

Higher Intelligence Is Associated with Less Task-Related Brain Network Reconfiguration

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The human brain is able to exceed modern computers on multiple computational demands (e.g., language, planning) using a small fraction of the energy. The mystery of how the brain can be so efficient is compounded by recent evidence that all brain regions are constantly active as they interact in so-called resting-state networks (RSNs). To investigate the brain's ability to process complex cognitive demands efficiently, we compared functional connectivity (FC) during rest and multiple highly distinct tasks. We found previously that RSNs are present during a wide variety of tasks and that tasks only minimally modify FC patterns throughout the brain. Here, we tested the hypothesis that, although subtle, these task-evoked FC updates from rest nonetheless contribute strongly to behavioral performance. One might expect that larger changes in FC reflect optimization of networks for the task at hand, improving behavioral performance. Alternatively, smaller changes in FC could reflect optimization for efficient (i.e., small) network updates, reducing processing demands to improve behavioral performance. We found across three task domains that high-performing individuals exhibited more efficient brain connectivity updates in the form of smaller changes in functional network architecture between rest and task. These smaller changes suggest that individuals with an optimized intrinsic network configuration for domain-general task performance experience more efficient network updates generally. Confirming this, network update efficiency correlated with general intelligence. The brain's reconfiguration efficiency therefore appears to be a key feature contributing to both its network dynamics and general cognitive ability.

Key words: brain connectivity; cognitive control; fMRI; individual differences; intelligence; task switching

Significance Statement

The brain's network configuration varies based on current task demands. For example, functional brain connections are organized in one way when one is resting quietly but in another way if one is asked to make a decision. We found that the efficiency of these updates in brain network organization is positively related to general intelligence, the ability to perform a wide variety of cognitively challenging tasks well. Specifically, we found that brain network configuration at rest was already closer to a wide variety of task configurations in intelligent individuals. This suggests that the ability to modify network connectivity efficiently when task demands change is a hallmark of high intelligence.

Introduction

The energy consumption of the brain under the extreme demands of a cognitively challenging task is not much greater than

that during rest conditions (Fox and Raichle, 2007). This constant activity during rest has been the target of extensive research. This work has focused primarily on functional connectivity (FC), the temporal correlation of activity between distinct locations in the brain. FC collected during rest has been used to identify several distinct functional brain networks, defined as clusters of brain regions with high FC (De Luca et al., 2005; Wang et al., 2008; Power et al., 2011; Yeo et al., 2011). These networks are functionally meaningful because they include sets of regions that serve common functions, as indicated by task activation patterns (Smith et al., 2009).

FC methods have also been applied to task data. For example, changes in FC patterns have been used to predict how well a

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participant learns (Bassett et al., 2011). As another example, patterns in FC strength between the frontoparietal control network (FPN) and the rest of the brain have been used to decode which tasks were being performed (Cole et al., 2013b). FC data can also be used to decode various stimulus-response mappings and cognitive states (Heinzle et al., 2012; Shirer et al., 2012). These results suggest that FC architecture during the performance of a task is related to specific task demands and is behaviorally relevant.

We recently found, however, that the FC structure during task performance is highly correlated ($r = 0.9$) with the FC structure observed at rest (Cole et al., 2014a). Despite this level of similarity, there were small but reliable differences in task FC structure relative to rest across different task demands. Whereas task FC changes are subtle when examining patterns across the whole brain (Cole et al., 2014b; Krienen et al., 2014), task FC has been shown to vary in specific networks under different task demands (Kinnison et al., 2012; McMenamin et al., 2014). The degree of similarity between rest and task FC across the whole brain suggests that much of the brain's network structure is evident at rest, but that updates to this FC structure result in updates to task representations. We therefore expected that the nature of the updating of the brain's functional network architecture from rest to task would be strongly related to task performance.

