

Supplementary Information

4.11 Supplementary Figures

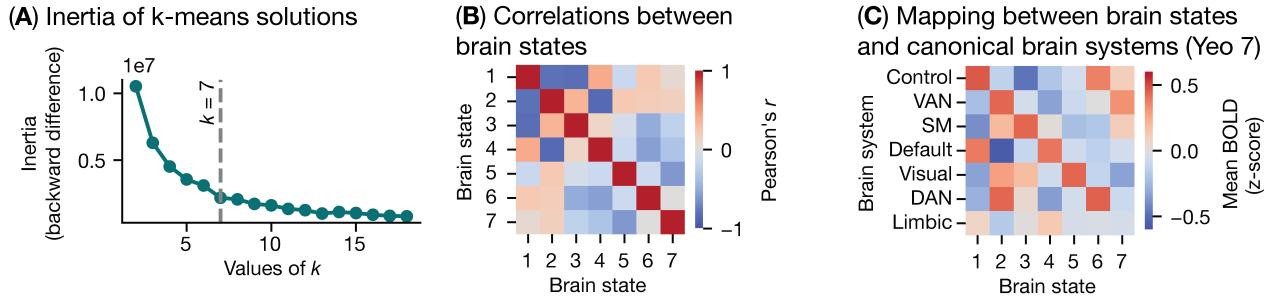


Figure S1. Characteristics of seven empirically-derived brain states using. (A) Inertia of k -means clustering solutions as a function of k . For each k , we calculated the inertia as the sum of squared distances between fMRI time points and their assigned cluster. Then, we examined the difference in inertia between k and $k + 1$ and determined that $k = 7$ was the optimal solution. (B) Pairwise spatial correlations between brain states. These correlations index brain states' similarity. (C) Overlap between brain states and seven canonical brain systems [54]. Z-scored fMRI activity from each brain state was averaged over regions that comprised each canonical system. State 1 and 2 are mirror images of one another, with State 1 consisting of activation of the control and default networks as well as deactivation of the ventral attention network (VAN), somatomotor network (SM), visual system, and the dorsal attention network (DAN). By contrast, state 2 shows strong deactivation of the default network, and activation of the VAN, SM, visual system, and DAN. Thus, states 1 and 2 capture activity broadly cycling between the control/default networks and the rest of the brain, which is a common motif in resting-state brain dynamics. States 3 through 6 map predominantly onto the SM, default network, visual system, and the DAN, respectively. Finally, state 7 jointly captures the control, VAN, and SM. No state specifically captures activation of the limbic system.

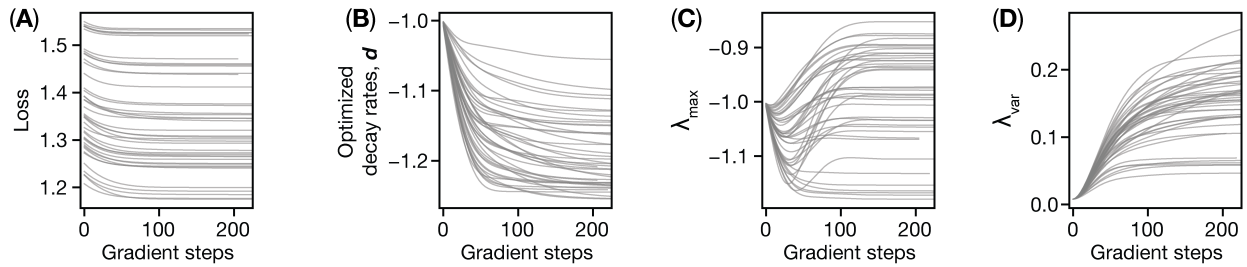


Figure S2. Parameters from the $INT_{\text{optimized}}$ model plotted as a function of training. In each subplot, gray lines represent different state transitions. (A) Optimization loss as a function training. Here, loss is a combination of the reference state cost function ($\mathcal{L}_{\text{ref}}$) and the eigenvalue cost function ($\mathcal{L}_{\text{eig}}$); see Materials and Methods for more details. (B) Optimized decay rates, d , plotted as function of training averaged over brain regions. (C) The maximum eigenvalue of the optimized connectome plotted as a function of training. (D) Variance in the eigenvalues of the optimized connectome plotted as a function of training. In C and D, eigenvalues were calculated by setting the diagonal of A_{norm} to d at each gradient step. The results presented here reveal the following insights. First, that our $INT_{\text{optimized}}$ model stabilized quickly and early during training, with loss for each state transition reaching a plateau after ~ 100 gradient steps in A. Second, that our model increased the overall strength of nodes' self-inhibition throughout training (i.e., more negative optimized decay rates in B). Third, that the dominant mode of system dynamics remained inclined towards self-inhibition (i.e., negative $\lambda_{\max}$ in C) despite modifying nodes' intrinsic dynamics. Finally, that the variability in system dynamics increased throughout training (i.e., greater λ_{var} in D). This last result demonstrates that our $INT_{\text{optimized}}$ model gave rise to more diverse system-wide neural dynamics.

