

Correction

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Correction for “Cognitive relevance of the community structure of the human brain functional coactivation network,” by Nicolas A. Crossley, Andrea Mechelli, Petra E. Vértes, Toby T. Winton-Brown, Ameera X. Patel, Cedric E. Ginestet, Philip McGuire, and Edward T. Bullmore, which appeared in issue 28, July 9, 2013, of *Proc Natl Acad Sci USA* (110:11583–11588; first published June 24, 2013; 10.1073/pnas.1220826110).

The authors note that on page 11587, right column, first full paragraph, line 8–9, “All functional metadata were extracted from the BrainMap database” should instead appear as “All coordinate data and functional metadata were provided by the BrainMap database.”

Also, the authors note that the following statement should be added to the Acknowledgments: “Comprehensive access to the BrainMap database was authorized by a collaborative-use license agreement. BrainMap is supported by National Institutes of Health/ National Institute of Mental Health Award R01 MH074457.”

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Cognitive relevance of the community structure of the human brain functional coactivation network

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There is growing interest in the complex topology of human brain functional networks, often measured using resting-state functional MRI (fMRI). Here, we used a meta-analysis of the large primary literature that used fMRI or PET to measure task-related activation (>1,600 studies; 1985–2010). We estimated the similarity (Jaccard index) of the activation patterns across experimental tasks between each pair of 638 brain regions. This continuous coactivation matrix was used to build a weighted graph to characterize network topology. The coactivation network was modular, with occipital, central, and default-mode modules predominantly coactivated by specific cognitive domains (perception, action, and emotion, respectively). It also included a rich club of hub nodes, located in parietal and prefrontal cortex and often connected over long distances, which were coactivated by a diverse range of experimental tasks. Investigating the topological role of edges between a deactivated and an activated node, we found that such competitive interactions were most frequent between nodes in different modules or between an activated rich-club node and a deactivated peripheral node. Many aspects of the coactivation network were convergent with a connectivity network derived from resting state fMRI data ($n = 27$, healthy volunteers); although the connectivity network was more parsimoniously connected and differed in the anatomical locations of some hubs. We conclude that the community structure of human brain networks is relevant to cognitive function. Deactivations may play a role in flexible reconfiguration of the network according to cognitive demand, varying the integration between modules, and between the periphery and a central rich club.

connectome | economy | small world | workspace

Our understanding of human brain network organization has advanced considerably in the last decade (1). Graph theory has been increasingly used to describe the topological properties of anatomical and functional networks, typically based on estimates of structural or functional brain connectivity from MRI data (2). Several studies have confirmed that human brain networks have complex topological properties (3)—including small worldness; high-degree hub nodes; and a community structure that can be decomposed as a set of modules (4), or as a small rich club and a large periphery (5).

It remains an open question how the complex topological properties of human brain networks are related to their capacity for information processing or for adapting to changing cognitive demands. It has been shown that higher intelligence quotient is correlated with shorter topological path length of structural and functional networks, which would facilitate globally efficient, integrative processing (6, 7). Other studies have shown network changes under contrasting experimental conditions (8–10). However, the reliance on resting-state functional MRI (fMRI) as the experimental basis for most work on functional networks has limited the extent to which the topology of brain graphs has been related to cognitive tasks, or to other aspects of brain function,

such as local deactivations, which are well-established findings in task-related fMRI studies (11).

Meta-analysis is a powerful way of combining data from functional neuroimaging studies that have located task-related brain activations and deactivations. For example, it has been shown meta-analytically that deactivations elicited by a wide range of tasks are frequently located in the “default-mode network” (12, 13). Meta-analyses of task-related fMRI data have also estimated the frequency with which two brain regions are consistently activated across different tasks. This provides an alternative measure of functional connectivity between regions, without describing a possible direction of the influence (unlike causal or effective connectivity) (14). Such meta-analytic measures of task-related coactivation have been explored using “seed-based” analysis (identifying which other regions are coactivated with an arbitrary region or “seed”) (15, 16) and by independent component analysis (ICA) (identifying a set of components or systems of regions that are consistently coactivated with each other) (17). Thus, it has been shown that brain coactivation components can be meta-analytically linked to specific cognitive domains (18) and that they are anatomically similar to the systems identified by ICA of resting-state fMRI data (17).