Given the importance of FC updates to task set updates, one might expect that larger changes in FC are associated with larger (and therefore more optimal/specific) updates from rest, leading to improved behavioral performance. Alternatively, smaller changes in FC structure could be associated with better behavioral performance because less effort/energy would be required to update FC to a task-optimal state. Somewhat consistent with this possibility, more intelligent participants have been characterized as having more efficient (i.e., smaller in amplitude) task-evoked brain activations based on functional MRI (fMRI) studies (Haier et al., 1988, 1992; Neubauer and Fink, 2009). Critically, these prior results focused on activation amplitudes and did not address the nature of brain network updates underlying task set reconfigurations (Cole et al., 2013a, b). Further, by focusing on activation amplitudes, these prior results did not address the updating of task information, which is encoded in activity and FC patterns (Kriegeskorte et al., 2008; Shirer et al., 2012; Cole et al., 2013c). We therefore investigated whole-brain FC pattern updates between rest and several functionally distinct tasks. We then tested for a relationship between these network dynamics and task performance.

Based on evidence of the relationship between activation efficiency and general intelligence, we hypothesized that higher-performing participants would be characterized by smaller changes in FC patterns (reconfiguration efficiency) when comparing task and rest FC architectures (see Fig. 1A). Note that we use rest FC as an estimate of intrinsic (context independent) FC, but we also include analyses with the across-task average FC as an alternative estimate of intrinsic FC (Cole et al., 2014a). In addition, we tested the novel hypothesis that the expected efficiency effect may be driven by high-performing individuals exhibiting a resting-state FC structure that is closer, or preconfigured, to task FC configurations. This would suggest that highly intelligent individuals have effective resting-state/intrinsic network configurations for shifting to a wide variety of tasks.

Materials and Methods

Participants. Data were collected through the Washington University–Minnesota Consortium Human Connectome Project (Van Essen et al., 2013). The participants were recruited from the Washington University

campus and surrounding area. All participants supplied informed consent. The data were from the “500 Subject” release. We used data from the “100 Unrelated Subjects” set, which excludes family relations, because we wanted a sample representative of the general population. The sample consists of 54 females and 46 males.

MRI parameters. Whole-brain echoplanar scans were acquired with a 32 channel head coil on a modified 3 T Siemens Skyra with TR = 720 ms, TE = 33.1 ms, flip angle = 52°, BW = 2290 Hz/Px, in-plane FOV = 208 × 180 mm, 72 slices, 2.0 mm isotropic voxels, with a multiband acceleration factor of 8 (Uğurbil et al., 2013). Data were collected across 2 d. On each day, 28 min of rest (eyes open with fixation) fMRI data were collected across two runs (56 min total), followed by 30 min of task fMRI data collection (60 min total). Each of the seven tasks was completed over two consecutive fMRI runs. Details regarding the resting-state data collection for this dataset were described previously (Smith et al., 2013), as well as details about the tasks (Barch et al., 2013).

Task fMRI details. These data were part of the Human Connectome Project and included data from rest and from seven diverse tasks (Barch et al., 2013). These seven tasks were selected to tap into different cognitive processes, as well as the different neural circuitry that supports those functions and includes tasks related to emotion perception, reward learning, language processing, motor responses, relational reasoning, social cognition, and working memory. We focused primarily on the language, reasoning, and working memory tasks due to statistical issues with the behavioral accuracy distributions for the other tasks (see Results for details).

fMRI preprocessing. We used a minimally preprocessed version of the data, which was the result of standard procedures including: spatial normalization to a standard template, motion correction, and intensity normalization. These steps have been described previously (Glasser et al., 2013). We performed analyses on the volume version of these minimally preprocessed data using AFNI (Cox, 1996). We removed variables of no interest from the time series using linear regression, including: motion estimates, ventricle and white matter signals, and derivatives. Ventricle, white matter, gray matter, and anatomical structures were identified for each subject using FreeSurfer (Fischl et al., 2002, 2004). Note that whole-brain global signal was not removed due to controversy regarding this preprocessing step (Murphy et al., 2009). The linear trend was removed from the signal and the data were spatially smoothed (FWHM = 4 mm). Resting fMRI data are also typically filtered temporally to isolate the low-frequency component of the time series. We did not apply a temporal filter to the data due to the possibility that task data may contain meaningful higher frequency information. In the interest of treating the task and rest data in a similar manner, we did not use a temporal filter.