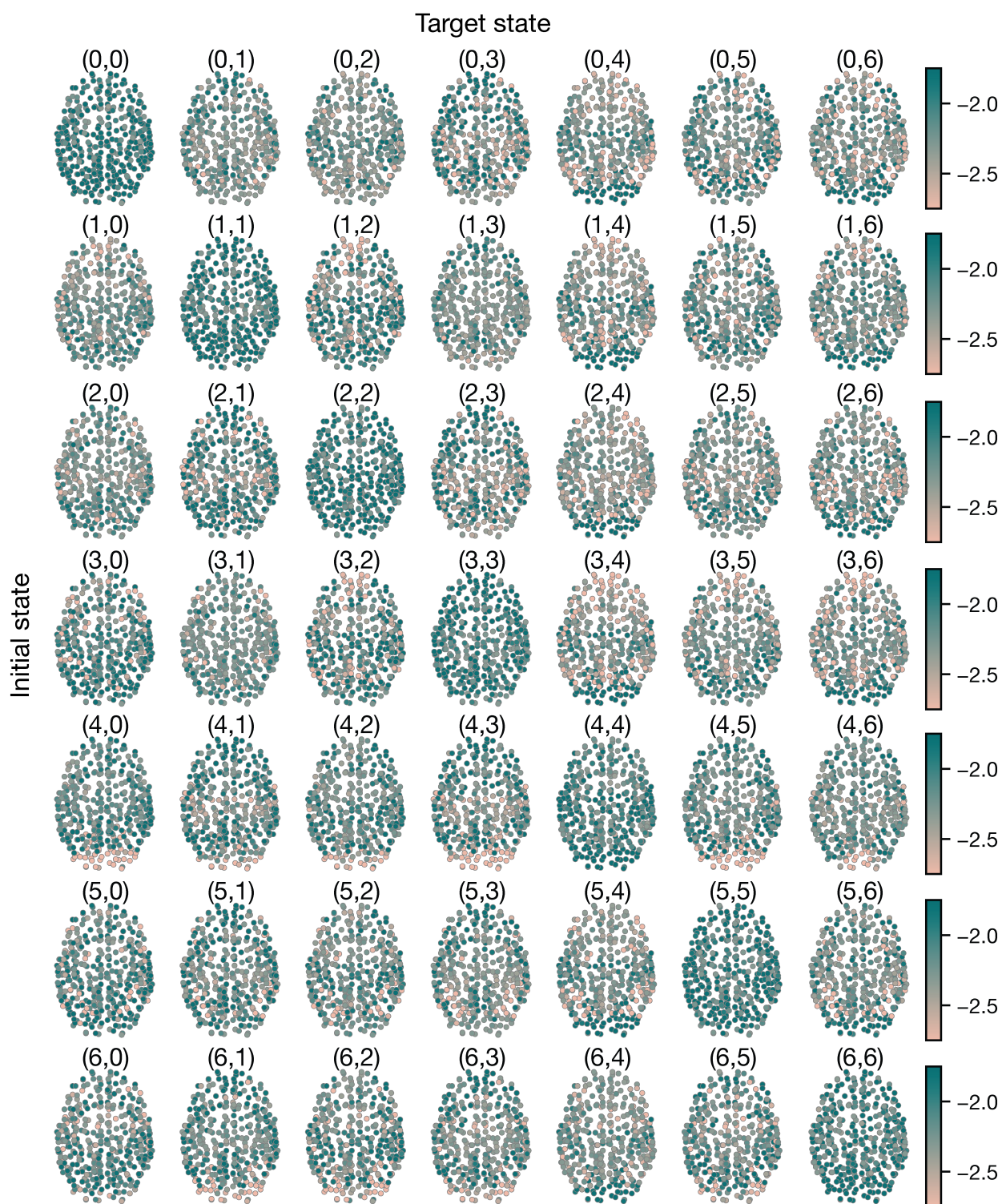


Figure S3. Optimized decay rates from the $INT_{\text{optimized}}$ model for each state transition.

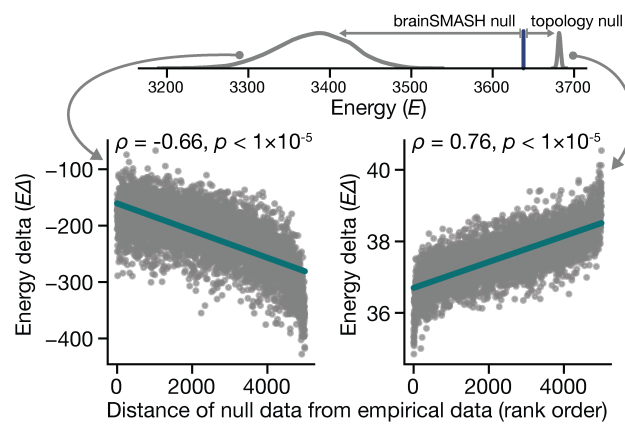
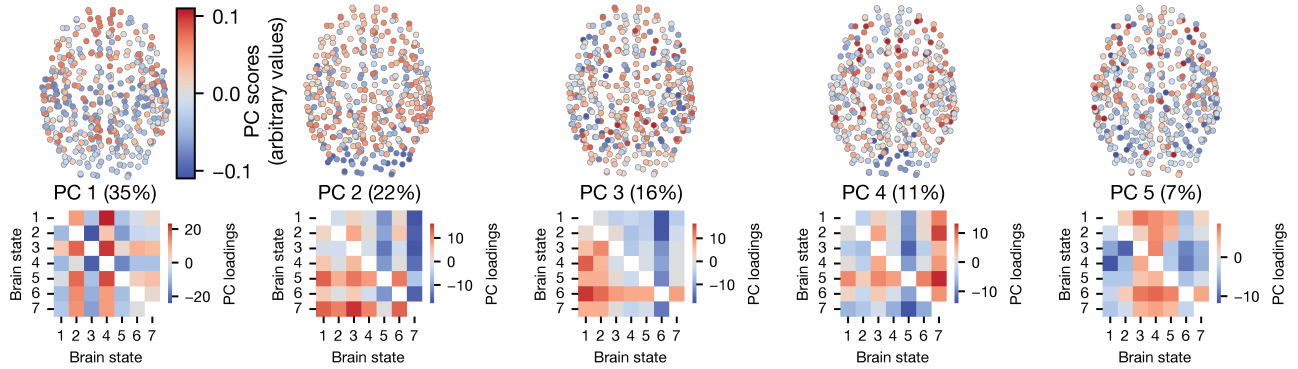
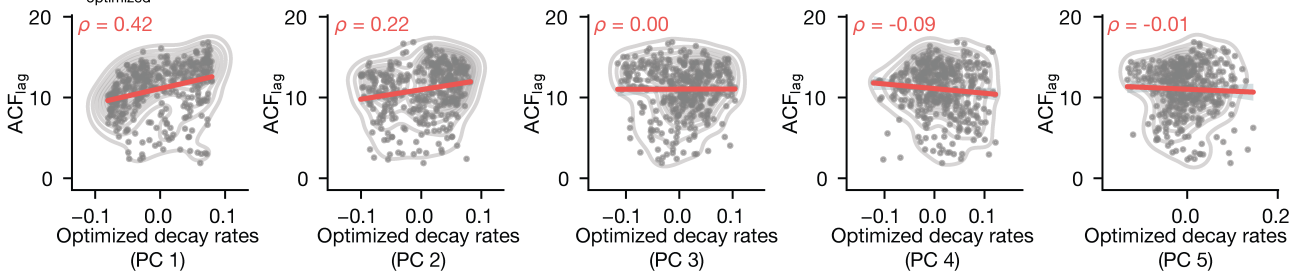


Figure S4. Control energy from the $INT_{\text{optimized}}$ model diverges in opposite directions under twin null models. We compared control energy against two null models, one that permuted the brain states (brainSMASH null) and another that permuted the connectome (topology null). see Main Text for details. Here, for both null models, we plot the difference between observed and null energy (y-axis) separately for each individual permutation, where permutations were ranked according to the distance between the corresponding observed and permuted data (x-axis). For the brainSMASH null (left), this involved computing the l_2 norm of the difference between the target states and the corresponding permuted target states. For the topology null (right), this involved computing the l_2 norm of the difference between the connectome and the permuted connectome. Together, these plots show that as the distance between the observed and permuted data grows, so too does the difference in control energy, just in different directions. In turn, this results demonstrates that the opposing effect of our twin null models on control energy is graded.

