Title: Network variants are similar between task and rest states

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Abstract: Recent work has demonstrated that individual-specific variations in functional networks can be reliably identified in individuals using functional magnetic resonance imaging (fMRI). These individual differences in functional connectivity have been termed network variants and exhibit reliability across time with resting-state fMRI data. These properties have suggested that network variants may be relatively trait-like markers of individual differences in brain organization. Another test of this conclusion would be to examine if network variants are stable between task and rest states. Here, we use precision data from the Midnight Scan Club (MSC) to demonstrate that (1) task data can be used to identify network variants reliably, (2) these network variants show substantial spatial overlap with those observed in rest, although state-specific effects are present, (3) network variants assign to similar canonical functional networks across states, and (4) single tasks or a combination of multiple tasks produce similar network variants to rest. Together, these findings further reinforce the trait-like nature of network variants and demonstrate the utility of using task data to define network variants.

1 Introduction

An important issue in contemporary cognitive neuroscience is how to best identify individual differences in human brain organization that may be relevant to individual differences in behavior. It has long been established that measuring functional brain networks via fMRI can identify regions with correlated activity (i.e., "functional connectivity") that support common functions such as motor processing and cognitive control (Biswal et al., 1995; Dosenbach et al., 2007). This organization of human brain networks has been mapped in multiple large groups (Power et al., 2011; Yeo et al., 2011) and more recently has been extended to individual-level brain networks (Braga & Buckner, 2017; Finn et al., 2015; Gordon, Laumann, Gilmore, et al., 2017; Gratton et al., 2019; Greene et al., 2019; Kong et al., 2019; Laumann et al., 2015, 2016; Marek et al., 2018; Miranda-Dominguez et al., 2014; Mueller et al., 2013; Poldrack et al., 2015; Seitzman et al., 2019; Sylvester et al., 2020). These networks can be measured during tasks or during a resting-state (Gratton et al., 2018), where participants are asked to lie in the scanner without performing any particular task.

While there are many commonalities in network organization across individuals, some locations show large variations (Braga & Buckner, 2017; Gordon, Laumann, Adeyemo, Gilmore, et al., 2017; Gordon, Laumann, Adeyemo, & Petersen, 2017; Gordon, Laumann, Gilmore, et al., 2017; Gratton et al., 2018; Kong et al., 2019; Mueller et al., 2013; Seitzman et al., 2019). This variability across individuals is consistently larger than that found within individuals, suggesting that these individual variations represent meaningful "trait-like" differences in brain organization (Gratton et al., 2018; Seitzman et al., 2019). Individual differences in network organization are even sufficiently large to identify individuals based on their functional connectivity profile alone (Finn et al., 2015; Miranda-Dominguez et al., 2014).

A recent paper investigated the "trait-like" characteristics of individual differences in brain networks in additional detail (Seitzman et al., 2019). The authors found that particular punctate locations showed very large individual differences in functional network organization relative to the group (with correlations $r<0.3$), that they termed "network variants". All individuals showed evidence of network variants, although particular variants differed in location, size, number, and network association across individuals. Importantly, the authors demonstrated that not only were network variants common, but they were also quite reliable within individuals over resting-state scans, given sufficient data (achieving $r> .8$ with 40 min. of data).

However, one outstanding question concerning the "trait-like" nature of network variants is whether they are stable across different states, such as during task performance. In order to have utility as biomarkers, ideally network variants would not depend on ongoing cognition, such as what a person is thinking about during a scan session (Gratton et al., 2018). To date, network variants have only been identified using resting state fMRI data (Seitzman et al., 2019), and it is unknown whether similar variants can also be identified using task fMRI data. Recent evidence suggests that functional connectivity as a whole is stable between states with only small observable task-dependent changes (Cole et al., 2014; Gratton et al., 2018; Krienen et al., 2014), although individually-specific task dependent changes were somewhat larger (Gratton et al., 2018). Thus, we sought to test whether these findings would also generalize to network variants.

A related practical consideration is that most existing datasets do not have sufficient resting-state data to achieve high reliability at the individual level (most have 5-10 min. of data, where reliability is poor; (Elliott et al., 2019; Gordon, Laumann, Gilmore, et al., 2017; Laumann et al., 2015; Noble et al., 2017). However, many of these datasets have additional task data. Moreover, in populations where excessive motion is an issue, it can be difficult to collect resting state data

whereas task fMRI may be more feasible (Greene et al., 2018; Vanderwal et al., 2019). One possibility is to combine rest and task data together to achieve higher reliability for network variants (as has been suggested by Elliot et al. (2019) for the connectome as a whole), which seems like a promising approach. However, for this approach to be effective, it is important to understand the degree to which the specific network properties under investigation are state dependent. While Gratton et al. (2018) demonstrated that task effects on functional connectivity as a whole were modest, they were present and significant. Thus, an important question for practical identification of network variants in other datasets, especially those of clinical interest, is to what degree their locations and network properties are state-dependent and can be computed from task-based measures instead. If task data can be used to identify similar network variants as observed in resting state data, this would make many more datasets which contain large amounts of task data suitable for this individual-specific analysis.

To address these theoretical and practical questions, we utilized data from the Midnight Scan Club (MSC). The MSC dataset is well-suited to examine these issues as it includes data from 10 individuals across 10 different sessions with over 10 hours of fMRI data across 4 task states and rest. With such a large amount of data for task and rest states, we can compare (1) reliability of network variants identified using task data, (2) similarity in the *locations* of network variants between task and rest states, (3) similarity of network variant *connectivity profiles* between task and rest states, and (4) whether network variants identified in individual tasks differ from each other. Jointly, these analyses suggest that network variants are largely trait-like and that task data can be reasonably used for their identification and analysis.

2 Methods

2.1 Overview

The ability to use task data to measure network variants was investigated using several methods. (1) In the first analysis, we quantified the reliability (within-state) of network variants identified with task data (Figure 2). (2) Next, we examined the stability (between-state) of network variant locations during task and rest (Figure 4). (3) Third, we measured the stability (between-state) of network affiliations for variants (Figure 5). (4) To examine whether network variants show greater stability than expected relative to other areas of cortex, we compared the stability of network variant locations to the rest of the vertices on the cortex (Figure 6). (5) Finally, we examined whether network variants showed task-specific patterns of deviation from group functional connectivity (Figure 7). These analyses quantify both the degree to which network variants show trait-like stability and the feasibility of using task data to identify network variants.

2.2 Datasets

The primary data used in this manuscript are from the Midnight Scan Club (MSC) dataset (Gordon, Laumann, Gilmore, et al., 2017). This dataset contains 5 hours of resting state data and 6 hours of task data across 4 tasks (semantic, dot coherence, motor, categorization/implicit memory) for 10 participants, collected across 10 separate fMRI sessions. One participant was excluded from analysis for excessive head motion and drowsiness (Gordon, Laumann, Gilmore, et al., 2017; Laumann et al., 2016). A separate secondary dataset comprised of 120 neurotypical adults was used as the “group average” reference and is referred to as the WashU 120 (Power et al., 2013). These datasets are described in more detail elsewhere (Gordon, Laumann, Gilmore, et al., 2017; Power et al., 2013). The MSC dataset is described briefly below, while a similar

description of the WashU 120 dataset is available in the *Supplementary Methods*. All data collection was approved by the Washington University Internal Review Board.

2.3 fMRI Acquisition

The acquisition parameters for the MSC dataset have been fully described elsewhere (Gordon, Laumann, Gilmore, et al., 2017). In brief high-resolution T1-weighted, T2-weighted, and resting-state BOLD data were collected on a Siemens 3T Magnetom Tim Trio with a 12-channel head coil (gradient-echo EPI sequence, isotropic 4 mm^3 voxels, TE of 27ms, and TR of 2.2s).

2.4 Task Designs and Analysis

The MSC dataset includes five different conditions. The conditions in the MSC dataset are described in more detail elsewhere (Gordon, Laumann, Gilmore, et al., 2017; Gratton et al., 2018), but are briefly outlined below.

2.4.1 Resting State

Each session began with a 30-minute scan where participants were instructed to focus on a white fixation superimposed on a black background.

2.4.2 Task Data

The MSC dataset contained data from four different tasks presented in counterbalanced order. Briefly, the motor task included two runs in each session (15.6 minutes total) of a blocked motor task adapted from the Human Connectome Project (Barch et al., 2013) where participants were cued to move either hands, feet, or tongue. The semantic and coherence tasks were presented as separate counter-balanced blocks in the same run two times in each session (14.2 minutes total). In the semantic task, participants responded to whether each word was a verb or a noun (both presented at 50% frequency). In the coherence task, Glass patterns were presented as

white dots on a black screen (Glass, 1969). These dots varied how concentrically they were arranged, with either a 50% or 0% coherence to a concentric arrangement (both presented at 50% frequency). The semantic and coherence tasks were analyzed together as a mixed block-event related analysis (Gordon, Laumann, Gilmore, et al., 2017) and are referred to collectively as the "mixed" task in this manuscript. The memory task included three runs in each session (~15 minutes total) with a different stimulus type (faces, scenes, words) presented in each run. In each run, participants were presented with 24 images, each of which was presented 3 times. Participants were asked to indicate whether the faces were male or female, the scenes were indoor or outdoor, and whether the words were abstract or concrete. Task activations were not analyzed in this manuscript, but task-related activity was regressed out from the timeseries via a general linear model as reported in Gratton et al. (2018).

2.5 Data and Code Availability

All of the data have been made publicly available (MSC and code: https://openneuro.org/datasets/ds000224/versions/00002; WashU 120: https://legacy.openfmri.org/dataset/ds000243/). Code for analysis related to network variants in MATLAB is available at: https://github.com/GrattonLab/SeitzmanGratton-2019-PNAS; other code related to MSC processing can be found at: https://github.com/MidnightScanClub. Code related specifically to the analyses in this paper will be located at this link upon publication: https://github.com/GrattonLab/.

2.6 MRI Processing

Data processing for the MSC dataset is explained in detail elsewhere (Gordon, Laumann, Gilmore, et al., 2017). The relevant details of the data processing are outlined below.

2.6.1 Structural MRI Processing

The T1-weighted images for both datasets were processed via automatic segmentation of the white matter, grey matter, and ventricles in Freesurfer 5.3 (Fischl et al., 2002). The default recon-all command in Freesurfer was then applied to recreate the anatomical surface for each participant (Dale et al., 1999), and these surfaces were subsequently hand edited to improve the quality of registration. These surfaces were then registered to the fs_LR_32k surface space using the procedure described in Glasser et al. (2013). Using a separate calculation, a T1-to-Talairach transform was also performed (Talairach, 1988). This same transform was then applied to the fs_LR_32k surfaces.

2.6.2 Functional MRI Processing

The BOLD fMRI data from different runs in each session were concatenated within participants and pre-processed in the volume. First, a slice timing correction was applied, and the data were aligned to the first frame of the first run via rigid body transforms and then normalized to mode 1000 (Miezin et al., 2000). The functional data were then registered to the T2 image and subsequently to the T1 image, which was previously registered to template space. The data were then resampled to 3mm isotropic resolution and registered to the Talairach atlas (Smith et al., 2004). Distortion correction was also applied in this step (Gordon, Laumann, Gilmore, et al., 2017).

The task fMRI data were processed in the volume via a finite impulse response general linear model (GLM) approach as described elsewhere (Gratton et al., 2018). The residuals from the GLM were used to compute task functional connectivity using the “background connectivity” approach (Al-Aidroos et al., 2012; Fair et al., 2007). Subsequently, task residual processing was identical to the resting state data (i.e., completing all steps in the following section).

2.6.3 Functional Connectivity Processing

In the volume, additional preprocessing steps were applied to the data to remove artifacts from the data as outlined elsewhere (Gordon, Laumann, Gilmore, et al., 2017; Power et al., 2014). These steps included (1) the removal of nuisance signals via regression from the white matter, ventricles, global signal, motion parameters, as well as their derivatives, (2) removal of frames with high motion (FD > .2 mm, along with sequences containing less than 5 contiguous low motion frames, the first 30 seconds of each run, and runs with < 50 low motion frames (Power et al., 2014), and (3) bandpass filtering of the data (.009 Hz to .08 Hz). For MSC03 and MSC10, the motion parameters were low-pass filtered (below .1 Hz) before FD calculations to address respiratory activity in the motion traces (Fair et al., 2020; Gordon, Laumann, Gilmore, et al., 2017; Gratton et al., 2018, 2020; Laumann et al., 2016). After this preprocessing, the cortical functional data were registered to the surface. The cortical surfaces were transformed into the CIFTI data format in Connectome Workbench (Marcus et al., 2011). Lastly, a geodesic Gaussian smoothing kernel was applied (FWHM = 6mm, sigma = 2.55) using 2-D smoothing on the cortical surface.