Further data analysis was completed by sampling from a set of 264 regions to capture and explore regional and systems level questions. These 264 regions were identified independently (Power et al., 2011). Using this approach reduces the chance of blurring signal from neighboring regions with different functional profiles (Wig et al., 2011). The 264 regions were identified and classified using resting-state functional connectivity parcellation (Cohen et al., 2008) and a task-based neuroimaging meta-analysis (Power et al., 2011). The mean time series from all of the voxels within each of these 264 regions was then calculated and used in all subsequent analyses (see Fig. 1B). Data analysis at this point was conducted with MATLAB 2014b (The MathWorks). We removed average task-related signals from the task data by using the residuals of a standard general linear model regression of task events, as described previously (Cole et al., 2014a). This method has been shown to increase the reliability of task FC estimates (Cao et al., 2014). We then calculated Pearson's correlations between all pairs of ROIs for each subject and for each task. To better match the data going into task and rest FC matrices, we calculated a separate rest FC matrix for each task. Specifically, each rest matrix was calculated using the same number of time points (starting from the beginning of the first rest scan) as the to-be-tested task. Pearson's correlation values were then normalized using a Fisher's Z transformation. These normalized values were used for all statistical tests.

Cognitive measures. Several cognitive measures were retrieved from the Connectome Database (<https://db.humanconnectome.org>). We used data from the NIH Toolbox Picture Sequence Memory Test, NIH Tool-

box Dimensional Change Card Sort Test, PMAT, NIH Toolbox Picture Vocabulary Test, Penn Word Memory Test, and NIH Toolbox List Sorting Working Memory Test. In all cases, we used the raw, unadjusted values. We used the raw number of correct responses for the PMAT.

Task fMRI behavioral data. Behavioral data collected during fMRI scans were retrieved from the Connectome Database. Accuracy scores across each of the tasks were *z*-scored. Median reaction times across each of the tasks were also recorded and *z*-scored.

FC similarity/distance. We focused on the similarity of FC patterns as a measure of functional network updates. This has the advantage of creating a single continuous value per measured update (rather than a separate value for each connection). Pattern similarity can be equivalently considered as (the inverse of) distance in state space, which has a long methodological history in mathematics and other fields (Cha, 2007). Pearson's correlation was used as a distance measure based on its ability to isolate patterns as opposed to, for example, mean differences (as would be the case with Euclidean distance). Note that, when used as a distance measure, Pearson's correlation does not require normally distributed data unless statistical significance is assessed (Ahlgren et al., 2003). We do not assess statistical significance using the similarity values directly, but rather based on distributions of those values across subjects using a second-level correlation. Because this second-level analysis requires approximately normally distributed data, we applied the Fisher's *z*-transform to the Pearson's correlation similarity values. Note that the use of Fisher's *z*-transform limited us to similarity values rather than the standard $1 - r$ (subtraction of Pearson's correlation from 1) distance values because *z*-transformed values range from negative to positive infinity.

We calculated similarity between FC structures for each participant separately. We only considered the upper triangle of the FC matrix, excluding redundant connections and self-connections (the diagonal). We then vectorized these values before calculating a Pearson's correlation between them. Due to the number of statistical tests, we report false discovery rate (FDR)-corrected *p*-values for primary analyses (Benjamini and Hochberg, 1995). Follow-up or control analyses were not independent of the primary tests and are thus not corrected.

Testing the influence of rest and task FC structure on FC reconfiguration efficiency. In this analysis, we sought to test whether high performers perform well because their rest FC structure is optimized (preconfigured) for a given task, such that it does not need to be changed much to achieve that task's FC structure. Alternatively, high performers possessing a task FC structure that is modified to a lesser degree from their rest FC structure could drive the FC reconfiguration efficiency effects. In other words, the observed behavior-correlated rest-to-task FC similarity could be driven by variation in rest FC, task FC, or both. To isolate the source of variance, we held across-subject variance constant for rest FC and task FC separately. If the behavior-similarity correlation still holds when rest FC is held constant (with task FC varying), this suggests that task FC was driving the effect. Alternatively, if the behavior-similarity correlation still holds when task FC is held constant (with rest FC varying), this suggests that rest FC was driving the effect. It is also possible that both sources of variance were driving the effect if the behavior-similarity correlation is eliminated (or stands) in both scenarios. In each case, the source of variance was held constant using a leave-one-subject-out approach. This involved averaging rest FC across all other individuals (aside from the tested individual) when focusing on task FC variance and averaging task FC across all other individuals when focusing on rest FC variance.

