

Distinct Functional Connectivity Mode during Viewing Natural Scenes Revealed by Principal Component Analysis

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1 **Abstract**

2 A fundamental question in systems neuroscience is how spontaneous activity at rest is
3 reorganized during task performance. Recent studies suggest a strong relationship between
4 resting and task FC. Furthermore, the relationship between resting and task FC has been
5 shown to reflect individual differences. Particularly, various studies have demonstrated that the
6 FC has higher reliability and provides enhanced detection of individual differences while
7 viewing natural scenes. Although the large-scale organization of FC during rest and movie-
8 viewing conditions have been well studied in relation to individual variations, the re-organization
9 of FC during viewing natural scenes have not been studied in depth. In this study, we used
10 principal component analysis on FC during rest and movie-viewing condition to characterize
11 the dimensionality of FC patterns across conditions and subjects. We found that the variations
12 in FC patterns related to viewing natural scenes can be explained by a single component, which
13 enables identification of the task over subjects with 100% accuracy. We showed that the FC
14 mode associated to viewing natural scenes better reflects individual variations. Furthermore,
15 we investigated the signatures of movie-viewing-specific functional modes in dynamic FC
16 based on phase-locking values between brain regions. We found that the movie-specific
17 functional mode is persistent across time; suggesting the emergence of a stable processing
18 mode. To explain the reorganization of whole-brain FC through the changes in local dynamics,
19 we appeal to a large-scale computational model. This modelling suggested that the
20 reorganization of whole-brain FC is associated to the interaction between frontal-parietal and
21 frontal-temporal activation patterns.

22

23 Introduction

24 Neural dynamics underwrite information processing at multiple spatiotemporal scales. The
25 neural correlates of information processing at a local scale have been widely studied. However,
26 the integration of information in whole-brain level is also crucial for understanding brain function
27 (Baars, 1993; Tononi, 2004). Long-range synchronization of oscillatory activity has been
28 proposed as dynamical mechanism for mediating the interaction between brain areas in a task-
29 dependent manner (Engel et al., 2001; Fries, 2005). Recent studies showed that neuronal
30 synchronization mediates neuronal communication in large-scale cortical networks during task
31 performance (Betti et al., 2013) and resting state (de Pasquale et al., 2010).

32

33 Resting state functional connectivity (rs-FC) is a powerful technique to characterize large-scale
34 organization of brain activity based on the temporal correlations between blood oxygen level-
35 dependent (BOLD) signals (Biswal et al., 1995). Rs-FC patterns have been shown to provide
36 'fingerprints' for the functional brain organization of individuals (Finn et al., 2015). Furthermore,
37 recent studies showed strong relationship between the FC during resting state and task
38 performance (Betti et al., 2013; Cole et al., 2014, 2016; Rosenberg et al., 2015). The
39 relationship between resting state and task FC has been shown to reflect individual differences
40 (Tavor et al., 2016). In particular, experimental paradigms such as viewing natural scenes (i.e.
41 movie watching) are of interest due to their ecological validity (Betti et al., 2013). Several studies
42 found that FC has higher reliability and provides enhanced detection of individual differences
43 while viewing natural scenes (Kim et al., 2017; Vanderwal et al., 2015, 2017). However, the
44 features underlying the enhanced reliability of FC are not clear given that the large-scale
45 organization of FC is very similar during rest and viewing natural scenes. Theoretical studies
46 have proposed that entropy of the cortical activity space is reduced during task (Ponce-Alvarez
47 et al., 2015). Therefore, the functional reorganization during viewing natural scenes is expected
48 to reflect not only individual subject-specific variations but also task-specific variations.
49 Nevertheless, the task-dependent reorganization of FC during viewing natural scenes and its
50 relationship to individual subject-specific variations are poorly understood.

51

52 Understanding the organization of whole-brain FC during distinct conditions is challenging
53 because of enormous dimensionality, which increases quadratically with the number of brain
54 regions. Principal component analysis (PCA) is widely known and intuitive mathematical
55 procedure to characterize the dimensionality of data. PCA transforms a set of observations into
56 orthogonal components and allows characterizing the relationship between these orthogonal
57 components and the projections of individual observations. PCA and associated techniques
58 have been used to characterize resting-state fluctuations (Carbonell et al., 2011), whole-brain
59 connectivity dynamics (Allen et al., 2012) and disease-related rs-FC states (Craddock et al.,
60 2009). In this paper, we used PCA to investigate the dimensionality of FC during rest and
61 movie-viewing condition. Based on the projections of individual subjects and sessions on
62 principal components, we identified FC-states specific to natural viewing condition. Then, we

63 studied the consistency of this principal component across sessions, subjects, and under
64 different preprocessing approaches.

65

66 Another important question related to the task-dependent reorganization of FC is whether
67 alterations in grand-average FC (over the whole session) reflect a persistent (temporally stable)
68 functional state or they reflect the emergence of various functional states fluctuating over time
69 (Gonzalez-Castillo et al., 2015). To answer this question, we extended our analysis beyond
70 grand-average FC states and investigated the temporal fluctuations in FC states based on the
71 dynamics of phase-coupling among brain regions.

72

73 Although empirical findings provide insights on the task-dependent reorganization of whole-
74 brain FC, these results may not offer a mechanistic understanding. We therefore adopted a
75 mechanistic approach for task-dependent reorganization of whole-brain FC using large-scale
76 by physically plausible modelling framework. We constraint the long-range interactions
77 between brain regions by diffusion weight imaging-derived (DWI) structural connectivity, and
78 studied the alterations in local dynamics of each brain regions during natural viewing conditions.

79

80 **Results**

81 **Principal component analysis reveals distinctive FC mode during movie watching** 82 **condition**

83 The grand average FC during resting state and movie exhibited similar patterns ($r = 0.8$, p -
84 value < 0.0001) (Figure 1A). However, the similarity across FCs of individual subjects was
85 substantially higher under the same condition (resting state $r = 0.46 \pm 0.06$; movie $r = 0.49 \pm$
86 0.06) than across conditions ($r = 0.40 \pm 0.07$). To characterize the variations in FC during rest-
87 state and movie viewing conditions, we performed principal component analysis (PCA) across
88 FCs of individual subjects (Figure 1B-C).

89
90 We concatenated FCs of 21 individuals during 2 separate sessions of resting state and movie
91 watching conditions and then employed PCA. We found that the first principal component (PC-
92 1) explaining 25.8% of the variance (Figure 2A) reflected the dominant FC pattern that were
93 conserved over conditions. The projections of PC-1 were significantly correlated with global
94 signal standard deviations of individual subjects/session ($r = 0.99$, p -value < 0.0001) (Figure
95 2J). This result suggested that the principal mode of variation in FC reflects the global signal
96 variance and associated overall synchronization levels. However, the second principal
97 component (PC-2) (Figure 2C) explaining 7.2% of the variance clearly distinguished the movie
98 condition from resting state. Based on the projections of two principal components (i.e. 2-
99 dimensional projections of subject/session data on principal components), we found that movie-
100 specific PC-2 separates the two conditions with 100% accuracy (Figure 2D).

101
102 Previous studies have shown restricted subject movements and increased arousal while
103 watching natural scenes (Vanderwal et al., 2015). Therefore, the movie-specific PC may also
104 reflect the contributions of artefactual signal changes. To rule out possible artefactual
105 contributions, we repeated the analyses after regressing out the global signal (Figure 2E-H).
106 We found that after global signal regression (GSR) the first principal component (PC-1)
107 explaining 9.69% of the variance reflected movie-specific variations in FC. The projections of
108 PC-1 separated two conditions with 100% accuracy (Figure 2H). Furthermore, the topologies
109 of movie-specific component modes were highly consistent with and without GSR ($r = 0.81$, p -
110 value < 0.0001). These results showed that the movie-specific variations in FC patterns can be
111 explained by a single dimension.

112 113 **Movie-specific FC variations are consistent across sessions and they reflect individual** 114 **variations better than non-specific principal components**

115 We repeated the PCA (with and without GSR) using 2 sessions separately. For both sessions
116 we found the movie-specific and non-specific components without GSR (Figure 3A-B) and with
117 GSR (Figure 3C-D). Without GSR, PC-1 (global signal component) of session 1 and session 2
118 was significantly correlated ($r = 0.75$, p -value < 0.0001). However, the similarity between movie-
119 specific PC-2 of session 1 and session 2 was substantially higher than that of PC-1 ($r = 0.83$,

120 $p < 0.0001$). Similarly, with GSR, we found higher similarity between session 1 and session 2
121 for movie-specific PC-1 ($r = 0.82$, p -value < 0.0001) than for non-specific PC-2 ($r = 0.54$, p -
122 value < 0.0001). These results show that the movie-specific principal component is highly
123 consistent across sessions.

124

125 To investigate the individual variations associated to each principal component, we compared
126 the PC projections across sessions. We found that the projections of movie-specific
127 components were highly consistent across sessions (without GSR $r = 0.92$, p -value < 0.0001 ;
128 with GSR $r = 0.93$, p -value < 0.0001), and the correlations were substantially higher than those
129 of non-specific components (without GSR $r = 0.76$, p -value < 0.0001 ; with GSR $r = 0.52$, p -
130 value < 0.0001). These results show that the FC topography related to movie-watching
131 conditions reflects individual variations better than that related to resting condition.

