a need to re-conceptualize the nature of DN-DAN interactions, our limited range of task conditions means that we cannot specify the principles by which these interactions vary across different cognitive states. Interestingly, we did observe that the SVM classifier was most accurate in distinguishing the conditions that were rated as least difficult and had the least inter-subject variability—the movie and artwork conditions. It is possible that participants were better able to adopt the desired cognitive states in these conditions, providing clear and specific patterns of FC. On the other hand, it is possible that the classifier performed worse at distinguishing the shopping and intro-spection conditions because participants were less able to consistently adopt the desired cognitive states, resulting in less differentiable FC patterns. Thus, the ease with which participants can perform different instructed tasks may influence the extent to which it is possible to detect reliable variation in FC patterns across contexts. Another possibility is that the movie and artwork conditions were associated with better classification because they were the most structured and stimulus driven and may have constrained FC patterns more than the other conditions that allowed more room for cognitive variability.

4.4. Temporal co-evolution of large-scale network interactions

Network organization dynamically changes across time (Allen et al., 2014; Betzel et al., 2016; Hutchison et al., 2013; Liegeois et al., 2015; Poldrack et al., 2015; Zalesky et al., 2014), with higher-order association cortices exhibiting considerable flexibility (Braun et al., 2015; Cole et al., 2013), which may contribute to the context-dependent regulation of thought and perception (Duncan, 2010; Miller and Cohen, 2001). Thus, network neuroscience is now demonstrating a correspondence between the dynamic landscape of network properties and the dynamic nature of cognitive processing. Prior work has shown that sets of functional connections change in strength across time in parallel (Bassett et al., 2014; Davison et al., 2015), and that global brain dynamics exhibit shifts between periods of segregation and integration (Betzel et al., 2016; Liegeois et al., 2015; Shine et al., 2016; Shine et al., 2016; Zalesky et al., 2014), with between-network connections exhibiting the strongest time-varying dynamics (Zalesky et al., 2014). Although DN-DAN anticorrelation is thought to be a robust feature of brain organization, we observed that DN-DAN interactions alternated across time between periods of anticorrelation and periods of positive correlation. In fact, we found positive FC ($r > 0$) in about 50% of windows for each of the DN subsystems (slightly fewer windows for the Core subsystem). This suggest frequent transitions between periods of segregation and periods of integration. Prior work offered suggestive evidence that negative FC involving the DN varies across time (Allen et al., 2014; Chang and Glover, 2010). Here, we extend this work by using well-established network boundaries and quantifying the number of windows exhibiting departures from negative FC. Time-dependent interactions between the DN and DAN may provide a balance between functional specialization, and the opportunity for information exchange that allows perception to inform internally-oriented thinking and vice versa.

Using a hypothesis-driven approach, we further found that variation across time in the strength of DN-DAN FC was related to larger patterns of temporal co-evolution between large-scale networks. While prior work has investigated the co-evolution patterns of node-to-node connections across the brain (Bassett et al., 2014; Davison et al., 2015), here we expand on this approach and demonstrate that additional information can be gleaned by constraining such analyses based on theoretical predictions and knowledge of network organization (Yeo et al., 2011). Moreover, our focus on network interactions obviates the need to perform a large number of statistical tests on all time-dependent node-to-node interactions. Within each context, we found that as the FPCN became more anticorrelated with the DAN, the DAN became more anticorrelated with the DN Core and dorsomedial prefrontal subsystems. Interestingly, FPCN interactions with the DN subsystems were not coordinated with DAN-DN interactions suggesting that network co-evolution does not merely represent global changes across the brain, but rather, is spatially specific. It is possible that different network relationships could emerge in other contexts (e.g., greater positive FPCN-DAN coupling may be associated with stronger DAN-Core anticorrelation during a visuospatial working memory task). However, the key point is that our findings provide novel evidence for coordinated changes in FC strength across multiple large-scale networks. Importantly, we found that these temporal changes in between-network FC were uncorrelated with temporal changes in participant motion, suggesting that they are not artifactual.