2.7 Network Variants

2.7.1 Functional Connectivity: Creation of Temporal Correlation Matrices

To quantify functional connectivity, a pairwise temporal correlation matrix was calculated for each participant between every pair of cortical surface vertices (59412 x 59412). This matrix was created by taking temporal Pearson correlations between pairs of vertices after censoring high motion frames. The correlation matrix was then Fisher transformed. Thus, each row of this matrix represents a seed map for a given seed (vertex) to all other vertices on the surface (Figure 1A; (Seitzman et al., 2019). We also created a similar correlation matrix for the WashU 120, but

in this case, the individual correlation matrices were averaged together to create a single group average matrix (Figure 1B).

In the MSC dataset, correlation matrices were created for each participant for task and rest data separately, with the amount of data in task and rest matched within each participant, within each session where possible, and across participants (80.6 minutes for each matrix per participant). For the "task" functional connectivity matrix, the amount of data for each individual task was equally sampled sequentially from the beginning of each session for each participant, except for MSC09. This participant had a very low amount of low-motion data in the motor task, so the mixed and memory tasks were equally sampled to supplement the low amount of motor data for analysis (see *Table S1* for more details on the data used for each analysis).

2.7.2 Spatial Correlations to the Group Average

In order to identify regions with strong dissimilarity from the typical functional connectivity profile (i.e., network variants), each MSC participant's correlation matrix was contrasted with the group average correlation matrix from the WashU 120 dataset using a spatial correlation. To compute the correlation, the seed map for each vertex (i.e., a row of the correlation matrix) in a given individual was correlated with the corresponding vertex's seed map in the WashU 120 group data, yielding one spatial correlation value per vertex (Figure 1C). This was repeated for each individual in the MSC (Seitzman et al., 2019). Vertices with low signal (mean BOLD signal < 750 after mode 1000 normalization) were masked (Gordon et al., 2016; Ojemann et al., 1997).

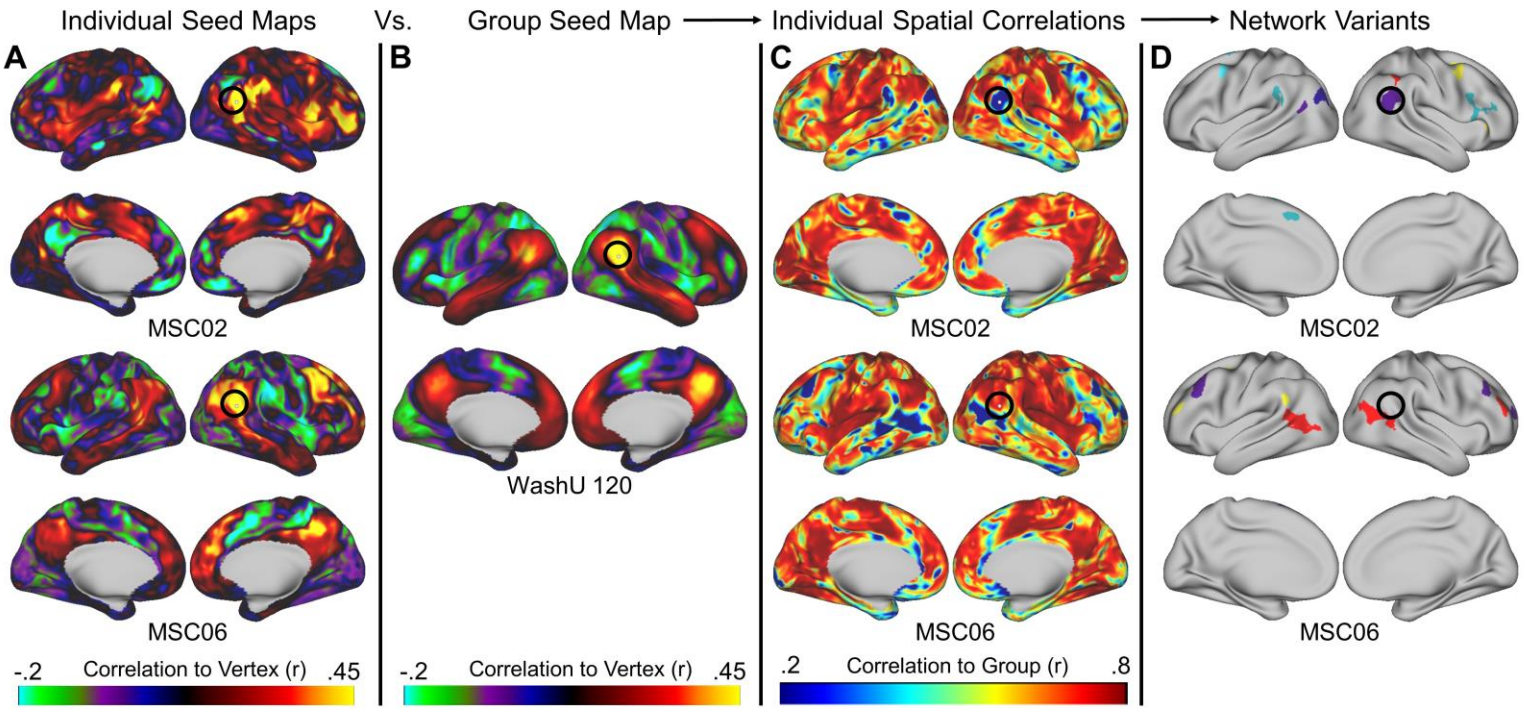

Figure 1. The process for generating network variants. First, a seed map is generated containing the correlations of every vertex to every other vertex within each individual during either task or rest (A) and the group average (B). Next, a spatial correlation between these maps is created and the degree of similarity between each individual and the group is created (C). Finally, regions with the lowest correlations (5%) with the group are selected as variants (D; small variants and locations in low signal regions are excluded). The seed maps shown here are for the vertex inside the black circles. This vertex corresponds to a network variant in MSC02 but not in MSC06.

2.7.3 Calculation of Network Variants

Next, in order to select regions that were most different from the group ("network variants"), the spatial correlation maps were binarized to keep only the lowest 5% of correlations to the group for each participant (values in the lowest 5% were set to 1, all other vertices were set to 0; Figure 1D; note this threshold differs slightly from Seitzman et al. (2019) due to small changes in the processing stream of the MSC data). Variants composed of less than 50 contiguous vertices and vertices with an SNR < 750 were excluded from analysis (Seitzman et al., 2019). The remaining vertices in the lowest 5% of correlations were then considered for further analysis. This procedure was used to create network variants in both task and rest data separately. To confirm the findings were not dependent on threshold, the analyses reported here

are also shown at a 2.5% threshold in the *Supplementary Results*. For the 2.5% threshold, variants were required to be larger than 25 contiguous vertices.

2.8 Stability of Functional Connectivity During Tasks to Group Average Data

If task data is to be considered suitable for identifying network variants, the functional connectivity matrices derived from it must show similar (within-state) reliability as resting state data. To test how much task data is necessary to achieve reliable estimates of functional connectivity within an individual, each participant's data was divided into split-halves composed of either odd or even numbered sessions. Data from all 3 tasks was used in the task analyses unless otherwise noted.

Following Laumann (2015) and Gordon (2017), functional connectivity for each even numbered session split half was estimated using all of the available task data and this was treated as the best estimate of "true" functional connectivity. In each odd numbered session split-half, data was consecutively sampled starting with the first session in 5 minute increments (Seitzman et al., 2019). When all of the task data in a session was exhausted, data was then sampled from the next session until either 100 minutes of task data was sampled, or no more task data was available (see *Table S1* for details on the data sampling of each analysis).

For each functional connectivity matrix in both segments of data, a spatial correlation map versus a group average was computed using the steps outlined above. The similarity of the individual-to-group spatial correlation maps was then compared between the "truth" half and progressive amounts of data from the other split-half via a Pearson correlation. Network variants were created using the procedure outlined in section 2.7.3, only no exclusion for size was applied. These binarized maps were compared between the "truth" and other half via a Dice-Sorenson correlation (Dice, 1945; Sorensen, 1948).

2.9 Comparing Variants Between States

2.9.1 Comparison of Variant Locations

To inspect the similarity of network variant locations across task and rest states, spatial overlap maps were created for each participant. These maps were created by determining which vertices on the surface were considered variants in both task and rest states within each participant. To quantify the amount of spatial overlap between states, variants were separately defined for rest and task states in each split half resulting in 4 variant maps (35.2 minutes total for each split-half matrix per participant). This was done for each split-half of each participant's data separately. Then, a Dice correlation was calculated to determine the similarity in variant locations within each state and between states for each participant.

2.9.2 Between State Comparison

To compare the amount of spatial overlap of variants between task and rest, each split-half of rest data was separately compared to each split-half of task data. This process was repeated for both pairs of split-halves (odd rest split-half to even task split-half and even rest split-half to odd task split-half) to produce two comparisons per participant. The overlap of the split-halves between states was computed via a Dice correlation. Paired t-tests were performed using the averaged value of the between-state comparisons within each participant.

2.9.3 Within State Comparison

To compare the amount of spatial overlap of variants within task and rest, the split-halves of rest and task were both separately compared (odd rest split-half to even rest split-half and odd task split-half to even task split-half) to produce two comparisons per participant. The overlap of the split-halves within states was computed via a Dice correlation. Paired t-tests were reported using the averaged values from the within each state comparisons within each participant.

2.9.4 Across Subject Comparison

To better evaluate the relative similarity of variants within participants (within and between states), we created a comparison benchmark of the similarity of variant locations across subjects. A given participant's variants (computed from a single split-half) were compared to the variants from other participants (also computed from a single split half, from the opposite state). For instance, one split-half of the task data for MSC01 was compared with the corresponding split-half of rest data for MSC02. The similarity in variant maps was computed with a Dice correlation. This was repeated for all combinations of subjects and split-halves, yielding 128 comparisons. This benchmark described the likelihood of observing variants in the same location across subjects which could be used as a comparison for the likelihood of observing variants in the same location within subjects (either within or between states). To compute t-statistics for this comparison, all of the comparisons for each participant's data were averaged into one value for that subject.

2.9.5 Comparison of Variant Magnitude Differences Across States

To compare the magnitude of individual differences between states, variants were defined using the procedure outlined in section 2.7.3. Then, the spatial correlation magnitude at each of these vertices was calculated in both states. Finally, the mean absolute difference between rest and task magnitudes was calculated.

To test whether these values were bigger than what would be expected in other areas of the cortex, the variants in each participant were randomly rotated, thereby matching for variant size and shape in the null distribution (Gordon, Laumann, Adeyemo, Gilmore, et al., 2017). Within each participant, 1000 rotations were randomly generated and performed within each hemisphere. In the case that a rotation resulted in parcels that overlapped with the medial wall,

this rotation was recalculated until none of the rotated parcels overlapped with each other or the medial wall. For each of the 1000 rotations, the mean absolute difference between task and rest magnitudes was calculated. These values were then compared to the mean absolute difference of variant locations in each participant.

2.10 Network Variants Versus Other Vertices

An outstanding issue in the measurement of network variants is whether they are more similar between states than would be expected from regions with more similarity to the group. Such a finding would provide evidence for their trait-like stability, as posited elsewhere (Seitzman et al., 2019). In order to examine this issue, we thresholded maps at 2.5% increments starting with the lowest 2.5% of spatial correlation values versus the group average for each split-half within each participant (e.g., bin 1: 0-2.5% similarity to the group, bin 2: 2.5-5%, bin 3: 5-7.5%, …, etc.). For each 2.5% increment, we computed the Dice correlation for the comparisons within-state, between-state, and across-subjects. The average value for each of these comparisons was then plotted with their associated standard error (across subjects). No size exclusion based on a minimum number of contiguous vertices was applied to this analysis.

2.11 Similarity of Individual Tasks Versus Multiple Tasks

We also evaluated the degree to which variants at rest are similar to variants from a single task versus variants from multiple tasks averaged together. For this analysis, the amount of data was matched across individual tasks and participants. Data were sampled consecutively from the beginning of each session and were matched across sessions to produce two independent "split-half" samples. This same procedure was also applied to sample an equal amount of data from all three tasks combined. The amount of data for each individual task and for all three tasks combined was 11.3 minutes total per split-half for each task per participant. MSC09 was not

used in this analysis due to the small amount available for this participant (1.25 minutes in the smaller split-half). Dice correlations were used to quantify the overlap within-state, between-state, and across-subjects. Within subject ANOVAs were used to test for differences between states. Due to the small amount of data available for this analysis, the results should be interpreted with some caution.

2.12 Similarity of network variant assignments between states

We next asked whether network variants also showed similar network assignments between states. To test this, each variant was assigned to a network, and the similarity of these networks assignments between states was evaluated.