132

133 **Movie-specific FC patterns are temporally stable**

134 We investigated whether the movie-specific FC patterns are temporally stable in time or
135 whether they emerge as a consequence of the fluctuations in FC (i.e. collection of single or
136 multiple transient states). We constructed dynamic FC (dFC) based on the time-dependent
137 fluctuations in phase-locking values (PLVs) between brain regions. First, we band-pass filtered
138 the BOLD time-series in 0.04-0.07Hz narrow-band. After employing Hilbert transform, we
139 calculated the PLVs at each time point using instantaneous phases of each brain region (Figure
140 4A). Then, we calculated the correlation between the instantaneous PLVs and average PLVs
141 of resting state and movie sessions. To avoid any session-specific bias, we calculated the
142 correlations between average PLVs of resting state and movie from session 1 and
143 instantaneous PLVs of session 2 (and vice versa). We also repeated the PCA on average PLV
144 matrices for session 1 and session 2 (Figure 4C, F). We found that the principal components
145 based on PLVs exhibit movie condition specificity for both sessions. Furthermore, movie-
146 specific PC of PLVs were highly correlated with that of Pearson correlation based FC ($r = 0.88$,
147 p -value < 0.0001).

148

149 For resting state sessions, the correlations between PLVs and average PLVs of movie sessions
150 were significantly lower than that for resting state sessions across time points (Wilcoxon signed-
151 rank test p -value < 0.0001 , for both session 1 and session 2). For movie sessions, the
152 correlations between PLVs and average PLVs of movie sessions were significantly higher than
153 that for resting state sessions across time points (Wilcoxon signed-rank test p -value < 0.0001 ,
154 for both session 1 and session 2) (Figure 4D-E). The results were the same when the analyses
155 were repeated using movie-specific and non-specific principal components instead of average
156 PLVs (Supplementary Figure 1). In addition, we constructed the average dFC across subjects
157 and estimated the correlation between the average PLVs at each time-point and average PLVs
158 of resting-state and movie sessions. We found that for both resting state and movie sessions,
159 the PLVs at each time-point exhibited higher correlations with grand-average PLVs of matching

160 condition (Supplementary Figure 1). We further employed PCA over the PLV fluctuations
161 concatenated across sessions for each subject. The trajectories of the principle components
162 revealed emergence of movie-specific FC as a distinct mode for most of the subjects
163 (Supplementary Figure 2). Nevertheless, we did not find task-specific components for PLVs
164 concatenated across all subjects and all sessions. These results suggest that the movie-
165 specific FC pattern emerges as a temporally stable mode during movie watching sessions,
166 although the time-resolved FC states is difficult to estimate.

167

168 **Large-scale computational modelling of the regional dynamics underlying movie-** 169 **watching FC**

170 We used a large-scale computational model to characterize the alterations in regional dynamics
171 associated to the movie-watching condition. We used Hopf normal model to characterize the
172 BOLD activity of each region (Deco et al., 2017). The regions were coupled to each other via
173 DWI-derived structural connectivity scaled by a global coupling parameter (Figure 5A). The
174 dynamics of each region were governed by local bifurcation parameter (a). The local bifurcation
175 parameters (a) reflects whether an individual region is dominantly in a noise-driven regime (a
176 < 0), oscillatory regime ($a > 0$), or alternates between the two regimes ($a \sim 0$) (Figure 5A). We
177 estimated the optimal global coupling and local bifurcation parameters of each subject/session
178 by maximizing the similarity (i.e. Pearson correlation) between empirical and model FCs using
179 gradient-descent optimization. There was no significant difference in the model fit for resting-
180 state ($r = 0.518 \pm 0.057$) and movie sessions ($r = 0.497 \pm 0.045$) ($T = 1.256$, p -value = 0.219,
181 permutation t-test).

182

183 To characterize the overall topology underlying each condition, first we estimated the optimal
184 global coupling parameter (g) and optimal bifurcation parameters (a) for resting state and movie
185 watching condition based on the similarity between average empirical and model FC. At rest,
186 the average optimal bifurcation parameters were low in parietal and temporal regions, whereas
187 they were higher in occipital and frontal regions (Figure 5B). For movie condition, the bifurcation
188 parameters were increased in parietal and temporal regions and decreased in anterior
189 cingulate, lateral prefrontal cortices and in supramarginal gyrus (Figure 5C). There was no
190 significant difference between the mean optimal bifurcation parameters of rest and movie
191 conditions (Figure 5D).

192

193 To quantify the group differences, we compared regional optimal bifurcation parameters of
194 resting state and movie sessions (Figure 6A). We found no significant differences in global
195 coupling parameters between rest and movie conditions (Figure 6B). In movie condition, the
196 local bifurcation parameters were significantly decreased towards negative values in bilateral
197 caudal anterior and posterior cingulate, right supramarginal gyrus, and left post- and para-
198 central cortices (Figure 6D). In contrast, the bifurcation parameters were significantly increased
199 in bilateral orbital frontal cortex, right lateral orbital frontal cortex, right middle rostral frontal

200 cortex, right superior parietal cortex, right fusiform gyrus, and left frontal pole and left medial
201 temporal cortex (Figure 6D).

202

203 Finally, we repeated the PCA on optimal bifurcation parameters across subjects and conditions
204 (Figure 6E-G). The first principal component (PC-1) explaining 41.77% of the variation and the
205 second principal component (PC-2) explaining 10.25% of the variation were both significantly
206 correlated with the contrast between average bifurcation parameters of movie and resting-state
207 sessions (PC-1 $r = 0.38$, p -value = 0.002; PC-2 $r = 0.73$, p -value < 0.0001). The first principal
208 component (PC-1) exhibited a strong positive peak in precuneus and isthmus of cingulate,
209 slightly higher values in medial frontal and temporal regions, which is very similar to default
210 mode network (DMN) topography (Figure 6E). The second principal component (PC-2) showed
211 higher values in temporal and frontal regions (Figure 6F). Furthermore, the second principal
212 component (PC-2) exhibited movie specificity (Figure 6G). This result shows that the alterations
213 in regional dynamics in the movie-condition reflect at enhanced influence of frontal-temporal
214 brain regions on whole-brain dynamics.

215 **Discussion**

216 We characterized the reorganization of FC during natural viewing condition compared to resting
217 state. Using principal component analysis, we found that the alterations in FC during natural
218 viewing condition can be explained along a single dimension or mode of variation (i.e. a
219 condition-specific pattern of connectivity that captures the variations across subjects). The
220 projections of the FCs of each subject on the movie-specific principal component provided a
221 clear separation between conditions with classification accuracy of 100%.

222

223 **FC signatures of viewing natural scenes**

224

225 The movie-specific FC topology exhibited enhanced connectivity between occipital-temporal
226 regions and frontal-parietal regions (Supplementary Figure 3). This result can be interpreted as
227 enhanced communication between sensory and association regions during natural viewing
228 condition. Previous studies reported that the subjects show decreased head movements and
229 higher arousal while natural viewing condition (Vanderwal et al., 2015). Therefore, the
230 exceptionally high classification power can also reflect systematic artifacts. To rule of this
231 possibility we repeated the analysis after global signal regression (GSR), separate sessions,
232 bandpass filtered signals, and phase-locking values. We found that the results are invariant to
233 different preprocessing approaches. Furthermore, the movie-specific FC mode was highly
234 consistent before and after GSR, and across sessions. The correlations between movie-
235 specific components across sessions were higher than those for non-specific components.
236 These findings confirmed previous studies showing the enhanced reliability and individual
237 subject detection during natural viewing conditions (Kim et al., 2017; Vanderwal et al., 2017).
238 In addition, we showed that the enhanced reliability and individual subject detection during
239 natural viewing conditions are driven by task-specific reorganization of FC, which is distinct
240 from the resting-state related individual variations.

241

242 Before GSR, the first principal component reflected the overall synchronization in FC (as well
243 as global signal variance). This was an expected result, since the global signal was consistently
244 reported as explaining the large amount of variation in BOLD signals (Carbonell et al., 2011).
245 However, our results showed that the global signal component is not related to the movie
246 condition. After GSR the global synchronization component disappeared, whereas the movie-
247 specific component remained intact. It is important to note that the global signal component
248 reflects the common FC topology across subjects and it was strongly correlated across
249 sessions. The high correlations between the projections of global signal components across
250 sessions suggest that the global signal component also explains individual variations. In other
251 words, the variations and similarities across subjects during resting-state are mostly driven by
252 the differences in global signal variance. However, in this study, it cannot be known to what
253 extend the global signal-related component and individual variations reflect neural,
254 hemodynamic and/or artefactual differences. The relationship between global signal

255 fluctuations and whole-brain synchronization is essential to understand individual subject
256 variations at resting-state.