Here, we combined a meta-analysis of cognitive task-related regional coactivation with a graph theoretical analysis of the topological properties of weighted functional coactivation networks. The strength of functional coactivation was estimated by the Jaccard index (range [0,1]), a measure of similarity between the patterns of activation of two regions reported across a large number of experimental contrasts in the primary literature of 1,641 task-related fMRI or PET studies published between 1985 and 2010, and collated in the BrainMap database (19, 20). From these data, we estimated the Jaccard index between each pair of 638 regional nodes covering the whole brain, collated these pairwise association measures in a continuous association matrix, and then built a weighted graph to investigate topological and spatial network properties in relation to the various cognitive tasks studied in the primary experiments. This method also allowed us to analyze the network position or topological role of cognitively deactivated nodes. We additionally compared the results to a functional connectivity network constructed from correlations between regional fMRI times series, measured at the same 638 nodal locations as in the coactivation analysis, from 27 healthy volunteers scanned in the resting state.

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Global and Nodal Properties of Coactivation and Connectivity

Networks. The coactivation network was topologically complex in several ways. The nodal degree distribution was fat-tailed with high-degree hub nodes located in: thalamus; putamen; insula; prefrontal, premotor, and precentral cortex; inferior parietal cortex; and ventral occipital cortex (Fig. 1*A* and *C*). Physically, this topology was embedded parsimoniously, in terms of the connection distance between coactivated nodes (Fig. 1*D*). Most connections or edges were short distance (median length of 57 mm; significantly shorter than random networks; $P < 10^{-3}$, permutation test). Relatively few edges were long distance, and these were often interhemispheric projections between bilaterally homotopic regions [14% of longest connections (defined as top 10 percentile) were homotopic; significantly more than random; $P < 10^{-3}$, permutation test]. Although the network cost was overall low, as measured by the distance of connections, the network topology still managed to balance integration and segregation between all brain regions: the clustering of the network thresholded at sparse levels was much higher than random, while retaining a similar path length, i.e., it was small world (21) (Fig. S1).

Partially for these respects, the organization of the coactivation network was convergent with properties of a comparable functional connectivity network generated from resting-state fMRI data. As known from prior studies (22, 23), and reproduced here, resting-state fMRI networks are small world, with fat-tailed degree distributions and parsimonious distance distributions (Fig. 1 C and D, and Fig. S1).

The correspondence between coactivation and connectivity networks was confirmed more quantitatively. The measure of functional coactivation (Jaccard index) was positively correlated with the functional connectivity measure (Z-normalized Pearson's correlation): strongly connected regions in the resting-state data tended to be strongly coactivated in the meta-analysis ($r = 0.49$; Fig. 1B). Both networks had fat-tailed degree distributions. The nodal degrees were significantly correlated between the two networks (Spearman's $\rho = 0.27$ for degree; $\rho = 0.3$ for weighted degree). These results indicate that nodes that were high-degree hubs in one network tended also to be hubs in the other, although the correspondence was not perfect. There were also differences in the length of connections, with the coactivation network having more long-range edges (Fig. 1D), particularly when considering the most strongly coactivated pairs of nodes (Fig. S2).

Modularity of Coactivation and Connectivity Networks. By a classical Newman decomposition (24), the coactivation network was found to be modular ($Q = 0.47$). It comprised four large modules, labeled anatomically: occipital, central (including sensorimotor areas), frontoparietal, and default mode (including medial frontal cortex, precuneus and posterior cingulate cortex, lateral parietal and temporal cortex, amygdala, and hippocampus) (25). The connectivity network derived from resting-state data were also modular ($Q = 0.49$), with four modules that approximated anatomically to the modules of the coactivation network (Fig. 1A and Fig. S3). The correspondence between coactivation and connectivity network modular decompositions