(A) Principal component analysis of optimized decay rates



(B) $INT_{\text{optimized}}$ decay rates correlate with empirical neural time scales



(C) Overlap between principal components of optimized decay rates and canonical brain systems

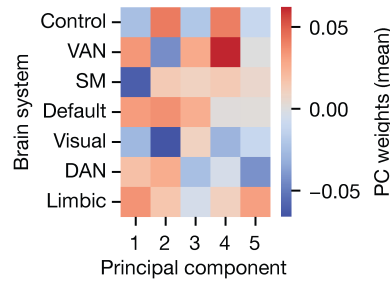


Figure S5. Model-based intrinsic neural time scales (INTs) correlate with empirically-measured INTs. (A) We used principal component analysis (PCA) to characterize variance in optimized decay rates over all state transitions. We extracted 5 PCs that explained 91% of the variance in optimized decay rates. (B) Correlations between PCs of optimized decay rates and empirically-measured INTs, as indexed by ACF_{lag} (see Main Text). (C) Overlap between PCs of optimized decay rates and canonical brain systems. Here, we plot the PC scores for each PC (x-axis) averaged over regions that comprise seven canonical brain systems (y-axis).

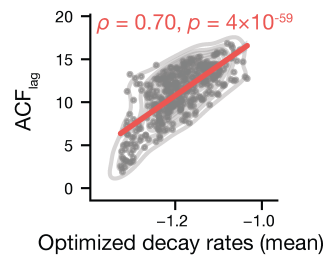


Figure S6. Model-based intrinsic neural time scales (INTs) correlate with mean empirically-measured INTs. Here, we show the correlation between optimized decay rates averaged over all transitions and empirical INTs estimated using ACF_{lag} (see Main Text).

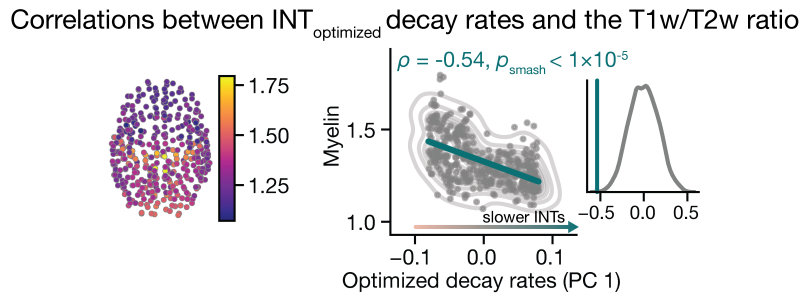


Figure S7. Model-based intrinsic neural time scales correlate with intracortical myelin content. Correlations between PC 1 of optimized decay rates (taken from Fig. 4) and the T1w/T2w ratio. The p -value was assigned using brainSMASH.

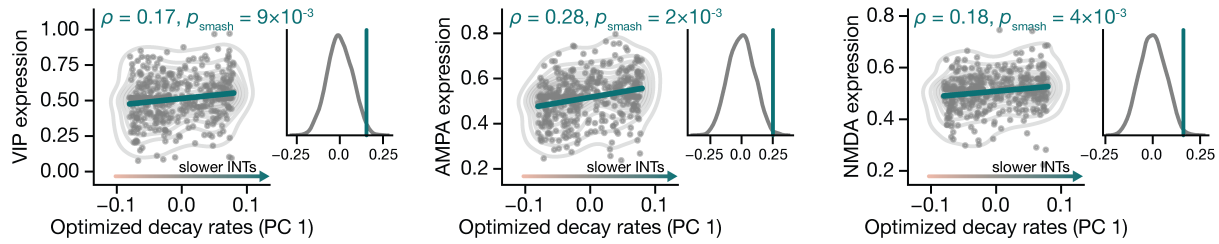


Figure S8. Model-based intrinsic neural time scales correlate with whole-brain maps of gene expression. Correlations between PC 1 of optimized decay rates (taken from Fig. 4) and whole-brain maps of gene expression extracted from the Allen Human Brain Atlas [46]. We correlated PC 1 with gene transcripts for vasoactive intestinal peptide interneurons (VIP, left) as well as groups of excitatory AMPA (middle) and NMDA (right) receptor subunits. Following [68], we averaged over the expression of GRIA1, GRIA2, GRIA3, and GRIA4 to estimate AMPA expression, as well as over the expression of GRIN1, GRIN2A, GRIN2B, and GRIN2C to estimate NMDA expression. We assigned p -values to these correlations using brainSMASH [58].

