

1 **High-level cognition during story listening is reflected in
2 high-order dynamic correlations in neural activity patterns**

3 Lucy L. W. Owen¹, Thomas H. Chang^{1,2}, and Jeremy R. Manning^{1,†}

¹Department of Psychological and Brain Sciences,
Dartmouth College, Hanover, NH

²Amazon.com, Seattle, WA

†Address correspondence to jeremy.r.manning@dartmouth.edu

4 May 31, 2021

5 **Abstract**

6 Our thoughts arise from coordinated patterns of interactions between brain structures that change
7 with our ongoing experiences. High-order dynamic correlations in neural activity patterns reflect different
8 subgraphs of the brain's functional connectome that display homologous lower-level dynamic correlations.
9 We tested the hypothesis that high-level cognition is reflected in high-order dynamic correlations in brain
10 activity patterns. We developed an approach to estimating high-order dynamic correlations in timeseries
11 data, and we applied the approach to neuroimaging data collected as human participants either listened to
12 a ten-minute story or listened to a temporally scrambled version of the story. We trained across-participant
13 pattern classifiers to decode (in held-out data) when in the session each neural activity snapshot was
14 collected. We found that classifiers trained to decode from high-order dynamic correlations yielded the best
15 performance on data collected as participants listened to the (unscrambled) story. By contrast, classifiers
16 trained to decode data from scrambled versions of the story yielded the best performance when they
17 were trained using first-order dynamic correlations or non-correlational activity patterns. We suggest that
18 as our thoughts become more complex, they are reflected in higher-order patterns of dynamic network
19 interactions throughout the brain.

20 **Introduction**

21 A central goal in cognitive neuroscience is to elucidate the *neural code*: the mapping between (a) mental
22 states or cognitive representations and (b) neural activity patterns. One means of testing models of the
23 neural code is to ask how accurately that model is able to "translate" neural activity patterns into known
24 (or hypothesized) mental states or cognitive representations (e.g., Haxby et al., 2001; Huth et al., 2016, 2012;
25 Kamitani & Tong, 2005; Mitchell et al., 2008; Nishimoto et al., 2011; Norman et al., 2006; Pereira et al., 2018;
26 Tong & Pratte, 2012). Training decoding models on different types of neural features (Fig. 1a) can also help to
27 elucidate which specific aspects of neural activity patterns are informative about cognition and, by extension,
28 which types of neural activity patterns might compose the neural code. For example, prior work has used
29 region of interest analyses to estimate the anatomical locations of specific neural representations (e.g., Etzel
30 et al., 2009), or to compare the relative contributions to the neural code of multivariate activity patterns

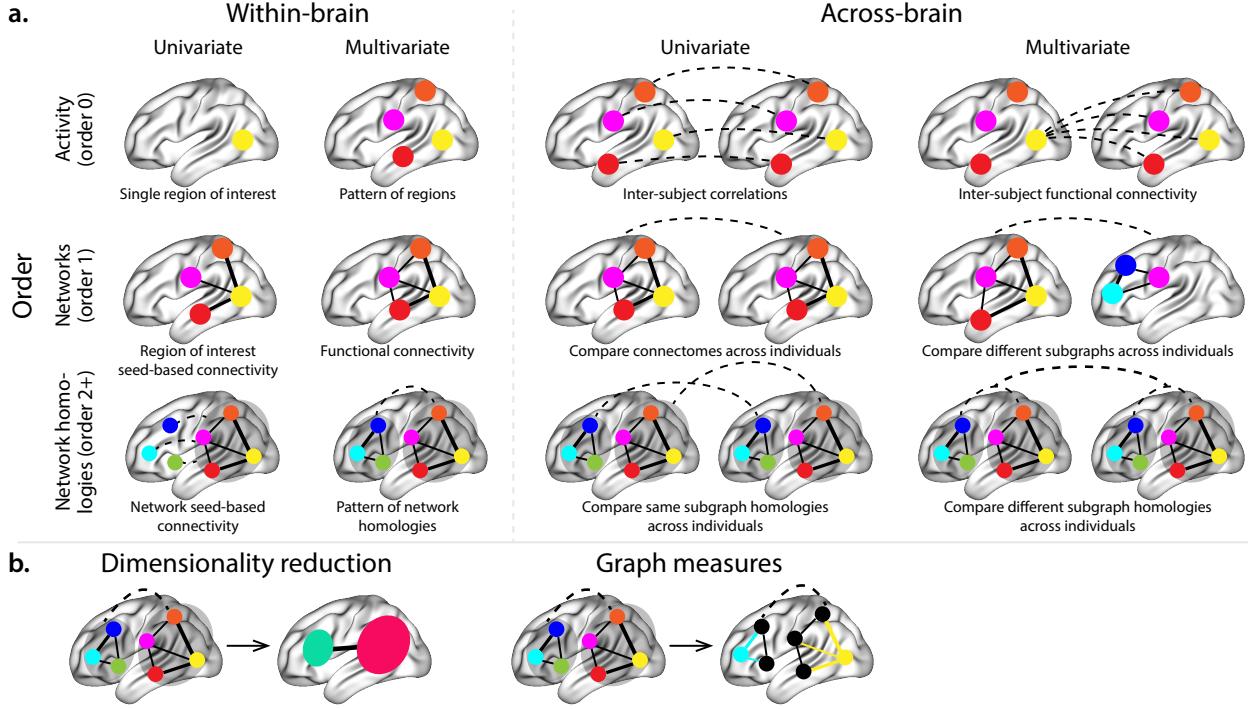


Figure 1: Neural patterns. a. A space of neural features. Within-brain analyses are carried out within a single brain, whereas across-brain analyses compare neural patterns across two or more individuals' brains. Univariate analyses characterize the activities of individual units (e.g., nodes, small networks, hierarchies of networks, etc.), whereas multivariate analyses characterize the patterns of activity across units. Order 0 patterns involve individual nodes; order 1 patterns involve node-node interactions; order 2 (and higher) patterns relate to interactions between homologous networks. Each of these patterns may be static (e.g., averaging over time) or dynamic. **b. Summarizing neural patterns.** To efficiently compute with complex neural patterns, it can be useful to characterize the patterns using summary measures. Dimensionality reduction algorithms project the patterns onto lower-dimensional spaces whose dimensions reflect weighted combinations or non-linear transformations of the dimensions in the original space. Graph measures characterize each unit's participation in its associated network.

31 versus dynamic correlations between neural activity patterns (e.g., Fong et al., 2019; Manning et al., 2018).

32 An emerging theme in this literature is that cognition is mediated by dynamic interactions between brain

33 structures (Bassett et al., 2006; Bressler & Kelso, 2001; Demertzi et al., 2019; Friston, 2000; Grossberg, 1988;

34 Lurie et al., 2018; Mack et al., 2017; McIntosh, 2000; Preti et al., 2017; Solomon et al., 2019; Sporns & Honey,

35 2006; Turk-Browne, 2013; Zou et al., 2019).

36 Studies of the neural code to date have primarily focused on univariate or multivariate neural pat-
 37 terns (for review see Norman et al., 2006), or (more recently) on patterns of dynamic first-order corre-
 38 lations (i.e., interactions between pairs of brain structures; Demertzi et al., 2019; Fong et al., 2019; Lurie et al.,
 39 2018; Manning et al., 2018; Preti et al., 2017; Zou et al., 2019). What might the future of this line of work
 40 hold? For example, is the neural code implemented through higher-order interactions between brain struc-

41 tures (e.g., see Reimann et al., 2017)? Second-order correlations reflect *homologous* patterns of correlation.
42 In other words, if the dynamic patterns of correlations between two regions, *A* and *B*, are similar to those
43 between two other regions, *C* and *D*, this would be reflected in the second-order correlations between (*A*–*B*)
44 and (*C*–*D*). In this way, second-order correlations identify similarities and differences between subgraphs
45 of the brain’s connectome. Analogously, third-order correlations reflect homologies between second-order
46 correlations—i.e., homologous patterns of homologous interactions between brain regions. More generally,
47 higher-order correlations reflect homologies between patterns of lower-order correlations. We can then ask:
48 which “orders” of interaction are most reflective of high-level cognitive processes?

49 One reason one might expect to see homologous networks in a dataset is related to the notion that
50 network dynamics reflect ongoing neural computations or cognitive processing (e.g., Beaty et al., 2016). If
51 the nodes in two brain networks are interacting (within each network) in similar ways then, according to
52 our characterization of network dynamics, we refer to the similarities between those patterns of interaction
53 as higher-order correlations. When higher-order correlations are themselves changing over time, we can
54 also attempt to capture and characterize those high-order dynamics.

55 Another central question pertains to the extent to which the neural code is carried by activity patterns
56 that directly reflect ongoing cognition (e.g., following Haxby et al., 2001; Norman et al., 2006), versus the
57 dynamic properties of the network structure itself, independent of specific activity patterns in any given
58 set of regions (e.g., following Bassett et al., 2006). For example, graph measures such as centrality and
59 degree (Bullmore & Sporns, 2009) may be used to estimate how a given brain structure is “communicating”
60 with other structures, independently of the specific neural representations carried by those structures.
61 If one considers a brain region’s position in the network (e.g., its eigenvector centrality) as a dynamic
62 property, one can compare how the positions of different regions are correlated, and/or how those patterns
63 of correlations change over time. We can also compute higher-order patterns in these correlations to
64 characterize homologous subgraphs in the connectome that display similar changes in their constituent
65 brain structures’ interactions with the rest of the brain.

66 To gain insights into the above aspects of the neural code, we developed a computational framework
67 for estimating dynamic high-order correlations in timeseries data. This framework provides an important
68 advance, in that it enables us to examine patterns of higher-order correlations that are computationally
69 intractable to estimate via conventional methods. Given a multivariate timeseries, our framework pro-
70 vides timepoint-by-timepoint estimates of the first-order correlations, second-order correlations, and so
71 on. Our approach combines a kernel-based method for computing dynamic correlations in timeseries
72 data with a dimensionality reduction step (Fig. 1b) that projects the resulting dynamic correlations into
73 a low-dimensional space. We explored two dimensionality reduction approaches: principle components

74 analysis (PCA; Pearson, 1901), which preserves an approximately invertible transformation back to the
75 original data (e.g., this follows related approaches taken by Gonzalez-Castillo et al., 2019; McIntosh & Jirsa,
76 2019; Toker & Sommer, 2019); and a second non-invertible algorithm for computing dynamic patterns in
77 eigenvector centrality (Landau, 1895). This latter approach characterizes correlations between each feature
78 dimension's relative *position* in the network (at each moment in time) in favor of the specific activity histories
79 of different features (also see Betzel et al., 2019; Reimann et al., 2017; Sizemore et al., 2018).

80 We validated our approach using synthetic data where the underlying correlations were known. We
81 then applied our framework to a neuroimaging dataset collected as participants listened to either an audio
82 recording of a ten-minute story, listened to a temporally scrambled version of the story, or underwent a
83 resting state scan (Simony et al., 2016). Temporal scrambling has been used in a growing number of studies,
84 largely by Uri Hasson's group, to identify brain regions that are sensitive to higher-order and longer-
85 timescale information (e.g., cross-sensory integration, rich narrative meaning, complex situations, etc.)
86 versus regions that are primarily sensitive to low-order (e.g., sensory) information. For example, Hasson et
87 al. (2008) argues that when brain areas are sensitive to fine versus coarse temporal scrambling, this indicates
88 that they are "higher order" in the sense that they process contextual information pertaining to further-
89 away timepoints. By contrast, low-level regions, such as primary sensory cortices, do not meaningfully
90 change their responses (after correcting for presentation order) even when the stimulus is scrambled at fine
91 timescales.

92 We used a subset of the story listening and rest data to train across-participant classifiers to decode
93 listening times (of groups of participants) using a blend of neural features (comprising neural activity
94 patterns, as well as different orders of dynamic correlations between those patterns that were inferred
95 using our computational framework). We found that both the PCA-based and eigenvector centrality-based
96 approaches yielded neural patterns that could be used to decode accurately (i.e., well above chance). Both
97 approaches also yielded the best decoding accuracy for data collected during (intact) story listening when
98 high-order (PCA: second-order; eigenvector centrality: fourth-order) dynamic correlation patterns were
99 included as features. When we trained classifiers on the scrambled stories or resting state data, only
100 (relatively) lower-order dynamic patterns were informative to the decoders. Taken together, our results
101 indicate that high-level cognition is supported by high-order dynamic patterns of communication between
102 brain structures.

103 **Results**

104 We sought to understand whether high-level cognition is reflected in dynamic patterns of high-order
105 correlations. To that end, we developed a computational framework for estimating the dynamics of stimulus-
106 driven high-order correlations in multivariate timeseries data (see *Dynamic inter-subject functional connectivity*
107 (*DISFC*) and *Dynamic higher-order correlations*). We evaluated the efficacy of this framework at recovering
108 known patterns in several synthetic datasets (see *Synthetic data: simulating dynamic first-order correlations* and
109 *Synthetic data: simulating dynamic higher-order correlations*). We then applied the framework to a public fMRI
110 dataset collected as participants listened to an auditorily presented story, listened to a temporally scrambled
111 version of the story, or underwent a resting state scan (see *Functional neuroimaging data collected during story*
112 *listening*). We used the relative decoding accuracies of classifiers trained on different sets of neural features
113 to estimate which types of features reflected ongoing cognitive processing.