257

258 **Stable task-specific FC patterns in dynamic FC**

259

260 We also investigated how movie-specific FC topography relates to the dynamic FC. We used
261 Hilbert transform on narrowband filtered time-series and characterized dynamic FC based on
262 phase-locking values across time. We found that the movie-specific principal components also
263 appear in FC and average PLVs of the narrowband filtered time-series. Then, we calculated
264 the similarity between grand-average PLVs of resting state and movie during one session and
265 the PLV fluctuations during the other session. We found that for movie sessions the PLV of
266 each time point was persistently more similar to the average PLVs of the movie sessions than
267 to those of the resting state sessions. In contrast, for resting sessions the PLV of each time
268 point was more similar to the resting state FC than to the movie FC. Overall, these results
269 showed that during natural viewing condition the FC is persistently reorganized into its
270 associated mode. One limitation of this approach is the substantial observation noise of
271 instantaneous PLVs in conjunction with limited variance explained by the PCs, which leads to
272 very low correlations between instantaneous PLVs. The stability of task-related FC patterns is
273 important for the assumptions behind large-scale computational modeling. Our results suggest
274 that whole-brain FC (at the time-scale of BOLD signals) is persistently reconfigured into a
275 distinct mode rather than an epiphenomenon reflecting activation of several transient states.

276

277 **Computational modeling of task-specific alterations**

278

279 Although variations related to the natural viewing condition can be explained in a single
280 dimension, it is very difficult interpret a whole-brain connectivity pattern. We proposed a
281 computational model to link the alterations in local dynamics to reorganization of whole-brain
282 FC. We used Hopf normal model to characterize BOLD signals. The motivation behind using
283 this model was that noise-driven and oscillatory dynamics can be modeled using a single
284 parameter (local bifurcation parameter). When the local bifurcation parameter of a particular
285 region is negative, the region exhibits noise-driven dynamics. For positive bifurcation parameter
286 values, the region exhibits sustained oscillations. Therefore, higher parameters values of a
287 region in the model indicate that the region has higher influence on its connected regions. The
288 model revealed significant decreases in bifurcation parameters particularly in cingulate cortex
289 (anterior and posterior cingulate) and in supramarginal gyrus. In contrast, the bifurcation
290 parameters significantly increased in lateral prefrontal cortex, medial temporal cortex and
291 superior parietal regions. These results showed that during movie condition, the influence of
292 frontal, temporal and parietal association regions on the whole-brain FC is enhanced.
293 Nevertheless, it is important to note that the model describes the BOLD signals in the
294 associated low-frequency narrow-band. Therefore, higher values of the bifurcation parameters

295 can also be interpreted as the contribution of low-frequency fluctuations in the regions is
296 enhanced since hemodynamic responses act as a low-pass filter. Furthermore, BOLD signals
297 are known to have negative relationship with the neural activity in middle frequency ranges
298 (Schölvinck et al., 2013). Therefore, the increased/decreased local bifurcation parameters
299 should be interpreted only in relation to low-frequency fluctuations.

300

301 Since the empirical data provided a clear separation of rest and movie conditions, we also
302 employed PCA on the bifurcation parameters of the model. The first PC mode showed a typical
303 pattern associated to the default mode network (DMN), in which the high values were observed
304 in isthmus cingulate, precuneus, medial frontal and temporal cortices. The second principal
305 component mode, characterized by higher bifurcation parameter values in temporal and frontal
306 regions, showed movie-specificity. These results suggested that the variations in bifurcation
307 parameters in frontal-parietal and frontal-temporal networks have exclusive contributions to the
308 organization of whole-brain FC during movie-viewing condition. Furthermore, we found that the
309 projections of the first and second principal components on movie sessions were negatively
310 correlated (spearman rank $r = -0.496$, p -value= 0.02). Therefore, the variations across both
311 task-specific and DMN-like activation patterns, and the antagonistic relationship between these
312 patterns are associated to task-related organization of FC. Nevertheless, based on these
313 results, it is not possible to draw conclusions on the causal mechanisms that drive the
314 relationship between DMN and task-related networks. The results may indicate that several
315 regions of DMN (particularly precuneus) having a role in mediating the switch between distinct
316 functional states, which is consistent with previous studies showing that precuneus dynamically
317 binds to distinct functional networks (Utevsy et al., 2014). An alternative explanation may
318 involve the variations of arousal and vigilance levels. This explanation is consistent with a
319 selective neuromodulatory enabling of intrinsic synaptic connections by ascending modulatory
320 neurotransmitter systems (e.g., noradrenaline). This is particularly relevant in light of the
321 systematic changes in the local bifurcation parameter that showed regionally-specific and
322 condition-sensitive effects in our modelling analyses.

323

324 **Limitations**

325

326 One limitation of our modeling results is that the model relies on DWI-derived SC, which has
327 limited performance on detecting interhemispheric connections, individual variations, and also
328 directions of the connections. In addition, the changes in directed effective connectivity may
329 also play role in defining the reorganization of FC during task (Gilson et al., 2017). We re-
330 analyzed the alterations in EC (Gilson et al., 2017) based on our current findings: the PCA
331 analysis of EC exhibited a better and clearer separation between resting-state and movie
332 sessions than FC (Supplementary Figure 4). Furthermore, the movie-specific principal
333 component of EC revealed enhanced connectivity from frontal regions towards parietal and
334 occipital brain regions, and from occipital and temporal regions toward parietal and frontal

335 regions (Supplementary Figure 3). Therefore, during natural viewing condition lower sensory
336 regions in occipital and temporal regions project to frontal and parietal higher-order association
337 regions, and that this pattern is completed as a recurrent loop by the frontal regions projecting
338 towards parietal regions and parietal regions projecting towards temporal and occipital regions.
339 These results are consistent with the alterations that we found in the local dynamics (i.e. under
340 fixed-connectivity assumption) such that frontal and parietal regions play crucial role in re-
341 organization of FC during task. In contrast, the model based on local dynamics cannot resolve
342 the alterations in sensory regions. Effective connectivity – as assessed using dynamic causal
343 modelling studies of the resting state – again point to a modulation of regional excitability by
344 different components of the default mode. For example, previous studies revealed that the
345 influence of the SN (salience network) and DAN (dorsal attention network) on the DMN (default
346 mode network) regions is inhibitory; whereas the DMN exerted an excitatory influence on the
347 SN and DAN regions (Zhou et al., 2018). Therefore, we speculate that the alterations in higher-
348 order association regions are better captured by the local dynamics because these regions
349 contribute to whole-brain organization through strong bidirectional connections across the
350 cortex, whereas the influence of sensory regions is dominantly unidirectional.

351

352 **Conclusion and future directions**

353

354 Current experimental paradigms are optimal to study task-dependent changes in BOLD signals,
355 but these are not optimal to study task-dependent re-organization of whole-brain FC.
356 Naturalistic condition, such as movie watching, that is comparable to the resting-state, may
357 have important implications on understanding the dynamic organization of whole-brain activity.
358 Here, we proposed a novel approach to link task-dependent functional organization and
359 dynamic functional connectivity. Nevertheless, it may not be possible to exploit the full potential
360 of dynamic organization of the brain through natural viewing paradigms. The major limitation of
361 this approach is that the natural viewing condition is a trivial task. Future studies may explore
362 other natural experimental paradigms that involve more challenging conditions such as problem
363 solving, navigation, social interactions, task engagement during present distractors. We
364 speculate that sophisticated natural tasks that require enhanced cognitive control may reveal
365 richer dynamical manifestation of functional reorganization. For example, certain challenging
366 tasks may show a better picture of dynamic reorganization of the whole-brain such as
367 consolidation of particular functional states in time (i.e. slow adaptation) and/or emergence of
368 observable transient functional states (i.e. multistability).

369

370

371

372 **Materials and Methods**

373 **Study design**

374 The fMRI imaging data used in this paper have been described in details elsewhere (Betti et
375 al., 2013; Mantini et al., 2012). Twenty-four right-handed young, healthy volunteers (15
376 females, 20–31 years old) participated in the study. They were informed about the experimental
377 procedures, which were approved by the Ethics Committee of the Chieti University, and signed
378 a written informed consent. The study included a resting state and a natural vision condition. In
379 the resting state, participants fixated a red target with a diameter of 0.3 visual degrees on a
380 black screen. In the natural-vision condition, subjects watched (and listened) to 30 minutes of
381 the movie “The Good, the Bad and the Ugly” in a window of 24x10.2 visual degrees. Visual
382 stimuli were projected on a translucent screen using an LCD projector, and viewed by the
383 participants through a mirror tilted by 45 degrees. Auditory stimuli were delivered using MR-
384 compatible headphones.