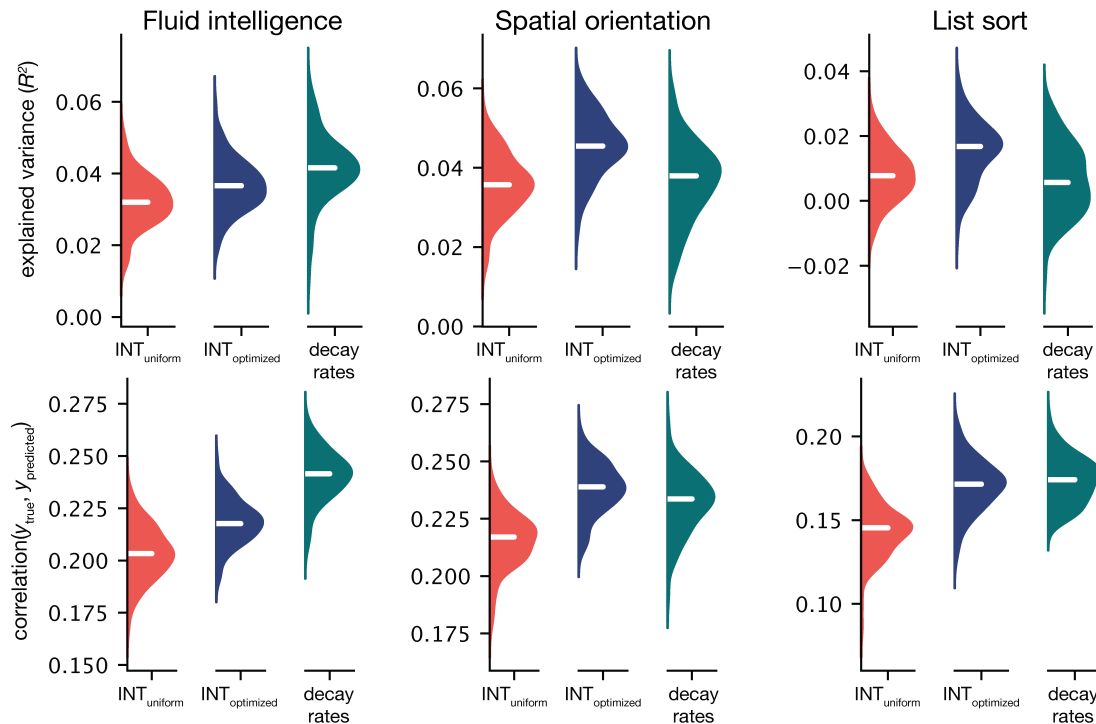


Figure S9. Brain-based predictive modeling analysis including subject-specific optimized decay rates. For each subject, we averaged optimized decay rates across brain regions and used these transition-specific whole-brain decay rates to predict cognition in the HCP-YA dataset. For completeness and visual comparison purposes, here we plot prediction performance for decay rates alongside that observed for control energy reported in Fig. 7 in the Main Text. Note, we also ran a prediction model that used both control energy and optimized decay rates together (results not shown). Combining these features into a single model conferred no significant performance gain.

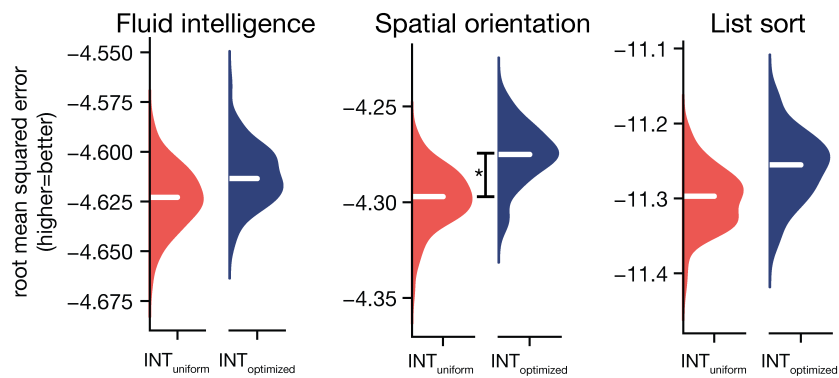


Figure S10. Brain-based predictive modeling analysis scored using root mean squared error (RMSE). Here, RMSE is shown with a negative sign so that higher scores equal better performance.

4.12 Sensitivity analysis

Below, we reproduce several of our key findings and figures in a series of replication analyses.

Different clustering solutions

In the main text, we presented our primary results by modeling state transitions between seven empirical brain states. These states were extracted by applying k -means clustering to rs-fMRI time series data with $k = 7$. Here, we replicate our analyses across $k = 2 - 13$. Figure S11 reproduces Figure S1C as a function of k by illustrating how brain states from each clustering solution aligned with canonical brain systems [54]. Figure S12 reproduces Figure 2C as a function of k , illustrating that control energy was lower for $INT_{\text{optimized}}$ compared to INT_{uniform} across $k = 2 - 13$. Finally, Figure S13 reproduces Figure 4 and Figure 5 as a function of k by showing that the first PC of optimized decay rates correlates consistently with ACF_{lag} , gene expression, and cell-type densities.

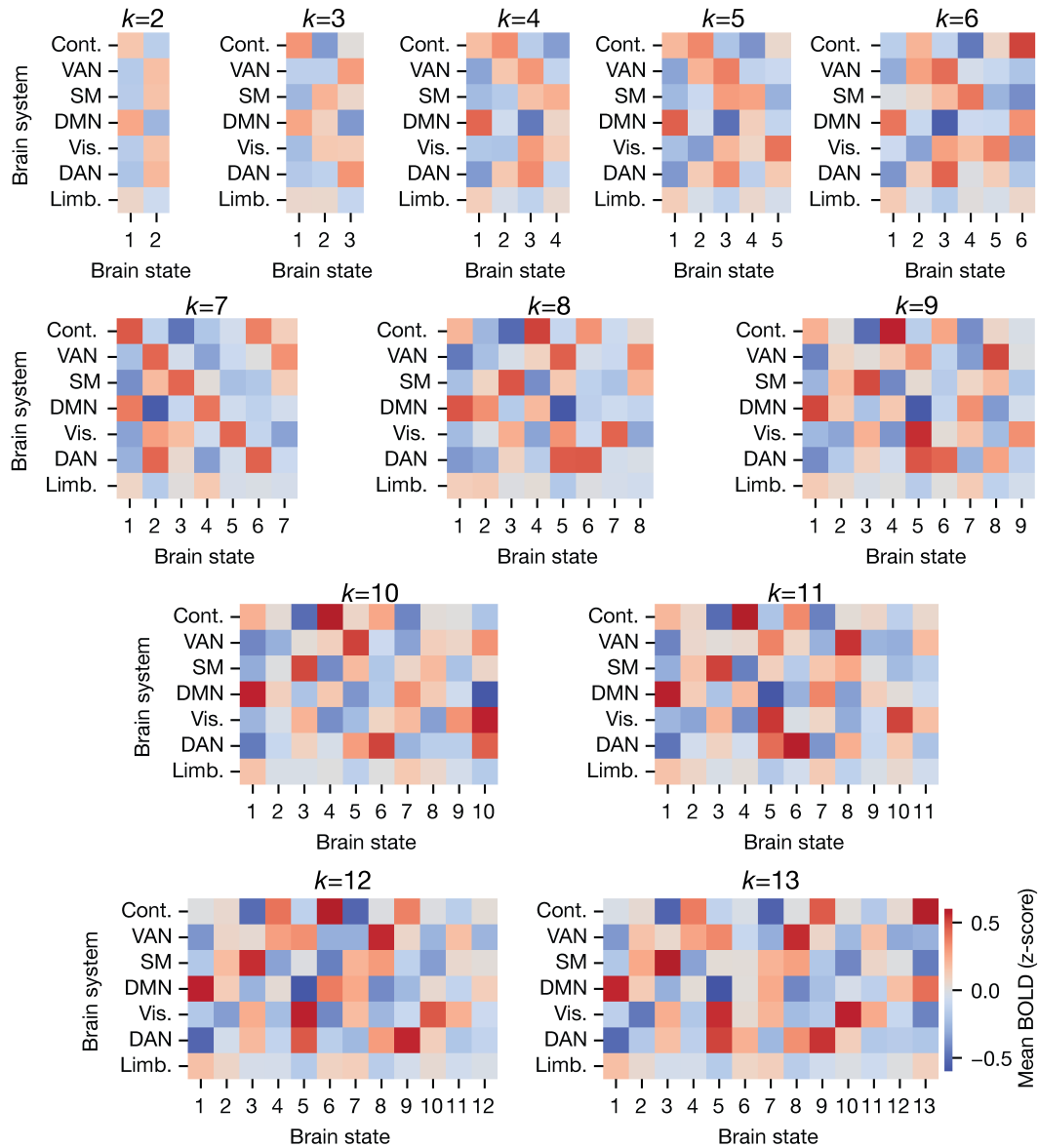


Figure S11. Overlap between seven canonical brain systems (rows) and brain states (columns) as a function of k .