114 **Recovering known dynamic correlations from synthetic data**

115 **Recovering dynamic first-order correlations**

116 We generated synthetic datasets that differed in how the underlying first-order correlations changed over
117 time. For each dataset, we applied Equation 4 with a variety of kernel shapes and widths. We assessed how
118 well the true underlying correlations at each timepoint matched the recovered correlations (Fig. 2). For every
119 kernel and dataset we tested, our approach recovered the correlation dynamics we embedded into the data.
120 However, the quality of these recoveries varied across different synthetic datasets in a kernel-dependent
121 way.

122 In general, wide monotonic kernel shapes (Laplace, Gaussian), and wider kernels (within a shape),
123 performed best when the correlations varied gradually from moment-to-moment (Figs. 2a, c, and d). In the
124 extreme, as the rate of change in correlations approaches 0 (Fig. 2a), an infinitely wide kernel would exactly
125 recover the Pearson's correlation (e.g., compare Eqns. 1 and 4).

126 When the correlation dynamics were unstructured in time (Fig. 2b), a Dirac δ kernel (infinitely narrow)
127 performed best. This is because, when every timepoint's correlations are independent of the correlations at
128 every other timepoint, averaging data over time dilutes the available signal. Following a similar pattern,
129 holding kernel shape fixed, narrower kernel parameters better recovered randomly varying correlations.

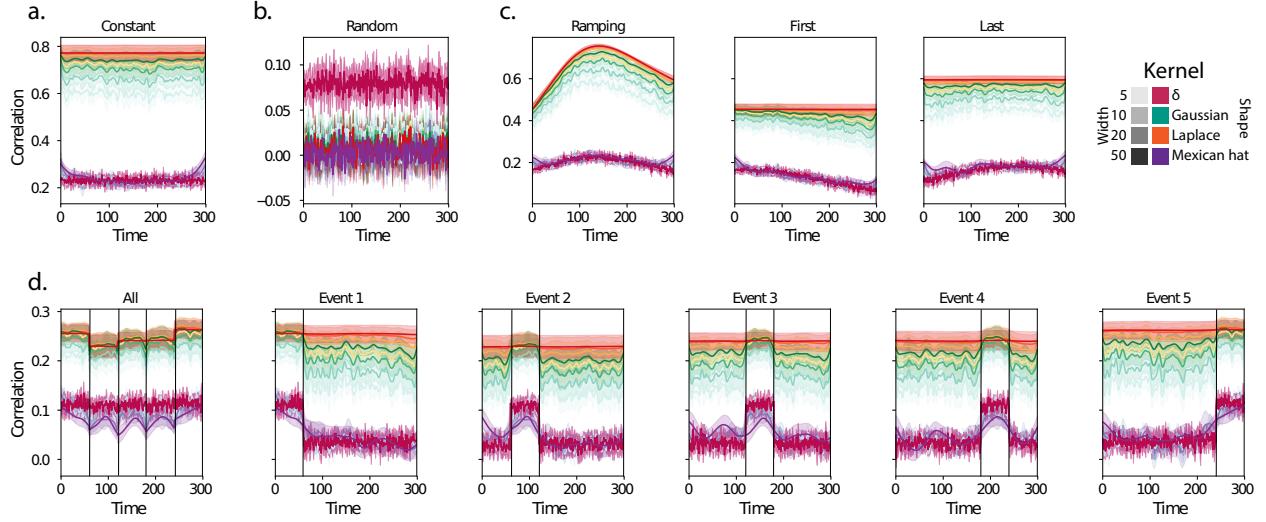


Figure 2: Recovering known dynamic first-order correlations from synthetic data. Each panel displays the average correlations between the vectorized upper triangles of the recovered correlation matrix at each timepoint and either the true underlying correlation at each timepoint or a reference correlation matrix. (The averages are taken across 10 different randomly generated synthetic datasets of the given category.) Error ribbons denote 95% confidence intervals (taken across datasets). Different colors denote different kernel shapes, and the shading within each color family denotes the kernel width parameter. For a complete description of each synthetic dataset, see *Synthetic data: simulating dynamic first-order correlations*.

a. Constant correlations. These datasets have a stable (unchanging) underlying correlation matrix. **b. Random correlations.** These datasets are generated using a new independently drawn correlation matrix at each new timepoint. **c. Ramping correlations.** These datasets are generated by smoothly varying the underlying correlations between the randomly drawn correlation matrices at the first and last timepoints. The left panel displays the correlations between the recovered dynamic correlations and the underlying ground truth correlations. The middle panel compares the recovered correlations with the *first* timepoint’s correlation matrix. The right panel compares the recovered correlations with the *last* timepoint’s correlation matrix. **d. Event-based correlations.** These datasets are each generated using five randomly drawn correlation matrices that each remain stable for a fifth of the total timecourse. The left panel displays the correlations between the recovered dynamic correlations and the underlying ground truth correlations. The right panels compare the recovered correlations with the correlation matrices unique to each event. The vertical lines denote event boundaries.

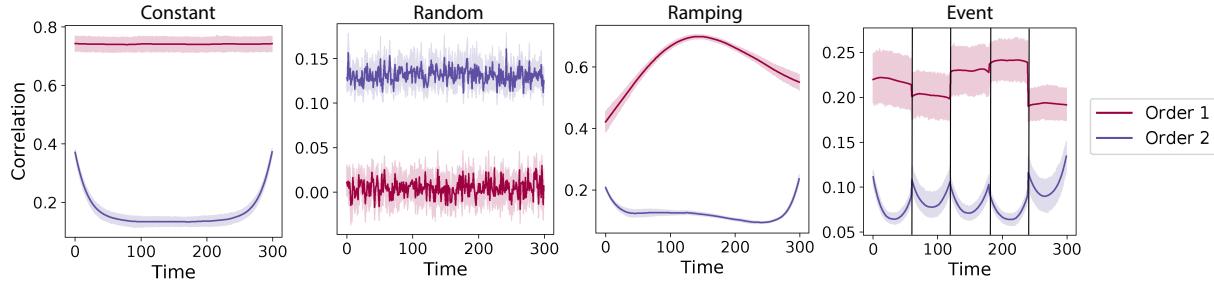


Figure 3: **Recovery of simulated first-order and second-order dynamic correlations.** Each panel displays the average correlations between the vectorized upper triangles of the recovered first-order and second-order correlation matrices and the true (simulated) first-order and second order correlation matrices at each timepoint and for each synthetic dataset. (The averages are taken across 10 different randomly generated synthetic datasets of the given category.) Error ribbons denote 95% confidence intervals (taken across datasets). For a complete description of each synthetic dataset, see *Synthetic data: simulating dynamic higher-order correlations*. All estimates represented in this figure were computed using a Laplace kernel (width = 20). **Constant.** These datasets have stable (unchanging) underlying second-order correlation matrices. **Random.** These datasets are generated using a new independently drawn second-order correlation matrix at each timepoint. **Ramping.** These datasets are generated by smoothly varying the underlying second-order correlations between the randomly drawn correlation matrices at the first and last timepoints. **Event.** These datasets are each generated using five randomly drawn second-order correlation matrices that each remain stable for a fifth of the total timecourse. The vertical lines denote event boundaries.

130 Recovering dynamic higher-order correlations

131 Following our approach to evaluating our ability to recover known dynamic first-order correlations from
 132 synthetic data, we generated an analogous second set of synthetic datasets that we designed to exhibit
 133 known dynamic first-order *and* second-order correlations (see *Synthetic data: simulating dynamic higher-*
 134 *order correlations*). We generated a total of 40 datasets that varied in how the first-order and second-order
 135 correlations changed over time. We then repeatedly applied Equation 4 using the overall best-performing
 136 kernel from our first-order tests (a Laplace kernel with a width of 20; Fig. 2) to assess how closely the
 137 recovered dynamic correlations matched the dynamic correlations we had embedded into the datasets.

138 Overall, we found that we could reliably recover both first-order and second-order correlations from
 139 the synthetic data (Fig. 3). When the correlations were stable for longer intervals, or changed gradually
 140 (constant, ramping, and event datasets), recovery performance was relatively high, and we were better able
 141 to recover dynamic first-order correlations than second-order correlations. This is because errors in our
 142 *estimation* procedure at lower orders necessarily propagate to higher orders (since lower-order correlations
 143 are used to estimate higher-order correlations). Conversely, when the correlations were particularly *unstable*
 144 (random datasets), we better recovered second-order correlations. This is because noise in our *data generation*
 145 procedure propagates from higher orders to lower orders (see *Synthetic data: simulating dynamic high-order*
 146 *correlations*).

147 We also examined the impact of the data duration (Fig. S3) and complexity (number of zero-order
148 features; Fig. S4) on our ability to accurately recover ground truth first-order and second-order dynamic
149 correlations. In general, we found that our approach better recovers ground truth dynamic correlations
150 from longer duration timeseries data.

151 We also found that our approach tends to best recover data generated using fewer zero-order features
152 (i.e., lower complexity), although this tendency was not strictly monotonic. Further, because our data
153 generation procedure requires $O(K^4)$ memory to generate a second-order timeseries with K zero-order
154 features, we were not able to fully explore how the number of zero-order features affects recovery accuracy
155 as the number of features gets larger (e.g., as it approaches the number of features present in the fMRI
156 data we examine below). Although we were not able to formally test this to our satisfaction, we expect
157 that accurately estimating dynamic high-order correlations would require data with many more zero-order
158 features than we were able to simulate. Our reasoning is that high-order correlations necessarily involve
159 larger numbers of lower-order features, so achieving adequate “resolution” high-order timeseries might
160 require many low-order features.

161 Taken together, our explorations using synthetic data indicated that we are able to partially, but not
162 perfectly, recover ground truth dynamic first-order and second-order correlations. This suggests that our
163 modeling approach provides a meaningful (if noisy) estimate of high-order correlations. We next turned
164 to analyses of human fMRI data to examine whether the recovered dynamics might reflect the dynamics of
165 human cognition during a naturalistic story-listening task.

166 Cognitively relevant dynamic high-order correlations in fMRI data

167 We used across-participant temporal decoders to identify cognitively relevant neural patterns in fMRI data
168 (see *Forward inference and decoding accuracy*). The dataset we examined (collected by Simony et al., 2016)
169 comprised four experimental conditions that exposed participants to stimuli that varied systematically in
170 how cognitively engaging they were. The *intact* experimental condition had participants listen to an audio
171 recording of a 10-minute story. The *paragraph*-scrambled experimental condition had participants listen to a
172 temporally scrambled version of the story, where the paragraphs occurred out of order (but where the same
173 total set of paragraphs were presented over the full listening interval). All participants in this condition
174 experienced the scrambled paragraphs in the same order. The *word*-scrambled experimental condition had
175 participants listen to a temporally scrambled version of the story where the words in the story occurred in a
176 random order. All participants in the word condition experienced the scrambled words in the same order.
177 Finally, in a *rest* experimental condition, participants lay in the scanner with no overt stimulus, with their

178 eyes open (blinking as needed). This public dataset provided a convenient means of testing our hypothesis
179 that different levels of cognitive processing and engagement are reflected in different orders of brain activity
180 dynamics.

181 In brief, we computed timeseries of dynamic high-order correlations that were similar across participants
182 in each of two randomly assigned groups: a training group and a test group. We then trained classifiers
183 on the training group’s data to match each sample from the test group with a stimulus timepoint. Each
184 classifier comprised a weighted blend of neural patterns that reflected up to n^{th} -order dynamic correlations
185 (see *Feature weighting and testing*, Fig. 10). We repeated this process for $n \in \{0, 1, 2, \dots, 10\}$. Our examinations
186 of synthetic data suggested that none of the kernels we examined were “universal” in the sense of optimally
187 recovering underlying correlations regardless of the temporal structure of those correlations. We found a
188 similar pattern in the (real) fMRI data, whereby different kernels yielded different decoding accuracies, but
189 no single kernel emerged as the clear “best.” In our analyses of neural data, we therefore averaged our
190 decoding results over a variety of kernel shapes and widths in order to identify results that were robust to
191 specific kernel parameters (see *Identifying robust decoding results*).

192 Our approach to estimating dynamic high-order correlations entails mapping the high-dimensional
193 feature space of correlations (represented by a T by $O(K^2)$ matrix) onto a lower-dimensional feature space
194 (represented by a T by K matrix). We carried out two sets of analyses that differed in how this mapping was
195 computed. The first set of analyses used PCA to find a low-dimensional embedding of the original dynamic
196 correlation matrices (Fig. 4a,b). The second set of analyses characterized correlations in dynamics of each
197 feature’s eigenvector centrality, but did not preserve the underlying activity dynamics (Fig. 4c,d).

