Connectivity Based on Multi-Voxel Patterns Can Selectively Identify Brain Networks Where Condition-based Functional Connectivity Does Not: Evidence from the Scene Network

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With a major focus of neuroimaging research on mapping brain network connectivity, it is essential that researchers use the most effective methods for determining which regions comprise functional networks. Here, we compare the functional magnetic resonance imaging (fMRI) brain networks that can be identified through shared fluctuations in regions' univariate responses to conditions (i.e., condition-based functional connectivity), with those identified by shared fluctuations in multivariate information. To do this, we compare brain networks generated by two approaches for measuring connectivity: psychophysiological interaction (PPI), which measures the effect of conditions on shared univariate responses, and informational connectivity (IC), which measures shared fluctuations in the discriminability of multi-voxel patterns. We compare the findings generated by applying these methods to data collected while people perceptually process scenes and control (pseudo) scenes. Prior work establishing the regions involved in scene processing give us an opportunity to compare the sensitivity and selectivity of these approaches to detect a stimulus-relevant network. We find that, while each measure produces useful information, the PPI method was less selective than IC in detecting scene-related regions. Using PPI led to identifying networks containing both scene and object regions, with little specificity in connections between scene regions. In contrast, the network identified by IC was more consistent with prior literature examining the brain's scene network. We recommend that – for conditions known to be

represented in multi-voxel patterns – researchers wishing to prioritize specificity in mapping networks should examine informational connectivity over univariate connectivity approaches such as PPI.

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Preface

I would like to thank all of those who helped me through the creation of this document. Thank you to my friends and family for their support, especially my sister Katie, who was always willing to lend an ear. Thank you to everyone in my lab and my advisor, Dr. Marc Coutanche, for their unmatched encouragement and guidance.

1.0 Introduction

Functional magnetic resonance imaging (fMRI) has long been a useful tool for gaining insight into the brain and how it processes various cognitive tasks. Traditionally, univariate analysis techniques have been used to compare a region's average blood oxygen-level-dependent (BOLD) signal reactivity to certain stimuli (DeYoe, Bandettini, Neitz, Miller, & Winans, 1994). These types of analyses have proven very useful in identifying regions involved with different types of processing. For example, the parahippocampal place area (PPA) was originally identified as a scene-processing region when univariate comparisons showed that the region responds more to scenes than to other visual stimuli (Epstein & Kanwisher, 1998). Since this early work, the idea of examining the multi-voxel pattern of activity across a region's voxels has become increasingly popular. Instead of examining average signal differences between conditions, multivariate techniques, including multivoxel pattern analysis (MVPA), allow for more fine-grained comparisons between conditions and stimuli, by establishing if a region's activity patterns are able to distinguish different conditions (Haynes & Rees, 2006). For example, beyond knowing that a region's activation level distinguishes scenes from non-scenes, MVPA is able to decode forests from buildings from mountains (Walther, Caddigan, Fei-Fei, & Beck, 2009). This development allows investigators to probe a level of neural specificity that is more closely analogous to the cognitive specificity humans use during real-world cognitive processing. For instance, it is typically not informative for a human to recognize that they are viewing "an" environment, or "an" object. Instead, recognizing an environment as a forest, or an object as a hammer, is more frequently cognitively relevant. Multi-voxel patterns can track these more specific distinctions, in ways that univariate approaches cannot.

Over the last twenty years, cognitive neuroscientists have become increasingly interested in understanding how regions of the brain work together to achieve cognition. In a similar fashion to investigations of individual brain regions, multiple analysis techniques have been developed to measure “connectivity” between regions. While connectivity analyses have historically drawn on univariate techniques, newer techniques have recently emerged that allow us to investigate how the *information* in a region co-varies with others (Anzellotti & Coutanche, 2018). Here, we compare a popular approach to measuring connectivity based on univariate differences with a more recent approach that draws on multivariate information.

Psychophysiological interaction (PPI), an arm of functional connectivity, is an established univariate measure of context-based connectivity (Friston et al., 1997; Gitelman, Penny, Ashburner, & Friston, 2003). This measure allows for the investigation of how the time course of BOLD activity correlates between regions depending on condition. A currently favored form of PPI, generalized PPI (gPPI), has been shown to produce results that are more reliable than earlier versions (Cisler, Bush, & Steele, 2014; McLaren, Ries, Xu, & Johnson, 2012).