Results

Better task performance is related to more efficient (smaller) FC reconfiguration

Previous studies have found a high correlation between FC during rest and during the performance of a variety of tasks. However, consistent differences between task and rest FC have also been detected (Cole et al., 2014a). We sought to identify the behavioral relevance of these FC differences between rest and task. Specifically, we looked for individual difference correlations between task performance and the similarity (i.e., distance) between rest and task FC architectures.

We used data from the Human Connectome Project, which consists of rest and seven distinct tasks. To assess task performance, we focused on accuracy measures collected during these tasks. We found that three of the tasks (language, relational reasoning, and working memory) had accuracy score distributions that were approximately normally distributed and were therefore suitable for computing correlations with FC updates. The accuracy distributions for the other four tasks either were not recorded (for the motor task) or were not normally distributed. The gambling task accuracies were not normally distributed due to accuracies being approximately equal across subjects (this task was designed to equate the number of wins and losses across participants). The accuracy data for the emotion task showed a strong ceiling effect ($M = 0.98$, $SD = 0.02$). Visual inspection of the accuracy data from the social task revealed a negatively skewed distribution and a Kolmogorov–Smirnov (K-S) test confirmed that it was not normally distributed ($p < 0.0001$). The following analyses were therefore focused on the language, reasoning, and working memory tasks. Across-subject mean accuracy scores were well above chance for all three tasks (language task: $M = 0.89$, $SD = 0.07$; reasoning task: $M = 0.76$, $SD = 0.12$; working memory task: $M = 0.88$, $SD = 0.08$). The language and reasoning task accuracy data were normally distributed as confirmed by a K-S test (smallest $p = 0.13$). The working memory accuracy data were slightly skewed as evidenced by a K-S test ($p = 0.03$). However, we observed similar FC reconfiguration efficiency results on the working memory task data when we correlated it with a measure of general intelligence rather than accuracy (see Results for more details).

We hypothesized that the similarity between whole-brain rest and task FC states, the efficiency of whole-brain rest to task FC updates, is related to task performance. However, this relationship could be driven by task performance correlations with any individual connection during either rest or task alone. To help rule out this possibility, we tested the relationship between each connection's FC strength and task performance. This analysis was conducted for both rest and task. We calculated the Pearson's correlation between each connection's FC weight in the 264-by-264 matrix and performance on each of the three tasks (FDR corrected for multiple comparisons). None of these corrected *p*-values were significant for the rest or task FC matrix for any of the three tasks. We did not find any support suggesting that the observed correlations between FC reconfiguration and task performance were driven by an association between individual FC weights and performance during either rest or task individually.

FC reconfiguration efficiency was calculated by comparing the whole-brain FC configuration during each task with the whole-brain FC configuration during rest (Fig. 1A). This produced a similarity score for each subject based on a correlation coefficient between the pattern of rest FC values and the pattern of task FC values. This correlation coefficient is a distance metric that quantifies the similarity of the pattern of FC across the entire matrix (see Materials and Methods for more details). We found that the similarity between rest and task FC structure was positively correlated with behavioral performance on all three of the tasks considered (language task: $r = 0.31$, corrected $p = 0.01$; reasoning task: $r = 0.247$, corrected $p = 0.022$; working memory task: $r = 0.23$, corrected $p = 0.029$; Fig. 2). These results suggest that more efficient whole-brain FC reconfiguration, or a smaller FC reconfiguration distance, is related to better task behavioral performance.

Are reconfiguration efficiency results driven by other factors?

We have shown that individuals exhibiting more accurate performance on tasks show more efficient whole-brain FC pattern reconfiguration. However, increased accuracy is typically accompanied by decreased reaction time. One possible explanation for our efficiency results could be that higher-performing individuals are responding more quickly and spending less time performing the task. These individuals would therefore have more idle “rest” time during the task run, which may make their FC structure more similar to rest FC than lower-performing individuals. To rule out this possibility, we calculated the median reaction time for each subject and regressed that factor out of our efficiency measure. We then correlated the residual (efficiency with the influence of reaction time removed) with behavioral performance. We found that the relationship between FC reconfiguration efficiency and performance accuracy remained for the language task ($r = 0.26$, $p = 0.008$) and the reasoning task ($r = 0.25$, $p = 0.012$). Once reaction time on the working memory task was removed from the efficiency measure, however, it was no longer correlated with behavioral accuracy ($r = 0.01$, $p = 0.91$). Whereas the amount of time on task may be influencing the relationship between efficiency and behavioral performance on the working memory task, it was not a factor for either the language or reasoning task. One possible explanation for the lack of effect on the working memory task is that the speed accuracy tradeoff is stronger on this task than it is on the language or reasoning task (Heitz, 2014). By removing the variance attributed to reaction time in the working memory task, we may also be removing variance related to task performance.