One possibility is that these structured temporal changes in large-scale network interactions reflect *shifting attentional priorities*. Abundant evidence suggests that the FPCN encodes task demands, and transmits signals about the current relevance of stimuli, actions, and outcomes to other regions, thus coordinating processing across the cortex (Buschman and Miller, 2007; Cole et al., 2015; Crowe et al., 2013; Dixon and Christoff, 2012, 2014; Dixon et al., 2014a; Duncan, 2010; Miller and Cohen, 2001; Tomita et al., 1999). Here, we extend these findings by demonstrating that FPCN FC patterns are tightly

coupled with the strength of DN-DAN FC changes across time. The large-scale network co-evolution we observed here could potentially reflect moment-to-moment shifts in the distribution of attention between perceptual information and internally-oriented conceptual thought. One possibility is that periods of stronger anticorrelation between the FPCN and DAN occurring in concert with stronger anticorrelation between the DAN and the Core and dorsomedial prefrontal subsystems could potentially reflect a state characterized by a decoupling between perceptual processing and abstract thoughts related to self-reflection or mental state inference. Indeed, given that the same relationship was not observed with the medial temporal lobe subsystem, this suggests that the observed network dynamics may relate to the complexity or abstractness of representations, given the roles of the Core and dorsomedial prefrontal subsystems in processing high-level conceptual information related to the self and others (Andrews-Hanna et al., 2014; Binder et al., 2009; D'Argembeau et al., 2012; D'Argembeau et al., 2010; Denny et al., 2012; Hassabis et al., 2013; Simony et al., 2016, but see Konishi et al. (2015)). More broadly, examining the temporal co-evolution of network interactions may shed new light on the neural architecture of different cognitive states and how they evolve across time.

4.5. Limitations

A limitation of the current study is the lack information about the nature and timing of ongoing cognitive activity, and how it relates to variability in DN-DAN interactions. To directly compare FC patterns during various cognitive states and rest, we did not have participants make responses. However, the lack of behavioral data meant that we could not link variation in FC patterns to behavioral performance. Other work has drawn links between task performance and FC patterns (Braun et al., 2015; Cole et al., 2012; Fornito et al., 2012; Kucyi et al., 2016; Schultz and Cole, 2016; Shine et al., 2016), and future studies could further benefit from the use of online experience sampling (Christoff, 2012; Fazelpour and Thompson, 2014) to map the relationship between FC patterns and cognitive states as they evolves across time. Additionally, experimenter controlled variations in task demands on the scale of tens of seconds could also be useful in linking FC patterns to mental states (Gonzalez-Castillo et al., 2015). A second limitation is that we used a limited range of task conditions and cannot specify the principles by which DN-DAN interactions vary across different cognitive states. While we used a hypothesis-driven approach to examine our prediction that DN-DAN interactions are not stable but vary depending on cognitive state, future work could use a range of tasks that systematically vary the required cognitive operations in order to provide additional evidence about the factors that govern contextual variability in DN-DAN interactions. A third limitation pertains to individual variability in network organization. Although we have characterized DN-DAN interactions in relation to well-established network boundaries (Yeo et al., 2011), these boundaries vary across individuals (Mueller et al., 2013). Future work could improve precision by using individually-tailored network ROIs (Wang et al., 2015). Finally, it could be argued that the contextual variation in DN-DAN FC that we observed was due to idiosyncratic numbers of attentional lapses in each context. However, several factors make this very unlikely. First, and foremost, the effect of context was not uniform across all DN-DAN functional connections. For example, from rest to the movie condition, some DN-DAN functional connections exhibited stronger negative FC, while others exhibited weaker negative FC or no change at all. This finding is inconsistent with a general, non-specific factor such as arousal driving the effect of context on anticorrelations. Second, participants reported high levels of attention during the conditions requiring an external focus. Finally, the machine learning classifier was able to accurately discriminate mental states for each participant based on the data from other participants, implying that there was structure in how DN-DAN FC varied across contexts. Thus,

changes in DN-DAN FC across contexts appear to be specifically related to differences in the required cognitive demands.

4.6. Conclusions

To summarize, we have found that the DN and DAN have a largely independent relationship when GSR is not used as part of preprocessing. Additionally, DN-DAN interactions are more variable than previously appreciated, suggesting that these networks and the functions they support are not strictly competitive. DN-DAN interactions varied across the three DN subsystems, exhibited a high degree of flexibility across different cognitive states, and alternated across time from positive to negative functional coupling. Finally, we found that these changes across time were systematically related to larger patterns of dynamic network co-evolution involving the FPCN, perhaps reflecting shifting attentional priorities. Together, these findings highlight the complexity of interactions between large-scale networks underlying thought and perception.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuroimage.2016.12.073.

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