Another measure of connectivity, informational connectivity (IC), builds on the previously discussed multivariate developments in fMRI analyses, by incorporating a multivariate approach into examinations of connectivity (Anzellotti & Coutanche, 2018; Coutanche & Thompson-Schill, 2013, 2014). Several studies have used the method to identify regions that show common fluctuations in multi-voxel information over time (Aly & Turk-Browne, 2016; Huffman & Stark, 2014). Just as functional connectivity has allowed researchers to measure connectivity by predicting, or correlating, the mean activity in different ROIs across time (dependent on condition, in the case of PPI), informational connectivity correlates the time course of regions' multi-voxel pattern discriminability, which varies over time, in a manner similar to that of univariate responses.

In this study, we compare the types of brain networks identified by univariate and multivariate approaches– in this case, networks detected through PPI and IC . To do so, we used both measures to attempt to identify the brain's scene network based on data collected while participants viewed different scenes and pseudoscenes during an fMRI scan. The scene network is a good choice for comparing connectivity approaches, as it has been well established in the literature, with investigations of scene processing frequently identifying the occipital place area (OPA), parahippocampal place area (PPA), and retrosplenial cortex (RSC) as core parts of this network (Aminoff & Tarr, 2015; Groen, Silson, & Baker, 2017). The OPA is thought to serve as the first stage in the scene perception system (Dilks, Julian, Paunov, & Kanwisher, 2013). The PPA processes rich, viewpoint specific visual details of a scene, while the RSC is involved in viewpoint-invariant navigation and route learning (Epstein, Higgins, Jablonski, & Feiler, 2007; Park & Chun, 2009).

As a point of comparison, we also probed the object network as a control network. Although regions in the scene and object networks likely communicate with each other during perception, scene processing should typically elicit relatively more connectivity within the scene network (by definition), than with other networks, when scene processing is being performed. For key nodes of the object network, we examined two subregions of the lateral occipital complex (LOC), the LO and posterior fusiform gyrus (pFs), and the anterior temporal lobe (ATL). The LO is sensitive to size and location of objects, while the pFs is involved in processing illumination and viewpoint (Grill-Spector et al., 1999). The ATL has been shown to act as a convergence zone for processing different features of objects (Coutanche & Thompson-Schill, 2015).

Our goal for this study was to compare two connectivity measures in their abilities to effectively extract the scene network from the object network when tasked with distinguishing between scenes and pseudoscenes. We predicted that informational connectivity would more reliably detect the scene network than psychophysiological interactions based on its greater access to the scene-specific information that is represented in multi-voxel patterns.

2.0 Methods

Data from this study were originally collected and reported by Aminoff and Tarr (2015). It was later acquired by the authors via Open fMRI. Full experimental details are available from the original manuscript employing this data (Aminoff & Tarr, 2015), but the relevant elements are as follows.

Data from 15 participants (12 females; one left-handed; age range 18–33, M = 24) were collected with approval of the Carnegie Mellon Institutional Review Board. Participants gave their written informed consent and were monetarily compensated for participating. Scanning data were collected with a 3T Siemens Verio MR scanner. Functional data were collected with 2mm x 2mm x 3mm slice thickness, while the T1-weighted MPRAGE with 1mm x 1mm x 1mm.

2.1 Stimuli and Experimental Design

2.1.1 Pre-scan training and testing

Prior to the scan, participants were presented with “pseudoscenes” that we used as control stimuli for real scenes. These pseudoscenes were arrangements of shapes with predictable spatial relations between them (in a similar fashion as real scenes, in which objects are arranged with predictable spatial relations). In a pseudoscene, the same shapes were consistently presented in the same arrangements (see Figure 1). In this sense, the shape patterns contained scene-like information – they had consistent identity and location information. Just as objects tend to appear in consistent locations across scenes, these pseudoscenes had the same shapes appearing in consistent locations. Our use of pseudoscenes allowed for a scene-related contrast between pseudoscenes and scenes that would effectively draw upon the scene network.