As another alternative explanation for the observed effects, the efficiency of FC pattern reconfiguration could be influenced by a more general FC configuration stability trait. For example, it could be that a more stable, or less volatile, FC structure is beneficial to behavioral performance rather than FC updating efficiency. To address this possibility, we compared the FC patterns during each subject’s first rest scan to that subject’s second rest scan (each lasting 14 min, collected during the same fMRI session). We found that the similarity in FC structure across these two resting-state scans (i.e., the stability of the FC structure) was not related to behavioral performance on any of the three tasks (largest $r = 0.15$, $p = 0.13$). This suggests that the similarity between task and rest FC configurations does not simply reflect FC configuration stability over time.

FC reconfiguration distance could potentially be driven by network patterns that are specific to rest, rather than being a truly intrinsic (i.e., context independent) network structure. Recent

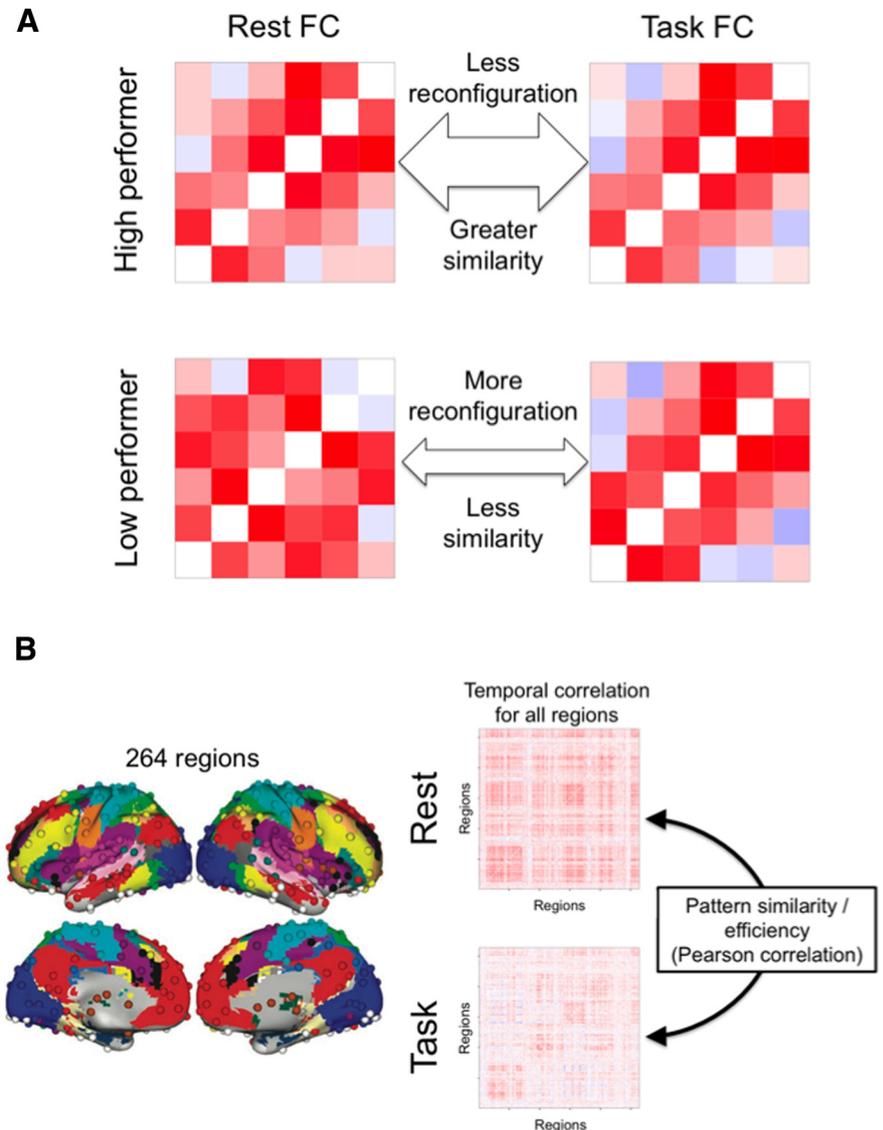


Figure 1. Assessing FC network architecture reconfiguration “distance”. **A**, We hypothesized that high-performing individuals would be characterized by more efficient FC updates, as indicated by a smaller reconfiguration distance and therefore a greater degree of similarity between rest FC and task FC structure. Note that we also used across-task average FC in place of rest FC to better isolate truly intrinsic (context independent) FC. This conceptual figure illustrates our hypotheses on a matrix representing FC strengths between six nodes. **B**, The mean time series from 264 regions of interest were extracted and all pairwise correlations were calculated for task and rest for each participant. We then calculated the FC reconfiguration efficiency by calculating the similarity of task and rest FC patterns (the upper triangles of the depicted matrices).