198 Both sets of temporal decoding analyses yielded qualitatively similar results for the auditory (non-rest)
199 conditions of the experiment (Fig. 4: pink, green, and teal lines; Fig. 5: three leftmost columns). The highest
200 decoding accuracy for participants who listened to the intact (unscrambled) story was achieved using high-
201 order dynamic correlations (PCA: second-order; eigenvector-centrality: fourth-order). Scrambled versions
202 of the story were best decoded by lower-order correlations (PCA/paragraph: first-order; PCA/word: order
203 zero; eigenvector centrality/paragraph: order zero; eigenvector centrality/word: order zero). The two sets
204 of analyses yielded different decoding results on resting state data (Fig. 4: purple lines; Fig. 5: rightmost
205 column). We note that, while the resting state times could be decoded reliably, the accuracies were only very
206 slightly above chance. We speculate that the decoders might have picked up on attentional drift, boredom,
207 or tiredness; we hypothesize that these all increased throughout the resting state scan. The decoders might
208 be picking up on aspects of these loosely defined cognitive states that are common across individuals. The
209 PCA-based approach achieved the highest resting state decoding accuracy using order zero features (non-
210 correlational, activation-based), whereas the eigenvector centrality-based approach achieved the highest

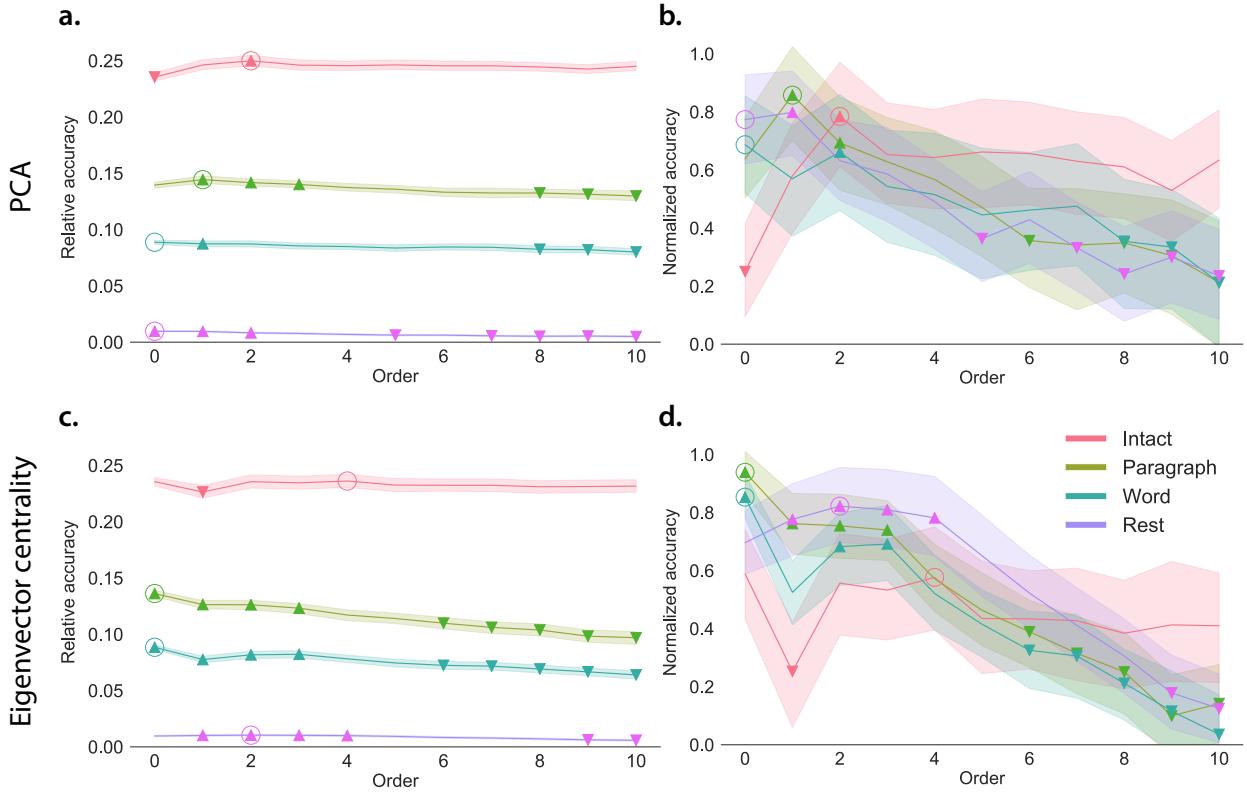


Figure 4: Across-participant timepoint decoding accuracy varies with correlation order and cognitive engagement. **a. Decoding accuracy as a function of order: PCA.** Order (*x*-axis) refers to the maximum order of dynamic correlations that were available to the classifiers (see *Feature weighting and testing*). The reported across-participant decoding accuracies are averaged over all kernel shapes and widths (see *Identifying robust decoding results*). The *y*-values are displayed relative to chance accuracy (intact: $\frac{1}{300}$; paragraph: $\frac{1}{272}$; word: $\frac{1}{300}$; rest: $\frac{1}{400}$; these chance accuracies were subtracted from the observed accuracies to obtain the relative accuracies reported on the *y*-axis). The error ribbons denote 95% confidence intervals across cross-validation folds (i.e., random assignments of participants to the training and test sets). The colors denote the experimental condition. Arrows denote sets of features that yielded reliably higher (upward facing) or lower (downward facing) decoding accuracy than the mean of all other features (via a two-tailed *t*-test, thresholded at $p < 0.05$). Figure 5 displays additional comparisons between the decoding accuracies achieved using different sets of neural features. The circled values represent the maximum decoding accuracy within each experimental condition. **b. Normalized timepoint decoding accuracy as a function of order: PCA.** This panel displays the same results as Panel a, but here each curve has been normalized to have a maximum value of 1 and a minimum value of 0 (including the upper and lower bounds of the respective 95% confidence intervals). Panels a and b used PCA to project each high-dimensional pattern of dynamic correlations onto a lower-dimensional space. **c. Timepoint decoding accuracy as a function of order: eigenvector centrality.** This panel is in the same format as Panel a, but here eigenvector centrality has been used to project the high-dimensional patterns of dynamic correlations onto a lower-dimensional space. **d. Normalized timepoint decoding accuracy as a function of order: eigenvector centrality.** This panel is in the same format as Panel b, but here eigenvector centrality has been used to project the high-dimensional patterns of dynamic correlations onto a lower-dimensional space. See Figures S1 and S2 for decoding results broken down by kernel shape and width, respectively.

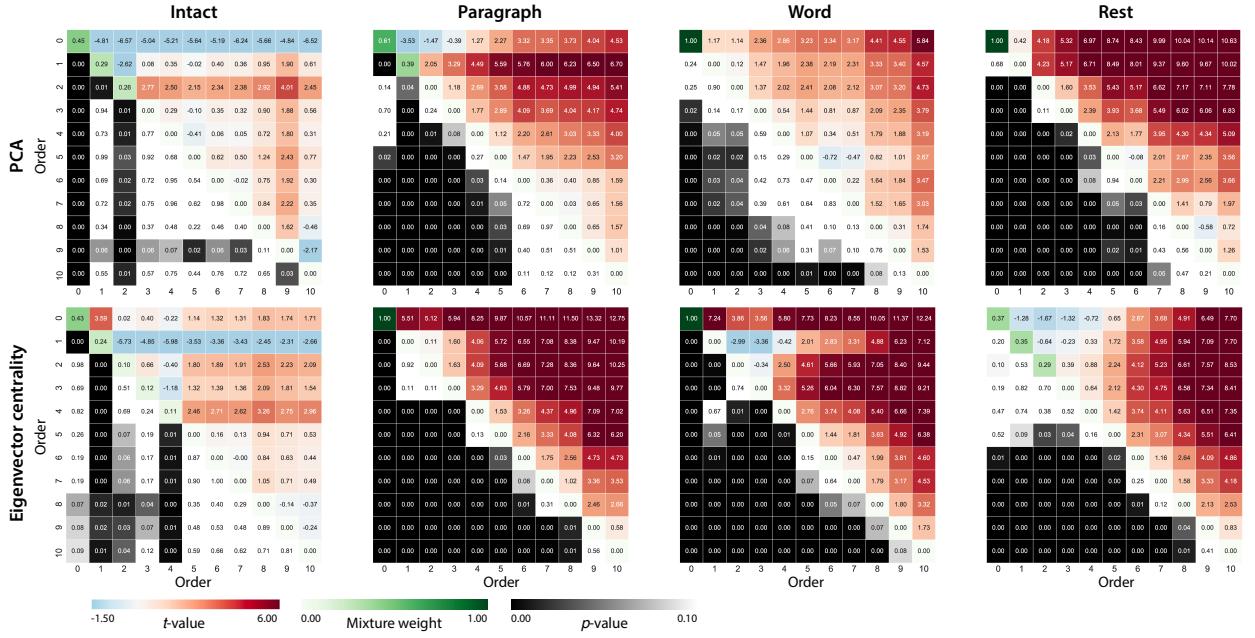


Figure 5: Statistical summary of decoding accuracies for different neural features. Each column of matrices displays decoding results for one experimental condition (intact, paragraph, word, and rest). We considered dynamic activity patterns (order 0) and dynamic correlations at different orders (order > 0). We used two-tailed t -tests to compare the distributions of decoding accuracies obtained using each pair of features. The distributions for each feature reflect the set of average decoding accuracies (across all kernel parameters), obtained for each random assignment of training and test groups. In the upper triangles of each matrix, warmer colors (positive t -values) indicate that the neural feature indicated in the given row yielded higher accuracy than the feature indicated in the given column. Cooler colors (negative t -values) indicate that the feature in the given row yielded lower decoding accuracy than the feature in the given column. The lower triangles of each map denote the corresponding p -values for the t -tests. The diagonal entries display the relative average optimized weight given to each type of feature in a decoder that included all feature types (see *Feature weighting and testing*).

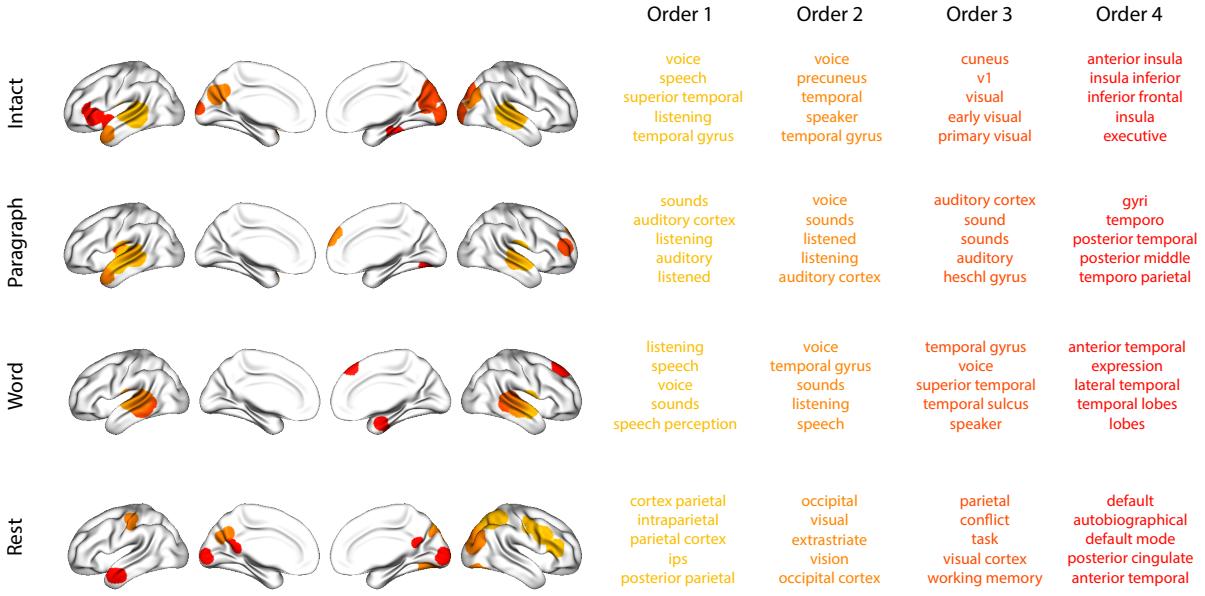


Figure 6: Top terms associated with the most strongly correlated nodes at each order. Each color corresponds to one order of inter-subject functional correlations. To calculate the dynamic correlations, eigenvector centrality has been used to project the high-dimensional patterns of dynamic correlations onto a lower-dimensional space at each previous order, which allows us to map the brain regions at each order by retaining the features of the original space. The inflated brain plots display the locations of the endpoints of the 10 strongest (absolute value) correlations at each order, thresholded at 0.999, and projected onto the cortical surface (Combrisson et al., 2019). The lists of terms on the right display the top five Neurosynth terms (Rubin et al., 2017) decoded from the corresponding brain maps for each order. Each row displays data from a different experimental condition. Additional maps and their corresponding Neurosynth terms may be found in the *Supplementary materials* (intact: Fig. S5; paragraph: Fig. S6; word: Fig. S7; rest: Fig. S8).

resting state decoding accuracy using second-order correlations. Taken together, these analyses indicate that high-level cognitive processing (while listening to the intact story) is reflected in the dynamics of high-order correlations in brain activity, whereas lower-level cognitive processing (while listening to scrambled versions of the story that lack rich meaning) is reflected in the dynamics of lower-order correlations and non-correlational activity dynamics. Further, these patterns are associated both with the underlying activity patterns (characterized using PCA) and also with the changing relative positions that different brain areas occupy in their associated networks (characterized using eigenvector centrality).

Having established that patterns of high-order correlations are informative to decoders, we next wondered which specific networks of brain regions contributed most to these patterns. As a representative example, we selected the kernel parameters that yielded decoding accuracies that were the most strongly correlated (across conditions and orders) with the average accuracies across all of the kernel parameters we examined. Using Figure 4c as a template, the best-matching kernel was a Laplace kernel with a width of 50 (Fig. 9d; also see Fig. S9). We used this kernel to compute a single K by K n^{th} -order DISFC matrix for each

224 experimental condition. We then used Neurosynth (Rubin et al., 2017) to compute the terms most highly
225 associated with the most strongly correlated pairs of regions in each of these matrices (Fig. 6; see *Reverse*
226 *inference*).