385

386 **Data acquisition**

387 Functional imaging was performed with a 3T MR scanner (Achieva; Philips Medical Systems,
388 Best, The Netherlands) at the Institute for Advanced Biomedical Technologies in Chieti, Italy.
389 The functional images were obtained using T2*-weighted echo-planar images (EPI) with BOLD
390 contrast using SENSE imaging. EPIs comprised of 32 axial slices acquired in ascending order
391 and covering the entire brain (32 slices, 230 x 230 in-plane matrix, TR/TE=2000/35, flip angle
392 = 90°, voxel size=2.875x2.875x3.5 mm³). For each subject, 2 and 3 scanning runs of 10
393 minutes duration were acquired for resting state and natural vision, respectively. Each run
394 included 5 dummy volumes – allowing the MRI signal to reach steady state, and an additional
395 300 functional volumes that were used for analysis. Eye position was monitored during
396 scanning using a pupil-corneal reflection system at 120 Hz (Iscan, Burlington, MA, USA). A
397 three-dimensional high-resolution T1-weighted image, for anatomical reference, was acquired
398 using an MP-RAGE sequence (TR/TE=8.1/3.7, voxel size=0.938x0.938x1 mm³) at the end of
399 the scanning session.

400

401 **Data preprocessing**

402 Data preprocessing was performed using SPM5 (Wellcome Department of Cognitive
403 Neurology, London, UK) running under MATLAB (The Mathworks, Natick, MA). The
404 preprocessing steps involved the following: (1) correction for slice-timing differences (2)
405 correction of head-motion across functional images, (3) coregistration of the anatomical image
406 and the mean functional image, and (4) spatial normalization of all images to a standard
407 stereotaxic space (Montreal Neurological Institute, MNI) with a voxel size of 3x3x3 mm³.
408 Furthermore, the BOLD time series in MNI space were subjected to spatial independent
409 component analysis (ICA) for the identification and removal of artifacts related to blood
410 pulsation, head movement and instrumental spikes (Smith et al., 2010). This BOLD artifact

411 removal procedure was performed by means of the GIFT toolbox (Medical Image Analysis Lab,
412 University of New Mexico). No global signal regression or spatial smoothing was applied.
413 For each recording session (subject and run), we extracted the mean BOLD time series from
414 the 66 regions of interest (ROIs) of the brain atlas (Hagmann et al., 2008)(see Supplementary
415 Table 1). 2 subjects were excluded due to signal dropout and 1 subject was excluded due to
416 substantial spikes in the time-series.

417

418 **Anatomical Connectivity**

419 Anatomical connectivity was estimated from Diffusion Spectrum Imaging (DSI) data collected
420 in five healthy right-handed male participants (Hagmann et al., 2008; Honey et al., 2009). The
421 grey matter was first parcellated into 66 ROIs, using the same low-resolution atlas used for the
422 FC analysis. For each subject, we performed white matter tractography between pairs of
423 cortical areas to estimate a neuroanatomical connectivity matrix. The coupling weights between
424 two brain areas were quantified using the fiber tract density, and were proportional to a
425 normalized number of detected tracts. The structural matrix (SC) was then obtained by
426 averaging the matrices over subjects.

427

428 **Principal component analysis**

429 For all subjects and sessions (i.e. 21 subjects, 2 resting state and 2 movie sessions) the
430 functional connectivity matrices were constructed based on Pearson correlation coefficient
431 between all pairs of ROIs.

432 The upper triangular parts of FC (i.e. $66(66 - 1)/2$ connections) matrices were concatenated
433 across subjects/sessions (21x4 session/subjects) leading to the feature matrix with dimensions
434 2145 x 84 (number of connections x number of sessions/subjects). Then, principal component
435 analysis was applied to the resulting feature matrix. The analyses were repeated for 1000
436 surrogates time-series with preserved power-spectrum based on each session/subject. The
437 dimensionality of the data was characterized by explained variance of the principal components
438 that are larger than those of the surrogates.

439 To quantify the consistency of principal components, we repeated the analysis using 2 separate
440 sessions. For both sessions, the feature matrices comprised the concatenated upper triangular
441 FC matrices of 1 resting state session and 1 movie session (i.e. 2145 x 42 matrices). The
442 consistency across sessions was quantified as Pearson correlation coefficients of the
443 components and the projection of components between sessions.

444 Since during natural viewing condition the individuals are shown to have restricted movements
445 and increase arousal (Vanderwal et al., 2015), the differences in FC can be substantially
446 affected by underlying artifacts. For this reason, we repeated all the analyses after regressing
447 out global signal from the time-series of each ROI.

448

449 **Dynamic functional connectivity**

450 Preprocessed time series were band-pass filtered in 0.04-0.07Hz range in order to reduce the

451 effects of low-frequency drift and high-frequency noise (Glerean et al., 2012). Then, Hilbert
452 transform was used for the assessment of dynamic functional connectivity (Demirtaş et al.,
453 2016; Glerean et al., 2012). The Hilbert transform, $S(t) = A\cos(\varphi(t))$ of the preprocessed
454 BOLD time series broke the signal down to an analytical signal $S(t)$ with an instantaneous phase
455 $\varphi(t)$ and amplitude A . For each time point t , the difference $\Delta\varphi_{ij}(t)$ between the phases of the
456 respective ROIs was calculated, where i and j are the indices of each ROI. The phase
457 differences were adjusted between 0 and π such that:

458

$$459 \quad \Delta\varphi_{ij}(t) = \begin{cases} |\varphi_i(t) - \varphi_j(t)|, & \text{if } |\varphi_i(t) - \varphi_j(t)| \leq \pi \\ 2\pi - |\varphi_i(t) - \varphi_j(t)|, & \text{otherwise} \end{cases} \quad 1$$

460

461 Then, the phase-locking values (PLVs), $PLV_{ij}(t)$ were constructed using the phase differences
462 normalized between 0 and 1, thereby representing perfect anti-synchronization and perfect
463 synchronization respectively, such that: $PLV_{ij}(t) = 1 - \Delta\varphi_{ij}(t)/\pi$.

464 We computed the grand-average PLVs for each session (i.e. resting state and movie watching).
465 Then, for each subject, we calculated the similarity (Pearson correlation coefficient) between
466 grand-average PLVs and time-resolved PLVs. In brief, for each subject two quantities were
467 estimated and compared as a function of time: the correlation between instantaneous PLVs
468 and grand-average PLVs for resting state and that for movie condition. To avoid the bias caused
469 by shared variability within each session, we calculated the grand-average PLVs of one
470 session, and then the similarities were calculated for the other session. Therefore, the analysis
471 was performed twice: the grand-average PLVs of session 1 projected to the PLVs of session 2
472 and the grand-average PLVs of session 2 projected to the PLVs of session 1. To provide a
473 better illustration for the magnitudes of correlations, we performed a same analysis averaging
474 the time-resolved PLVs across subjects (Supplementary Figure 1).

475 The principal component analysis was repeated for band-pass filtered time-series and average
476 PLVs. Since the PLVs were much more sensitive to global synchronization levels, we
477 subtracted the mean from each average PLV matrix. We also repeated the time-resolved
478 analysis using movie-specific and non-specific principal component instead of grand-average
479 PLVs. After identifying the principal component whose projections distinguish the resting
480 condition from movie condition, we re-projected each component on the instantaneous PLVs
481 using Pearson correlation coefficient (Supplementary Figure 1). We also performed PCA over
482 the concatenated time courses (i.e. 2 resting state and 2 movie sessions) of individual subject
483 PLVs. The trajectories of the first 2 principal components were plotted to illustrate the switch
484 between resting and movie watching conditions (Supplementary Figure 2).

485

486 **Computational modeling**

487 We modeled the whole-brain rs-fMRI BOLD signals using 66 nodes. Each node was coupled
488 with each other via DWI-derived structural connectivity (SC) matrix. We described the local
489 dynamics of each individual node using normal form of a supercritical Hopf bifurcation (Deco

490 et al., 2017). The advantage of this model is that it allows transitions between asynchronous
 491 noise activity and oscillations. Where ω is the intrinsic frequency of each node, a is the local
 492 bifurcation parameter, η is additive Gaussian noise with standard deviation β , the temporal
 493 evolution of the activity, z , in node j is given in complex domain as:

$$494 \quad \frac{dz_j}{dt} = [a_j + i\omega_j - |z_j|^2] + \beta\eta_j(t) \quad 2$$

495

496 and,

$$497 \quad z_j = \rho_j e^{i\theta_j} = x_j + iy_j \quad 3$$

498

499 This system shows a supercritical bifurcation at $a_j = 0$. Being specific, if a_j is smaller than 0, the
 500 local dynamics has a stable fixed point at $z_j = 0$, and for a_j values larger than 0, there exists a
 501 stable limit cycle oscillation with a frequency $f = \omega/2\pi$. Finally, the whole-brain dynamics is
 502 described by the following coupled equations:

$$503 \quad \frac{dx_j}{dt} = [a_j - x_j^2 - y_j^2]x_j - \omega_j y_j + g \sum_i C_{ij}(x_i - x_j) + \beta\eta_{x_j}(t) \quad 4$$

504

$$505 \quad \frac{dy_j}{dt} = [a_j - x_j^2 - y_j^2]y_j + \omega_j x_j + g \sum_i C_{ij}(y_i - y_j) + \beta\eta_{y_j}(t) \quad 5$$

506

507 Where C_{ij} is the Structural Connectivity (SC) between nodes i and j , g is the global coupling
 508 factor, and the standard deviation of Gaussian noise, $\beta = 0.02$. The natural frequency (f) of
 509 each region was taken as the peak frequency in the given narrowband of the corresponding
 510 region in the empirical time-series.