studies have shown that FC maps averaged across a variety of tasks have a very high correlation with rest FC maps (Cole et al., 2014a; Krienen et al., 2014), suggesting that this is a way to estimate the brain’s intrinsic FC structure independently of rest data. We therefore repeated our main analysis using the across-task average FC structure in place of rest FC. Note that the to-be-compared task’s FC was withheld from the mean task FC estimates to remove circularity from the analysis. As expected, we found that FC reconfiguration distance between task FC and the mean task FC (of the remaining six tasks) was positively correlated with behavioral performance for the language task ($r = 0.24$, $p = 0.017$), the reasoning task ($r = 0.28$, $p = 0.005$), and the working memory task ($r = 0.24$, $p = 0.018$). This suggests that the observed correlation between FC update efficiency and behavioral performance was not driven by a unique feature of rest FC structure, but likely by the underlying intrinsic FC structure.

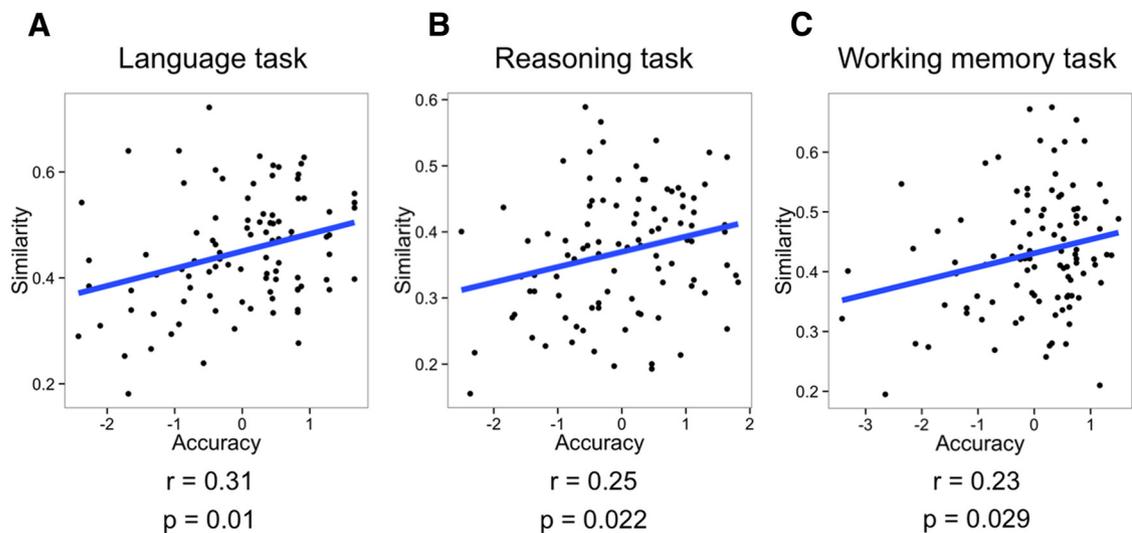


Figure 2. FC reconfiguration efficiency is related to behavioral performance on three different tasks. **A**, Correlation between accuracy on the language task and similarity between rest FC structure and language task FC structure. **B**, Correlation between accuracy on the reasoning task and similarity between rest FC structure and reasoning task FC structure. **C**, Correlation between accuracy on the working memory task and similarity between rest FC structure and working memory task FC structure. Note that these effects were also present when using across-task average FC in place of rest FC, suggesting that effects are driven by intrinsic (i.e., context independent) FC rather than rest FC per se.