Participants were incidentally presented with pseudoscenes among three other conditions over a period of about 25 minutes. The three other conditions were similar to pseudoscenes in that they were arrangements of shapes in particular manners, but differed in how they were arranged. Four pseudoscenes were learned over 30 presentations. All stimuli were preceded by a central fixation cross for 250 ms and a 250 ms blank screen, followed by the stimulus appearing on the screen for 2500 ms. While viewing the pseudoscenes, participants were asked to imagine 4 equally-sized quadrants dividing the screen presenting the stimuli. During each presentation, they were instructed to indicate how many of the quadrants contains at least one shape.

2.1.2 **Scanning**

Data from the main experiment was collected through 2 runs with a 2 second TR using a block design for a 224 TR run length. Each trial, a stimulus was presented with a fixation cross overtop for 2s. Participants passively viewed one of nine stimulus conditions at a time and were instructed to press a button when the fixation cross changed color (twice per block). For the present study, we used data from three of these conditions: scenes, pseudoscenes, and objects. In the original study, there were two blocks of each of the nine stimuli presented each run. Our scene condition collapsed across 3 conditions in the original experiment: hallways, roads, and intersections (i.e., there were 6 blocks of scenes and 2 of all other conditions in each run). Objects were everyday objects placed on a white background, with “weak-contextual associations” (as determined by the original authors), such as a garbage can or clock (Aminoff & Tarr, 2015).

Pseudoscenes were the arranged shapes participants trained on prior to their scan. Other conditions (not examined here) included the other shape arrangements from training and scrambled objects.

After the experimental functional runs, a separate localizer run consisting of 152 TRs was used (TR = 2.3s). It consisted of 84 scenes (indoor and outdoor) and 84 objects with weak contextual associations on a gray background (Aminoff & Tarr, 2015). The run was used to functionally define the scene network ROIs. Localizer data were collected using a block design with 12 stimuli blocks in one run. Half of the stimuli blocks were scene blocks and half were object blocks, which alternated and were interleaved by 8s of fixation. Participants completed a one-back task (two repeats per block) while viewing 16 stimuli (14 unique) in each block. Each stimulus was presented for 1s.

2.2 **Magnetic Resonance Imaging Preprocessing**

Imagining data were preprocessed using the Analysis of Functional NeuroImages (AFNI) software package (Cox, 1996). Slice-time and motion corrections were applied to all functional images so as to register them to a mean functional volume. A high-pass filter was used to remove low-frequency trends below 0.01 Hz from all runs. Activation for all voxels was scaled to a mean of 100 and a maximum activation limit of 200 was imposed. The time series was shifted by 2 TRs to account for hemodynamic lag.

2.3 **Regions of Interest**

Six regions of interest were created for each subject and used for analysis. The scene network consisted of the occipital place area (OPA), parahippocampal place area (PPA), and retrosplenial cortex (RSC). The object network included the LO and pFs (two subregions of the lateral occipital cortex, LOC) and the anterior temporal lobe (ATL). All ROIs consist of two spheres, one placed in each hemisphere. The PPA had an average of 259 voxels (*SD* = 26.03), the OPA, 248 (*SD* = 8.19), and the RSC, 250 (*SD* = 9.66). The LO was made up of 272 voxels on average (*SD* = 18.72), while the pFs had an average of 250 (*SD* = 11.08) and the ATL 259 (*SD* = 22.58). Importantly, the ROIs were identical for the two compared connectivity approaches. Thus, both connectivity approaches had the same potential for detecting networks.

The OPA, PPA, and RSC were functionally defined using univariate measures from the localizer run. A contrast of scenes minus objects was conducted and peak beta coefficients located in clusters in regions expected based on prior work were used as the center points for newly created ROIs. The RSC for subject 1, PPA in subject 10, and OPA for subjects 9 and 10 could not be functionally localized after cluster correction and so coordinates from previous papers were used (Bainbridge & Oliva, 2015; Frost & Goebel, 2012; Park & Chun, 2009). The LO and pFs were defined using coordinates from a previous paper (Grill-Spector, Kushnir, Hendler, & Malach, 2000), as was the ATL (Coutanche & Thompson-Schill, 2015).