511 Following a similar approach previously employed on biophysically-based computational model
 512 (Deco et al., 2014), we analytically estimated the model FC using linearization of the system
 513 around a stable fix point. Where $\delta\mathbf{u} = \{\delta x_1 \dots \delta x_{66}, \delta y_1 \dots \delta y_{66}\}$ represents the Taylor expansion
 514 of the system, \mathbf{A} is the Jacobian matrix, and $\varepsilon(t)$ is the noise term, the fluctuations around the
 515 fix point can be described as:

$$516 \quad \frac{d\delta\mathbf{u}}{dt} = \mathbf{A}\delta\mathbf{u} + \varepsilon(t) \quad 6$$

517 Where the deterministic parts of right-hand side of equations 4 and 5 are described by $-F_j$ and
 518 $-G_j$, respectively, the Jacobian matrix of the system evaluated at the fixed point $\hat{x}_j, \hat{y}_j, j \in$
 519 $\{1 \dots 66\}$ can be constructed as:

$$\mathbf{A} = \begin{bmatrix} \frac{\partial F_1}{\partial x_1} & \dots & \frac{\partial F_1}{\partial x_N} & \frac{\partial F_1}{\partial y_1} & \dots & \frac{\partial F_1}{\partial y_N} \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ \frac{\partial F_N}{\partial x_1} & \dots & \frac{\partial F_N}{\partial x_N} & \frac{\partial F_N}{\partial y_1} & \dots & \frac{\partial F_N}{\partial y_N} \\ \frac{\partial G_j}{\partial x_1} & \dots & \frac{\partial G_j}{\partial x_N} & \frac{\partial G_j}{\partial y_1} & \dots & \frac{\partial G_j}{\partial y_N} \\ \frac{\partial G_1}{\partial x_1} & \dots & \frac{\partial G_1}{\partial x_N} & \frac{\partial G_1}{\partial y_1} & \dots & \frac{\partial G_1}{\partial y_N} \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ \frac{\partial G_N}{\partial x_1} & \dots & \frac{\partial G_N}{\partial x_N} & \frac{\partial G_N}{\partial y_1} & \dots & \frac{\partial G_N}{\partial y_N} \\ \frac{\partial G_N}{\partial x_1} & \dots & \frac{\partial G_N}{\partial x_N} & \frac{\partial G_N}{\partial y_1} & \dots & \frac{\partial G_N}{\partial y_N} \end{bmatrix}$$

521 Where $i, j \in \{1 \dots 66\}$, each element of matrix \mathbf{A} can be calculated as:

$$522 \quad \frac{\partial F_j}{\partial x_j} = \frac{\partial G_j}{\partial y_j} = a - g \sum_k C_{jk} \quad 7$$

523

$$524 \quad \frac{\partial F_j}{\partial x_l} = \frac{\partial G_j}{\partial y_l} = gC_{jl} \quad 8$$

525

$$526 \quad \frac{\partial F_j}{\partial y_j} = -\omega_0 \quad 9$$

527

$$528 \quad \frac{\partial G_j}{\partial y_j} = \omega_0 \quad 10$$

529

$$530 \quad \frac{\partial F_j}{\partial x_l} = \frac{\partial G_j}{\partial y_l} = 0 \quad 11$$

531

532 Where \mathbf{Q} is the noise covariance matrix, the covariance matrix of the system \mathbf{P} can be estimated
533 by solving Lyapunov equation:

$$534 \quad \mathbf{AP} + \mathbf{PA}^T = -\mathbf{Q} \quad 12$$

535

536

537 Finally, the model correlation matrix (FC) can be extracted from the covariance matrix as:

$$538 \quad mFC_{ij} = \frac{P_{ij}}{\sqrt{P_{ii}P_{jj}}}, i, j \in \{1 \dots 66\} \quad 13$$

539

540 We estimated the model optimal parameters a and g by maximizing the similarity between
541 model FC (equation 13) and empirical FC using gradient descent optimization. To avoid the
542 solutions reflecting a local minimum, for each subject/session we estimated the best solution
543 after repeating the optimization with 100 random initial conditions. The similarity between model
544 FC and empirical FC was quantified as Pearson correlation coefficient. For each subject, the
545 empirical functional connectivity was calculated as the average FC across the corresponding
546 conditions (i.e. resting state or movie sessions) of the corresponding subject.

547 The group comparisons for resting state versus movie sessions (optimal bifurcation parameters
548 and global coupling parameter) were done using permutation t-test (5000 permutations). For

549 optimal bifurcation parameters, the p-values were corrected using FDR approach with
550 Benjamini&Hochberg algorithm if necessary (Hochberg and Benjamini, 1990).

551

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553

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556

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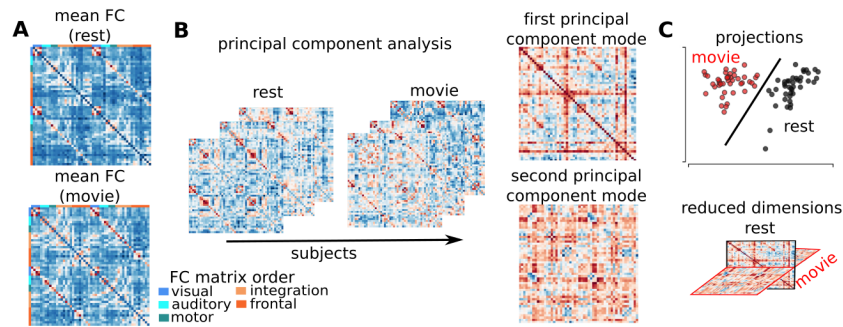
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658 **Figures and captions**

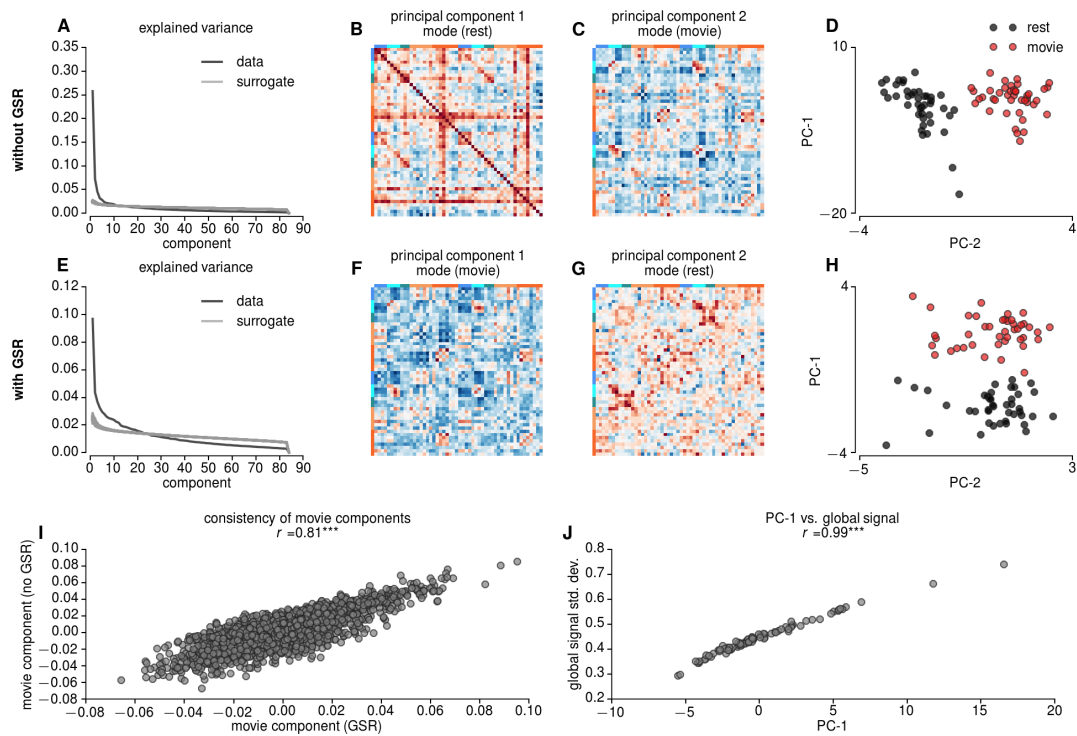
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661 **Figure 1.** Conceptual overview. **A** Mean FC across subjects during resting state (top) and
662 movie (bottom) sessions. For convenience the matrices were ordered by pre-defined networks
663 involving visual, auditory, motor, integration and frontal regions. **B-C** Overview of principal
664 component analysis (PCA). The FCs of the subjects at each session were concatenated into a
665 single feature matrix. Then PCs of the feature matrix was calculated (**B**). Note that the
666 (vectorized) FC features pertain to correlations over the number of regions squared. However,
667 the principal components of these FC features can be reorganized into a connectivity matrix
668 that has the same size as the number of connections – as shown on the right (of panel B). The
669 projections of each subject/session of the first two principal components were plotted against
670 each other (**C**). The second principal component projections revealed a clear distinction
671 between rest and movie sessions (top) leading to representation of FC variations in two
672 dimensions (bottom).