227 For all of the story listening conditions (intact, paragraph, and word; top three rows of Fig. 6), we
228 found that first- and second-order correlations were most strongly associated with auditory and speech
229 processing areas. During intact story listening, third-order correlations reflected integration with visual
230 areas, and fourth-order correlations reflected integration with areas associated with high-level cognition
231 and cognitive control, such as the ventrolateral prefrontal cortex. However, when participants listened to
232 temporally scrambled stories, these higher-order correlations instead involved interactions with additional
233 regions associated with speech and semantic processing (second and third rows of Fig. 6). By contrast, we
234 found a much different set of patterns in the resting state data (Fig. 6, bottom row). First-order resting state
235 correlations were most strongly associated with regions involved in counting and numerical understand-
236 ing. Second-order resting state correlations were strongest in visual areas; third-order correlations were
237 strongest in task-positive areas; and fourth-order correlations were strongest in regions associated with
238 autobiographical and episodic memory. We carried out analogous analyses to create maps (and decode
239 the top associated Neurosynth terms) for up to fifteenth-order correlations (Figs. S5, S6, S7, and S8). Of
240 note, examining fifteenth-order correlations between 700 nodes using conventional methods would have
241 required storing roughly $\frac{700^{2 \times 15}}{2} \approx 1.13 \times 10^{85}$ floating point numbers—assuming single-precision (32 bits
242 each), this would require roughly 32 times as many bits as there are molecules in the known universe!
243 Although these fifteenth-order correlations do appear (visually) to have some well-formed structure, we
244 provide this latter example primarily as a demonstration of the efficiency and scalability of our approach.

245 Discussion

246 We tested the hypothesis that high-level cognition is reflected in high-order brain network dynamics (e.g.,
247 see Reimann et al., 2017; Solomon et al., 2019). We examined high-order network dynamics in functional
248 neuroimaging data collected during a story listening experiment. When participants listened to an auditory
249 recording of the story, participants exhibited similar high-order brain network dynamics. By contrast,
250 when participants instead listened to temporally scrambled recordings of the story, only lower-order brain
251 network dynamics were similar across participants. Our results indicate that higher orders of network
252 interactions support higher-level aspects of cognitive processing (Fig. 7).

253 The notion that cognition is reflected in (and possibly mediated by) patterns of first-order network
254 dynamics has been suggested by or proposed in myriad empirical studies and reviews (e.g., Bressler &

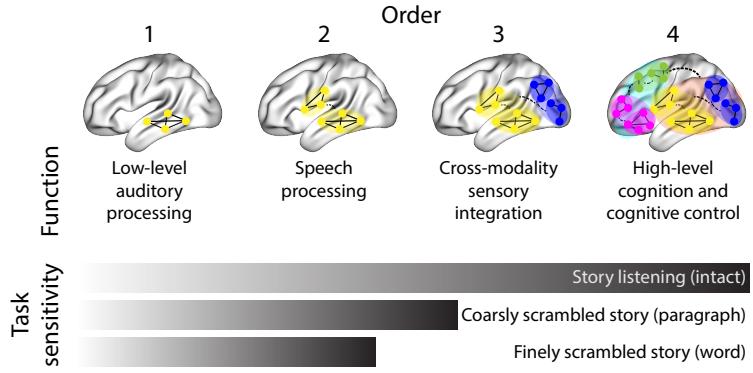


Figure 7: Proposed high-order network dynamics underlying high-level cognition during story listening. Schematic depicts higher orders of network interactions supporting higher-level aspects of cognitive processing. When tasks evoke richer, deeper, and/or higher-level processing, this is reflected in higher-order network interactions.

255 Kelso, 2001; Chang & Glover, 2010; Demertzi et al., 2019; Fong et al., 2019; Gonzalez-Castillo et al., 2019;
 256 Liégeois et al., 2019; Lurie et al., 2018; Manning et al., 2018; McIntosh, 2000; Park et al., 2018; Preti et
 257 al., 2017; Roy et al., 2019; Turk-Browne, 2013; Zou et al., 2019). Our study extends this line of work by
 258 finding cognitively relevant *higher-order* network dynamics that reflect ongoing cognition. Our findings
 259 also complement other work that uses graph theory and topology to characterize how brain networks
 260 reconfigure during cognition (e.g., Bassett et al., 2006; Betzel et al., 2019; McIntosh & Jirsa, 2019; Reimann et
 261 al., 2017; Sizemore et al., 2018; Toker & Sommer, 2019; Zheng et al., 2019).

262 An open question not addressed by our study pertains to how different structures integrate incom-
 263 ing information with different time constants. For example, one line of work suggests that the cortical
 264 surface comprises a structured map such that nearby brain structures process incoming information at
 265 similar timescales. Low-level sensory areas integrate information relatively quickly, whereas higher-level
 266 regions integrate information relatively slowly (Baldassano et al., 2017; Chien & Honey, 2019; Hasson et
 267 al., 2015, 2008; Honey et al., 2012; Lerner et al., 2014, 2011). A similar hierarchy appears to play a role in
 268 predicting future events (C. S. Lee et al., 2020). Other related work in human and mouse brains indicates
 269 that the temporal response profile of a given brain structure may relate to how strongly connected that
 270 structure is with other brain areas (Fallon et al., 2020). Further study is needed to understand the role of
 271 temporal integration at different scales of network interaction, and across different anatomical structures.
 272 Importantly, our analyses do not speak to the physiological basis of higher-order dynamics, and could
 273 reflect nonlinearities, chaotic patterns, non-stationarities, and/or multistability, etc. However, our decoding
 274 analyses do indicate that higher-order dynamics are consistent across individuals, and therefore unlikely to
 275 reflect non-stimulus-driven dynamics that are unlikely to be similar across individuals.

276 Another potential limitation of our approach relates to recent work suggesting that the brain undergoes

277 rapid state changes, for example across event boundaries (e.g., Baldassano et al., 2017). Shappell et al.
278 (2019) used hidden semi-Markov models to estimate state-specific network dynamics (also see Vidaurre et
279 al., 2018). Our general approach might be extended by considering putative state transitions. For example,
280 rather than weighting all timepoints using a similar kernel (Eqn. 4), the kernel function could adapt on a
281 timepoint-by-timepoint basis such that only timepoints determined to be in the same “state” were given
282 non-zero weight.

283 Identifying high-order network dynamics associated with high-level cognition required several impor-
284 tant methods advances. First, we used kernel-based dynamic correlations to extended the notion of (static)
285 inter-subject functional connectivity (Simony et al., 2016) to a dynamic measure of inter-subject functional
286 connectivity (DISFC) that does not rely on sliding windows (e.g., as in Manning et al., 2018), and that may
287 be computed at individual timepoints. This allowed us to precisely characterize stimulus-evoked network
288 dynamics that were similar across individuals. Second, we developed a computational framework for
289 efficiently and scalably estimating high-order dynamic correlations. Our approach uses dimensionality
290 reduction algorithms and graph measures to obtain low-dimensional embeddings of patterns of network
291 dynamics. Third, we developed an analysis framework for identifying robust decoding results by carrying
292 out our analyses using a range of parameter values and identifying which results were robust to specific
293 parameter choices. By showing that high-level cognition is reflected in high-order network dynamics, we
294 have elucidated the next step on the path towards understanding the neural basis of cognition.

295 Methods

296 Our general approach to efficiently estimating high-order dynamic correlations comprises four general
297 steps (Fig. 8). First, we derive a kernel-based approach to computing dynamic pairwise correlations in
298 a T (timepoints) by K (features) multivariate timeseries, \mathbf{X}_0 . This yields a T by $O(K^2)$ matrix of dynamic
299 correlations, \mathbf{Y}_1 , where each row comprises the upper triangle and diagonal of the correlation matrix at
300 a single timepoint, reshaped into a row vector (this reshaped vector is $(\frac{K^2-K}{2} + K)$ -dimensional). Second,
301 we apply a dimensionality reduction step to project the matrix of dynamic correlations back onto a K -
302 dimensional space. This yields a T by K matrix, \mathbf{X}_1 , that reflects an approximation of the dynamic correlations
303 reflected in the original data. Third, we use repeated applications of the kernel-based dynamic correlation
304 step to \mathbf{X}_n and the dimensionality reduction step to the resulting \mathbf{Y}_{n+1} to estimate high-order dynamic
305 correlations. Each application of these steps to a T by K time series \mathbf{X}_n yields a T by K matrix, \mathbf{X}_{n+1} , that
306 reflects the dynamic correlations between the columns of \mathbf{X}_n . In this way, we refer to n as the *order* of the
307 timeseries, where \mathbf{X}_0 (order 0) denotes the original data and \mathbf{X}_n denotes (approximated) n^{th} -order dynamic

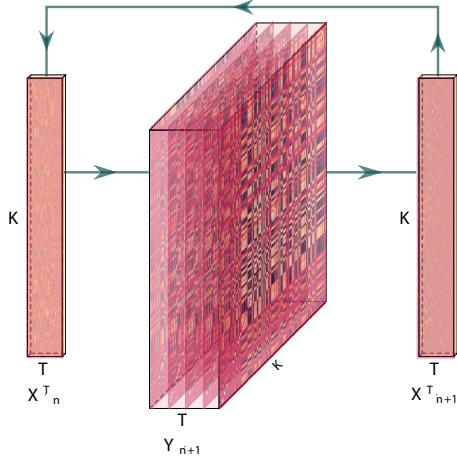


Figure 8: Estimating dynamic high-order correlations. Given a T by K matrix of multivariate timeseries data, \mathbf{X}_n (where $n \in \mathbb{N}, n \geq 0$), we use Equation 4 to compute a timeseries of K by K correlation matrices, \mathbf{Y}_{n+1} . We then approximate \mathbf{Y}_{n+1} with the T by K matrix \mathbf{X}_{n+1} . This process may be repeated to scalably estimate iteratively higher-order correlations in the data. Note that the transposes of \mathbf{X}_n and \mathbf{X}_{n+1} are displayed in the figure for compactness.

correlations between the columns of \mathbf{X}_0 . Finally, we use a cross-validation-based decoding approach to evaluate how well information contained in a given order (or weighted mixture of orders) may be used to decode relevant cognitive states. If including a given \mathbf{X}_n in the feature set yields higher classification accuracy on held-out data, we interpret this as evidence that the given cognitive states are reflected in patterns of n^{th} -order correlations.

All of the code used to produce the figures and results in this manuscript, along with links to the corresponding datasets, may be found at github.com/ContextLab/timecorr-paper. In addition, we have released a Python toolbox for computing dynamic high-order correlations in timeseries data; our toolbox may be found at timecorr.readthedocs.io.

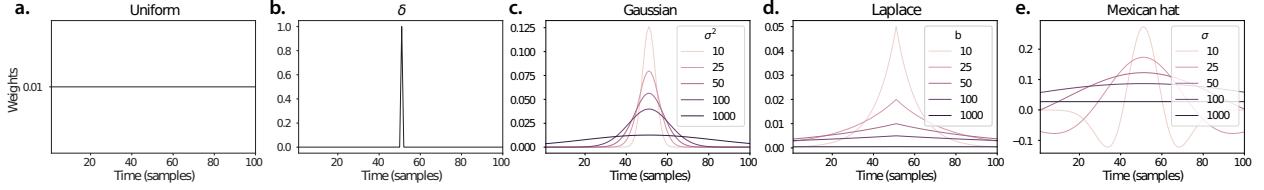


Figure 9: Examples of kernel functions. Each panel displays per-timepoint weights for a kernel centered at $t = 50$, evaluated at 100 timepoints ($\tau \in [1, \dots, 100]$). **a. Uniform kernel.** The weights are timepoint-invariant; observations at all timepoints are weighted equally, and do not change as a function of τ . This is a special case kernel function that reduces dynamic correlations to static correlations. **b. Dirac δ kernel.** Only the observation at timepoint t is given a non-zero weight (of 1). **c. Gaussian kernels.** Each kernel's weights fall off in time according to a Gaussian probability density function centered on time t . Weights derived using several different example width parameters (σ^2) are displayed. **d. Laplace kernels.** Each kernel's weights fall off in time according to a Laplace probability density function centered on time t . Weights derived using several different example width parameters (b) are displayed. **e. Mexican hat (Ricker wavelet) kernels.** Each kernel's weights fall off in time according to a Ricker wavelet centered on time t . This function highlights the *contrasts* between local versus surrounding activity patterns in estimating dynamic correlations. Weights derived using several different example width parameters (σ) are displayed.

317 Kernel-based approach for computing dynamic correlations

Given a T by K matrix of observations, \mathbf{X} , we can compute the (static) Pearson's correlation between any pair of columns, $\mathbf{X}(\cdot, i)$ and $\mathbf{X}(\cdot, j)$ using (Pearson, 1901):

$$\text{corr}(\mathbf{X}(\cdot, i), \mathbf{X}(\cdot, j)) = \frac{\sum_{t=1}^T (\mathbf{X}(t, i) - \bar{\mathbf{X}}(\cdot, i))(\mathbf{X}(t, j) - \bar{\mathbf{X}}(\cdot, j))}{\sqrt{\sum_{t=1}^T \sigma_{\mathbf{X}(\cdot, i)}^2 \sigma_{\mathbf{X}(\cdot, j)}^2}}, \text{ where} \quad (1)$$

$$\bar{\mathbf{X}}(\cdot, k) = \frac{1}{T} \sum_{t=1}^T \mathbf{X}(t, k), \text{ and} \quad (2)$$

$$\sigma_{\mathbf{X}(\cdot, k)}^2 = \frac{1}{T} \sum_{t=1}^T (\mathbf{X}(t, k) - \bar{\mathbf{X}}(\cdot, k))^2 \quad (3)$$

- 318 We can generalize this formula to compute time-varying correlations by incorporating a *kernel function* that
 319 takes a time t as input, and returns how much the observed data at each timepoint $\tau \in [-\infty, \infty]$ contributes
 320 to the estimated instantaneous correlation at time t (Fig. 9; also see Allen et al., 2012, for a similar approach).