2.12.1 Assigning Network Variants to Functional Networks

Each variant was assigned to functional networks via a winner take all algorithm. This algorithm assigned variants to one of 14 group average template networks (Gordon, Laumann, Adeyemo, Gilmore, et al., 2017). The templates for matching the network variants were the spatial maps of the group average canonical networks from the group average of the WashU 120 dataset. First, a seed map was generated for all the vertices composing a given variant. These seed maps were then averaged together to form one seed map for each network variant (Seitzman et al., 2019). For each map and the template, the highest 5% of correlations with the rest of the surface were binarized. Next, we computed the similarity (Dice correlation) between the binarized network variant map and the templates. Vertices within 30mm geodesic distance from any vertex in each variant were excluded from the variant seed map and template seed map (Gordon, Laumann, Adeyemo, Gilmore, et al., 2017). Each network variant was assigned to the winning template with the largest Dice correlation. If no good "winning" template was found based on the lowest 5% of Dice correlations with the winning network (Dice < 0.1394 at 5%

threshold) or multiple networks tied for the highest value, then the variant was assigned to an "unknown" network. In addition, network variants were also removed if their assigned network overlapped at least 50% with the group average network (11/125 = 9% in rest, 11/123 = 9% in task; (Seitzman et al., 2019).

2.12.2 Evaluating Variant Network Assignment Consistency Between States

We next asked whether a particular variant showed the same network assignments between states. To do this, first variants in task and rest were assigned to networks according to the procedure above. Next, the same vertices that each variant was composed of were selected in the other state (e.g., the variant locations from a task were applied to the resting state data), and the network assignment procedure was repeated for these vertices in the other state. If the network assignments were the same between states, both values were set to 1. Otherwise, the value for the network assignment in the other state was set to 0. A Dice correlation was then used to quantify the likelihood of the same vertices between states being assigned to the same network.

3 Results

3.1 High Amounts of Task Data Can Produce Reliable Estimates of Network Variants

The overarching question of this manuscript is whether network variants are similar between task and rest states, indicating that they are trait-like and that task data may be used to identify variants. As a first step, we asked if task data can produce reliable (i.e., high within-state similarity) estimates of network variants, as has been shown for rest data. Following Gordon et al. (2017) and Laumann et al. (2015), reliability was estimated using a split-half procedure. Specifically, task data from each participant was divided into two halves. Variants were created from one entire half of the data; these variants were treated as our best estimate of "true" variants. The other half was incrementally sampled in 5 minute increments of data; each

incremental sample was used to generate a new estimate of network variants. This incremental sample estimate was then compared to the other full half (the "true" estimate). The same procedure was conducted both for the comparisons of the continuous spatial correlation maps (Figure 2A, compared using Pearson correlations) and for the binarized network variants (Figure 2B, compared using Dice correlations).

The general trend is that as the data quantity increases (x-axis), the similarity between the two halves of data also increases (y-axis) before reaching an asymptote, typically around 40 min. of data. In particular, with > 40 minutes the continuous spatial correlation maps reach reliabilities with $r > .8$ (Figure 2A). In addition, the binary overlap between the lowest 5% of correlations between the group average also becomes stable with high amounts of data (Figure 2B; note that however these values typically asymptote at a lower level, around Dice correlation = 0.7, likely due to instability caused by the thresholding operation). However, reaching stability for the binarized data requires additional time beyond what is necessary to achieve reliable spatial correlation maps (> 70 minutes). This task reliability profile is similar to what is seen with rest (*Figure S1*). Thus, high amounts of task data can produce reliable measures of network deviation in individuals with respect to the group average, similar to rest.

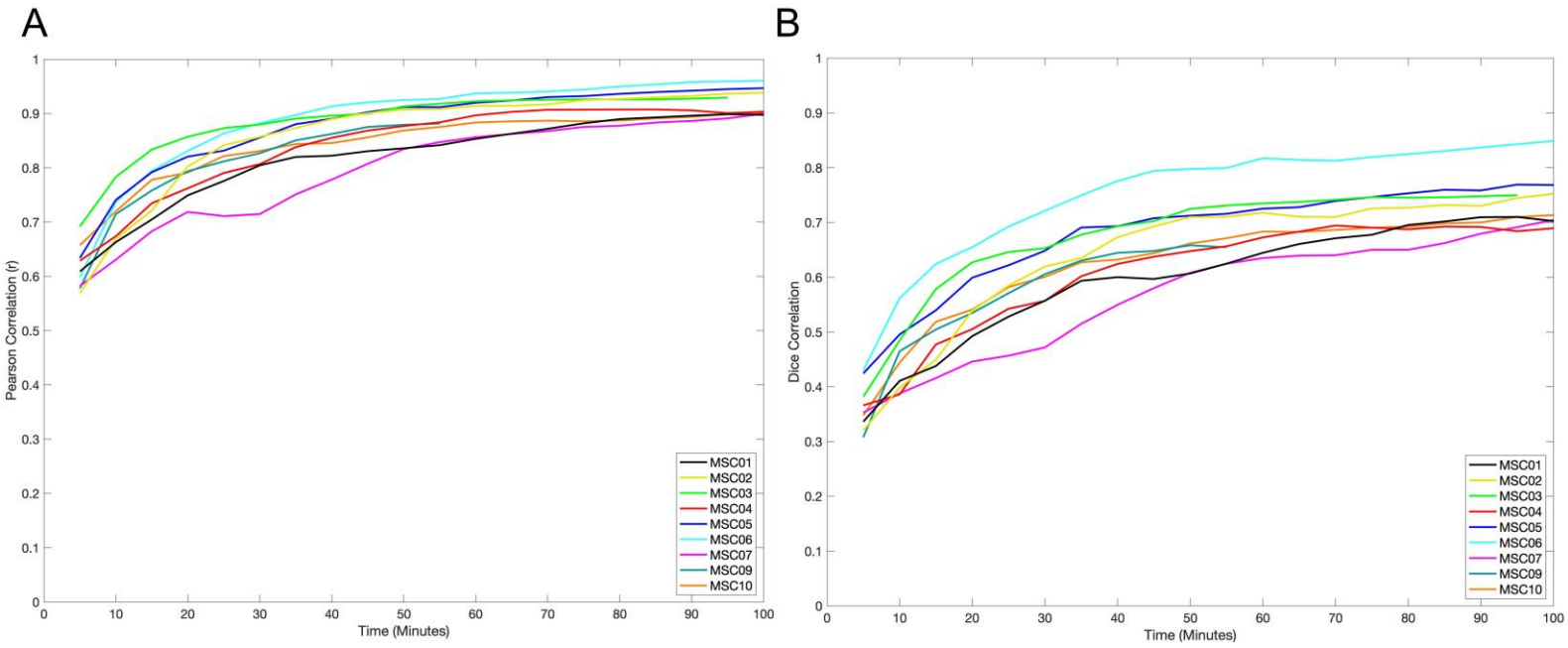

Figure 2. Reliability of network variants measured from task data. (A) Comparisons of individual-to-group spatial correlation maps from task data are shown for 5 minute increments for each participant. The similarity between maps is calculated via Pearson correlation. Spatial correlation maps begin to plateau around 30-40 minutes at r>0.8. (B) Comparisons of network variant maps (after binarization of the spatial correlations to the bottom 5% of locations) from task data are shown in 5 minute increments for each participant. The similarity between binarized locations is calculated via Dice correlations. Binarized maps take longer (50-70 min.) and reach a slightly lower asymptote (Dice > 0.65), likely due to instability in the thresholding operation. A similar pattern was observed for the reliability of network variants in rest data (Figure S2). Note that MSC09 (55 minutes) and MSC03 (95 minutes) did not have 100 minutes of data in their respective split-halves.

3.2 Network Variants Occur in Relatively Similar Locations Across States

Next, we examined whether network variants occur in the same locations between task and rest, addressing the extent to which they are dependent on state. If network variants are trait-like, then their vertices would be expected to overlap at a significantly greater rate between states (within a person) than across people. Consistent with this pattern, Figure 3A,B shows that network variants appear in similar locations between task and rest states in single individuals (see *Figure S2* for variant overlap for the other participants).

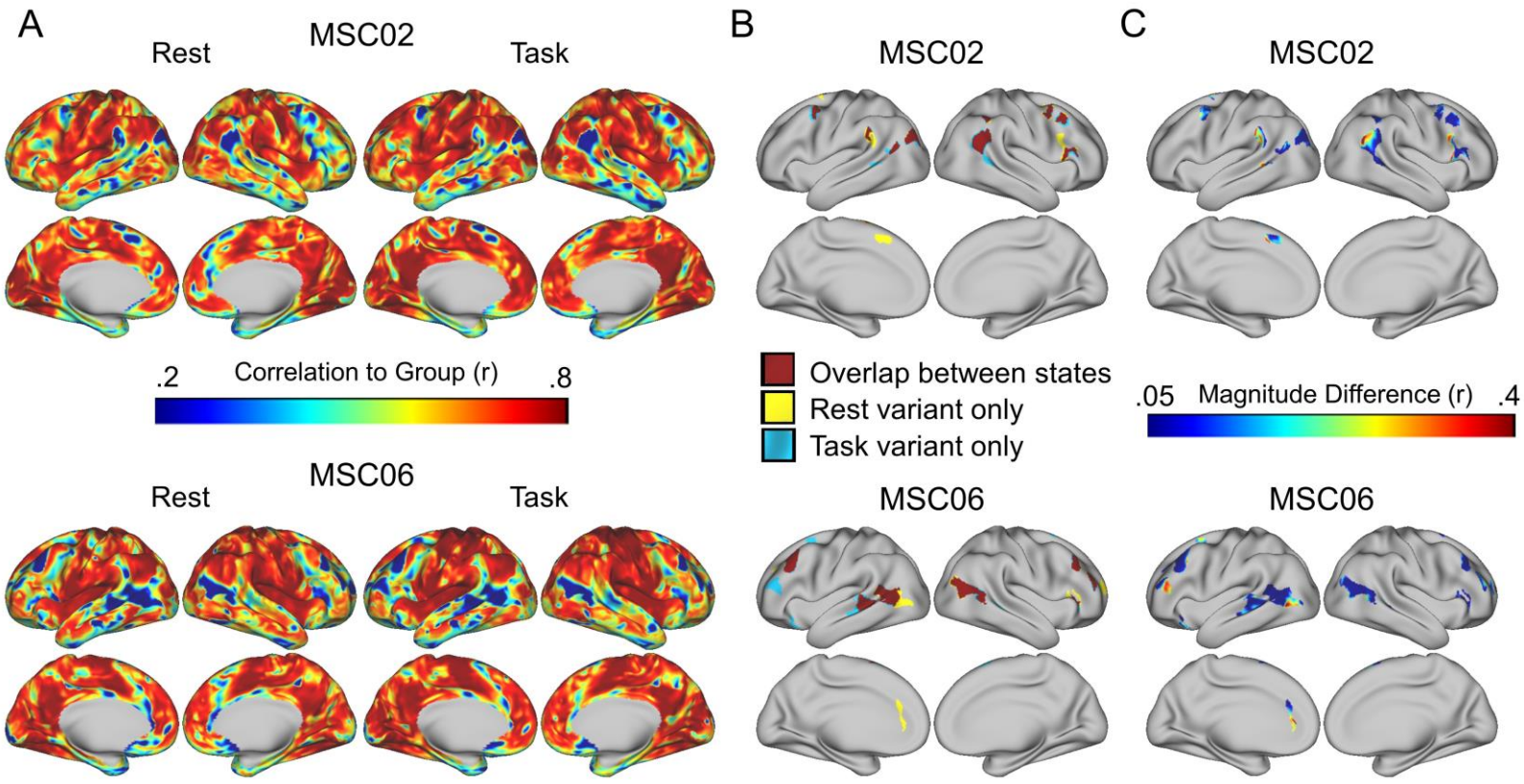

Figure 3. Comparison of network variant locations between task and rest states. (A) Individual-to-group spatial correlation maps are shown separately for task and rest states in MSC02 and MSC06; note the strong similarity in map profiles. (B) These maps are binarized (bottom 5%) to generate network variants for each state. The overlap between states is shown in red, and variant locations seen in only one state are shown in yellow (for rest) and blue (for task). (C) For each location labeled as a variant in either task or rest state, we have plotted the absolute difference in magnitude of the spatial correlations between states. Most locations show small magnitude differences, but a small number show more sizeable differences.