2.4 **Connections of Interest**

We compared connectivity between scene regions (PPA to OPA, PPA to RSC, OPA to RSC), between object regions (LO to pFs, LO to ATL, pFs to ATL), and between inter-network regions (PPA to LO, PPA to pFs, PPA to ATL, OPA to LO, OPA to pFs, OPA to ATL, RSC to LO, RSC to pFs, RSC to ATL). Note that the order in which the connections are presented does not imply directionality.

2.5 **Decoding Analyses**

All MVPA analyses were conducted using MATLAB_R2017b with the Princeton MVPA Toolbox (Detre, et al., 2006). Analyses were conducted using ridge regression with an optimal penalty applied (Coutanche, Thompson-Schill, & Schultz, 2011).

A 2-fold cross-validation was conducted (training on 1 run, testing on the second) with a ridge regression applied with an optimal penalty to classify each TR as that of a pseudoscene or a scene in each ROI. The optimal penalty was selected using the training data only. The classifier was trained and tested on vectors of BOLD activity values within the ROIs. Because there were more scene blocks per run (6) than pseudoscene blocks per run (2), this decoding was done 10 times in each participant, where two of the scene blocks were randomly selected to be included in the cross-validation each time. The final decoding performance of an ROI was defined as the average output of each iteration. A one-way t-test was conducted in each ROI, testing the average decoding performances against chance (50%).

This process was repeated for pseudoscene-versus-object contrasts, instead training and testing on pseudoscene and object TRs. Because there were an equal number of object and pseudoscene presentations, however, the cross-validated decoding was conducted only once. After the 2-fold cross-validation, the final decoding performance for an ROI was defined as the group average of the classifier performance. A one-way t-test was again conducted in each ROI against chance (50%).

2.6 **Connectivity Analyses**

2.6.1 **Psychophysiological interaction**

Generalized PPI was conducted using AFNI in each subject's native space (Cox, 1996). Drift and motion regressors were first removed to create a fitted time series. Analyses were conducted with each of the six ROIs acting as the seed region. During each iteration, the time series of the seed was deconvolved with a Gamma basis function. We calculated the interaction of this output with each of the seven conditions separately, treating all scenes as one condition. The resulting interactions were convolved with the HRF. Each iteration, we conducted a regression predicting functional activity using each condition's timing information, head motion, the seed time series, and the interactions we calculated as predictors.

For each ROI seed and each condition of interest (objects, scenes, pseudoscenes), the interaction predictor beta weights were extracted from the other ROIs. Because connections between each ROI pair were each produced twice (once while the first ROI was the seed and again when the second ROI was the seed), we averaged the results between the ROI pairs to get a final

PPI connectivity value for each ROI-ROI connection for each condition of interest. To get the final difference scores, which reflects the impact of conditions upon functional connectivity, each subject's averaged beta values for the pseudoscene interaction were subtracted from those of the scene interaction. This was repeated with an object minus pseudoscene difference score. Significance tests for these difference scores were conducted via one-way t-tests against 0.

2.6.2 **Informational connectivity**

All IC analyses were conducted using MATLAB_R2017b with the Princeton MVPA Toolbox (Detre, et al., 2006) and the Informational Connectivity Toolbox (Coutanche & Thompson-Schill, 2013).

Informational connectivity is a way of using multivoxel patterns to assess whether regions in the brain are able to discriminate conditions from one another concurrently (i.e., have shared time courses of discriminability). Discriminability values reflect a classifiers "confidence" in its guess on each trial where higher discriminability values represent a region's greater ability to discriminate conditions from one another (Coutanche & Thompson-Schill, 2014). Here, discriminability values across time were correlated between regions to produce informational connectivity. IC was calculated twice: once for pseudoscenes versus scenes and again for comparing pseudoscenes versus objects.

To assess statistical significance of the IC results, we conducted permutation testing. First, each subject's classifier testing labels were scrambled 100 times so that any block in the experiment could be labeled as either of the conditions of interest for the given contrast. Informational connectivity was repeated for each new set of labels, each set being held constant for both training and testing. To obtain a group *p*-value, a null distribution was generated by randomly sampling a classification accuracy value from every subject's 100 means 10,000 times, giving 10,000 permutated group means (each reflecting the average of one permuted value per subject). The group *p*-value was then calculated from this distribution by comparing the real group mean to this null distribution.