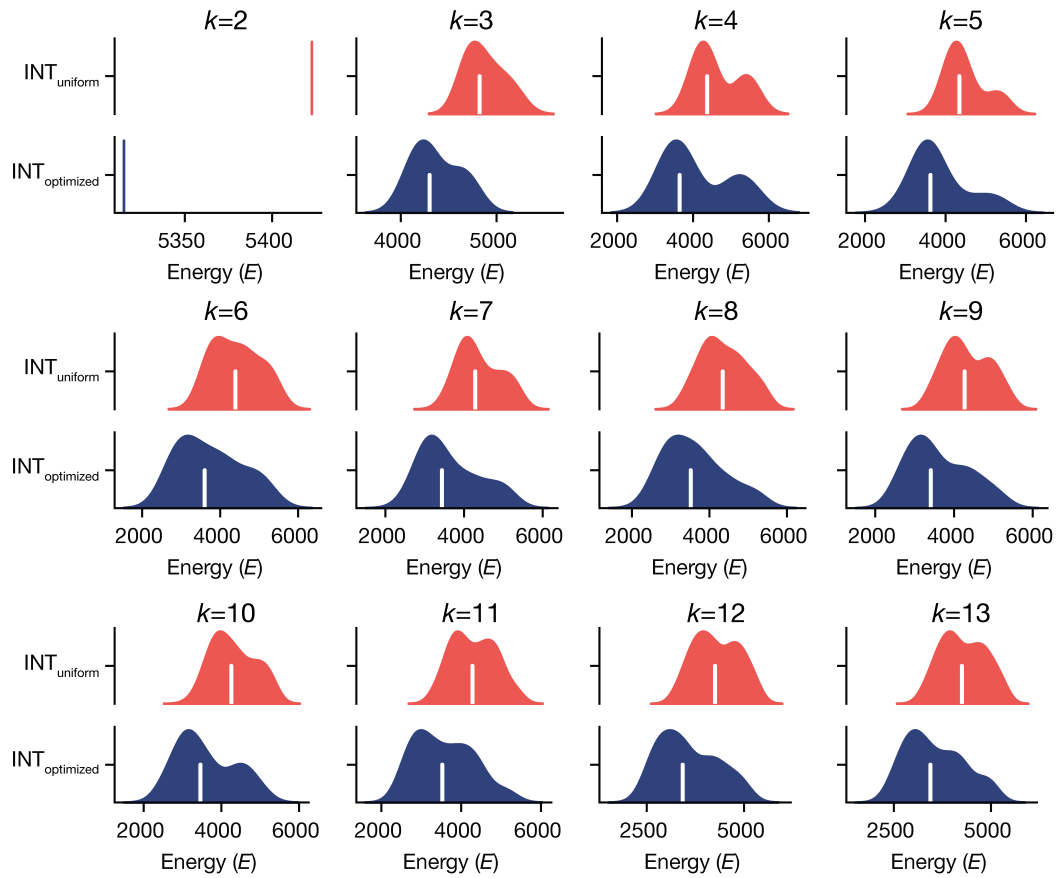


Figure S12. Control energy for the INT_{uniform} and $INT_{\text{optimized}}$ models plotted as a function of k .

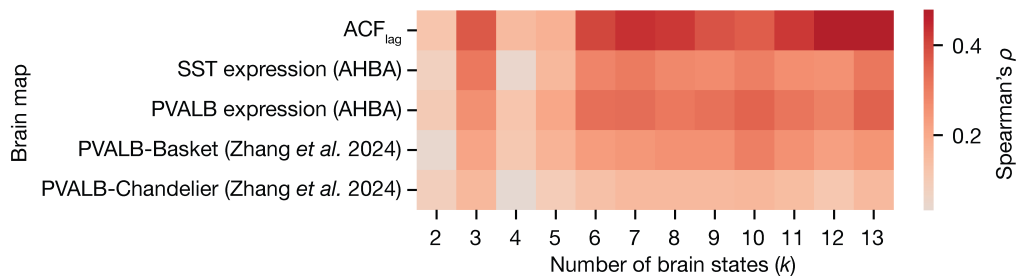


Figure S13. Correlations between optimized decay rates and empirical brain maps as a function of k . For each clustering solution, k , we extracted the first principal component of the optimized decay rates across all state transitions. Then, we correlated that principal component map with the five empirical brains maps discussed in the main text. Note, owing to the fact that the axes of a given principal component analysis are arbitrary, here we plot the absolute Spearman correlation coefficients.

Replication datasets

Below, we replicate our main findings using our replication dataset (see Section 4.1.2).

Using the MICA-MICs dataset [51], we reproduced Fig. 2 and Fig. S2 (Fig. S14). Specifically, we extracted brain states using k -means clustering applied to the MICA-MICs rs-fMRI data and fit the INT_{uniform} and $INT_{\text{optimized}}$ models to the $k = 5$ solution. We found that our results replicated, with the $INT_{\text{optimized}}$ model yielding lower control energy across all state transitions. We also observed that average optimized decay rates from the HCP-YA dataset (taken from Fig. 2B) correlated positively with average optimized decay rates from the MICA-MICs dataset ($r = 0.50, p = 1 \times 10^{-26}$; $\rho = 0.50, p = 4 \times 10^{-26}$). These replication efforts demonstrate that our findings were robust to differences in sample characteristics, data acquisition, data processing, and state definition.