To quantify this similarity, we calculated the Dice coefficient between task and rest state network variants. We benchmarked this between-state overlap against two comparisons: (a) within-state overlap (how similar network variants are across two different samples from the same state, e.g., between two halves of resting state data from MSC01) and (b) across-subject overlap (how similar network variants are between subjects, e.g., between a task split half of MSC01 and a rest split half from MSC02). These comparisons allowed us to determine if network variants were more trait-like (showing relatively similar variants between states, but distinct variants across people) or state-like (showing relatively distinct variants between states,

closer to the level seen across people). Importantly, data quantities were matched for all comparison samples within and across individuals.

The results showed that variants were more likely to overlap between states within subjects (M = .533, SD = .103) than across subjects (M = .068, SD = .025, $t(8) = 14.96$, $p < .0001$, d = 4.99), suggesting a large trait-like component to network variants. Variants were also significantly more likely to overlap within states (M = .641, SD = .082) than between states (M = .533, SD = .103, $t(8) = 6.38$, $p = .0002$, $d = 2.13$; see Figure 4), suggesting some state-dependence. However, the magnitude of the difference between states was substantially smaller than the magnitude of the difference across subjects. Similar results are also observed at a 2.5% threshold (see *Figure S3*) Jointly, these findings indicate that variant locations are affected by state, but are relatively more trait-like than state-like.

We also examined whether the magnitude of the spatial correlations differed between states at network variant locations more than from other areas of the cortex (Figure 3C). On average, the differences between states are relatively small for network variants (M = .115, SD = .091, *Skew* = 1.11). However, the tail of the distribution for magnitude differences is somewhat larger for network variants than would be expected by chance in other areas of the cortex (M = .063, SD = .057, *Skew* = 1.84), indicating that a subset of locations shows larger magnitude differences than might be expected for other areas of cortex (see *Figure S4*). This suggests that there may be an interaction between individual differences in functional connectivity and task state.

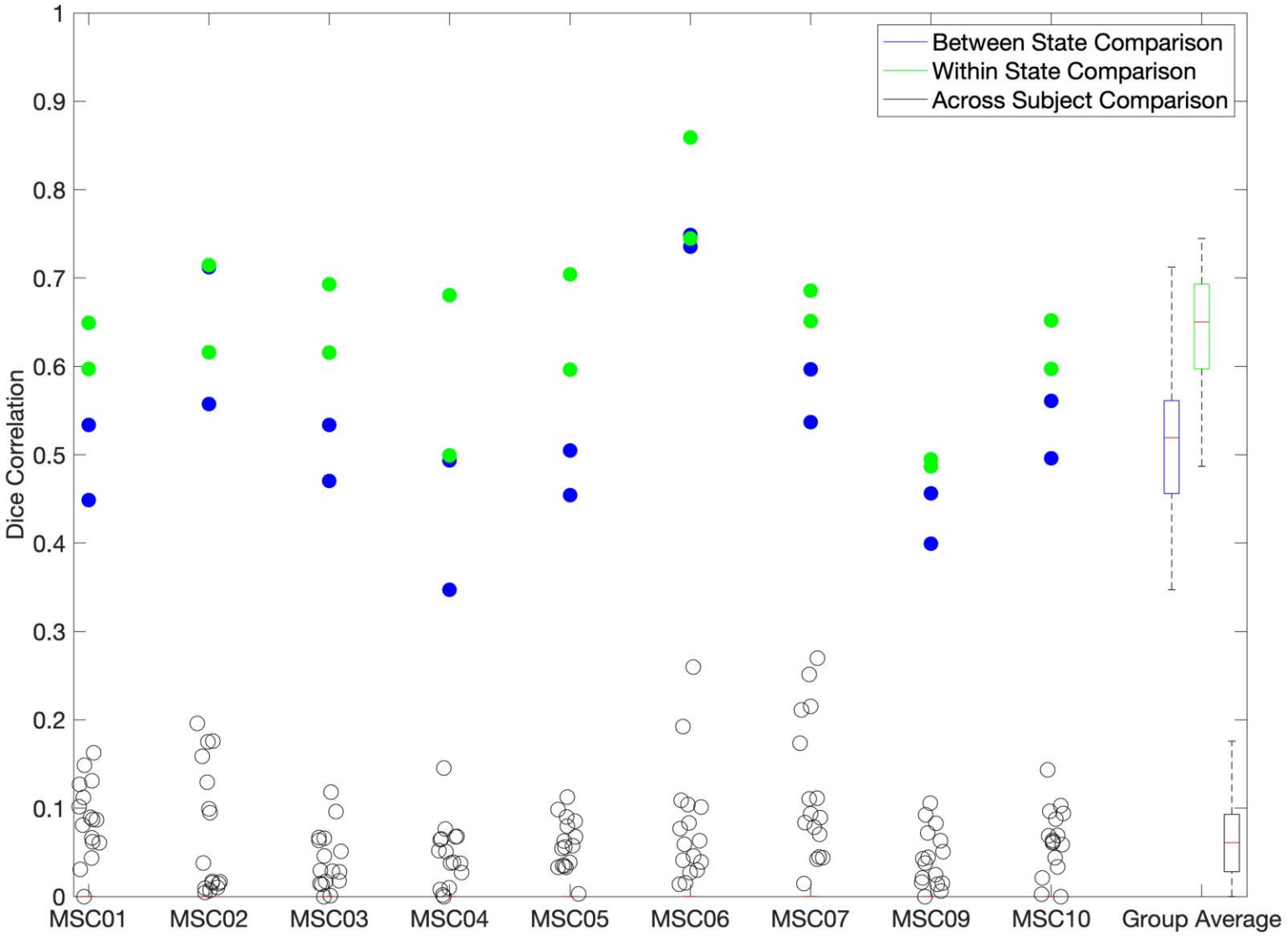

Figure 4. Network variant locations were compared using Dice correlation, for network variants between states (blue), within states (green), and across subjects (black). Values are plotted for each subject (columns) with the summary boxplot at the end. Within and between state comparisons are shown as two dots, one for each pair of split-halves tested (see sections 2.7.4 and 2.7.5).

3.3 Network Variants Associate with Similar Networks in Task and Rest

While the locations of network variants are relatively similar across states, it is still possible that the functional networks that these variants belong to may differ across states. To test this possibility, each variant was assigned to a template network using a winner-take-all procedure in

each state (see section 2.12.1). A Dice correlation was then used to quantify how often variants were assigned to the same network between states.

As shown in Figure 5B, the distribution of variant network assignments between states was similar. In addition, the likelihood of obtaining a matching network assignment for a variant using the same vertices in the opposite state was high (M = .832, SD = .075; Figure 5C). This shows that network variants tend to be assigned to the same network between states, providing evidence for their trait-like stability.

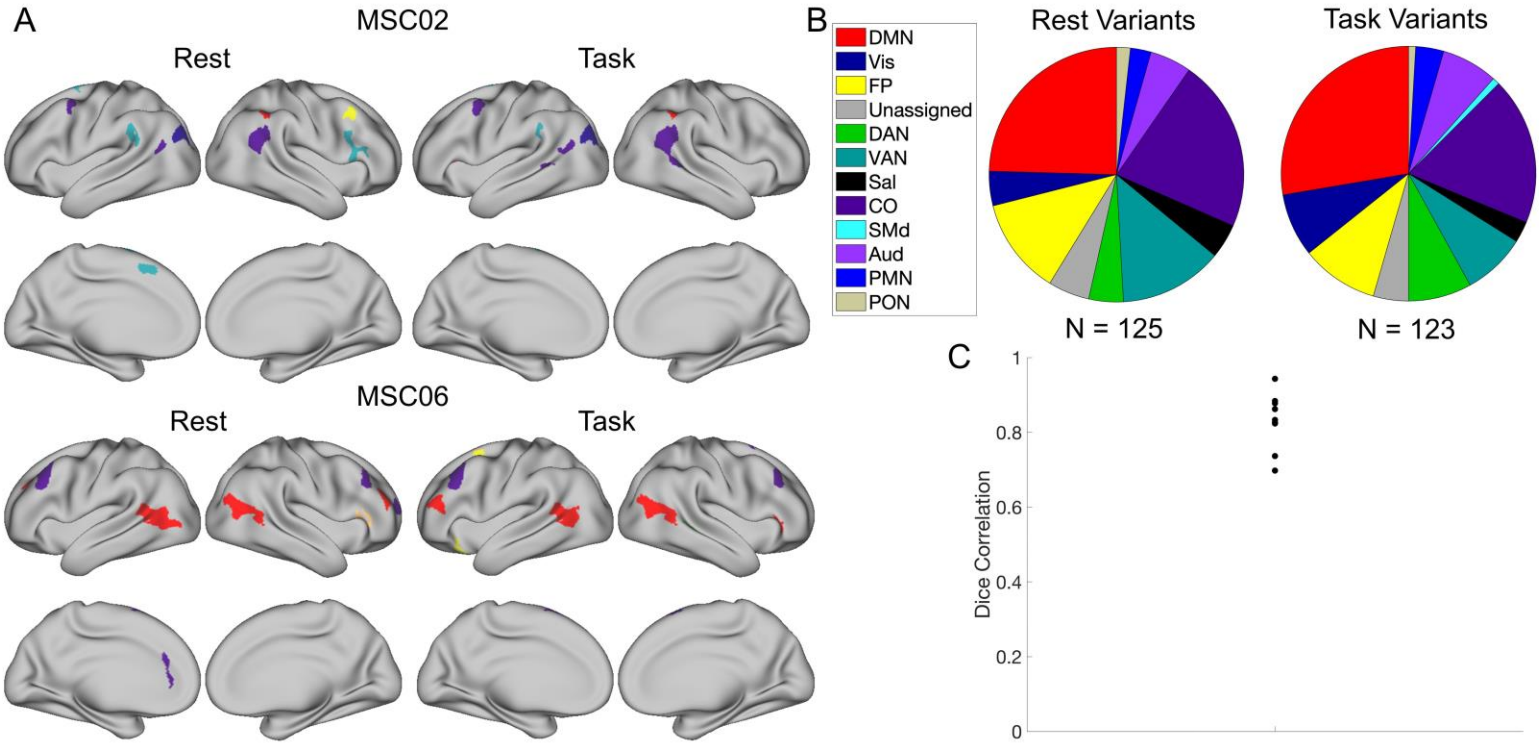

Figure 5. Comparison of network variant assignments between task and rest states. (A) The network assignments for variants are shown for task and rest states in MSC02 and MSC06. (B) The distributions of the networks that variants are assigned to for rest variants and task variant are also shown across all subjects. (C) The likelihood of a variant in one state being assigned to the same network in the opposite state is plotted for each participant (see *Figure S5* for a version of this figure with the participants labeled).

3.4 Network Variants are Highly Stable Compared to Vertices More Similar to the Group

Next, we looked at whether network variants are more trait-like than vertices selected based on having higher similarity to the group. To test this, we examined whether network variants (defined as the lowest 2.5 percentile bin of spatial correlations, showing the highest differences from the group) showed relatively strong state-stability compared with other brain locations binned by their similarity to the group (defined by taking 2.5% percentile bins in the comparison between individual and group networks, e.g., 2.5-5%, 5-7.5%, 7.5-10%, etc.; see *Figure S6* for example maps of these selected bins for MSC02).

The pattern of this analysis is shown in Figure 6. Interestingly, network variant locations (the left side of the curve) showed more stability between states, with higher within- and between-state similarity than almost any other percentile bin. The only other bins that showed as strong of stability were at the highest end of the spectrum: those with the most consistency to the group. This is likely driven by the fact that network variants (as well as the most group consistent regions) agglomerate into contiguous parcels, whereas other bins show a more scattered representation across cortex. This provides evidence for the distinctive and trait-like nature of network variants relative to other locations selected for their group similarity.