3.0 Results

3.1 **Decoding Performance**

All of the scene processing areas were able to decode scenes from pseudoscenes, OPA (M = .717, SD = .15, t(14) = 5.57, p < .001), PPA (M = .794, SD = .091, t(14) = 12.96, p < .001), RSC (M = .707, SD = .092, t(14) = 8.75, p < .001). Both LO (M = .617, SD = .092, t(14) = 4.90, p < .001) and the pFs (M = .570, SD = .114, t(14) = 2.34, p = .032) could also make this classification. The ATL was at chance, M = .501, SD = .069, t(14) = .058, p = .955).

Only LO (M = .572, SD = .094, t(14) = 2.96, p = .010) was able to decode pseudoscenes from objects. No other ROIs were able to make the discrimination, ps > .169.

3.2 **Connectivity**

3.2.1 **Psychophysiological interaction**

Multiple PPI results showed connections that had higher betas for scenes than pseudoscenes (see Figure 2). This included connections between regions of the scene network, as well as strong connections between the scene and object network regions. Notably, the strongest connection was between the two inter-network regions, the RSC and LO (M = .245, p = .001). There was a strong scene-network connection between the PPA and OPA (M = .182, p = .004). However, the PPA-LO connection (M = .182, p = .005) was stronger than those of the OPA-RSC

(M = .181, p = .006) and RSC-PPA (M = .161, p = .036). No other connections reached significance, ps > .171.

Four inter-network connections showed significant differences between PPI betas related to objects and pseudoscenes, (PPA-LO: M = .182, p = .024; PPA-pFs: M = .167, p = .031; RSC-LO: M = .147, p = .052; OPA-LO: M = .138, p = .015). No other regions showed significant differences, ps > .062.

3.2.2 **Informational connectivity**

Informational connectivity clearly and specifically identified the scene network. Strong connections were found between scene processing regions: PPA to OPA (M = .451, p < .001), PPA to RSC (M = .600, p < .001), and OPA to RSC (M = .336, p = .019. No significant levels of IC were determined between object processing regions, ps > .131, or between object and scene regions.

None of the regions were significantly informationally connected for the object vs. pseudoscene contrast, ps > .610.

4.0 Discussion

In this study, we examined how univariate and multivariate approaches to condition-based connectivity differ in identifying regions of the scene network. Using brain data collected while processing scenes and control stimuli ("pseudoscenes"), we found that inter-region connectivity based on shared fluctuations in multi-voxel pattern discriminability – informational connectivity – detected the scene network with greater specificity than did connectivity based on how shared univariate responses are modulated by condition (through PPI). Our IC findings showed strong connections between scene network regions. These results had a high degree of specificity: connections between object regions, and between object and scene regions, were not significant. While PPI results did indicate that the scene network was involved in the scene processing, they also implied strong connections existed among inter-network (i.e., object network – scene network and scene network – object network) connections. Moreover, the strongest connection in the PPI results was between the RSC (a scene processing region) and the LO (an object processing region). Our study aimed to compare the ability of IC and PPI to extract the scene network during a scene-relevant contrast. The scene network, which has been well-documented in the literature, provided us with a way of evaluating the effectiveness of our connectivity measures in identifying the network. We argue that the method of greatest value is that which offers the most interpretable results. Here, while the PPI results are reasonable, they do not effectively pull out the scene network. Our IC results, on the other hand, showed an easily interpretable pattern of results. The fact that we see the scene network specifically be identified with IC gives confidence that it would specifically identify networks in circumstances that are less well established. These results cannot be reduced to a result of thresholding. While it is true that some of the weaker connections in the

PPI results might disappear if we changed the threshold, the LO-RSC and LO-PPA connections would remain stronger than some of the intra-scene network connections.