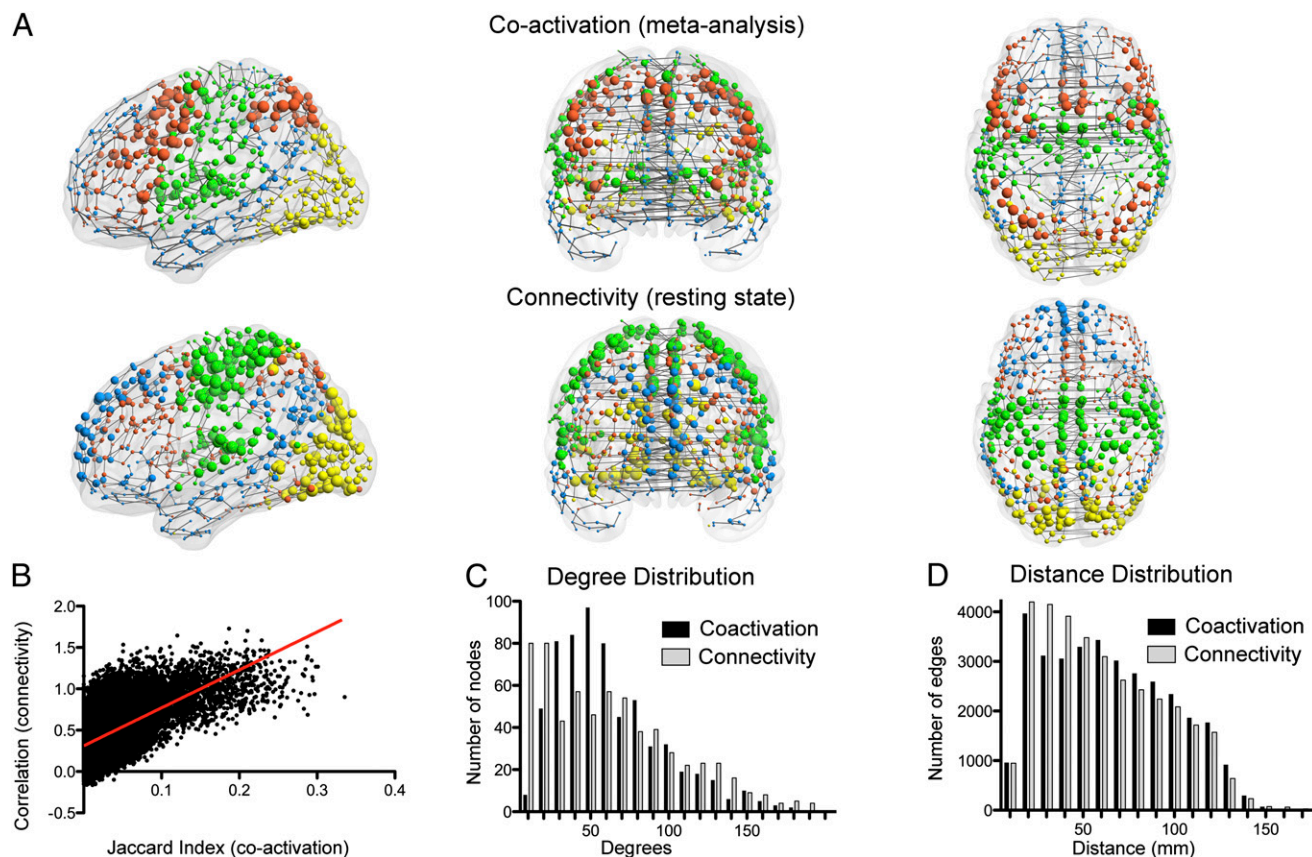
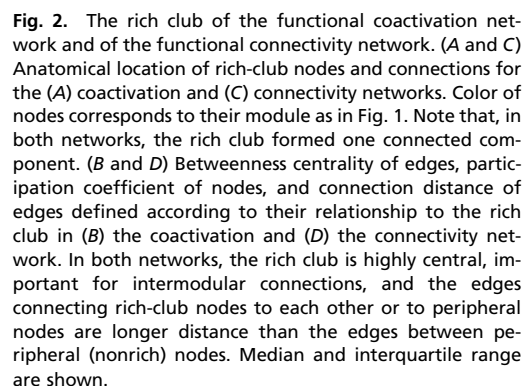