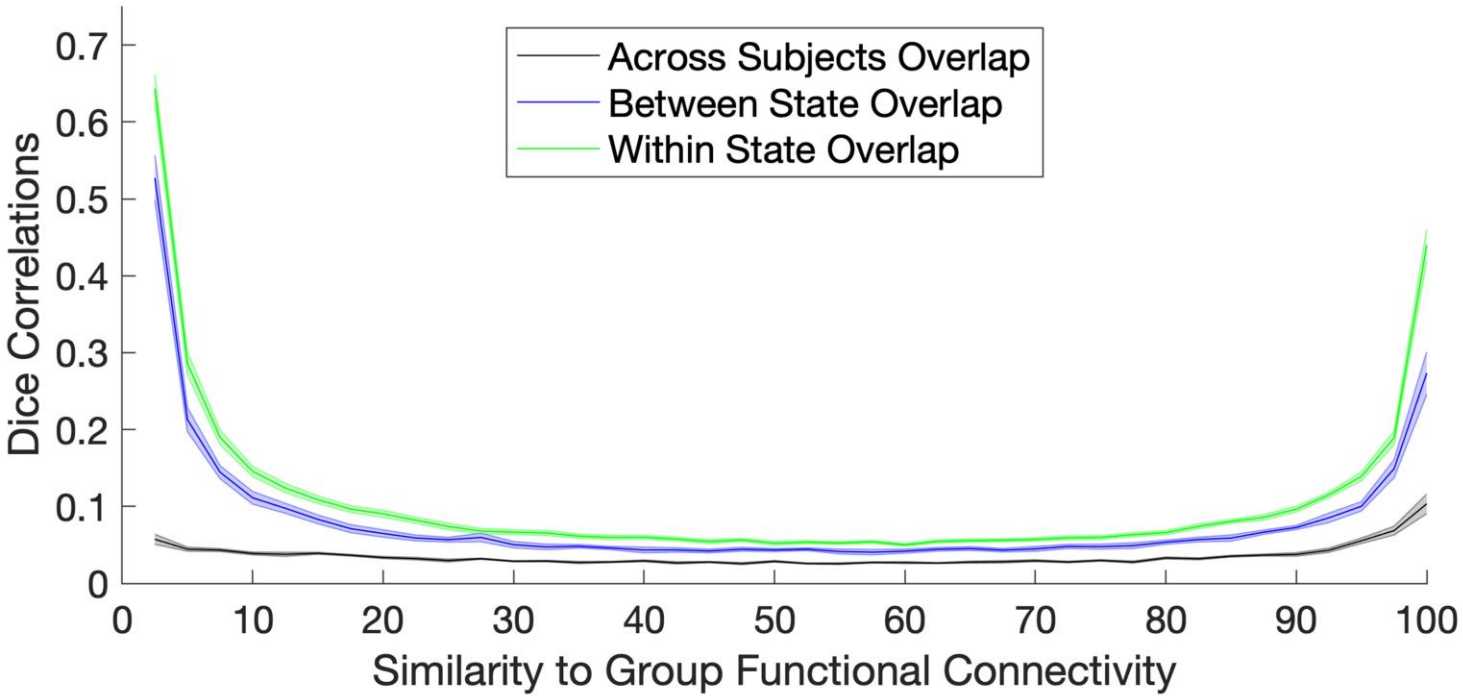

Figure 6. State/trait comparisons for locations binned by their similarity to the group (in 2.5% size bins). At each bin, split halves of the data were compared within state (green), between state (blue), and across subjects (black). Standard error bars are shown for each line. The areas that are the most similar and dissimilar to the group average functional connectivity show the most consistency and trait-like nature.

3.5 Network Variant Stability was Similar When Examined for Single Tasks

The last comparison tested was whether variant stability for task versus rest differed between any of the 4 tasks collected in the MSC. A significant effect would indicate that there were task-specific effects of how stable variants were across states. To test this effect, similar overlap analyses as those presented in Figure 4 were carried out, but with data separated by task rather than concatenating across all tasks. Note that, given the separation, this analysis was conducted on relatively less data (11.3 minutes per split-half) and thus the results should be interpreted with caution due to lower reliability.

Overall, the results suggest that variant similarity between task and rest does not significantly differ between tasks (Figure 7). A one-way within subjects ANOVA was used to

test whether the stability of network variants between individual task states. Greenhouse-Geisser corrections were applied where appropriate. The effect of task was not significant, ($F(1.631,11.418) = 1.565$, $p = .248$, $d = .95$), indicating that there were no significant differences in stability for any individual task versus rest. This suggests that there is no difference in the stability of network variants when using a single task versus multiple tasks compared to rest. Similar results are also seen when using a 2.5% threshold to identify network variants (see *Figure S7*).

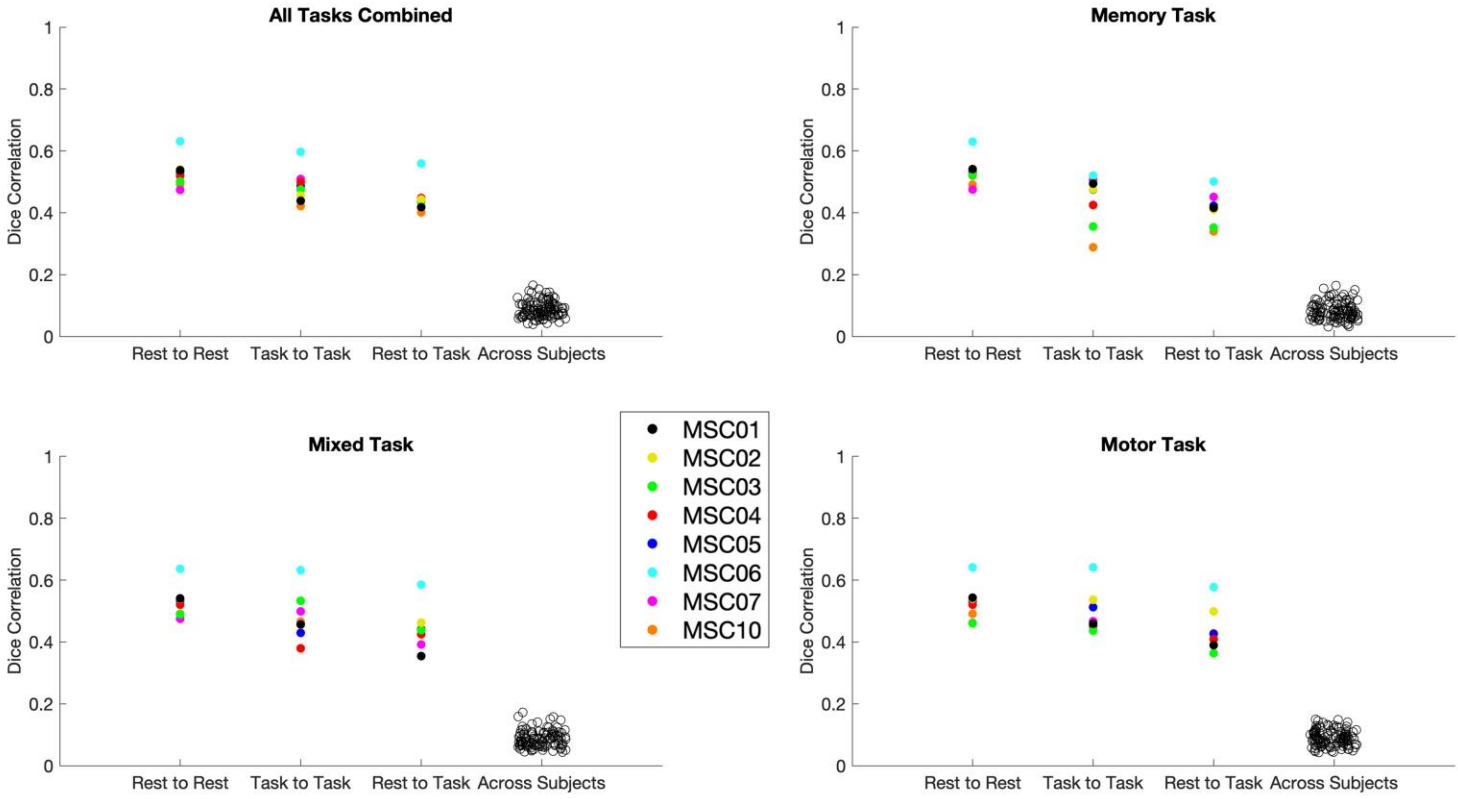

Figure 7. Comparison of network variant similarity in individual tasks relative to all tasks and rest. Dice correlations were used to compare network variants from data from all 3 tasks combined (upper left), the memory task (upper right), the mixed task (bottom left), and the motor tasks (bottom right). Each comparison shows the rest-to-rest, task-to-task (for the relevant task), rest-to-task (for the relevant task), and across subject comparisons of network variants. All comparisons were matched on amount of data within and across participants. Note that MSC09 was excluded from this analysis due to low amounts of high quality data in the motor task.

4 Discussion

This study examined whether network variants (locations where an individual's network organization differs markedly from the group) were susceptible to state-level changes induced by task demands. This question has bearing on both the trait-like aspects of network variants and on practical questions of whether task data can reasonably be used to identify network variants. To examine this question, we used resting state and task data from the Midnight Scan Club to define network variants. These network variants were then compared to each other in various ways to evaluate whether network variants showed trait-like stability between states. We found that (1) network variants defined from task data show similar reliability to resting state data, (2) network variants appear in similar locations between task and rest data, although with some small state-dependent effects, (3) the network assignments of variants are similar between task and rest, and (4) that there is similar stability for network variants identified from multiple or single tasks. Thus, our analyses suggest that while network variants show some differences that are due to state-level factors, they are predominantly stable between states, consistent with their trait-like properties. Importantly, these findings suggest that a reasonable approximation of network variants can be identified from task as well as rest.

4.1 Network Variants Are Largely Trait-like

The current findings add an additional piece of evidence to suggest that network variants are relatively trait-like in nature by demonstrating consistency across different task states. We found that individuals' network variants tend to occur in similar locations across different states as well as have similar network labels. These findings add to previous evidence from Seitzman et al. (2019) showing (a) that network variants are consistent across sessions within a state, even over a year, (b) that variants defined at rest can be used to predict default mode deactivations during a

task and (c) that variants can be used to separate individuals into sub-groups that relate to behavioral measures taken outside of the scanner. This consistency across states, high reliability, and relationship to brain activation and behavioral measures taken at other moments in time jointly suggest that network variants may be trait-like properties of brain networks, rather than functions of ongoing processing.

Although network variants exhibit primarily trait-like properties, it is also clear that they show some minor but significant state dependence. This is consistent with past work showing that the functional organization of the brain is largely stable, but can be modified to adjust to different task states (Cole et al., 2014; Gratton et al., 2016; Krienen et al., 2014). In the context of individual differences, recent work has emphasized that stable group and individual factors dominate brain networks, but more modest task-based effects are also present in functional organization between task and rest states across the full connectome (Gratton et al., 2018). These state-dependent changes in functional connectivity likely also contribute to differences in connectivity of network variants between different task states. Future work will be needed with a larger sample of tasks to further elucidate whether these changes in observed network variants across states are systematically related to unique strategies or task performance (performance on the current tasks, which were all relatively simple, was at ceiling and all MSC individuals are high IQ).

Taken together, these results suggest that the neurobiological underpinnings of network variants may stem from a systematic change in the function of underlying brain tissue from that which is neurotypically observed in the population, which then alters the Hebbian associations between brain regions and their functional connectivity properties (Gratton et al., 2019; Seitzman et al., 2019). Given their stability, these individual-level differences in brain network

organization may be due to differences in cortical organization driven by longer-term factors such as genetics, more prolonged life experiences, or other environmental factors.

Under this framework, network variants may be viewed as prime candidates for neural correlates of trait-like individual differences in behavior, such as cognitive ability and risk for psychopathology. However, as the pattern of functional connectivity of network variants is affected by task states, it is clear that they are somewhat dependent on state. One possible explanation for this finding is that areas identified as network variants may have shifted in their functions from their 'typical' role; this may also compound differences in coherence across regions during particular task states, including potentially, functional connections with multiple networks (e.g. a variant may include neurons which correspond both to the typical neural functions as well as atypical functions, connecting two different networks). This would cause network assignments to vary in some areas during task performance versus rest and impose some state-dependency on the characteristics of network variants. Additional investigations of network variants using different methodologies will be needed to further examine their underlying neurobiology.

4.2 Practical Considerations for Identifying Network Variants With Task Data

Due to the similarities of network variants between task and rest states, it seems reasonable that network variants can be estimated using task data. Network variants show substantial stability in location and network characteristics between rest and task states. In practice, there is approximately a 17% reduction in the stability of network variant location when examined between states versus within states. This is in contrast with network assignment, which shows a much higher stability between states. While identifying variants between states is not as consistent as identifying them from within the same state, the results suggest that it may be

reasonable to conduct network variant analyses across tasks if needed for data quantity reasons. Notably, spatial differences in network variants between states are much smaller than the differences observed in reliability from using small amounts of data (approximately 56% lower between 5 minutes and 70 minutes of data).

Critically, the finding that variants can be identified during task states with good correspondence to rest opens up new datasets for variant analysis that would not be available otherwise. While most currently available datasets only have small amounts of rest data (5-10 mins) which are insufficient to achieve high reliability (Fig. 2B, S1B), many have substantial additional task data. Moreover, while datasets from clinical populations are of great interest, it is may be particularly difficult to obtain large amounts of high quality resting state data in many of these populations (due to exacerbated head motion, compliance issues, etc. (Greene et al., 2018; Hodgson et al., 2017; Vanderwal et al., 2019)). Combining data across task and rest may be an effective strategy to increase functional connectivity reliability sufficient for network variant analyses without sacrificing substantial variability due to state differences.