321

Given a kernel function $\kappa_t(\cdot)$ for timepoint t , evaluated at timepoints $\tau \in [1, \dots, T]$, we can update the

static correlation formula in Equation 1 to estimate the *instantaneous correlation* at timepoint t :

$$\text{timecorr}_{\kappa_t}(\mathbf{X}(\cdot, i), \mathbf{X}(\cdot, j)) = \frac{\sum_{\tau=1}^T (\mathbf{X}(\tau, i) - \tilde{\mathbf{X}}_{\kappa_t}(\cdot, i))(\mathbf{X}(\tau, j) - \tilde{\mathbf{X}}_{\kappa_t}(\cdot, j))}{\sqrt{\sum_{\tau=1}^T \tilde{\sigma}_{\kappa_t}^2(\mathbf{X}(\cdot, i)) \tilde{\sigma}_{\kappa_t}^2(\mathbf{X}(\cdot, j))}}, \text{ where} \quad (4)$$

$$\tilde{\mathbf{X}}_{\kappa_t}(\cdot, k) = \sum_{\tau=1}^T \kappa_t(\tau) \mathbf{X}(\tau, k), \quad (5)$$

$$\tilde{\sigma}_{\kappa_t}^2(\mathbf{X}(\cdot, k)) = \sum_{\tau=1}^T (\mathbf{X}(\tau, k) - \tilde{\mathbf{X}}_{\kappa_t}(\cdot, k))^2. \quad (6)$$

322 Here $\text{timecorr}_{\kappa_t}(\mathbf{X}(\cdot, i), \mathbf{X}(\cdot, j))$ reflects the correlation at time t between columns i and j of \mathbf{X} , estimated using
 323 the kernel κ_t . We evaluate Equation 4 in turn for each pair of columns in \mathbf{X} and for kernels centered on each
 324 timepoint in the timeseries, respectively, to obtain a T by K by K timeseries of dynamic correlations, \mathbf{Y} . For
 325 convenience, we then reshape the upper triangles and diagonals of each timepoint's symmetric correlation
 326 matrix into a row vector to obtain an equivalent T by $(\frac{K^2-K}{2} + K)$ matrix.

327 Dynamic inter-subject functional connectivity (DISFC)

Equation 4 provides a means of taking a single observation matrix, \mathbf{X}_n and estimating the dynamic correlations from moment to moment, \mathbf{Y}_{n+1} . Suppose that one has access to a set of multiple observation matrices that reflect the same phenomenon. For example, one might collect neuroimaging data from several experimental participants, as each participant performs the same task (or sequence of tasks). Let $\mathbf{X}_n^1, \mathbf{X}_n^2, \dots, \mathbf{X}_n^P$ reflect the T by K observation matrices ($n = 0$) or reduced correlation matrices ($n > 0$) for each of P participants in an experiment. We can use *inter-subject functional connectivity* (ISFC; Simony & Chang, 2020; Simony et al., 2016) to compute the stimulus-driven correlations reflected in the multi-participant dataset at a given timepoint t using:

$$\tilde{\mathbf{C}}(t) = M \left(R \left(\frac{1}{2P} \sum_{p=1}^P Z(\mathbf{Y}_{n+1}^p(t))^\top + Z(\mathbf{Y}_{n+1}^p(t)) \right) \right), \quad (7)$$

where M extracts and vectorizes the upper triangle and diagonal of a symmetric matrix, Z is the Fisher z -transformation (Zar, 2010):

$$Z(r) = \frac{\log(1+r) - \log(1-r)}{2}, \quad (8)$$

R is the inverse of Z :

$$R(z) = \frac{\exp(2z - 1)}{\exp(2z + 1)}, \quad (9)$$

and $\mathbf{Y}_{n+1}^p(t)$ denotes the correlation matrix at timepoint t (Eqn. 4) between each column of \mathbf{X}_n^p and each column of the average \mathbf{X}_n from all *other* participants, $\bar{\mathbf{X}}_n^{\setminus p}$:

$$\bar{\mathbf{X}}_n^{\setminus p} = \frac{1}{P-1} \sum_{q \in \setminus p} \mathbf{X}_n^q, \quad (10)$$

where $\setminus p$ denotes the set of all participants other than participant p . In this way, the T by $\binom{K^2-K}{2} + K$ DISFC matrix $\bar{\mathbf{C}}$ provides a time-varying extension of the ISFC approach developed by Simony et al. (2016).

330 Low-dimensional representations of dynamic correlations

Given a T by $\binom{K^2-K}{2} + K$ matrix of n^{th} -order dynamic correlations, \mathbf{Y}_n , we propose two general approaches to computing a T by K low-dimensional representation of those correlations, \mathbf{X}_n . The first approach uses dimensionality reduction algorithms to project \mathbf{Y}_n onto a K -dimensional space. The second approach uses graph measures to characterize the relative positions of each feature ($k \in [1, \dots, K]$) in the network defined by the correlation matrix at each timepoint.

336 Dimensionality reduction-based approaches to computing \mathbf{X}_n

The modern toolkit of dimensionality reduction algorithms include Principal Components Analysis (PCA; Pearson, 1901), Probabilistic PCA (PPCA; Tipping & Bishop, 1999), Exploratory Factor Analysis (EFA; Spearman, 1904), Independent Components Analysis (ICA; Comon et al., 1991; Jutten & Herault, 1991), t -Stochastic Neighbor Embedding (t -SNE; van der Maaten & Hinton, 2008), Uniform Manifold Approximation and Projection (UMAP; McInnes et al., 2018), non-negative matrix factorization (NMF; D. D. Lee & Seung, 1999), Topographic Factor Analysis (TFA; Manning et al., 2014), Hierarchical Topographic Factor analysis (HTFA; Manning et al., 2018), Topographic Latent Source Analysis (TLSA; Gershman et al., 2011), dictionary learning (J. Mairal et al., 2009; J. B. Mairal et al., 2009), and deep auto-encoders (Hinton & Salakhutdinov, 2006), among others. While complete characterizations of each of these algorithms is beyond the scope of the present manuscript, the general intuition driving these approaches is to compute the T by K matrix, \mathbf{X} , that is closest to the original T by J matrix, \mathbf{Y} , where (typically) $K \ll J$. The different approaches place different constraints on what properties \mathbf{X} must satisfy and which aspects of the data are compared (and how) in order to optimize how well \mathbf{X} approximates \mathbf{Y} .

350 Applying dimensionality reduction algorithms to \mathbf{Y} yields an \mathbf{X} whose columns reflect weighted combi-
351 nations (or nonlinear transformations) of the original columns of \mathbf{Y} . This has two main consequences. First,
352 with each repeated dimensionality reduction, the resulting \mathbf{X}_n has lower and lower fidelity (with respect to
353 what the “true” \mathbf{Y}_n might have looked like without using dimensionality reduction to maintain tractability).
354 In other words, computing \mathbf{X}_n is a lossy operation. Second, whereas each column of \mathbf{Y}_n may be mapped
355 directly onto specific pairs of columns of \mathbf{X}_{n-1} , the columns of \mathbf{X}_n reflect weighted combinations and/or
356 nonlinear transformations of the columns of \mathbf{Y}_n . Many dimensionality reduction algorithms are invertible
357 (or approximately invertible). However, attempting to map a given \mathbf{X}_n back onto the original feature space
358 of \mathbf{X}_0 will usually require $O(TK^2)$ space and therefore becomes intractable as n or K grow large.

359 **Graph measure approaches to computing \mathbf{X}_n**

360 The above dimensionality reduction approaches to approximating a given \mathbf{Y}_n with a lower-dimensional
361 \mathbf{X}_n preserve a (potentially recombined and transformed) mapping back to the original data in \mathbf{X}_0 . We also
362 explore graph measures that instead characterize each feature’s relative *position* in the broader network of
363 interactions and connections. To illustrate the distinction between the two general approaches we explore,
364 suppose a network comprises nodes A and B , along with several other nodes. If A and B exhibit uncorrelated
365 activity patterns, then by definition the functional connection (correlation) between them will be close to
366 0. However, if A and B each interact with *other* nodes in similar ways, we might attempt to capture those
367 similarities between A ’s and B ’s interactions with those other members of the network.

368 In general, graph measures take as input a matrix of interactions (e.g., using the above notation, a K
369 by K correlation matrix or binarized correlation matrix reconstituted from a single timepoint’s row of \mathbf{Y}),
370 and return as output a set of K measures describing how each node (feature) sits within that correlation
371 matrix with respect to the rest of the population. Widely used measures include betweenness centrality (the
372 proportion of shortest paths between each pair of nodes in the population that involves the given node
373 in question; e.g., Barthélemy, 2004; Freeman, 1977; Geisberger et al., 2008; Newman, 2005; Opsahl et al.,
374 2010); diversity and dissimilarity (characterizations of how differently connected a given node is from others
375 in the population; e.g., Lin, 2009; Rao, 1982; Ricotta & Szeidl, 2006); eigenvector centrality and pagerank
376 centrality (measures of how influential a given node is within the broader network; e.g., Bonacich, 2007;
377 Halu et al., 2013; Lohmann et al., 2010; Newman, 2008); transfer entropy and flow coefficients (a measure of
378 how much information is flowing from a given node to other nodes in the network; e.g., Honey et al., 2007;
379 Schreiber, 2000); k -coreness centrality (a measure of the connectivity of a node within its local subgraph; e.g.,
380 Alvarez-Hamelin et al., 2005; Christakis & Fowler, 2010); within-module degree (a measure of how many

381 connections a node has to its close neighbors in the network; e.g., Rubinov & Sporns, 2010); participation
382 coefficient (a measure of the diversity of a node's connections to different subgraphs in the network; e.g.,
383 Rubinov & Sporns, 2010); and subgraph centrality (a measure of a node's participation in all of the network's
384 subgraphs; e.g., Estrada & Rodríguez-Velázquez, 2005); among others.

385 For a given graph measure, $\eta : \mathbb{R}^{K \times K} \rightarrow \mathbb{R}^K$, we can use η to transform each row of \mathbf{Y}_n in a way that
386 characterizes the corresponding graph properties of each column. This results in a new T by K matrix,
387 \mathbf{X}_n , that reflects how the features reflected in the columns of \mathbf{X}_{n-1} participate in the network during each
388 timepoint (row).

389 **Dynamic higher-order correlations**

390 Because \mathbf{X}_n has the same shape as the original data \mathbf{X}_0 , approximating \mathbf{Y}_n with a lower-dimensional \mathbf{X}_n
391 enables us to estimate high-order dynamic correlations in a scalable way. Given a T by K input matrix, the
392 output of Equation 4 requires $O(TK^2)$ space to store. Repeated applications of Equation 4 (i.e., computing
393 dynamic correlations between the columns of the outputted dynamic correlation matrix) each require
394 exponentially more space; in general the n^{th} -order dynamic correlations of a T by K timeseries occupies
395 $O(TK^{2^n})$ space. However, when we approximate or summarize the output of Equation 4 with a T by K matrix
396 (as described above), it becomes feasible to compute even very high-order correlations in high-dimensional
397 data. Specifically, approximating the n^{th} -order dynamic correlations of a T by K timeseries requires only
398 $O(TK^2)$ additional space— the same as would be required to compute first-order dynamic correlations. In
399 other words, the space required to store $n + 1$ multivariate timeseries reflecting up to n^{th} order correlations
400 in the original data scales linearly with n using our approach (Fig. 8).

401 **Data**

402 We examined two types of data: synthetic data and human functional neuroimaging data. We constructed
403 and leveraged the synthetic data to evaluate our general approach (for a related validation approach see
404 Thompson et al., 2018). Specifically, we tested how well Equation 4 could be used to recover known dynamic
405 correlations using different choices of kernel (κ ; Fig. 9), for each of several synthetic datasets that exhibited
406 different temporal properties. We also simulated higher-order correlations and tested how well Equation 4
407 could recover these correlations using the best kernel from the previous synthetic data analyses. We then
408 applied our approach to a functional neuroimaging dataset to test the hypothesis that ongoing cognitive
409 processing is reflected in high-order dynamic correlations. We used an across-participant classification test
410 to estimate whether dynamic correlations of different orders contain information about which timepoint in

411 a story participants were listening to.

412 **Synthetic data: simulating dynamic first-order correlations**

413 We constructed a total of 40 different multivariate timeseries, collectively reflecting a total of 4 qualitatively
414 different patterns of dynamic first-order correlations (i.e., 10 datasets reflecting each type of dynamic pat-
415 tern). Each timeseries comprised 50 features (dimensions) that varied over 300 timepoints. The observations
416 at each timepoint were drawn from a zero-mean multivariate Gaussian distribution with a covariance matrix
417 defined for each timepoint as described below. We drew the observations at each timepoint independently
418 from the draws at all other timepoints; in other words, for each observation $s_t \sim \mathcal{N}(\mathbf{0}, \Sigma_t)$ at timepoint t ,
419 $p(s_t) = p(s_t | s_{\setminus t})$.