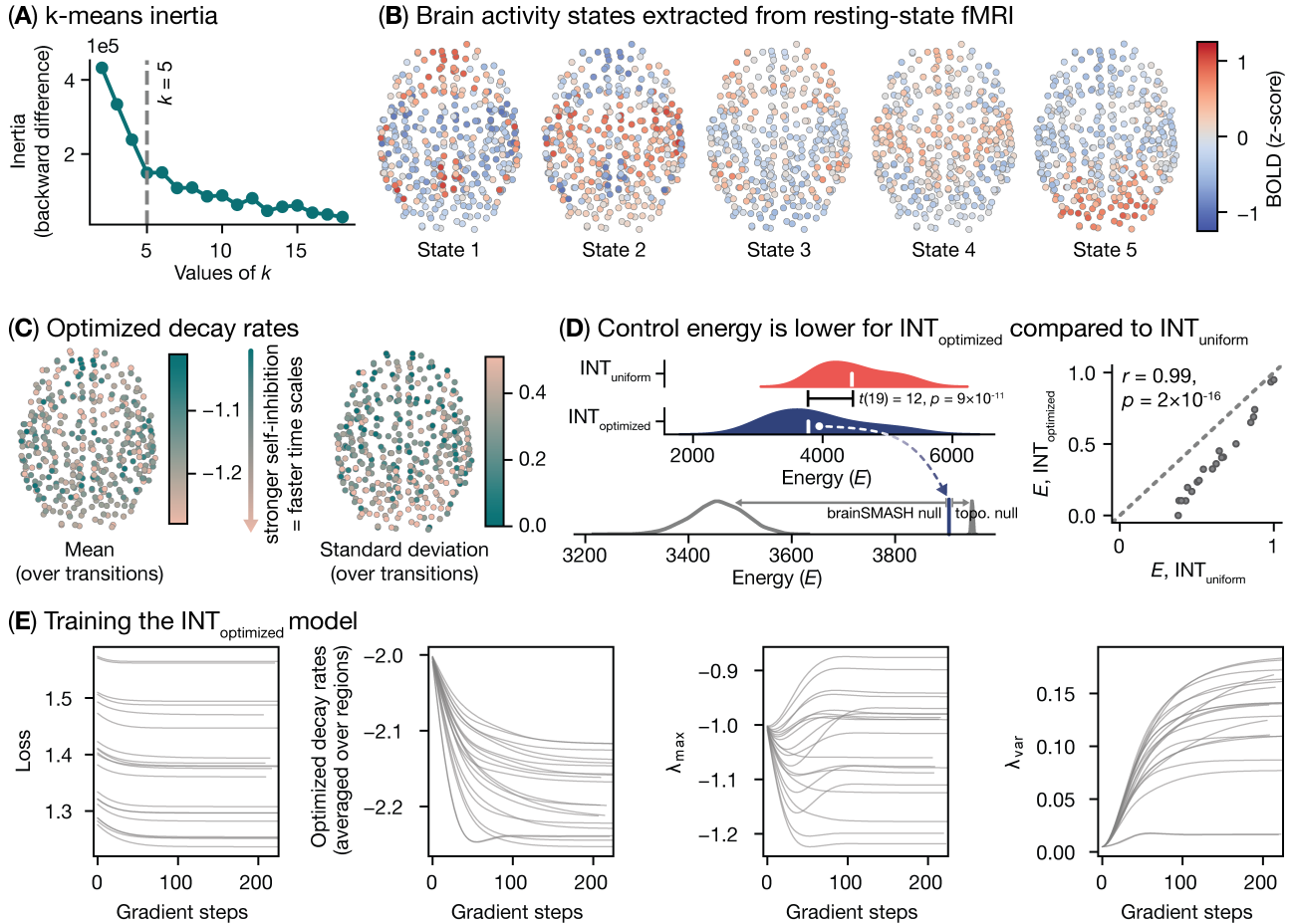


Figure S14. Replication dataset: MICA-MICs. (A) Inertia of k -means clustering solutions as a function of k . (B) Spatial topography of five empirically-derived brain states. (C) Fully-trained regional optimized internal decay rates. (D) Control energy associated with each state transition plotted for the $INT_{\text{optimized}}$ model compared to the standard INT_{uniform} model. (E) Parameters from the $INT_{\text{optimized}}$ model plotted as a function of training.

4.13 Assessing control node important using greedy search

In the main text, we demonstrated the ability of networks with optimized decay rates to better achieve state transitions from partial control sets (see Fig. 3). Here, to further explore the biological significance and correlates of these partial control sets, we implemented a greedy search algorithm that identified an ordering of control nodes from least to greatest impact on control. Specifically, using the adjacency matrix with the optimized decay rates, and beginning with a full control set ($B = I$), for each node we computed the change in control energy, ΔE_i , required to achieve a given state transition when control node i was removed. We then identified the node whose removal caused the smallest increase in control energy and permanently removed that node from the control set. We repeated this node removal process iteratively 350 times, resulting in an ordered list of 350 nodes (out of 400) that ranked nodes from the smallest to largest impact on control. The remaining 50 nodes had the greatest impact on control energy. Note, we stopped the procedure at 350 nodes because the computation of optimal control was no longer numerically stable after this point. We performed this whole procedure for all 42 state transitions separately, resulting in 42 lists of node importance. Finally, we averaged these lists over state transitions, and correlated nodes' mean control importance (Fig. S15A) with their empirical INTs (ACF_{lag}), myelin, and binary degree. We found a strong positive correlation between node importance (iteration removed) and ACF_{lag} (Fig. S15B; $r = 0.69, p = 3 \times 10^{-57}$), as well as weak negative correlations between node importance and myelin (Fig. S15C; $r = -0.14, p = 5 \times 10^{-3}$) and degree (Fig. S15D; $r = -0.12, p = 2 \times 10^{-2}$). These results indicate that nodes that are more important for control exhibit longer empirical INTs. More broadly, these results highlight that nodes' importance for control is coupled to a much greater extent with brain function than with brain structure (i.e., myelin, degree).

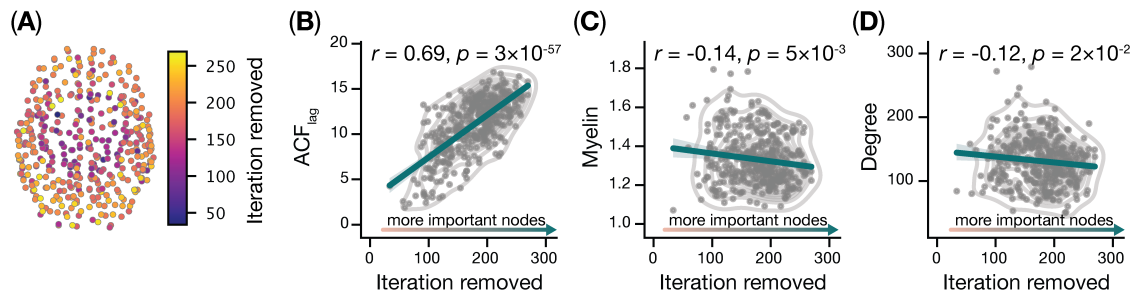


Figure S15. Nodes' importance for control couples tightly to brain function. (A) Node importance, indexed by iteration removed, plotted in brain space. (B) Correlation between node importance and empirical INTs (ACF_{lag}). (C) Correlation between node importance and intracortical myelin. (D) Correlation between node importance and unweighted degree.