Elliot and colleagues (2019) have shown that combining resting state data with background connectivity during task performance increases the reliability of functional connectivity data as a whole. Critically, this increase in reliability was also accompanied by an increase in the predictive utility of functional connectivity for cognitive measures and the heritability of functional connectivity. Additional work has also incorporated this strategy of analyzing functional connectivity data in developmental samples (Cui et al., 2020), demonstrating its utility in a dataset with a limited amount of resting-state fMRI data. Our results suggest that this method can also be used to identify network variants, which may yield new insights into neurologic and psychiatric disease.

4.3 Important Methodological Considerations for Identifying Network Variants

Despite this promise for using task data to identify network variants, some caveats for this approach are discussed below. First, while the reliability of functional connectivity in general becomes stable after >30 minutes of data (Gordon, Laumann, Gilmore, et al., 2017; Laumann et al., 2015), network variants appear to require more data to achieve an adequate reliability. From our estimates, it appears that >70 minutes of task data are required to achieve asymptotic reliability for network variants. This amount of data is very similar to that necessary for achieving acceptable reliability in rest as well. This added need for data is likely due to the thresholding procedure in defining network variants as spatial correlations maps (Fig. 2A, S1A) achieve high reliability more quickly. Combining task and rest data may be an effective strategy to achieve this amount of data in available datasets with insufficient rest.

In addition to combining rest and task data, our initial evidence suggests that it is possible to either use data from a single task or combine data from multiple tasks to generate network variants. We found no significant differences in the ability to identify network variants across 3 different tasks versus rest, indicating that all of the tasks performed relatively similarly. However, for this analysis we were restricted to using a small amount of data which complicates the interpretation of our analysis. It may be possible that with larger amounts of data or with different tasks, task-specific effects for network variants could be observed.

A final caveat of our analyses is that is important to match data in terms of both quantity and quality when comparing the reliability of fMRI data. Because reliability of a scan steadily increases with the amount of low-motion data (Elliott et al., 2019; Gordon, Laumann, Gilmore, et al., 2017; Laumann et al., 2015; Noble et al., 2017), it is necessary to match these attributes in order to make accurate comparisons. Recent work also highlights the importance of accounting

for the presence of task activations when using task data for functional connectivity (Cole et al., 2019). The background connectivity approach we used here is likely more informative about the relative merits of task vs. rest data from functional connectivity changes rather than activations themselves.

5 Limitations

We also note several limitations to the current study. First, although the MSC dataset has a large amount of resting state data, it is somewhat limited in the amount of available task data, especially for single tasks. This is particularly true of the motor task, which had a high number of frames lost due to movement. Therefore, we only draw limited inferences about task-specific effects on network variants from the current study.

Second, although we found some state-dependent changes in network variants, it was unclear what drove these differences. We did not find systematic patterns associated with particular networks or particular tasks. It is possible that future work with a broader set or more targeted tasks may help to identify these and shed light on state-dependent mechanisms.

Third, several of the analysis decisions in this paper are based on thresholding data which has the potential to systematically change patterns in the data. One example of this is the thresholding of network variants in individuals as the lowest 5% of correlations with group average networks. This decision was based off examining histograms of group correlations and finding the approximate tail of the distribution. In addition, we also demonstrated that the reported results replicate at a second threshold (2.5%) showing their robustness to this choice. Another thresholding choice was in the assignment of variants to networks, for which the top 5% of correlations with a seed region were selected for spatial overlap. It should be noted that the distribution of the network assignments closely mirrored past work (Seitzman et al., 2019), with

higher-level association networks making up the majority of network variants. To alleviate these concerns in future work, newer techniques such as bagging (Nikolaidis et al., 2020) may be used to enhance the reliability of processing steps which require thresholding.

Fourth, another possible limitation is the method used here to assign variants to networks. It is possible that network assignments may be poor or relatively ambiguous in some cases due to the winner-take-all method used. To mitigate this issue, we reassigned variants with a poor match to any canonical network as belonging to an "unassigned" network. Subsequent work may seek to incorporate newer techniques, such as "soft" multi-network assignments (Cui et al., 2020) for networks with an ambiguous pattern of connectivity.

6 Conclusion

Overall, these results suggest that network variants show trait-like stability between multiple states. Network variants measured with task data were reliable (given sufficient data) and appeared in similar locations with similar network assignment to that seen with rest data. There were also more minor state-dependent differences associated with network variants. Jointly this work suggests that combining rest and task data may be a reasonable strategy to identify network variants from datasets with insufficient rest.

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Supplementary Methods

WashU 120 Processing

The WashU 120 dataset is composed of resting state data from 120 neurotypical adults collected from several different studies. The data acquisition and processing of this data is fully described elsewhere (Power, Schlaggar, Lessov-Schlaggar, & Petersen, 2013). All data collection was approved by the Washington University Internal Review Board.

fMRI Acquisition

The acquisition parameters for this dataset have been fully described elsewhere. In brief, high-resolution T1-weighted, T2-weighted, and resting-state BOLD data were collected on a Siemens 3T Magnetom Tim Trio with a 12-channel head coil (gradient-echo EPI sequence, isotropic 4 mm^3 voxels, TE of 27ms, and TR of 2.5s).

Resting State

The WashU 120 dataset contains between one and four sessions of eyes-open resting state data per participant (average: 14 minutes, range: 7.67 minutes– 30.17 minutes).

MRI Processing

Data processing for the WashU 120 dataset (Power et al., 2013) is explained in more detail elsewhere. The relevant details of the data processing are outlined below.

Structural MRI Processing

The T1-weighted images for both datasets were processed via automatic segmentation of the white matter, grey matter, and ventricles in Freesurfer 5.3 (Fischl et al., 2002). The default recon-all command in Freesurfer was then applied to recreate the anatomical surface for each participant (Dale, Fischl, & Sereno, 1999). These surfaces were then registered to the fs_LR_32k

surface space (Glasser et al., 2013). Using a separate calculation, a T1-to-Talairach transform was also generated (Talairach, 1988).

Functional MRI Processing

The BOLD fMRI data were concatenated within participants and pre-processed in the volume. First, a slice timing correction was applied, and the data were aligned to the first frame of the first run via rigid body transforms and then normalized to mode 1000 (Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000). For the functional data in the WashU 120 dataset, the images were registered to both the T2 and T1 images. Both datasets were then resampled to 3mm isotropic resolution and registered to Talairach space (Smith et al., 2004). Distortion correction was not applied to the WashU 120 dataset as no field maps were collected.

Functional Connectivity Processing

In the volume, additional preprocessing steps were applied to the data to remove artifacts described elsewhere (Power et al., 2014, 2013). These steps included (1) the removal of nuisance signals via regression from the white matter, ventricles, and global signal, (2) removal of frames with high motion (FD > .2 mm), and (3) bandpass filtering of the data (.009 Hz to .08 Hz). After this preprocessing, the cortical functional data were registered to the surface. The cortical surfaces were transformed into the CIFTI data format in Connectome Workbench (Marcus et al., 2011). Lastly, a geodesic Gaussian smoothing kernel was applied (FWHM = 6mm, sigma = 2.55) using 2-D smoothing on the cortical surface.

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Supplementary Results

Analysis	Figure	Data Description	Data Amount
1	Figure 2	Data sampled in 5 minute increments equally from all 3 task states and compared to corresponding full split-half of task data. Data consecutively sampled from each session.	5-100 minutes of task data in one split-half for each individual except MSC03 (95 minutes total) and MSC09 (55 minutes). All task data sampled in corresponding split-half sampled for all participants.
2	Figure 4	Data matched within each split-half across participants and between states. Data consecutively sampled from each session.	35.2 minutes per split-half in each state for each individual.
3	Figure 5	Data matched across participants and between states. Data consecutively sampled from each session.	80.6 minutes per state for each individual.
4	Figure 6	Data matched within each split-half across participants and between states. Data consecutively sampled from each session.	35.2 minutes per split-half in each state for each individual.
5	Figure 7	Data matched within each split-half across tasks, participants, and between states. Data consecutively sampled from each session.	11.3 minutes per split-half in each task for each individual.

Supplementary Table 1 (S1). Data description for each analysis. The number for the analysis corresponds to the number in section 2.1 as well as the figure indicated.

Subject	Rest	Task	Total
MSC01	16	17	33
MSC02	13	11	24
MSC03	5	7	12
MSC04	16	14	30
MSC05	12	16	28
MSC06	10	11	21
MSC07	15	12	27
MSC09	14	14	28
MSC10	13	10	23
Total	114	112	226

Supplementary Table 2 (S2). The total number of variants is shown across task and rest states for each participant at a 5% threshold. These counts reflect variants that were excluded for being in low signal regions, small size, or overlapping more than 50% with the group network template.

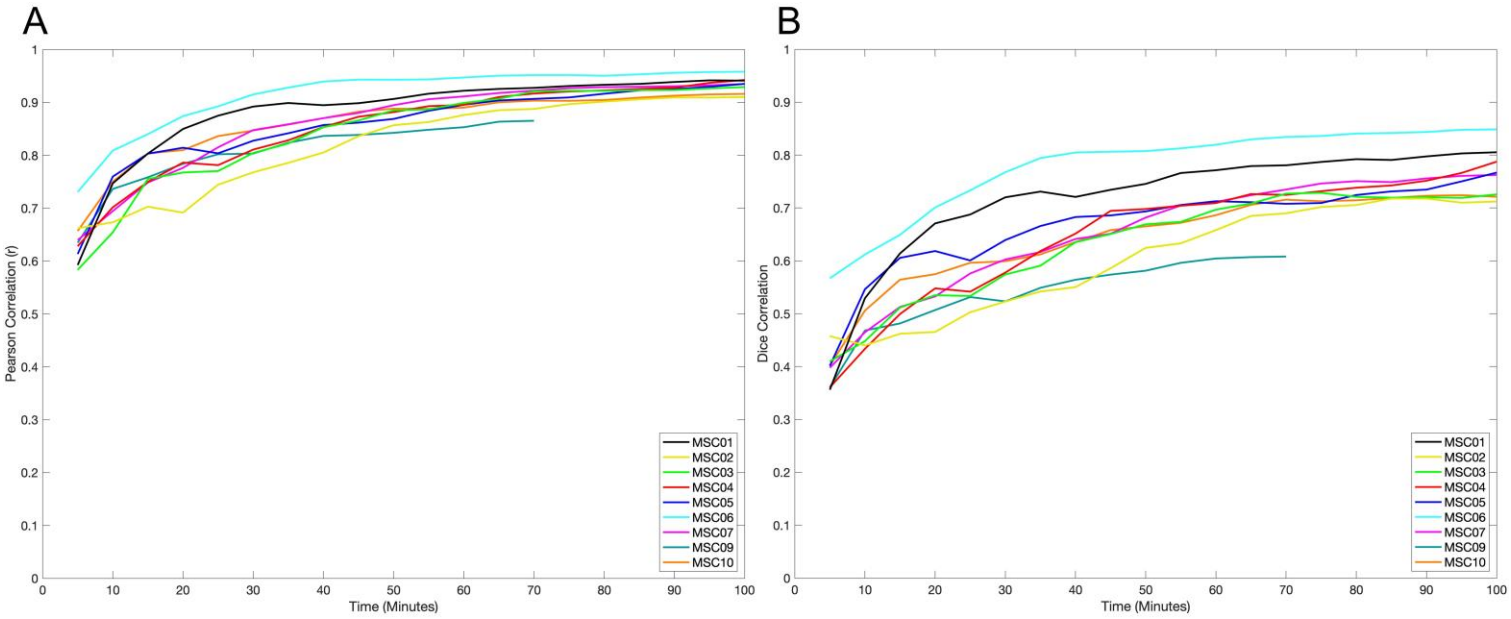

Figure S1. Reliability of network variants in rest data. (A) As for the task data in Figure 2, here the Pearson correlations between split-halves of rest data for each participant are shown for 5 minute increments. (B) The Dice correlations for the binarized maps containing the lowest 5% of correlations with the group average are also shown for each individual for 5 minute increments of rest data. Note that MSC09 (70 minutes) did not have 100 minutes of data in their split-half.