Fig. 1. The functional coactivation network based on meta-analysis of task-related fMRI studies has similar modularity and other properties to a functional connectivity network based on resting-state fMRI data. (A) Coactivation and connectivity networks plotted in anatomical space. The edges are defined by the minimum spanning tree for illustrative purposes. The size of the nodes is proportional to their weighted degree (strength), and their color corresponds to module membership. (B) Relationship between the coactivation metric (Jaccard index) and the connectivity metric (resting-state fMRI time series correlations) for every pair of regions. (C) Degree and (D) distance distributions of the coactivation network and a resting-state fMRI connectivity network.

Rich Clubs of Coactivation and Connectivity Networks. Rich-club analysis provides another perspective on the community structure of complex networks, describing networks that have an elite minority of highly interconnected hub nodes (the rich club) and a majority of less well-connected nodes (the poor periphery). The coactivation network had a rich club (Fig. S54), comprising

Likewise, the functional connectivity network derived from resting-state fMRI had a rich-club configuration (Fig. S5B). We first defined the rich club as the subset of the top 21 most highly connected nodes in the functional connectivity network. This size of club was chosen to facilitate comparison with the 21-node rich club of the coactivation network; for completeness, we also explored the rich-club organization of a larger subset of nodes in the fMRI connectivity network, but this did not substantively affect the results (SI Results and Fig. S6). The rich club ($n = 21$) was located in the central and occipital modules (Fig. 2C). Their edges also occupied a central position in the network (edge betweenness centrality greater than peripheral connections; $P < 10^{-3}$, permutation test; Fig. 2D); they were also important for intermodular connections (higher participation coefficient



in rich-club nodes than peripheral; $P < 10^{-4}$, permutation test), and they were more costly in the sense that the connection distance between rich-club nodes, and the distance of feeder connections, was greater than the distance of peripheral connections (both $P < 10^{-4}$, permutation tests).

For the coactivation network, we investigated the functional role of the rich club by analyzing the task-related contrasts that had generated edges between rich-club nodes. Rich-club nodes were most frequently coactivated by action (59%) or cognition tasks (30%), much less frequently by the other domains (Fig. S7A). It was also notable that the edges between rich-club nodes represented coactivation of pairs of regions by a more diverse range of task-related contrasts, whereas feeder or peripheral edges typically represented coactivations by experimental contrasts from a more restricted range of similar behavioral domains. The cognitive diversity of coactivation was quantified in the range [0,1], such that edges coactivated by only one behavioral domain scored 0 and edges diversely coactivated with equal frequency by all domains scored 1. We found that diversity was higher for rich-club connections (0.74) than for feeder (0.72) or peripheral connections (0.7; $P < 10^{-3}$ for both comparisons, permutation tests; Fig. S7B).

The Topological Role of Deactivations. We first looked at the role of deactivations (defined as fMRI signal greater during rest than during a task condition) by examining where they appeared in the coactivation network. In line with prior meta-analyses (12, 13), deactivations were most often located in nodes of the default-mode module (Fig. 3*B*).

Although coactivation of two regions indicates that they act “cooperatively” to perform a task, concomitant activation and deactivation of two regions could be described as a “competitive” interaction. To explore further the role of deactivations, we examined their relationship to those regions activated by the same task, and mapped these “competitive” activation/deactivation pairs to the coactivation network. Competitive interactions were significantly more likely to appear between nodes in different modules than nodes in the same module (odds ratio of 2.02; $P < 0.001$, permutation test). They were also much more likely to mediate a connection between an activated rich-club node and a deactivated peripheral node, than they were to mediate a connection between two peripheral or two rich-club nodes, or an activated peripheral node and a deactivated rich-club node (odds ratios of 4.4, 5.2, and 9.8, respectively; all $P < 0.01$, permutation tests, Bonferroni corrected; Fig. 3C).

