Article

Intrinsic and Task-Evoked Network Architectures of the Human Brain

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SUMMARY

Many functional network properties of the human brain have been identified during rest and task states, yet it remains unclear how the two relate. We identified a whole-brain network architecture present across dozens of task states that was highly similar to the resting-state network architecture. The most frequent functional connectivity strengths across tasks closely matched the strengths observed at rest, suggesting this is an "intrinsic," standard architecture of functional brain organization. Furthermore, a set of small but consistent changes common across tasks suggests the existence of a task-general network architecture distinguishing task states from rest. These results indicate the brain's functional network architecture during task performance is shaped primarily by an intrinsic network architecture that is also present during rest, and secondarily by evoked task-general and task-specific network changes. This establishes a strong relationship between resting-state functional connectivity and task-evoked functional connectivity—areas of neuroscientific inquiry typically considered separately.

INTRODUCTION

Recent advances in human neuroimaging have led to numerous studies characterizing interregional temporal relationships during task and resting states (Fox and Greicius, 2010; Friston, 2011). Initial functional connectivity (FC) studies focused on FC during task states (Friston, 1994), yet FC during the resting state has come to dominate the field (Biswal et al., 2010). There are many reasons for this shift in focus, although perhaps the most influential is the notion that resting-state FC may characterize an "intrinsic" functional network architecture that is present across many (or all) brain states (Fox and Raichle, 2007; Vincent et al., 2007), much like structural connectivity. If true, this would greatly simplify the study of functional brain organization—from needing to consider a virtually infinite variety of task states to

considering a state space strongly constrained by a single (or few) network architecture(s). Thus, determining the universality of the resting-state network architecture is an important step toward understanding the brain's functional organization.

Most comparisons between task and rest FC have observed high correspondence (Fair et al., 2007; Fox et al., 2007; Greicius et al., 2003), but these comparisons have been limited to small sets of task states and connections. More recent comparisons between task and rest FC have emphasized differences in FC patterns, also during a small number of task states (Buckner et al., 2013; Hermundstad et al., 2013; Mennes et al., 2013). Thus, some studies advocate a more universal architecture, while others advocate differential task and resting architectures.

We sought to test for universality of the resting-state network architecture in a more comprehensive manner by using large-scale graphs built from FC among hundreds of brain regions encompassing every major brain system (Power et al., 2011) across dozens of task states (Barch et al., 2013; Cole et al., 2010) and rest. We hypothesized that resting-state FC would reveal an intrinsic network architecture that would also be present across a wide variety of task states. We also hypothesized that some task-evoked FC changes from this intrinsic architecture would be evident ("evoked" network architectures) but that these evoked changes would tend to be small and be restricted to a relatively small number of connections for any given task. This would suggest that the intrinsic network architecture represents a standard state of brain organization that is modified as necessary to implement task demands. Generally, this would help bridge resting-state FC and task FC findings in the literature, facilitating a more comprehensive account of human brain organization.

RESULTS

Detecting the Human Brain's Intrinsic and Evoked Network Architectures

It may be that evoked FC changes occur in the presence of an intrinsic functional network architecture that extends across many or all brain states (e.g., rest and tasks). To address this question, we used fMRI to measure temporal relationships between hundreds of brain regions across dozens of task states and rest in single subjects. Two data sets were used. The first data set involved the permuted rule operations cognitive paradigm (Cole et al., 2010) that contained 12 rules that were
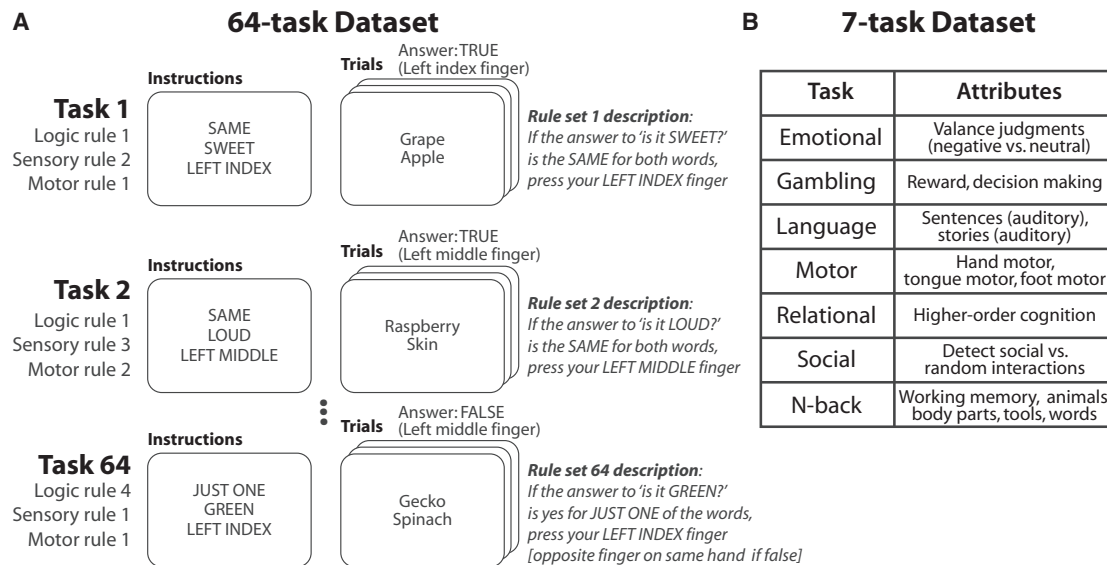
Figure 1. Testing Multiple Tasks per Subject