It is interesting that the object network did not appear in the IC results. We believe these results are largely due to the stimuli used in the object-pseudoscene comparison. While there are certainly differences between the object and pseudoscene stimuli, the pseudoscenes contain 3D shapes. On top of this, because the shapes were connected with meaningful information when they were associated in the pseudoscene context, they are quite object-like. This may have made it difficult for the classifier to distinguish between the conditions. The PPI results did show two connections for this contrast. This suggests that in situations where connections are weaker, PPI can provide information about connections.

Our findings suggest that both connectivity measures provide separate advantages. Each analysis provides complementary information: more sensitivity in the PPI measure and more specificity in the IC. Moving forward, we suggest that those looking to define new networks with conditions that are known to be represented within multi-voxel patterns (such as scenes) should consider multivariate approaches to connectivity to help with the interpretability of results and the accuracy of the regions included in the network.

Appendix A Figures

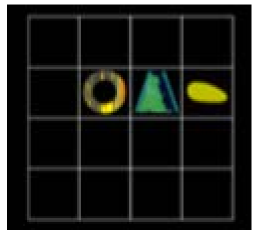

Figure 1 Example of a Single Pseudoscene

Figure edited from Aminoff & Tarr, 2015.

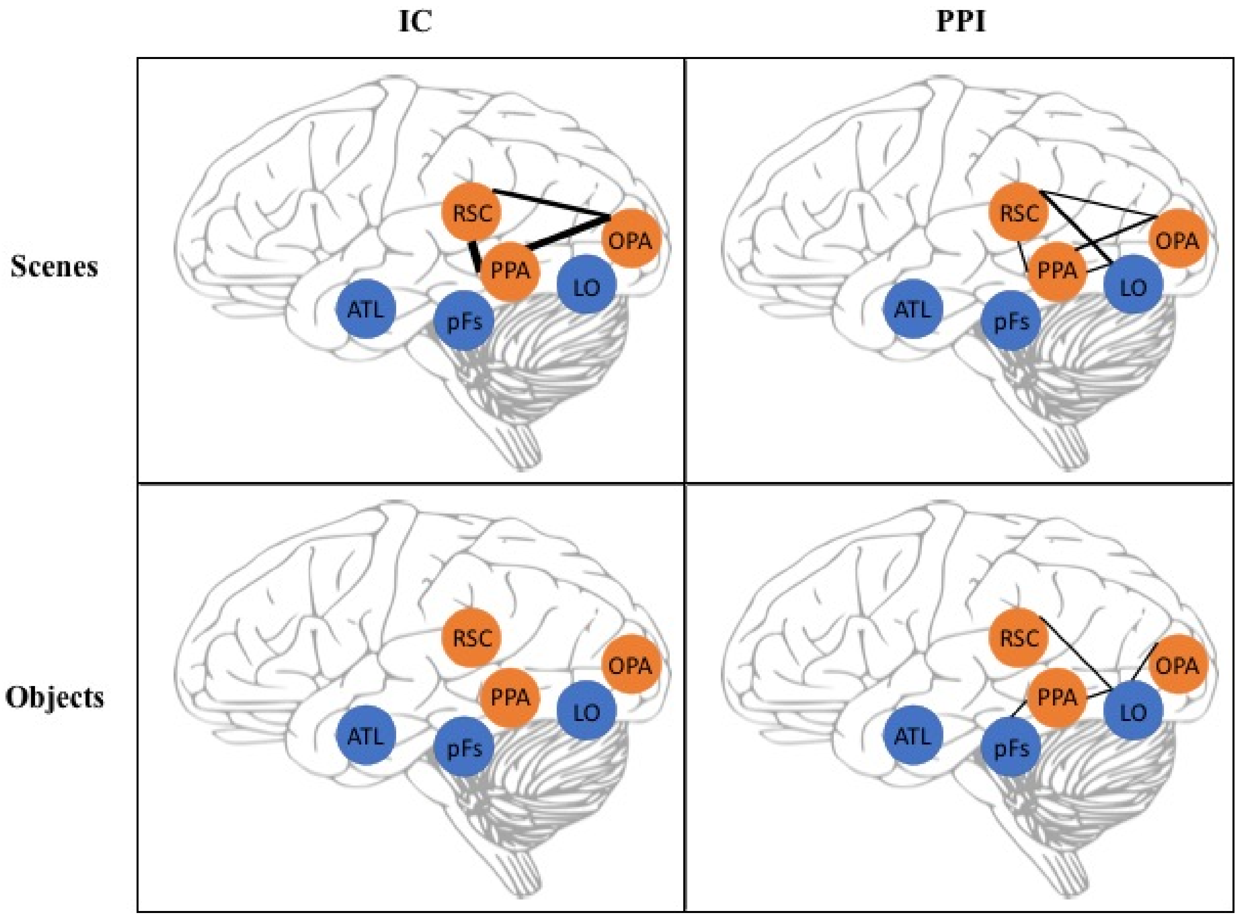

Figure 2 Connectivity Results from both Measures

IC = informational connectivity. PPI = psychophysiological interaction. Top row shows results from a contrast of scenes relative to pseudoscenes and bottom, objects and pseudoscenes. Line width indicates the average IC or PPI value in respective panels. Solid line indicates $p < .05$.

Appendix B Tables

Table 1 Ranked Connectivity Measures for Comparisons of Interest

Informational Connectivity				Psychophysiological Interaction			