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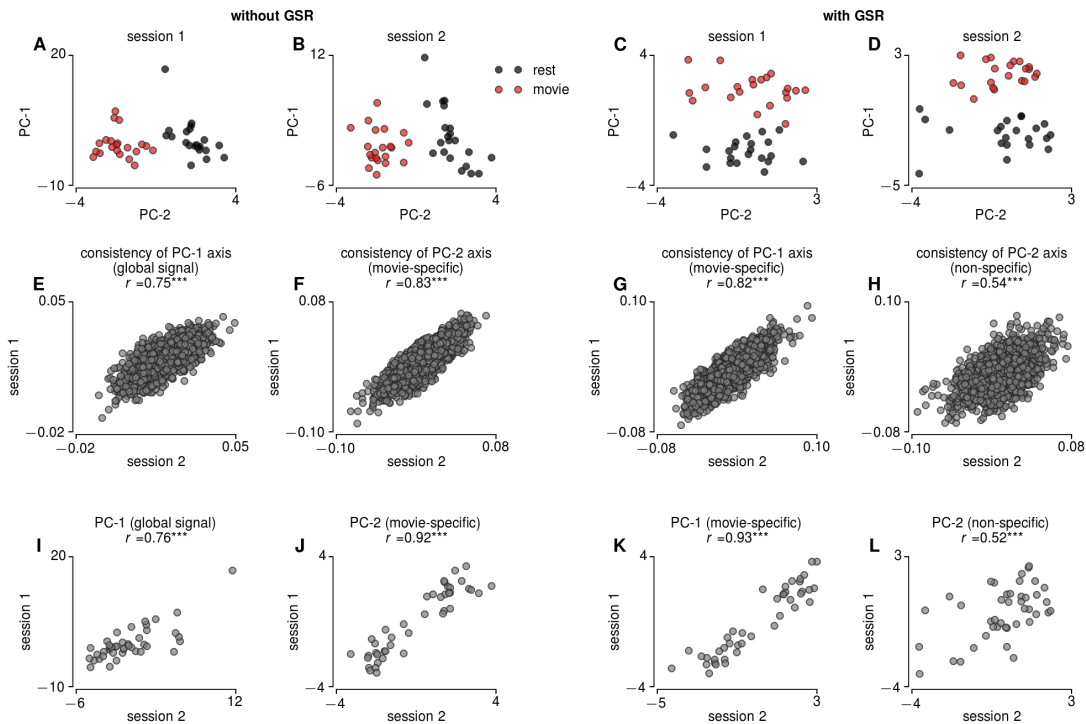
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Figure 2. Principal component analysis of FC based on 2 resting state and 2 movie sessions concatenated across 21 subjects. **A-D.** Results without global signal regression (GSR). **A** Explained variance by each PC (black) and random surrogates (gray) without GSR. Compared to 1000 random surrogates the dimensionality of FCs without GSR is 13. The first PC (**B**) explains 25.8% of the variation, whereas second PC (**C**) explains 7.2% of the variation. The projections of first two PCs reveals that the second component is specific to movie sessions (**D**). The first PC of the FCs without GSR reflects global signal standard deviation (**J**). **E-H.** Results with global signal regression (GSR). **E** Explained variance by each PC (black) and random surrogates (gray) with GSR. Compared to random surrogates the dimensionality of FCs with GSR is 22. The first PC, which is specific to movie sessions explains 9.69% of the variation (**F**). The movie-specific components with and without GSR is highly consistent. *** p-value < 0.0001.



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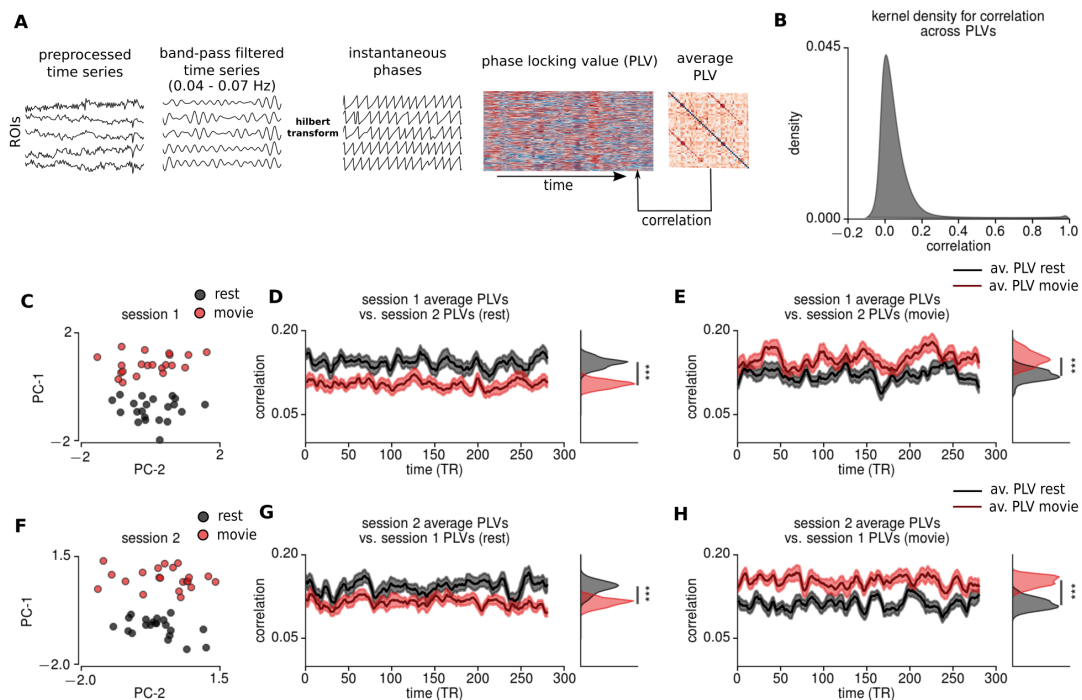
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Figure 3. The consistency of principal components across sessions. The second PC is specific to movie session in both session 1 (A) and session 2 (B) without GSR, whereas the first PC is movie-specific in session 1 (C) and session 2 (D) with GSR. The consistency of the movie-specific component (F without GSR; G with GSR) is substantially higher than that of the non-specific components (E without GSR; H with GSR). Similarly, the consistency of the projections for movie-specific component (J without GSR; K with GSR) is substantially higher than that of the non-specific components (I without GSR; L with GSR). *** p-value < 0.0001.



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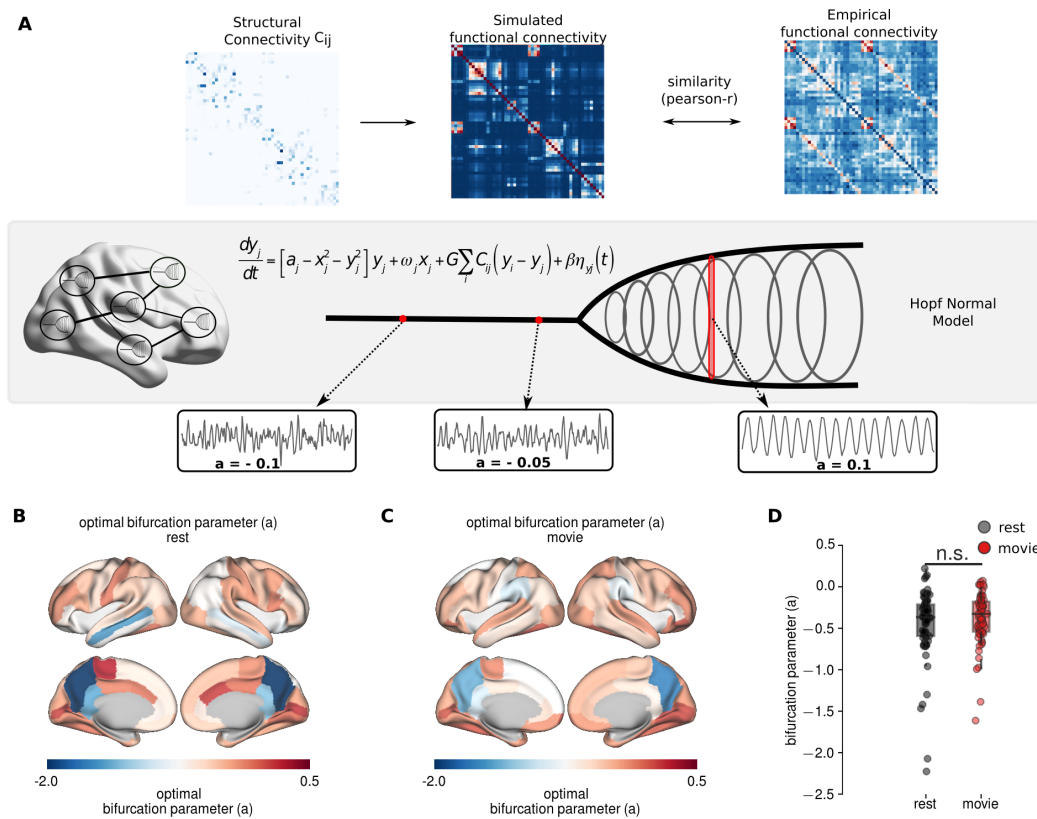
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Figure 4. Stability of movie-specific components in dynamic FC. **A** The schematic describing the derivation of phase-locking value (PLV) dynamics. **B** Kernel density estimates of the correlations across PLVs. **C** Components projections of session 1. **D** Correlations between average PLVs at rest (black), during movie condition (red) and PLVs of resting state session 2. **E** Correlations between average PLVs at rest (black), during movie condition (red) and PLVs of movie session 2. **F-H** The same procedure as C-E, where the average PLVs were calculated for session 2 and projected on session 1 PLVs. The similarity between average resting-state PLVs and instantaneous PLVs of resting state sessions are significantly higher than those of movie sessions (Wilcoxon signed-rank test, p -value < 0.0001) (**D,G**). Conversely, The similarity between average movie PLVs and instantaneous PLVs of movie sessions are significantly higher than those of resting state sessions (Wilcoxon signed-rank test, p -value < 0.0001) (**E,H**). Shaded regions indicate standard error of mean. *** indicates p -values < 0.0001 .