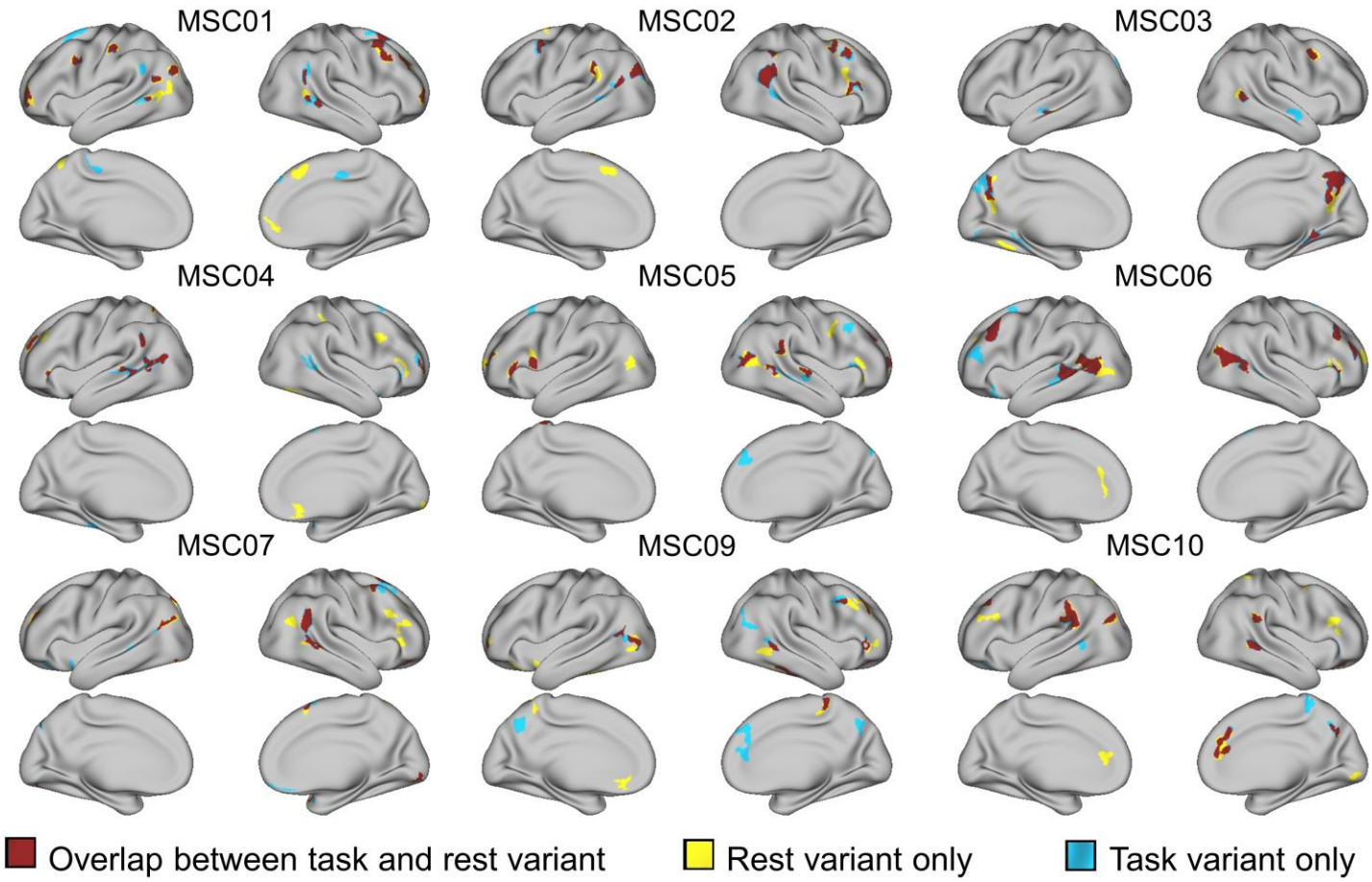

Figure S2. The overlap in variants between task and rest is shown for all included MSC subjects. Areas shaded in yellow represent variants that are only observed during the resting state, areas shaded in blue represent areas only observed in the task state, and areas shaded in red represent areas where variants are present in both task and rest states.

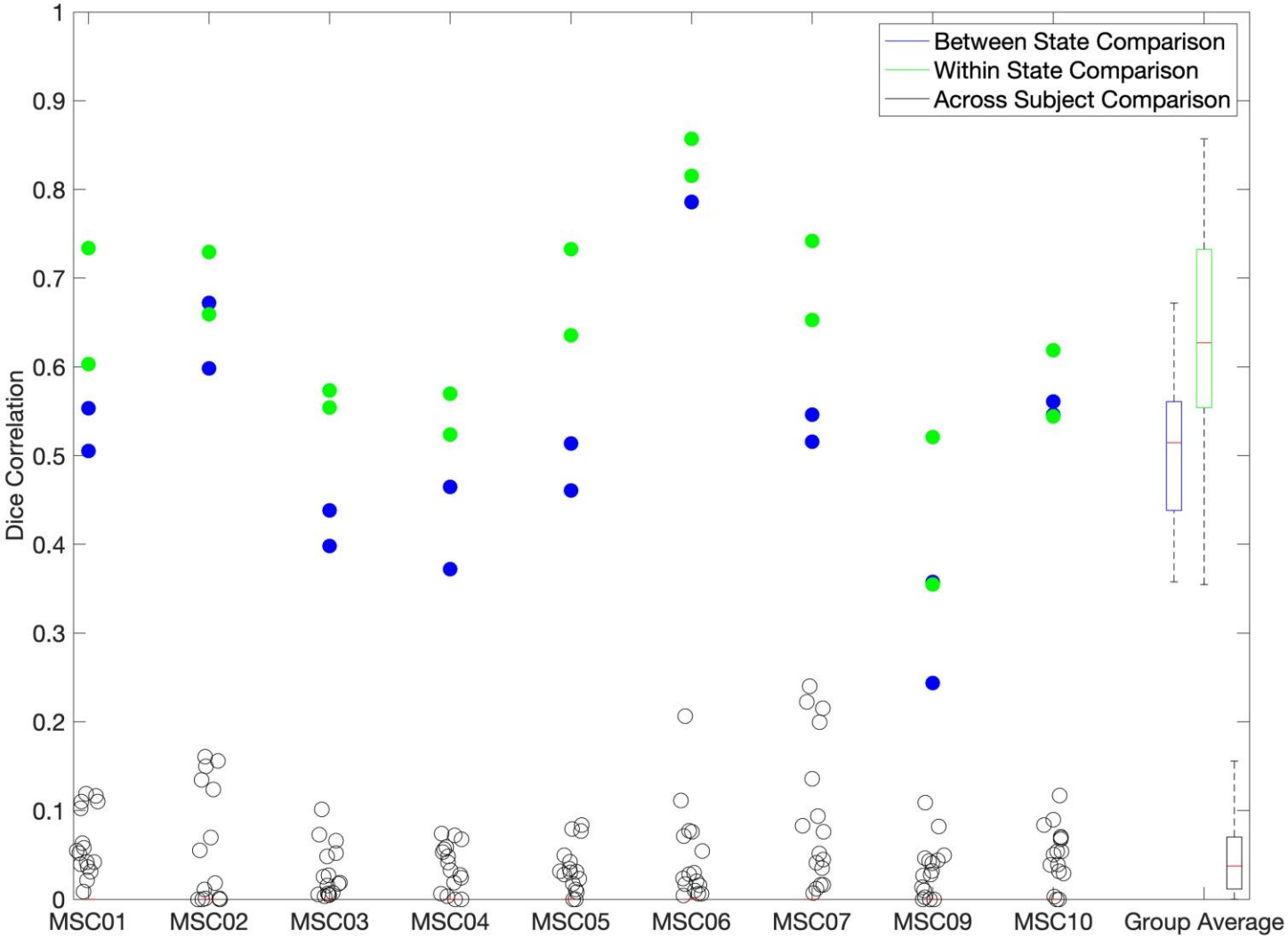

Figure S3. The Dice correlation of the overlap of vertices containing network variants between states and within states is plotted for variants thresholded at the 2.5% lowest values of each individual's spatial correlation map. The value for each individual participant is plotted for all of the comparisons, and the value of every across participant comparison is also plotted. Two dots are present for the between and within state comparisons as both pairs of split-halves were used (see sections 2.7.4 and 2.7.5).The results at the 2.5% threshold showed that variants were more likely to overlap between states within subjects (M = .518, SD = .139) than across subjects (M = .049, SD = .02, $t(8) = 10.56$ $p < .0001$, $d = 3.52$). Variants were also were significantly more likely to overlap within states (M = .635, SD = .115) than between states (M = .518, SD = .139, $t(8) = 6.1$, $p = .0003$, $d = 2.03$; see Figure 4). As with the 5% threshold, the magnitude of the difference between states was smaller than the magnitude of the difference across subjects.

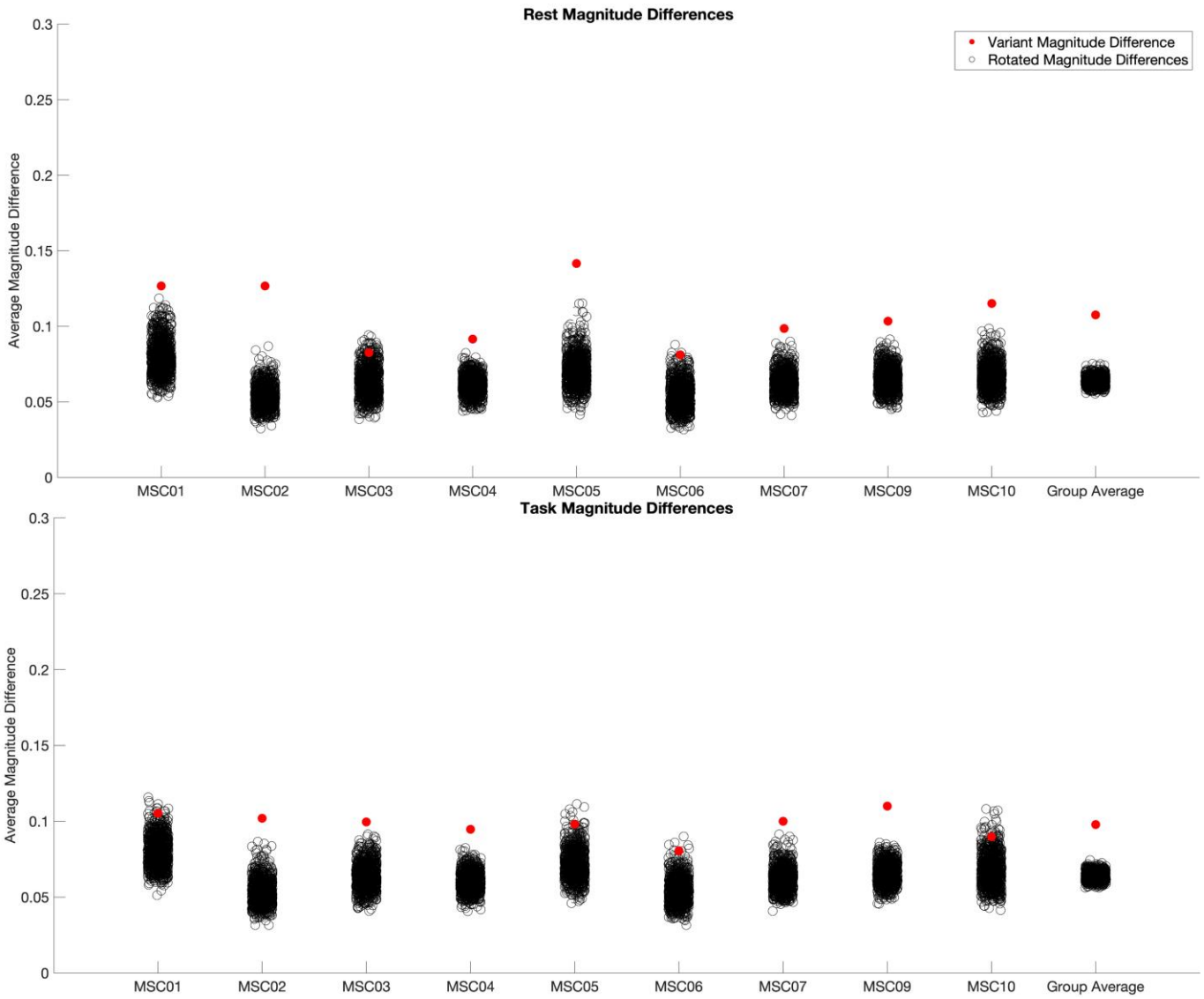

Figure S4. The difference in magnitude of the correlations with the group average networks between variants in rest and task states. In this analysis, the spatial correlations of the vertices identified as network variants during rest were subtracted from the spatial correlations of the same locations during task. Then the mean of the absolute value of this difference was calculated to obtain a mean difference in magnitude of the correlations between states (see Figure 3C). The magnitude difference is shown separately for variants identified in rest (top) and variants identified in task (bottom). To determine whether these values were different from what would be expected by chance (i.e., relative to other areas of the cortex), the network variants for each participant were rotated 1000 times and for each rotation the same operation was performed. Red dots represent the average (absolute) magnitude difference of the observed network variants and the black dots represent the average (absolute) magnitude difference of randomly rotated variants. The results of this analysis showed that network variants showed more variation than would be expected by chance for most participants. As can be seen in Figure 3C, most locations show small deviations (<0.1), but some locations show larger differences, likely driving this effect.