Scenes vs. Pseudoscenes							
Rank	**Connection**	**Average**	***p***	**Rank**	**Connection**	**Average**	***p***
1	RSC PPA	0.601	<.001	1	RSC LO	0.245	0.001
2	PPA OPA	0.451	<.001	2	PPA OPA	0.194	0.004
3	OPA RSC	0.336	<.001	3	PPA LO	0.182	0.005
4	PPA pFs	0.282	0.087	4	OPA RSC	0.181	0.006
5	OPA LO	0.210	0.357	5	RSC PPA	0.161	0.036
6	RSC pFs	0.207	0.128	6	PPA pFs	0.097	0.196
7	OPA pFs	0.184	0.843	7	RSC pFs	0.096	0.171
8	LO pFs	0.170	0.528	8	OPA LO	0.055	0.334
9	PPA ATL	0.152	0.159	9	LO ATL	0.020	0.726
10	pFs ATL	0.135	0.285	10	PPA ATL	0.019	0.823
11	RSC LO	0.117	0.880	11	OPA ATL	0.013	0.851
12	RSC ATL	0.113	0.619	12	RSC ATL	0.011	0.877
13	PPA LO	0.109	0.161	13	OPA pFs	0.011	0.855
14	OPA ATL	0.074	0.626	14	LO pFs	-0.047	0.344
15	LO ATL	0.049	0.845	15	pFs ATL	-0.067	0.358
Objects vs. Pseudoscenes							
Rank	**Connection**	**Average**	***p***	**Rank**	**Connection**	**Average**	***p***
1	PPA OPA	0.229	0.803	1	PPA LO	0.182	0.024
2	PPA pFs	0.221	0.710	2	PPA pFs	0.167	0.031
3	OPA pFs	0.208	0.813	3	RSC LO	0.147	0.052
4	RSC PPA	0.208	0.607	4	OPA LO	0.138	0.015
5	LO pFs	0.192	0.734	5	PPA OPA	0.119	0.064
6	OPA LO	0.191	0.940	6	OPA pFs	0.106	0.062
7	PPA LO	0.186	0.855	7	RSC ATL	0.063	0.487
8	OPA RSC	0.180	0.867	8	RSC PPA	0.057	0.189
9	pFs ATL	0.149	0.811	9	LO pFs	0.054	0.462
10	RSC pFs	0.122	0.892	10	OPA RSC	0.053	0.486
11	OPA ATL	0.109	0.968	11	RSC pFs	0.038	0.57
12	PPA ATL	0.100	0.971	12	OPA ATL	-0.027	0.756
13	RSC LO	0.083	0.965	13	PPA ATL	-0.030	0.723
14	RSC ATL	0.080	0.913	14	LO ATL	-0.049	0.627

15	LO ATL	0.034	0.915	15	pFs ATL	-0.185	0.097

Notes. Average IC and PPI values and significance values organized in ranked order from most strongly connected to least strongly connected. Connections in orange contain two ROIs in the scene network. Blue, two ROIs in the object network.

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