Robustness Analysis. We considered the effects of various possible confounding or methodological factors on these results (*SI Materials and Methods*). Main findings were robust to variation in

the brain template used, assumptions when modeling activations from peak coordinates, and to controlling the estimation of coactivation for possible biases due to the uneven number of primary studies across behavioral domains (Table S1).

This analysis of the human brain functional coactivation network revealed a community structure that was similar (but not identical) to that of the functional connectivity network derived from resting-state fMRI. Moreover, the meta-analytic network provided insight into the cognitive specialization (or generalization) of the modules and the rich club of human brain functional networks, as well as suggesting a network role for cognitive deactivations.

Relatively specialist roles in cognitive processing could be assigned to most modules. The occipital module was mostly coactivated by tasks involving perception, the central module by action, the default-mode module by emotion, and the fronto-parietal module by executive tasks demanding action or cognition. These results are broadly in agreement with those obtained by previous studies using ICA (17, 18). For example, each of the four modules defined by our analysis corresponds closely to one or more of the 10 independent components reported by Smith et al. (19) on a nearly identical sample of the BrainMap database (Fig. S8). (The methodological and substantive commonalities and differences between ICA and graph analysis of the functional coactivation and connectivity networks are detailed more extensively in *SI Discussion*.) Thus, the modularity results are not surprising discoveries, but they provide support for the cognitive relevance of the graphical analysis of the coactivation network and, by extension, of the fMRI connectivity network.

The use of graph analysis also provided us with opportunities to go beyond the description of these basic building blocks of the functional brain network as explored with modularity analysis or ICA. For example, in addition to the highly segregated modules, we discovered the existence of a rich club that represented a key integrative element of both coactivation and connectivity networks [as has been suggested previously by analysis of anatomical networks (5, 27, 28)]. We were also able to demonstrate that local activation or deactivation of brain regions in response to task/rest contrasts could be related to the topology of the networks, with many competitive edges linking an activated node of the rich club to a deactivated node in the periphery. In short, the community structure of human brain functional networks can be rendered as a set of functionally specialized and topologically peripheral modules ranged around a functionally generalized and topologically central rich club (Fig. 3*A*).

Because topological modules in brain networks are often anatomically colocalized, i.e., topologically neighboring nodes tend

Defining Competitive Edges of the Network. We identified a subset of 110 contrasts from 67 studies that used rest or fixation as task control, and that reported both activations (task > rest) and deactivations (rest > task) for the same contrast. Each pair of regions activated and deactivated by a contrast in the primary literature was linked by a competitive edge and the topological and functional roles of the competitive edges were defined in relation to the topology of the corresponding nodes in the coactivation network (*SI Materials and Methods* and *Fig. S10B*).

fMRI Data Acquisition and Analysis. fMRI data were acquired from 27 healthy volunteers (mean age, 24 y) using a 3T Siemens Tim Trio system while they lay quietly at rest in the scanner with eyes closed. Gradient-echo echo-planar imaging data sensitive to blood oxygenation level-dependent contrast were recorded for 5 min, 6 s with the following parameters: relaxation time of 2 s; echo times, 13 and 31 ms; flip angle, 80°; voxel size, 3.5 × 3.5 × 3 mm; in-plane field of view, 22.5 cm; 36 interleaved slices. Images were slice-time corrected, realigned, and normalized. Regional mean time series were estimated for each of 638 gray matter regions, corrected by regression for head movement parameters (rotations and translations in three dimensions and their first derivatives) and the mean ventricular cerebrospinal fluid time series, and bandpassed (0.01–0.1 Hz). There was no evidence for residual

effects of head movement on these corrected regional mean time series (49) (*SI Materials and Methods* and *Fig. S12*). Pearson's correlations between each pair of time series in each individual were estimated, and normalized by the Fisher transform before averaging over individuals to estimate the group mean functional connectivity matrix. We then used a global thresholding rule to build a weighted network of the same connection density as the coactivation network.

Data Availability. The functional coactivation matrix, the group functional connectivity matrix, and the stereotactically coordinated template used for brain parcellation, are all freely available for download from the Brain Connectivity Toolbox (50).

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