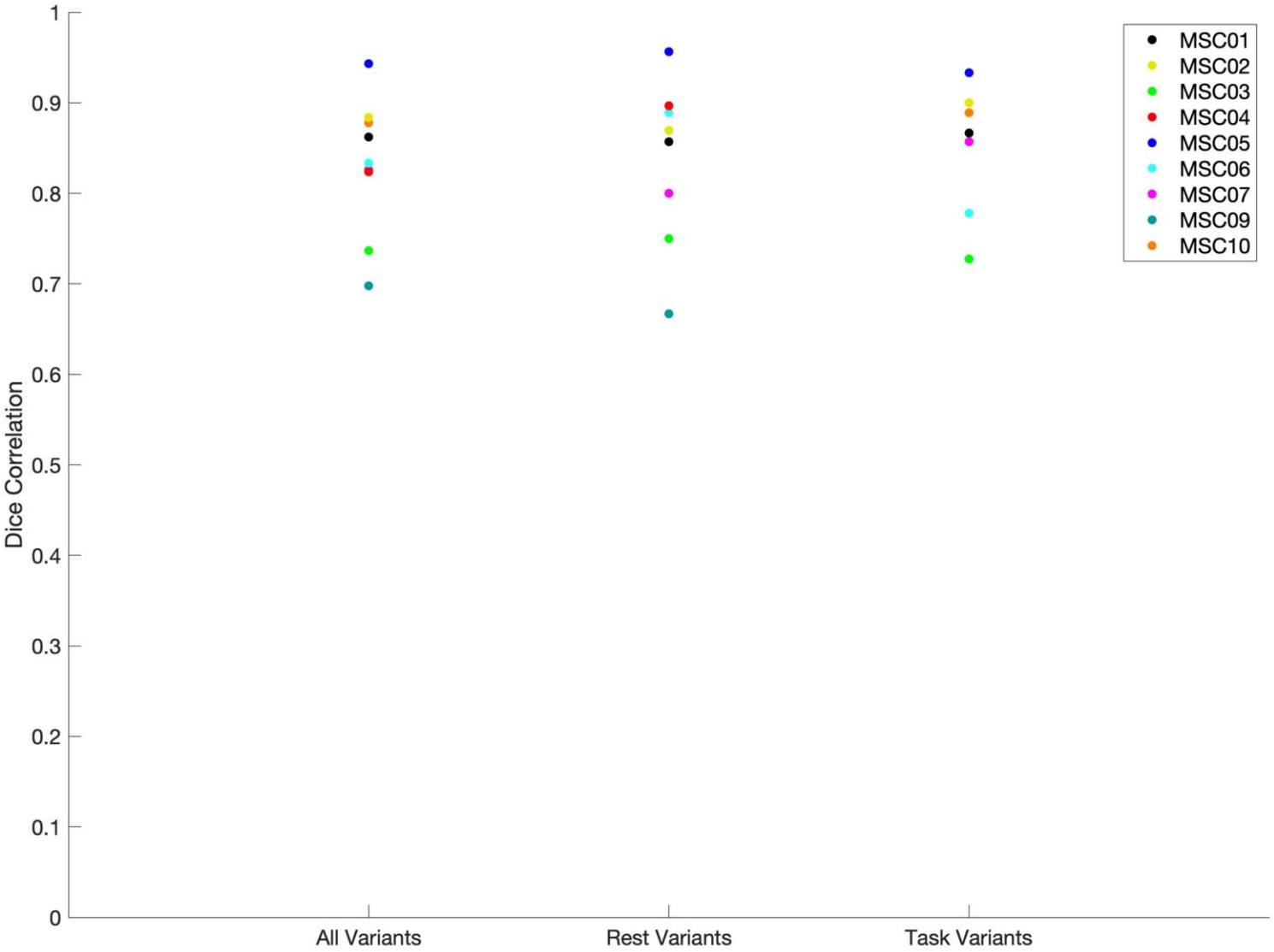

Figure S5. Plot from Figure 5C with each participant labeled by color. The likelihood of assignment to the same network for variants in both states is plotted under "All Variants". The same comparison is also shown separately for variants observed in rest (Rest Variants) and variants observed in task (Task Variants).

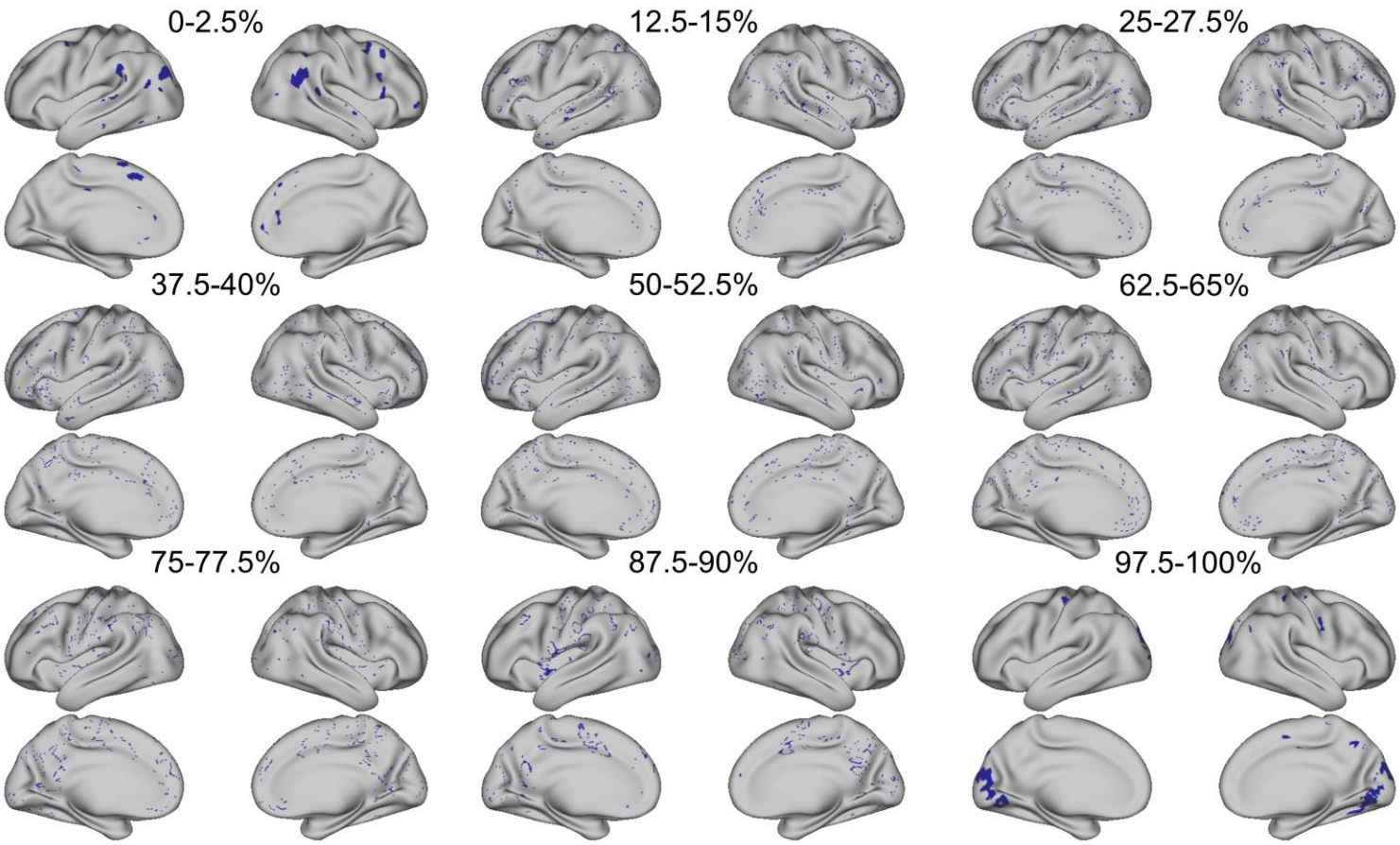

Figure S6. Spatial correlation maps corresponding to the bins plotted in Figure 6 for MSC02. In the bins that are most dissimilar and similar to the group average, the vertices form contiguous parcels. However, for the intermediate bins the vertices are dispersed over the cortex.

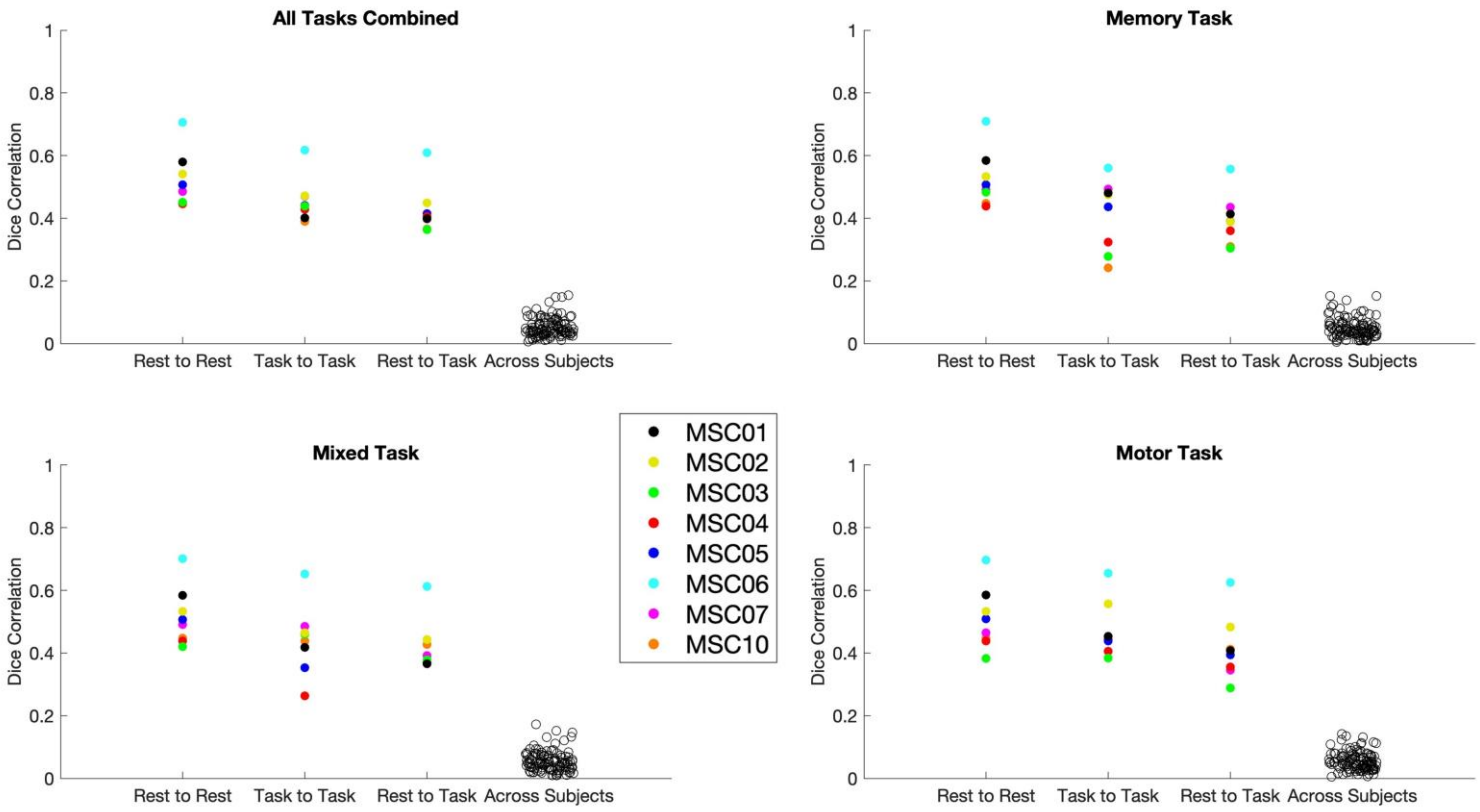

Figure S7. Dice correlations for the stability of all 4 tasks are shown using a 2.5% threshold of the lowest correlations with the group average to define network variants. The pattern shown is similar to that observed in Figure 7. As in section 3.5, a within-subject ANOVA was used to test for significant differences in the stability of variants between tasks using a 2.5% threshold for defining variants. A model with one independent variable (Task) was specified for the rest to task comparisons across all 4 tasks. This model was not significant, $F(3,21) = 1.193$, $p = .336$, $d = .83$, indicating that there were no differences in reliability between states in any of the four tasks. These results are the same as those observed at the 5% threshold, providing no evidence that there are task-specific effects on the stability of network variants between states.