Constant. We generated data with stable underlying correlations to evaluate how Equation 4 characterized correlation “dynamics” when the ground truth correlations were static. We constructed 10 multivariate timeseries whose observations were each drawn from a single (stable) Gaussian distribution. For each dataset (indexed by m), we constructed a random covariance matrix, Σ_m :

$$\Sigma_m = \mathbf{C}\mathbf{C}^\top, \text{ where} \quad (11)$$

$$\mathbf{C}(i, j) \sim \mathcal{N}(0, 1), \text{ and where} \quad (12)$$

420 $i, j \in [1, 2, \dots, 50]$. In other words, all of the observations (for each of the 300 timepoints) within each dataset
421 were drawn from a multivariate Gaussian distribution with the same covariance matrix, and the 10 datasets
422 each used a different covariance matrix.

423 **Random.** We generated a second set of 10 synthetic datasets whose observations at each timepoint were
424 drawn from a Gaussian distribution with a new randomly constructed (using Eqn. 11) covariance matrix.
425 Because each timepoint’s covariance matrix was drawn independently from the covariance matrices for all
426 other timepoints, these datasets provided a test of reconstruction accuracy in the absence of any meaningful
427 underlying temporal structure in the dynamic correlations underlying the data.

Ramping. We generated a third set of 10 synthetic datasets whose underlying correlations changed gradually over time. For each dataset, we constructed two *anchor* covariance matrices using Equation 11, Σ_{start} and Σ_{end} . For each of the 300 timepoints in each dataset, we drew the observations from a multivariate

Gaussian distribution whose covariance matrix at each timepoint $t \in [0, \dots, 299]$ was given by

$$\Sigma_t = \left(1 - \frac{t}{299}\right) \Sigma_{\text{start}} + \frac{t}{299} \Sigma_{\text{end}}. \quad (13)$$

428 The gradually changing correlations underlying these datasets allow us to evaluate the recovery of dynamic
429 correlations when each timepoint's correlation matrix is unique (as in the random datasets), but where the
430 correlation dynamics are structured and exhibit first-order autocorrelations (as in the constant datasets).

431 **Event.** We generated a fourth set of 10 synthetic datasets whose underlying correlation matrices exhibited
432 prolonged intervals of stability, interspersed with abrupt changes. For each dataset, we used Equation 11
433 to generate 5 random covariance matrices. We constructed a timeseries where each set of 60 consecutive
434 samples was drawn from a Gaussian with the same covariance matrix. These datasets were intended to
435 simulate a system that exhibits periods of stability punctuated by occasional abrupt state changes.

436 **Synthetic data: simulating dynamic high-order correlations**

437 We developed an iterative procedure for constructing timeseries data that exhibits known dynamic high-
438 order correlations. The procedure builds on our approach to generating dynamic first-order correlations.
439 Essentially, once we generate a timeseries with known first-order correlations, we can use the known first-
440 order correlations as a template to generate a new timeseries of second-order correlations. In turn, we can
441 generate a timeseries of third-order correlations from the second-order correlations, and so on. In general,
442 we can generate order n correlations given a timeseries of order $n - 1$ correlations, for any $n > 1$. Finally,
443 given the order n timeseries, we can reverse the preceding process to generate an order $n - 1$ timeseries, an
444 order $n - 2$ order timeseries, and so on, until we obtain an order 0 timeseries of simulated data that reflects
445 the chosen high-order dynamics.

446 The central mathematical operation in our procedure is the Kronecker product (\otimes). The Kronecker
447 product of a $K \times K$ matrix, m_1 , with itself (i.e., $m_1 \otimes m_1$) produces a new $K^2 \times K^2$ matrix, m_2 whose entries
448 reflect a scaled tiling of the entries in m_1 . If these tilings (scaled copies of m_1) are indexed by row and column,
449 then the tile in the i^{th} row and j^{th} column contains the entries of m_1 , multiplied by $m_1(i, j)$. Following this
450 pattern, the Kronecker product $m_2 \otimes m_2$ yields the $K^4 \times K^4$ matrix m_3 whose tiles are scaled copies of m_2 . In
451 general, repeated applications of the Kronecker self-product may be used to generate $m_{n+1} = m_n \otimes m_n$ for
452 $n > 1$, where m_{n+1} is a $K^{2^n} \times K^{2^n}$ matrix. After generating a first-order timeseries of dynamic correlations
453 (see *Synthetic data: simulating dynamic first-order correlations*), we use this procedure (applied independently
454 at each timepoint) to transform it into a timeseries of n^{th} -order correlations. When m_{n+1} is generated in this

455 way, the temporal structure of the full timeseries (i.e., constant, random, ramping, event) is preserved, since
456 changes in the original first-order timeseries are also reflected in the scaled tilings of itself that comprise the
457 higher-order matrices.

458 Given a timeseries of n^{th} -order correlations, we then need to work “backwards” in order to generate the
459 order-zero timeseries. If the n^{th} -order correlation matrix at a given timepoint is m_n , then we can generate an
460 order $n - 1$ correlation matrix (for $n > 1$) by taking a draw from $\mathcal{N}(0, m_n)$ and reshaping the resulting vector
461 to have square dimensions. Intuitively, the re-shaped matrix will look like a noisy version of the template
462 matrix, m_{n-1} . (When $n = 1$, no re-shaping is needed; the resulting K -dimensional vector may be used as the
463 observation at the given timepoint.) After independently drawing each timepoint’s order $n - 1$ correlation
464 matrix from that timepoint’s order n correlation matrix, this process can be applied repeatedly until $n = 0$.
465 This results in a K -dimensional timeseries of T observations containing the specified high-order correlations
466 at orders 1 through n . Following our approach to generating synthetic data exhibiting known first-order
467 correlations, we constructed a total of 40 additional multivariate timeseries, collectively reflecting a total of
468 4 qualitatively different patterns of dynamic correlations (i.e., 10 datasets reflecting each type of dynamic
469 pattern: constant, random, ramping, and event).

470 Functional neuroimaging data collected during story listening

471 We examined an fMRI dataset collected by Simony et al. (2016) that the authors have made publicly available
472 at arks.princeton.edu/ark:/88435/dsp015d86p269k. The dataset comprises neuroimaging data collected as
473 participants listened to an audio recording of a story (intact condition; 36 participants), listened to temporally
474 scrambled recordings of the same story (17 participants in the paragraph-scrambled condition listened to
475 the paragraphs in a randomized order and 36 in the word-scrambled condition listened to the words in a
476 randomized order), or lay resting with their eyes open in the scanner (rest condition; 36 participants). Full
477 neuroimaging details may be found in the original paper for which the data were collected (Simony et al.,
478 2016).

479 **Hierarchical topographic factor analysis (HTFA).** Following our prior related work, we used HTFA (Manning et al., 2018) to derive a compact representation of the neuroimaging data. In brief, this approach approximates the timeseries of voxel activations (44,415 voxels) using a much smaller number of radial basis function (RBF) nodes (in this case, 700 nodes, as determined by an optimization procedure described by Manning et al., 2018). This provides a convenient representation for examining full-brain network dynamics.
480 All of the analyses we carried out on the neuroimaging dataset were performed in this lower-dimensional
481 space. In other words, each participant’s data matrix, X_0 , was a number-of-timepoints by 700 matrix of

486 HTFA-derived factor weights (where the row and column labels were matched across participants). Code
487 for carrying out HTFA on fMRI data may be found as part of the BrainIAK toolbox (Capota et al., 2017),
488 which may be downloaded at brainiak.org.

489 **Temporal decoding**

490 We sought to identify neural patterns that reflected participants' ongoing cognitive processing of incoming
491 stimulus information. As reviewed by Simony et al. (2016), one way of homing in on these stimulus-driven
492 neural patterns is to compare activity patterns across individuals (e.g., using ISFC analyses). In particular,
493 neural patterns will be similar across individuals to the extent that the neural patterns under consideration
494 are stimulus-driven, and to the extent that the corresponding cognitive representations are reflected in
495 similar spatial patterns across people (also see Simony & Chang, 2020). Following this logic, we used an
496 across-participant temporal decoding test developed by Manning et al. (2018) to assess the degree to which
497 different neural patterns reflected ongoing stimulus-driven cognitive processing across people (Fig. 10). The
498 approach entails using a subset of the data to train a classifier to decode stimulus timepoints (i.e., moments
499 in the story participants listened to) from neural patterns. We use decoding (forward inference) accuracy
500 on held-out data, from held-out participants, as a proxy for the extent to which the inputted neural patterns
501 reflected stimulus-driven cognitive processing in a similar way across individuals.

502 **Forward inference and decoding accuracy**

503 We used an across-participant correlation-based classifier to decode which stimulus timepoint matched
504 each timepoint's neural pattern (Fig. 10). We first divided the participants into two groups: a template group,
505 $\mathcal{G}_{\text{template}}$ (i.e., training data), and a to-be-decoded group, $\mathcal{G}_{\text{decode}}$ (i.e., test data). We used Equation 7 to
506 compute a DISFC matrix for each group ($\bar{\mathbf{C}}_{\text{template}}$ and $\bar{\mathbf{C}}_{\text{decode}}$, respectively). We then correlated the rows of
507 $\bar{\mathbf{C}}_{\text{template}}$ and $\bar{\mathbf{C}}_{\text{decode}}$ to form a number-of-timepoints by number-of-timepoints decoding matrix, Λ . In this
508 way, the rows of Λ reflected timepoints from the template group, while the columns reflected timepoints
509 from the to-be-decoded group. We used Λ to assign temporal labels to each row $\bar{\mathbf{C}}_{\text{decode}}$ using the row of
510 $\bar{\mathbf{C}}_{\text{template}}$ with which it was most highly correlated. We then repeated this decoding procedure, but using
511 $\mathcal{G}_{\text{decode}}$ as the template group and $\mathcal{G}_{\text{template}}$ as the to-be-decoded group. Given the true timepoint labels (for
512 each group), we defined the *decoding accuracy* as the average proportion of correctly decoded timepoints,
513 across both groups. We defined the *relative decoding accuracy* as the difference between the decoding accuracy
514 and chance accuracy (i.e., $\frac{1}{T}$).

515 **Feature weighting and testing**

516 We sought to examine which types of neural features (i.e., activations, first-order dynamic correlations, and
517 higher-order dynamic correlations) were informative to the temporal decoders. Using the notation above,
518 these features correspond to $\mathbf{X}_0, \mathbf{X}_1, \mathbf{X}_2, \mathbf{X}_3$, and so on.

519 One challenge to fairly evaluating high-order correlations is that if the kernel used in Equation 4 is
520 wider than a single timepoint, each repeated application of the equation will result in further temporal
521 blur. Because our primary assessment metric is temporal decoding accuracy, this unfairly biases against
522 detecting meaningful signal in higher-order correlations (relative to lower-order correlations). We attempted
523 to mitigate temporal blur in estimating each \mathbf{X}_n by using a Dirac δ function kernel (which places all of its
524 mass over a single timepoint; Fig. 9b, 10a) to compute each lower-order correlation ($\mathbf{X}_1, \mathbf{X}_2, \dots, \mathbf{X}_{n-1}$). We
525 then used a new (potentially wider, as described below) kernel to compute \mathbf{X}_n from \mathbf{X}_{n-1} . In this way,
526 temporal blurring was applied only in the last step of computing \mathbf{X}_n . We note that, because each \mathbf{X}_n is a
527 low-dimensional representation of the corresponding \mathbf{Y}_n , the higher-order correlations we estimated reflect
528 true correlations in the data with lower-fidelity than estimates of lower-order correlations. Therefore, even
529 after correcting for temporal blurring, our approach is still biased against finding meaningful signal in
530 higher-order correlations.

531 After computing each $\mathbf{X}_1, \mathbf{X}_2, \dots, \mathbf{X}_{n-1}$ for each participant, we divided participants into two equally sized
532 groups (± 1 for odd numbers of participants): $\mathcal{G}_{\text{train}}$ and $\mathcal{G}_{\text{test}}$. We then further subdivided $\mathcal{G}_{\text{train}}$ into $\mathcal{G}_{\text{train}_1}$
533 and $\mathcal{G}_{\text{train}_2}$. We then computed Λ (temporal correlation) matrices for each type of neural feature, using $\mathcal{G}_{\text{train}_1}$
534 and $\mathcal{G}_{\text{train}_2}$. This resulted in $n + 1$ Λ matrices (one for the original timeseries of neural activations, and one
535 for each of n orders of dynamic correlations). Our objective was to find a set of weights for each of these
536 Λ matrices such that the weighted average of the $n + 1$ matrices yielded the highest decoding accuracy.
537 We used quasi-Newton gradient ascent (Nocedal & Wright, 2006), using decoding accuracy (for $\mathcal{G}_{\text{train}_1}$ and
538 $\mathcal{G}_{\text{train}_2}$) as the objective function to be maximized, to find an optimal set of training data-derived weights,
539 $\phi_{0,1,\dots,n}$, where $\sum_{i=0}^n \phi_i = 1$ and where $\phi_i \geq 0 \forall i \in [0, 1, \dots, n]$.

540 After estimating an optimal set of weights, we computed a new set of $n + 1$ Λ matrices correlating the
541 DISFC patterns from $\mathcal{G}_{\text{train}}$ and $\mathcal{G}_{\text{test}}$ at each timepoint. We use the resulting decoding accuracy of $\mathcal{G}_{\text{test}}$
542 timepoints (using the weights in $\phi_{0,1,\dots,n}$ to average the Λ matrices) to estimate how informative the set of
543 neural features containing up to n^{th} order correlations were.