4.14 Identifiability and robustness of optimized decay rates to random initial conditions

In the main text, we presented optimized diagonal weights, d , that minimize the distance between the controlled state trajectory and the reference state. Here, we provide evidence for the uniqueness and identifiability of the reported optimized weights. Specifically, we demonstrate that optimizing d from random initial conditions converges to the same value by computing the optimized decay rates under two different conditions. For the first condition, we initialized all decay rates uniformly at $d_{ii} = 1$ (just as we did in the Main Text), and computed the optimized decay rates separately for all state transitions. For the second condition, we initialized all decay rates randomly and uniformly between $d_{ii} \in [0, 1]$, and again computed the optimized decay rates for all state transitions. Finally, we correlated all optimized decay rates from all transitions across the two initialization conditions (Fig. S16, left). Additionally, for completeness, we also computed and correlated optimized decay rates for two separate runs of the random uniform initialization strategy (Fig. S16, right). As can be seen, whether initialized uniformly or randomly, the optimized decay rates converged to nearly the same value with a Pearson correlation coefficient of $\rho \approx 1.0$. Hence, the optimized decay rates exhibit almost no spread based on initialization strategy, providing strong evidence for identifiability.

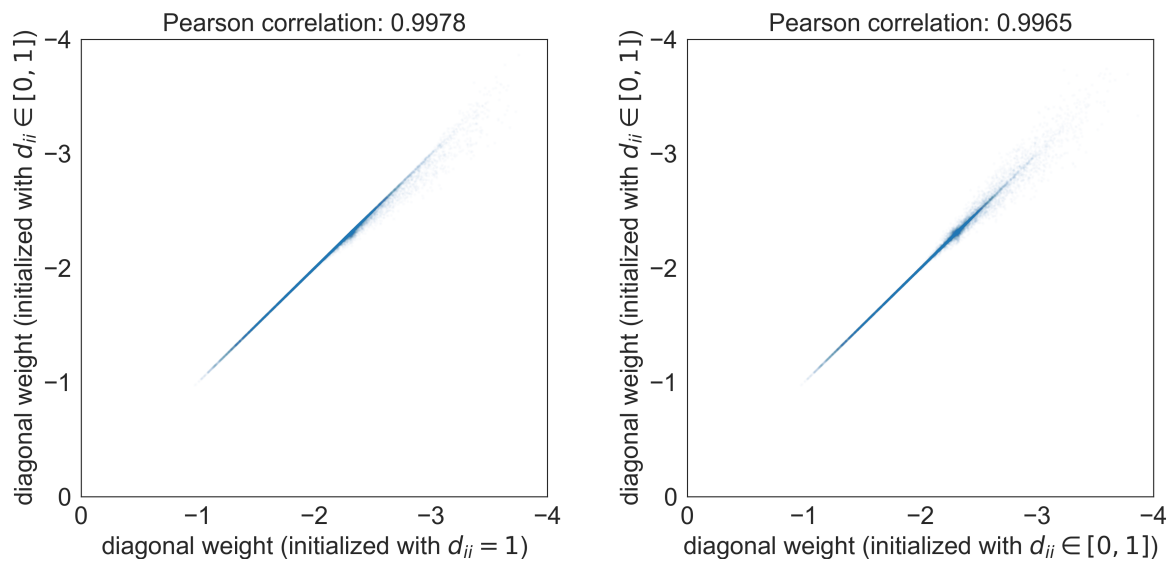


Figure S16. Identifiability of optimized decay rates across random initializations. (left): A scatterplot of the optimized decay rates between a uniform initialization (initial $d_{ii} = 1$) on the x-axis, and a random initialization (initial $d_{ii} \in [0, 1]$) on the y-axis, showing almost identical converged values and strong identifiability. (right): Same scatterplot between two random initializations also showing almost identical converged values and strong identifiability.

4.15 Boilerplate material

4.15.1 fMRIPrep

Some of the results included in this manuscript come from preprocessing performed using *fMRIPrep* 24.1.0 (Esteban et al. [106]; Esteban et al. [107]; RRID:SCR_016216), which is based on *Nipype* 1.8.6 (Gorgolewski et al. [108]; Gorgolewski et al. [109]; RRID:SCR_002502).

Preprocessing of B0 inhomogeneity mappings A total of 1 fieldmaps were found available within the input BIDS structure for this particular subject. A B0-nonuniformity map (or *fieldmap*) was estimated based on two (or more) echo-planar imaging (EPI) references with *topup* (Andersson et al. [110]; FSL None).

Anatomical data preprocessing A total of 2 T1-weighted (T1w) images were found within the input BIDS dataset. Each T1w image was corrected for intensity non-uniformity (INU) with *N4BiasFieldCorrection* [111], distributed with ANTs 2.5.3 [112, RRID:SCR_004757]. The T1w-reference was then skull-stripped with a *Nipype* implementation of the *antsBrainExtraction.sh* workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using *fast* [FSL (version unknown), RRID:SCR_002823, 113]. An anatomical T1w-reference map was computed after registration of 2 <module 'nipype.interfaces.image' from '/opt/conda/envs/fmriprep/lib/python3.11/site-packages/nipype/interfaces/image.py'> images (after INU-correction) using *mri_robust_template* [FreeSurfer 7.3.2, 114]. Brain surfaces were reconstructed using *recon-all* [FreeSurfer 7.3.2, RRID:SCR_001847, 115], and the brain mask estimated previously was refined with a custom variation of the method to reconcile ANTs-derived and FreeSurfer-derived segmentations of the cortical gray-matter of Mindboggle [RRID:SCR_002438, 116]. Volume-based spatial normalization to two standard spaces (MNI152NLin6Asym, MNI152NLin2009cAsym) was performed through nonlinear registration with *antsRegistration* (ANTs 2.5.3), using brain-extracted versions of both T1w reference and the T1w template. The following templates were selected for spatial normalization and accessed with *TemplateFlow* [24.2.0, 117]: *FSL's MNI ICBM 152 non-linear 6th Generation Asymmetric Average Brain Stereotaxic Registration Model* [Evans et al. [118], RRID:SCR_002823; TemplateFlow ID: MNI152NLin6Asym], *ICBM 152 Nonlinear Asymmetrical template version 2009c* [Fonov et al. [119], RRID:SCR_008796; TemplateFlow ID: MNI152NLin2009cAsym].