711

712 **Figure 5.** Large-scale computational modeling. **A** The schematic of the modeling framework.

713 The BOLD activity of each region was described using Hopf normal model, where the local

714 bifurcation parameters (a) mediate the local dynamics. Negative values of bifurcation

715 parameter, a, indicates noise-driven activity, whereas positive values indicate oscillatory activity

716 with increasing amplitude. Brain regions are coupled each other through DWI-derived SC

717 matrix. The optimal model parameters were estimated using gradient descent optimization,

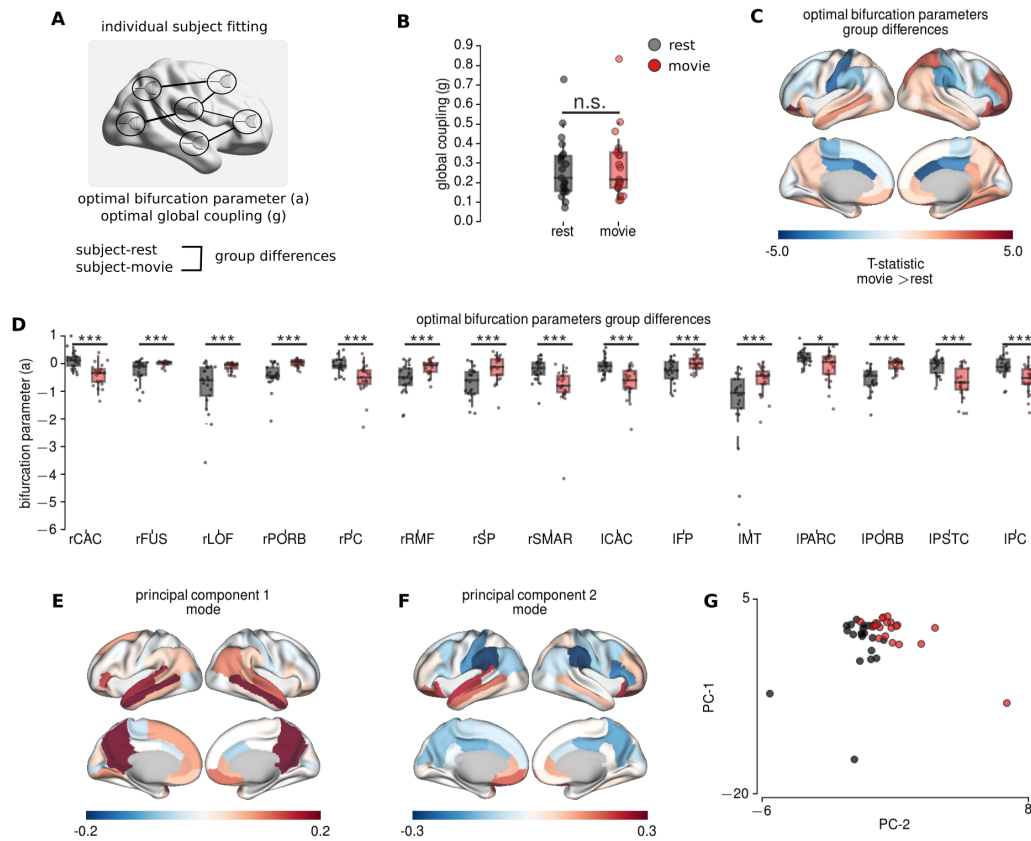
718 which maximizes the similarity between empirical and model FC. **B** Mean optimal bifurcation

719 parameter topography at resting state. **C** Mean optimal bifurcation parameter topography

720 during movie condition. **D** The distributions of the bifurcation parameters during movie condition

721 and resting state.

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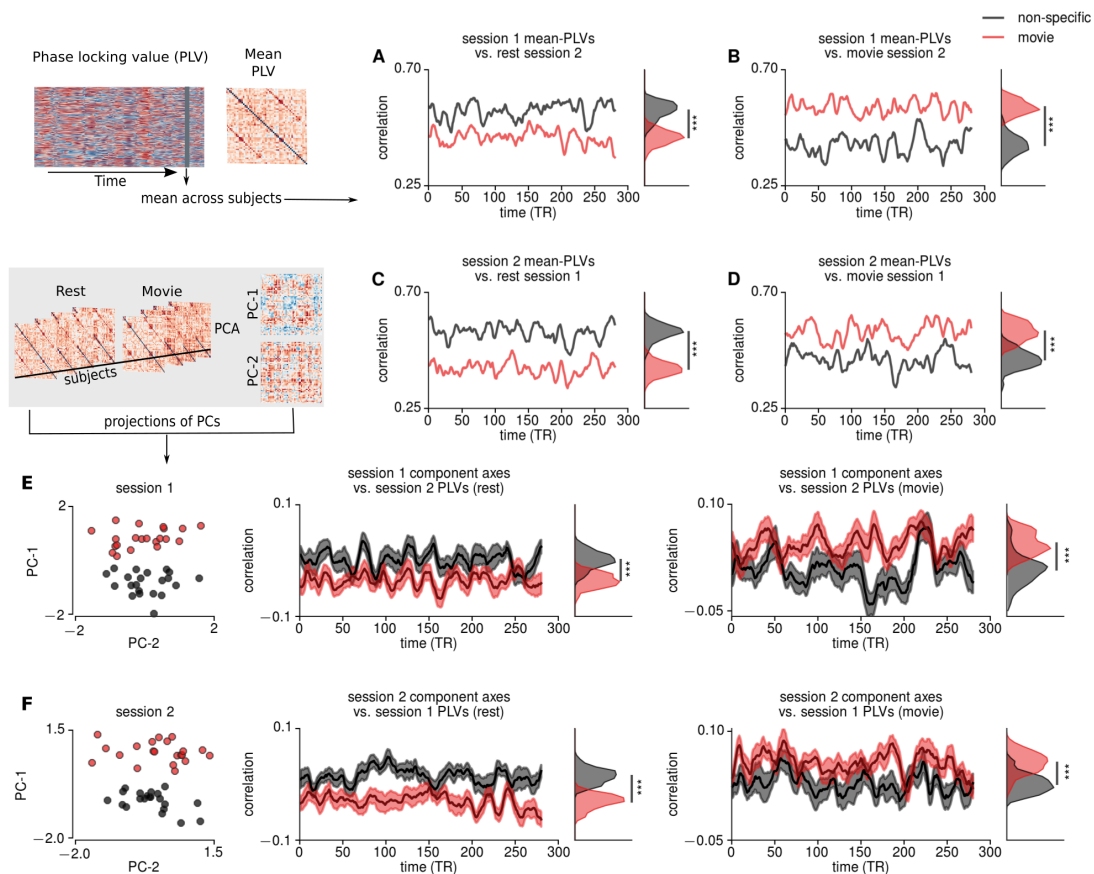


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724 **Figure 6.** Modeling results for individual subject fitting. **A** The schematic of individual subject
 725 fitting. **B** The group differences for global coupling parameters did not show significant
 726 difference. **C-D** The group differences between optimal bifurcation parameters at rest (black)
 727 and during movie condition (red) (permutation t-test, 5000 permutations). **C** The topography of
 728 the group differences (T-statistics; hot colors indicate larger values during movie condition). **D**
 729 Boxplots of the regions showing significantly difference after FDR correction. **E-G** Principal
 730 component analysis applied to optimal bifurcation parameters in the model. **E** The topography
 731 of the first principal component. **F** The topography of the second principal component. PC-1
 732 has higher values in precueus, posterior cingulate, medial temporal and frontal regions,
 733 exhibiting typical pattern associated to default mode network. PC-2 exhibit increased values in
 734 frontal and temporal regions, and decreased values particularly in supramarginal gyri and in
 735 medial brain regions. **G** The projections of the principal components on rest and movie
 736 sessions. *** indicate p-value < 0.0001.