544 We used a permutation-based procedure to form stable estimates of decoding accuracy for each set of
545 neural features. In particular, we computed the decoding accuracy for each of 10 random group assignments
546 of $\mathcal{G}_{\text{train}}$ and $\mathcal{G}_{\text{test}}$. We report the mean accuracy (along with 95% confidence intervals) for each set of neural

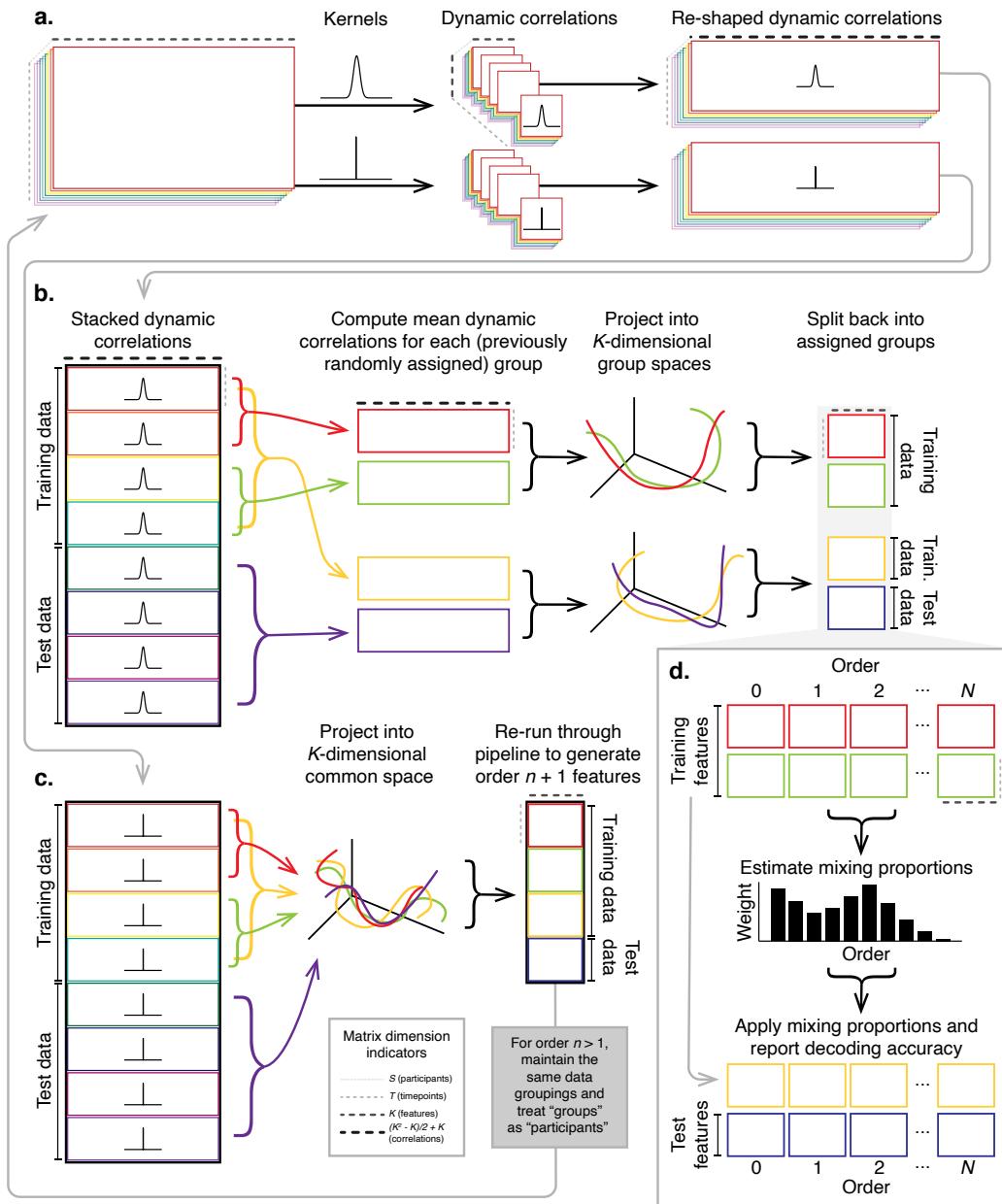


Figure 10: Decoding analysis pipeline. **a. Computing dynamic correlations from timeseries data.** Given a timeseries of observations as a $T \times K$ matrix (or a set of S such matrices), we use Equation 4 to compute each participant's DISFC (relative to other participants in the training or test sub-group, as appropriate). We repeat this process twice—once using the analysis kernel (shown here as a Gaussian in the upper row of the panel), and once using a δ function kernel (lower row of the panel). **b. Projecting dynamic correlations into a lower-dimensional space.** We project the training and test data into K -dimensional spaces to create compact representations of dynamic correlations at the given order (estimated using the analysis kernel). **c. Kernel trick.** We project the dynamic correlations computed using a δ function kernel into a common K -dimensional space. These low-dimensional embeddings are fed back through the analysis pipeline in order to compute features at the next-highest order. **d. Decoding analysis.** We split the training data into two equal groups, and optimize the feature weights (i.e., dynamic correlations at each order) to maximize decoding accuracy. We then apply the trained classifier to the (held-out) test data.

547 features.

548 **Identifying robust decoding results**

549 The temporal decoding procedure we use to estimate which neural features support ongoing cognitive
550 processing is governed by several parameters. In particular, Equation 4 requires defining a kernel function,
551 which can take on different shapes and widths. For a fixed set of neural features, each of these parameters
552 can yield different decoding accuracies. Further, the best decoding accuracy for a given timepoint may be
553 reliably achieved by one set of parameters, whereas the best decoding accuracy for another timepoint might
554 be reliably achieved by a different set of parameters, and the best decoding accuracy across *all* timepoints
555 might be reliably achieved by still another different set of parameters. Rather than attempting to maximize
556 decoding accuracy, we sought to discover the trends in the data that were robust to classifier parameters
557 choices. Specifically, we sought to characterize how decoding accuracy varied (under different experimental
558 conditions) as a function of which neural features were considered.

559 To identify decoding results that were robust to specific classifier parameter choices, we repeated our
560 decoding analyses after substituting into Equation 4 each of a variety of kernel shapes and widths. We
561 examined Gaussian (Fig. 9c), Laplace (Fig. 9d), and Mexican Hat (Fig. 9e) kernels, each with widths of 5, 10,
562 20, and 50 samples. We then report the average decoding accuracies across all of these parameter choices.
563 This enabled us to (partially) factor out performance characteristics that were parameter-dependent, within
564 the set of parameters we examined.

565 **Reverse inference**

566 The dynamic patterns we examined comprise high-dimensional correlation patterns at each timepoint. To
567 help interpret the resulting patterns in the context of other studies, we created summary maps by computing
568 the across-timepoint average pairwise correlations at each order of analysis (first order, second order, etc.).
569 We selected the 10 strongest (absolute value) correlations at each order. Each correlation is between the
570 dynamic activity patterns (or patterns of dynamic high-order correlations) measured at two RBF nodes
571 (see *Hierarchical Topographic Factor Analysis*). Therefore, the 10 strongest correlations involved up to 20 RBF
572 nodes. Each RBF defines a spatial function whose activations range from 0 to 1. We constructed a map
573 of RBF components that denoted the endpoints of the 10 strongest correlations (we set each RBF to have a
574 maximum value of 1). We then carried out a meta analysis using Neurosynth (Rubin et al., 2017) to identify
575 the 10 terms most commonly associated with the given map. This resulted in a set of 10 terms associated
576 with the average dynamic correlation patterns at each order.

577 **Acknowledgements**

578 We acknowledge discussions with Luke Chang, Vassiki Chauhan, Hany Farid, Paxton Fitzpatrick, Andrew
579 Heusser, Eshin Jolly, Aaron Lee, Qiang Liu, Matthijs van der Meer, Judith Mildner, Gina Notaro, Stephen
580 Satterthwaite, Emily Whitaker, Weizhen Xie, and Kirsten Ziman. Our work was supported in part by NSF
581 EPSCoR Award Number 1632738 to J.R.M. and by a sub-award of DARPA RAM Cooperative Agreement
582 N66001-14-2-4-032 to J.R.M. The content is solely the responsibility of the authors and does not necessarily
583 represent the official views of our supporting organizations.

584 **Author contributions**

585 Concept: J.R.M. Implementation: T.H.C., L.L.W.O., and J.R.M. Analyses: L.L.W.O. and J.R.M. Writing:
586 L.L.W.O. and J.R.M.

587 **References**

- 588 Allen, E. A., Damaraju, E., Plis, S. M., Erhardt, E. B., Eichele, T., & Calhoun, V. D. (2012). Tracking
589 whole-brain connectivity dynamics in the resting state. *Cerebral Cortex*, 24(3), 663–676.
- 590 Alvarez-Hamelin, I., Dall’Asta, L., Barrat, A., & Vespignani, A. (2005). *k*-corr decomposition: a tool for the
591 visualization of large scale networks. *arXiv*, cs/0504107v2.
- 592 Baldassano, C., Chen, J., Zadbood, A., Pillow, J. W., Hasson, U., & Norman, K. A. (2017). Discovering event
593 structure in continuous narrative perception and memory. *Neuron*, 95(3), 709–721.
- 594 Barthélémy, M. (2004). Betweenness centrality in large complex networks. *European Physical Journal B*, 38,
595 163–168.
- 596 Bassett, D., Meyer-Lindenberg, A., Achard, S., Duke, T., & Bullmore, E. (2006). Adaptive reconfiguration
597 of fractal small-world human brain functional networks. *Proceedings of the National Academy of Sciences,*
598 USA, 103(51), 19518–19523.
- 599 Beaty, R. E., Benedek, M., Silvia, P. J., & Schacter, D. L. (2016). Creative cognition and brain network
600 dynamics. *Trends in Cognitive Sciences*, 20(2), 87–95.
- 601 Betzel, R. F., Byrge, L., Esfahlani, F. Z., & Kennedy, D. P. (2019). Temporal fluctuations in the brain’s modular
602 architecture during movie-watching. *bioRxiv*, doi.org/10.1101/750919.

- 603 Bonacich, P. (2007). Some unique properties of eigenvector centrality. *Social Networks*, 29(4), 555–564.
- 604 Bressler, S. L., & Kelso, J. A. S. (2001). Cortical coordination dynamics and cognition. *Trends in Cognitive Sciences*, 5(1), 26–36.
- 606 Bullmore, E., & Sporns, O. (2009). Complex brain networks: graph theoretical analysis of structural and
607 functional systems. *Nature Reviews Neuroscience*, 10(3), 186–198.
- 608 Capota, M., Turek, J., Chen, P.-H., Zhu, X., Manning, J. R., Sundaram, N., . . . Shin, Y. S. (2017). *Brain imaging
609 analysis kit*.
- 610 Chang, C., & Glover, G. H. (2010). Time-frequency dynamics of resting-state brain connectivity measured
611 with fMRI. *NeuroImage*, 50, 81–98.
- 612 Chien, H.-Y. S., & Honey, C. J. (2019). Constructing and forgetting temporal context in the human cerebral
613 cortex. *bioRxiv*, doi.org/10.1101/761593.
- 614 Christakis, N. A., & Fowler, J. H. (2010). Social network sensors for early detection of contagious outbreaks.
615 *PLoS One*, 5(9), e12948.
- 616 Combrisson, E., Vallat, R., O'Reilly, C., Jas, M., Pascarella, A., l Saive, A., . . . Jerbi, K. (2019). Visbrain: a
617 multi-purpose GPU-accelerated open-source suite for multimodal brain data visualization. *Frontiers in
618 Neuroinformatics*, 13(14), 1–14.
- 619 Comon, P., Jutten, C., & Herault, J. (1991). Blind separation of sources, part II: problems statement. *Signal
620 Processing*, 24(1), 11–20.
- 621 Demertzi, A., Tagliazucchi, E., Dehaene, S., Deco, G., Barttfeld, P., Raimondo, F., . . . Sitt, J. D. (2019). Human
622 consciousness is supported by dynamic complex patterns of brain signal coordination. *Science Advances*,
623 5(2), eaat7603.
- 624 Estrada, E., & Rodríguez-Velázquez, J. A. (2005). Subgraph centrality in complex networks. *Physical Review E*, 71(5), 056103.
- 626 Etzel, J. A., Gazzola, V., & Keysers, C. (2009). An introduction to anatomical ROI-based fMRI classification.
627 *Brain Research*, 1281, 114–125.
- 628 Fallon, J., Ward, P. G. D., Parkes, L., & Oldham, S. (2020). Timescales of spontaneous fMRI fluctuations
629 relate to structural connectivity in the brain. *Network Neuroscience*, 4(3), 788–806.