Functional data preprocessing For each of the 1 BOLD runs found per subject (across all tasks and sessions), the following preprocessing was performed. First, a reference volume was generated, using a custom methodology of *fMRIPrep*, for use in head motion correction. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using *mcfliirt* [FSL, 120]. The estimated *fieldmap* was then aligned with rigid-registration to the target EPI (echo-planar imaging) reference run. The field coefficients were mapped on to the reference EPI using the transform. The BOLD reference was then co-registered to the T1w reference using *bregister* (FreeSurfer) which implements boundary-based registration [121]. Co-registration was configured with six degrees of freedom. Several confounding time-series were calculated based on the *preprocessed BOLD*: framewise displacement (FD), DVARS and three region-wise global signals. FD was computed using two formulations following Power (absolute sum of relative motions, Power et al. [122]) and Jenkinson (relative root mean square displacement between affines, Jenkinson et al. [120]). FD and DVARS are calculated for each functional run, both using their implementations in *Nipype* [following the definitions by 122]. The three global signals are extracted within the CSF, the WM, and the whole-brain masks. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction [*CompCor*, 123]. Principal components are estimated after high-pass filtering the *preprocessed BOLD* time-series (using a discrete cosine filter with 128s cut-off) for the two *CompCor* variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components are then calculated from the top 2% variable voxels within the brain mask. For aCompCor, three probabilistic masks (CSF, WM and combined CSF+WM) are generated in anatomical space. The implementation differs from that of Behzadi et al. in that instead

of eroding the masks by 2 pixels on BOLD space, a mask of pixels that likely contain a volume fraction of GM is subtracted from the aCompCor masks. This mask is obtained by dilating a GM mask extracted from the FreeSurfer's *aseg* segmentation, and it ensures components are not extracted from voxels containing a minimal fraction of GM. Finally, these masks are resampled into BOLD space and binarized by thresholding at 0.99 (as in the original implementation). Components are also calculated separately within the WM and CSF masks. For each CompCor decomposition, the k components with the largest singular values are retained, such that the retained components' time series are sufficient to explain 50 percent of variance across the nuisance mask (CSF, WM, combined, or temporal). The remaining components are dropped from consideration. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadratic terms for each [124]. Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardized DVARS were annotated as motion outliers. Additional nuisance timeseries are calculated by means of principal components analysis of the signal found within a thin band (*crown*) of voxels around the edge of the brain, as proposed by [125]. All resamplings can be performed with a *single interpolation step* by composing all the pertinent transformations (i.e. head-motion transform matrices, susceptibility distortion correction when available, and co-registrations to anatomical and output spaces). Gridded (volumetric) resamplings were performed using *nitransforms*, configured with cubic B-spline interpolation.

Many internal operations of *fMRIPrep* use *Nilearn* 0.10.4 [126, RRID:SCR_001362], mostly within the functional processing workflow. For more details of the pipeline, see [the section corresponding to workflows in fMRIPrep's documentation](#).

4.15.2 Post-processing of fmriprep outputs

The eXtensible Connectivity Pipeline- DCAN (XCP-D) [127–129] was used to post-process the outputs of *fMRIPrep* version 24.1.1 [130, 131, RRID:SCR_016216]. XCP-D was built with *Nipype* version 1.8.6 [108, RRID:SCR_002502].

Segmentations The following atlases were used in the workflow: the Schaefer Supplemented with Subcortical Structures (4S) atlas [132–136] at 3 different resolutions (156, 256, and 456 parcels), the Schaefer1007 atlas, the Schaefer2007 atlas, and the Schaefer4007 atlas. Each atlas was warped to the same space and resolution as the BOLD file.

Anatomical data Native-space T1w images were transformed to MNI152NLin2009cAsym space at 1 mm³ resolution.

Functional data For each of the one BOLD runs found per subject (across all tasks and sessions), the following post-processing was performed.

In total, 36 nuisance regressors were selected from the preprocessing confounds, according to the '36P' strategy. These nuisance regressors included six motion parameters, mean global signal, mean white matter signal, mean cerebrospinal fluid signal with their temporal derivatives, and quadratic expansion of six motion parameters, tissue signals and their temporal derivatives [129, 137].

The BOLD data were despiked with *AFNI*'s *3dDespike*.

Nuisance regressors were regressed from the BOLD data using a denoising method based on *Nilearn*'s approach. The timeseries were band-pass filtered using a(n) second-order Butterworth filter, in order to retain signals between 0.01-0.08 Hz. The same filter was applied to the confounds. The resulting time series were then denoised using linear regression. The denoised BOLD was smoothed using *Nilearn* with a Gaussian kernel (FWHM=6 mm).

The amplitude of low-frequency fluctuation (ALFF) [138] was computed by transforming the mean-centered, standard deviation-normalized, denoised BOLD time series to the frequency domain. The power spectrum was computed

within the 0.01-0.08 Hz frequency band and the mean square root of the power spectrum was calculated at each voxel to yield voxel-wise ALFF measures. The resulting ALFF values were then multiplied by the standard deviation of the denoised BOLD time series to retain the original scaling. The ALFF maps were smoothed with Nilearn using a Gaussian kernel (FWHM=6 mm). Regional homogeneity (ReHo) [139] was computed with neighborhood voxels using AFNI's *3dReHo* [140].

Processed functional timeseries were extracted from the residual BOLD signal with Nilearn's *NiftiLabelsMasker* for the atlases. Corresponding pair-wise functional connectivity between all regions was computed for each atlas, which was operationalized as the Pearson's correlation of each parcel's unsmoothed timeseries. In cases of partial coverage, uncovered voxels (values of all zeros or NaNs) were either ignored (when the parcel had >50.0% coverage) or were set to zero (when the parcel had <50.0% coverage).

Many internal operations of *XCP-D* use *AFNI* [141, 142], *ANTS* [143], *TemplateFlow* version 24.2.2 [144], *matplotlib* version 3.9.2 [145], *Nibabel* version 5.3.0 [146], *Nilearn* version 0.10.4 [147], *numpy* version 2.1.2 [148], *pybids* version 0.17.2 [149], and *scipy* version 1.14.1 [150]. For more details, see the *XCP-D* website (<https://xcp-d.readthedocs.io>).

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