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738 **Supplementary Figures**

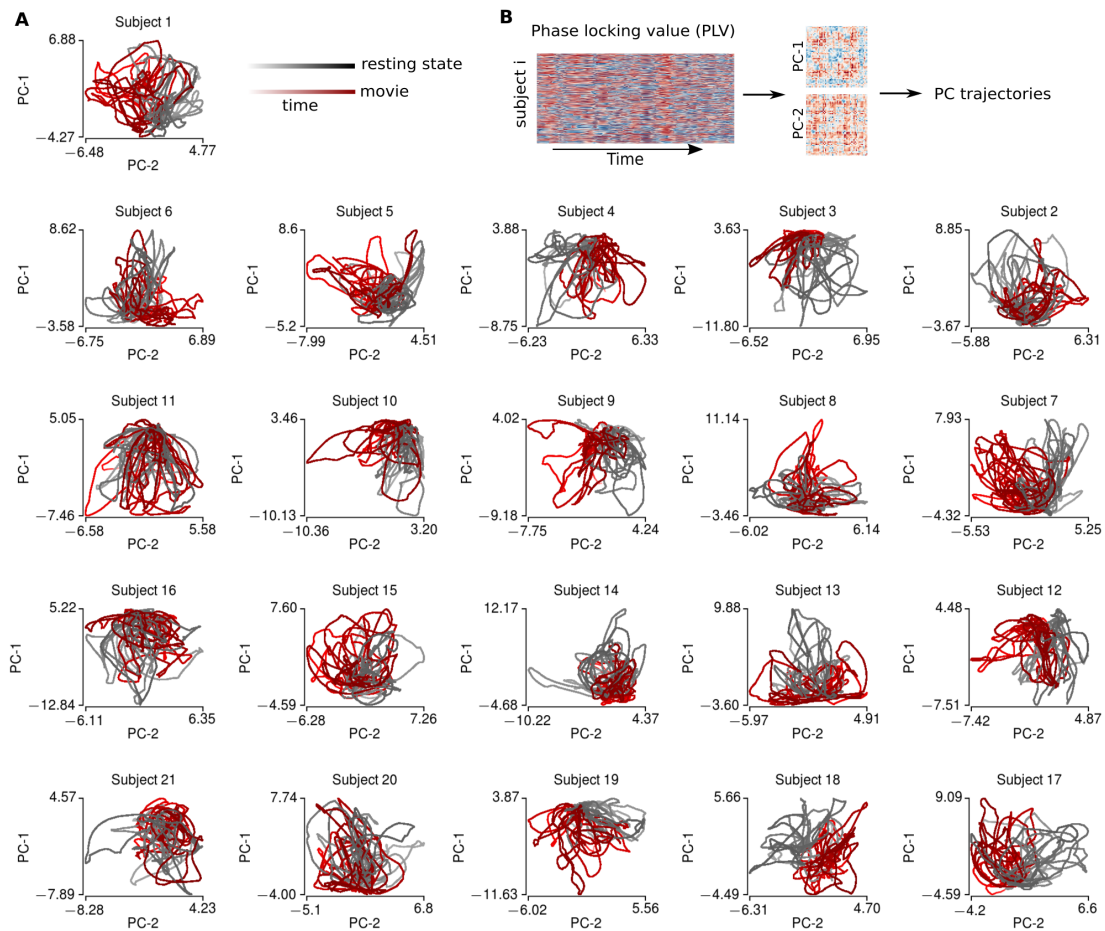


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Supplementary Figure 1. A-D The similarity between mean PLVs and instantaneous PLVs of each condition. The mean-PLVs were computed for resting-state and movie sessions, and then the correlation coefficient between condition-specific mean-PLVs and instantaneous PLVs (averaged across subjects) were calculated. Since higher correlations are expected between average and instantaneous PLVs for the same sessions, the analyses were done cross-sessions: We calculated the correlation between mean-PLVs of rest/movie sessions 1 and instantaneous PLVs of rest/movie sessions 2, and vice versa. E-F The similarity between movie-specific and non-specific principal components and instantaneous PLVs.

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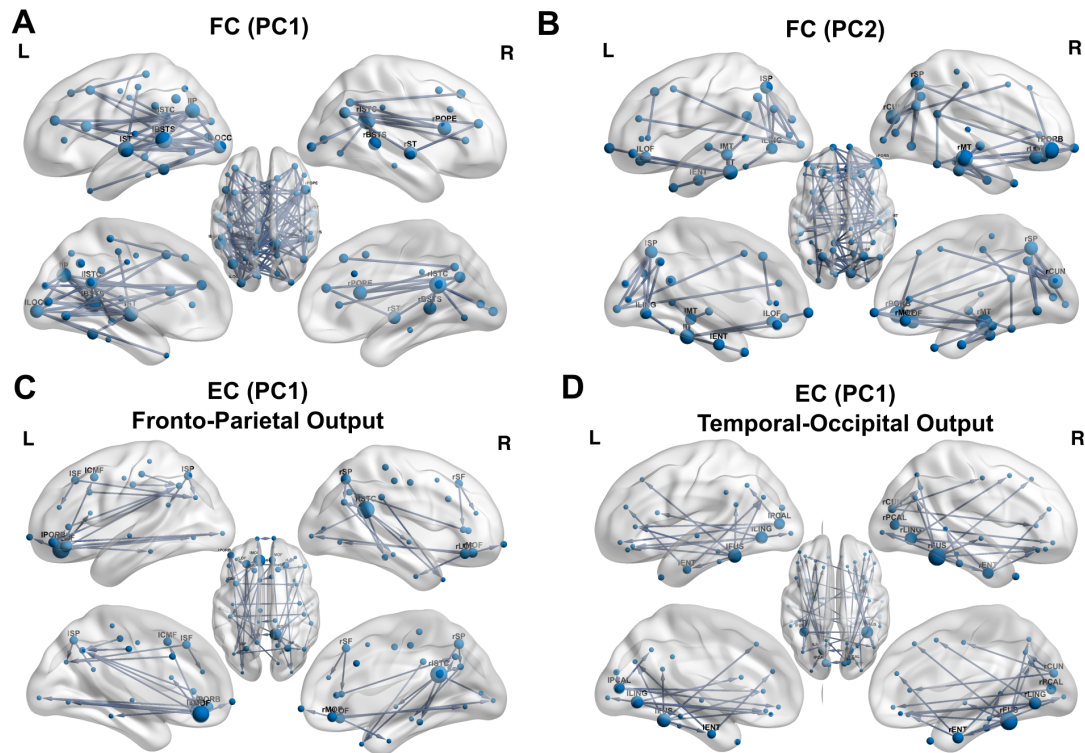


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Supplementary Figure 2. The trajectories extracted from the PCA on dynamic functional connectivity of each subject. Gray colors indicate the time course of the components at rest, red colors indicate time course of the components while watching movie.

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Supplementary Figure 3. The visualization of the highest 1% of the connections of PC-1 (A)

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and PC-2 (B) of FC, and PC-1 of EC (C-D). A The non-specific component of FC exhibits
757 larger connectivity strengths across posterior cingulate and precuneus, medial temporal and
758 frontal regions as well as occipital cortex, which suggests default-mode network connectivity.

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B The movie-specific component of FC shows high connectivity between occipital and
760 parietal regions, and between temporal and frontal regions. For effective connectivity (EC),

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movie-specific component reveals enhanced connectivity from frontal regions towards parietal

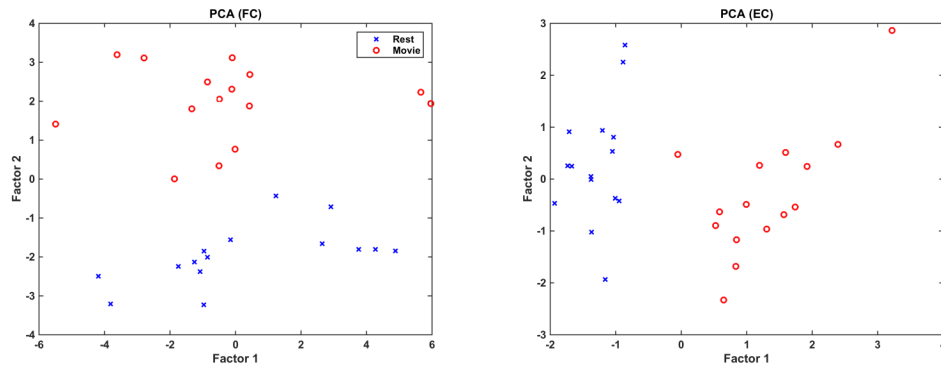
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and occipital brain regions (C), and enhanced connectivity from occipital and temporal

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regions toward parietal and frontal regions (D).

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766 **Supplementary Figure 4.** The PCA on functional connectivity (left) and effective connectivity

767 (right). The separation between resting-state and movie conditions are clearer in EC.

768 Furthermore, there is a strong correlation between the projections of movie-specific and non-

769 specific components only for movie sessions for effective connectivity.

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