- 630 Fong, A. H. C., Yoo, K., Rosenberg, M. D., Zhang, S., Li, C.-S. R., Scheinost, D., ... Chun, M. M. (2019).
631 Dynamic functional connectivity during task performance and rest predicts individual differences in
632 attention across studies. *NeuroImage*, 188, 14–25.
- 633 Freeman, L. C. (1977). A set of measures of centrality based on betweenness. *Sociometry*, 40(1), 35–41.
- 634 Friston, K. J. (2000). The labile brain. I. neuronal transients and nonlinear coupling. *Philosophical Transactions of the Royal Society of London*, 355B, 215–236.
- 635
- 636 Geisberger, R., Sanders, P., & Schultes, D. (2008). Better approximation of betweenness centrality. *Proceedings of the Meeting on Algorithm Engineering and Experiments*, 90–100.
- 637
- 638 Gershman, S. J., Blei, D. M., Pereira, F., & Norman, K. A. (2011). A topographic latent source model for
639 fMRI data. *NeuroImage*, 57, 89–100.
- 640 Gonzalez-Castillo, J., Caballero-Gaudes, C., Topolski, N., Handwerker, D. A., Pereira, F., & Bandettini, P. A.
641 (2019). Imaging the spontaneous flow of thought: distinct periods of cognition contribute to dynamic
642 functional connectivity during rest. *NeuroImage*, 202(116129).
- 643 Grossberg, S. (1988). Nonlinear neural networks: principles, mechanisms, and architectures. *Neural Networks*, 1(1), 17–61.
- 644
- 645 Halu, A., Mondragón, R. J., Panzarasa, P., & Bianconi, G. (2013). Multiplex PageRank. *PLoS One*, 8(10),
646 e78293.
- 647 Hasson, U., Chen, J., & Honey, C. J. (2015). Hierarchical process memory: memory as an integral component
648 of information processing. *Trends in Cognitive Sciences*, 19(6), 304–315.
- 649 Hasson, U., Yang, E., Vallines, I., Heeger, D. J., & Rubin, N. (2008). A hierarchy of temporal receptive
650 windows in human cortex. *The Journal of Neuroscience*, 28(10), 2539–2550.
- 651 Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and
652 overlapping representations of faces and objects in ventral temporal cortex. *Science*, 293, 2425–2430.
- 653 Hinton, G. E., & Salakhutdinov, R. R. (2006). Reducing the dimensionality of data with neural networks.
654 *Science*, 313(5786), 504–507.
- 655 Honey, C. J., Kotter, R., Breakspear, M., & Sporns, O. (2007). Network structure of cerebral cortex shapes
656 functional connectivity on multiple time scales. *Proceedings of the National Academy of Sciences, USA*,
657 104(24), 10240–10245.

- 658 Honey, C. J., Thesen, T., Donner, T. H., Silbert, L. J., Carlson, C. E., Devinsky, O., ... Hasson, U. (2012). Slow
659 cortical dynamics and the accumulation of information over long timescales. *Neuron*, 76, 423–434.
- 660 Huth, A. G., de Heer, W. A., Griffiths, T. L., Theunissen, F. E., & Gallant, J. L. (2016). Natural speech reveals
661 the semantic maps that tile human cerebral cortex. *Nature*, 532, 453–458.
- 662 Huth, A. G., Nisimoto, S., Vu, A. T., & Gallant, J. L. (2012). A continuous semantic space describes
663 the representation of thousands of object and action categories across the human brain. *Neuron*, 76(6),
664 1210–1224.
- 665 Jutten, C., & Herault, J. (1991). Blind separation of sources, part I: an adaptive algorithm based on
666 neuromimetic architecture. *Signal Processing*, 24(1), 1–10.
- 667 Kamitani, Y., & Tong, F. (2005). Decoding the visual and subjective contents of the human brain. *Nature
668 Neuroscience*, 8, 679–685.
- 669 Landau, E. (1895). Zur relativen Wertbemessung der Turnierresultate. *Deutsches Wochenschach*, 11, 366–369.
- 670 Lee, C. S., Aly, M., & Baldassano, C. (2020). Anticipation of temporally structured events in the brain.
671 *bioRxiv*, 10.1101/2020.10.14.338145.
- 672 Lee, D. D., & Seung, H. S. (1999). Learning the parts of objects by non-negative matrix factorization. *Nature*,
673 401, 788–791.
- 674 Lerner, Y., Honey, C. J., Katkov, M., & Hasson, U. (2014). Temporal scaling of neural responses to compressed
675 and dilated natural speech. *Journal of Neurophysiology*, 111, 2433–2444.
- 676 Lerner, Y., Honey, C. J., Silbert, L. J., & Hasson, U. (2011). Topographic mapping of a hierarchy of temporal
677 receptive windows using a narrated story. *The Journal of Neuroscience*, 31(8), 2906–2915.
- 678 Liégeois, R., Li, J., Kong, R., Orban, C., Van De Ville, D., Ge, T., ... Yeo, B. T. T. (2019). Resting brain
679 dynamics at different timescales capture distinct aspects of human behavior. *Nature Communications*,
680 10(2317), 1–9.
- 681 Lin, J. (2009). Divergence measures based on the Shannon entropy. *IEEE Transactions on Information Theory*,
682 37(1), 145–151.
- 683 Lohmann, G., Margulies, D. S., Horstmann, A., Pleger, B., Lepsius, J., Goldhahn, D., ... Turner, R. (2010).
684 Eigenvector centrality mapping for analyzing connectivity patterns in fMRI data of the human brain.
685 *PLoS One*, 5(4), e10232.

- 686 Lurie, D., Kessler, D., Bassett, D., Betzel, R., Breakspear, M., Keilholz, S., ... Calhoun, V. (2018). On the
687 nature of time-varying functional connectivity in resting fMRI. *PsyArXiv*, doi.org/10.31234/osf.io/xtzre.
- 688 Mack, M. L., Preston, A. R., & Love, B. C. (2017). Medial prefrontal cortex compresses concept representations
689 through learning. *bioRxiv*, doi.org/10.1101/178145.
- 690 Mairal, J., Ponce, J., Sapiro, G., Zisserman, A., & Bach, F. R. (2009). Supervised dictionary learning. *Advances*
691 in *Neural Information Processing Systems*, 1033–1040.
- 692 Mairal, J. B., Bach, F., Ponce, J., & Sapiro, G. (2009). Online dictionary learning for sparse coding. *Proceedings*
693 of the International Conference on Machine Learning, 689–696.
- 694 Manning, J. R., Ranganath, R., Norman, K. A., & Blei, D. M. (2014). Topographic factor analysis: a Bayesian
695 model for inferring brain networks from neural data. *PLoS One*, 9(5), e94914.
- 696 Manning, J. R., Zhu, X., Willke, T. L., Ranganath, R., Stachenfeld, K., Hasson, U., ... Norman, K. A. (2018).
697 A probabilistic approach to discovering dynamic full-brain functional connectivity patterns. *NeuroImage*,
698 180, 243–252.
- 699 McInnes, L., Healy, J., & Melville, J. (2018). UMAP: uniform manifold approximation and projection for
700 dimension reduction. *arXiv*, 1802(03426).
- 701 McIntosh, A. R. (2000). Towards a network theory of cognition. *Neural Networks*, 13(8–9), 861–870.
- 702 McIntosh, A. R., & Jirsa, V. K. (2019). The hidden repertoire of brain dynamics and dysfunction. *Network*
703 *Neuroscience*, doi.org/10.1162/netn_a_00107.
- 704 Mitchell, T. M., Shinkareva, S. V., Carlson, A., Chang, K. M., Malave, V. L., Mason, R. A., & Just, M. A.
705 (2008). Predicting human brain activity associated with the meanings of nouns. *Science*, 320(5880), 1191.
- 706 Newman, M. E. J. (2005). A measure of betweenness centrality based on random walks. *Social Networks*, 27,
707 39–54.
- 708 Newman, M. E. J. (2008). The mathematics of networks. *The New Palgrave Encyclopedia of Economics*, 2, 1–12.
- 709 Nishimoto, S., Vu, A. T., Naselaris, T., Benjamini, Y., Yu, B., & Gallant, J. L. (2011). Reconstructing visual
710 experience from brain activity evoked by natural movies. *Current Biology*, 21, 1–6.
- 711 Nocedal, J., & Wright, S. J. (2006). *Numerical optimization*. New York, NY: Springer.
- 712 Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern
713 analysis of fMRI data. *Trends in Cognitive Sciences*, 10(9), 424–430.

- 714 Opsahl, T., Agneessens, F., & Skvoretz, J. (2010). Node centrality in weighted networks: generalizing degree
715 and shortest paths. *Social Networks*, 32, 245–251.
- 716 Park, H.-J., Friston, K. J., Pae, C., Park, B., & Razi, A. (2018). Dynamic effective connectivity in resting state
717 fMRI. *NeuroImage*, 180, 594–608.
- 718 Pearson, K. (1901). On lines and planes of closest fit to systems of points in space. *The London, Edinburgh,
719 and Dublin Philosophical Magazine and Journal of Science*, 2, 559–572.
- 720 Pereira, F., Lou, B., Pritchett, B., Ritter, S., Gershman, S. J., Kanwisher, N., ... Fedorenko, E. (2018). Toward
721 a universal decoder of linguistic meaning from brain activation. *Nature Communications*, 9(963), 1–13.
- 722 Preti, M. G., Bolton, T. A. W., & Van De Ville, D. (2017). The dynamic functional connectome: state-of-the-art
723 and perspectives. *NeuroImage*, 160, 41–54.
- 724 Rao, C. R. (1982). Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology*,
725 21(1), 24–43.
- 726 Reimann, M. W., Nolte, M., Scolamiero, M., Turner, K., Perin, R., Chindemi, G., ... Markram, H. (2017).
727 Cliques of neurons bound into cavities provide a missing link between structure and function. *Frontiers
728 in Computational Neuroscience*, 11(48), 1–16.
- 729 Ricotta, C., & Szeidl, L. (2006). Towards a unifying approach to diversity measures: bridging the gap
730 between the Shannon entropy and Rao's quadratic index. *Theoretical Population Biology*, 70(3), 237–243.
- 731 Roy, D. S., Park, Y.-G., Ogawa, S. K., Cho, J. H., Choi, H., Kamensky, L., ... Tonegawa, S. (2019). Brain-
732 wide mapping of contextual fear memory engram ensembles supports the dispersed engram complex
733 hypothesis. *bioRxiv*, doi.org/10.1101/668483.
- 734 Rubin, T. N., Kyoejo, O., Gorgolewski, K. J., Jones, M. N., Poldrack, R. A., & Yarkoni, T. (2017). Decoding
735 brain activity using a large-scale probabilistic functional-anatomical atlas of human cognition. *PLoS
736 Computational Biology*, 13(10), e1005649.
- 737 Rubinov, M., & Sporns, O. (2010). Complex network measures of brain connectivity: uses and interpreta-
738 tions. *NeuroImage*, 52, 1059–1069.
- 739 Schreiber, T. (2000). Measuring information transfer. *Physical Review Letters*, 85(2), 461–464.
- 740 Shappell, H., Caffo, B. S., Pekar, J. J., & Lindquist, M. A. (2019). Improved state change estimation in
741 dynamic functional connectivity using hidden semi-Markov models. *NeuroImage*, 191, 243–257.

- 742 Simony, E., & Chang, C. (2020). Analysis of stimulus-induced brain dynamics during naturalistic paradigms.
743 *NeuroImage*, 216, 116461.
- 744 Simony, E., Honey, C. J., Chen, J., & Hasson, U. (2016). Dynamic reconfiguration of the default mode
745 network during narrative comprehension. *Nature Communications*, 7(12141), 1–13.
- 746 Sizemore, A. E., Giusti, C., Kahn, A., Vettel, J. M., Betzel, R. F., & Bassett, D. S. (2018). Cliques and cavities
747 in the human connectome. *Journal of Computational Neuroscience*, 44(1), 115–145.
- 748 Solomon, S. H., Medaglia, J. D., & Thompson-Schill, S. L. (2019). Implementing a concept network model.
749 *Behavior Research Methods*, 51, 1717–1736.
- 750 Spearman, C. (1904). General intelligence, objectively determined and measured. *American Journal of
751 Psychology*, 15, 201–292.
- 752 Sporns, O., & Honey, C. J. (2006). Small worlds inside big brains. *Proceedings of the National Academy of
753 Sciences, USA*, 103(51), 19219–19220.
- 754 Thompson, W. H., Richter, C. G., Plavén-Sigray, P., & Fransson, P. (2018). Simulations to benchmark
755 time-varying connectivity methods for fMRI. *PLoS Computational Biology*, 14(5), e1006196.
- 756 Tipping, M. E., & Bishop, C. M. (1999). Probabilistic principal component analysis. *Journal of Royal Statistical
757 Society, Series B*, 61(3), 611–622.
- 758 Toker, D., & Sommer, F. T. (2019). Information integration in large brain networks. *PLoS Computational
759 Biology*, 15(2), e1006807.
- 760 Tong, F., & Pratte, M. S. (2012). Decoding patterns of human brain activity. *Annual Review of Psychology*, 63,
761 483–509.
- 762 Turk-Browne, N. B. (2013). Functional interactions as big data in the human brain. *Science*, 342, 580–584.
- 763 van der Maaten, L. J. P., & Hinton, G. E. (2008). Visualizing high-dimensional data using t-SNE. *Journal of
764 Machine Learning Research*, 9, 2579–2605.
- 765 Vidaurre, D., Abeysuriya, R., Becker, R., Quinn, A. J., Alfaro-Almagro, F., Smith, S. M., & Woolrich, M. W.
766 (2018). Discovering dynamic brain networks from big data in rest and task. *NeuroImage*, 180, 646–656.
- 767 Zar, J. H. (2010). *Biostatistical analysis*. Prentice-Hall.
- 768 Zheng, M., Allard, A., Hagmann, P., & Serrano, M. . . A. (2019). Geometric renormalization unravels
769 self-similarity of the multiscale human connectome. *arXiv*, 1904.11793.

770 Zou, Y., Donner, R. V., Marwan, N., Donges, J. F., & Kurths, J. (2019). Complex network approaches to
771 nonlinear time series analysis. *Physics Reports*, 787, 1–97.