(A) The first fMRI data set involved 64 distinct tasks, composed of unique combinations of task rules (Cole et al., 2010). Each subject (n = 15) performed all 64 tasks.

(B) The second data set involved seven tasks chosen to elicit the involvement of all major cognitive domains and brain systems (Barch et al., 2013). Each subject (n = 118) performed all seven tasks.

permuted into 64 distinct task states in short task blocks (Figure 1A). Tasks were defined as distinct cognitive processes, such that the same stimuli could be presented across each of the 64 tasks, but distinct cognitive processes would be necessary to respond correctly to each one. Importantly, this paradigm isolated cognitive task set differences by minimizing perceptual changes across tasks (e.g., changes in visual field, sensory modality). To extend and test the robustness of findings from the 64-task data set, we also conducted analyses with a Human Connectome Project data set (118 subjects) that included rest and a set of seven tasks (Figure 1B) (Barch et al., 2013). The seven tasks were highly distinct from one another, although they also differed in basic perceptual aspects (e.g., changes in visual field, sensory modality), which could be a larger driver of FC differences than cognitive task set differences. FC was estimated as temporal correlations (Zalesky et al., 2012) among a set of 264 putative functional regions throughout the brain (defined independently to reduce potential statistical biases) (Power et al., 2011). These correlations were estimated for task FC after regressing out (across-trial mean) task-evoked activations and removing the short rest periods between task blocks from each region's time series.

In addition to testing for the existence of an intrinsic network architecture—an architecture common across rest and multiple task states—we sought to identify interregional connections unique to each task state, together comprising a set of evoked network architectures. To estimate both intrinsic and evoked architectures simultaneously, we used a tool (multislice community detection) developed to extract clusters and cluster changes in multinetwork systems (Mucha et al., 2010) and recently applied to neuroimaging data sets (Bassett et al., 2011) (Figure 2A). Unlike other clustering algorithms, this algorithm enabled us to identify network communities (putative functional modules) in brain networks both within and across task states. Using this approach, we identified network communities elicited differentially across tasks (using a low intertask coupling parameter), and we also identified consensus communities present across tasks (using a high intertask coupling parameter). The assignment of brain regions to communities is referred to as a "partition." The coupling parameter determines the extent to which identified partitions are constrained by multiple task states. We were most interested in low coupling parameters, in which all task states are considered separately, and also especially interested in high coupling parameters (identified by the production of a partition stable across additional increases in the coupling parameter), in which all task states are considered together. To examine the relationship between these community partitions and a previously defined resting-state FC community partition (Power et al., 2011) (Figure 2B), we calculated the partition similarity using the Z score of the Rand coefficient (Traud et al., 2011).

We hypothesized that there would be significant differences among the task partitions at low coupling parameters but that they would converge on a consensus partition similar to the resting-state FC community partition at high coupling parameters. Note that the multislice community detection approach forces a single consensus partition at high coupling parameters, but this approach does not require that the consensus partition look like any other particular partition (e.g., a resting-state FC partition). Furthermore, this approach does not require that partitions differentiate from any particular other partition at low coupling parameters.