Movement during a scan can influence measures of FC (Van Dijk et al., 2012) even after motion estimates have been entered into a regression as variables of no interest (Power et al., 2012). This suggests that our measure of FC structure similarity between task and rest could have been contaminated by motion artifacts. To address this possibility, we first examined whether behavioral performance was correlated with mean framewise displacement (FD) across participants. FD calculates the difference in head position at each time point in Euclidean distance from the current brain volume relative to the previous. The mean FD simply calculates the mean amount of movement in Euclidean distance across an entire scan. We found that motion was negatively correlated with performance on the language task ($r = -0.24$, $p = 0.016$), reasoning task ($r = -0.21$, $p = 0.042$), and working memory task ($r = -0.25$, $p = 0.012$). To determine whether motion was influencing the relationship between behavioral performance and the efficiency of FC reconfiguration from task to rest, we regressed the mean FD measures from the FC reconfiguration efficiency estimates. We then used the resulting residuals and investigated whether behavioral performance was still related to efficiency. We found that, even when the mean FD was regressed out of the similarity between the task and rest FC structure, there was still a significant positive correlation for the language task ($r = 0.31$, $p = 0.002$), the reasoning task ($r = 0.24$, $p = 0.016$), and the working memory task ($r = 0.24$, $p = 0.016$). In addition, we implemented a motion scrubbing strategy (Power et al., 2012). We first identified TRs exhibiting a high degree of FD (0.5). We eliminated these TRs as well as one prior and two TRs after the flagged time point. FC for rest and task was recalculated on the remaining time points and we recalculated the correlation between FC reconfiguration efficiency and behavioral performance. We found that motion scrubbing did not have an impact on the results because we observed a significant FC similarity–performance correlation for the language task ($r = 0.34$, $p = 0.0005$), the reasoning task ($r = 0.2$, $p = 0.045$), and the working memory task ($r = 0.22$, $p = 0.029$). This suggests that motion was unlikely to have driven the relationship between task performance and FC update efficiency.

Efficient FC pattern configuration updates in specific networks predict better task performance

We have shown that the FC pattern reconfiguration distance across the entire brain is correlated with behavioral performance. Next, we investigated whether this pattern across multiple nodes was driven by a subset of specific regions or if this efficiency effect is truly a general property across the entire brain. We assessed each network's contribution by calculating a whole-brain FC configuration similarity score for each network separately (as identified in Power et al., 2011; Cole et al., 2013b). This score was based on task–rest similarity of each network's FC pattern with the entire rest of the brain. We then tested for individual difference correlations between these scores and behavioral performance.

We found that some of these network-level update efficiencies were significantly correlated ($p < 0.05$, FDR corrected for multiple comparisons) with behavioral performance. For the language task, we found that reconfiguration efficiency was significantly related to behavior in the auditory (likely language-related), mouth somatomotor (likely language-related), dorsal attention, default mode, salience, and cingulo-opercular networks, along with a set of regions with unidentified network membership (Fig. 3A; lowest r -value = 0.23). For the reasoning task, performance was related to the mouth somatomotor, cingulo-opercular, visual, frontoparietal, salience, and subcortical networks (Fig. 3B; lowest r -value = 0.24). In the working memory task, performance was related to the default mode, parietal memory retrieval, visual, frontoparietal, and salience networks (Fig. 3C; lowest r -value = 0.23). These results suggest that FC reconfiguration efficiency is not a completely global phenomenon, such that the update efficiency of functional networks that are particularly important for a given task likely have privileged influences on performance of that task.

Rest and task FC structure both contribute to the relationship between FC reconfiguration efficiency and behavioral performance

We have provided evidence that FC reconfiguration efficiency is related to behavior. However, it is unclear whether efficiency in high performers is driven by differences in rest or task FC struc-

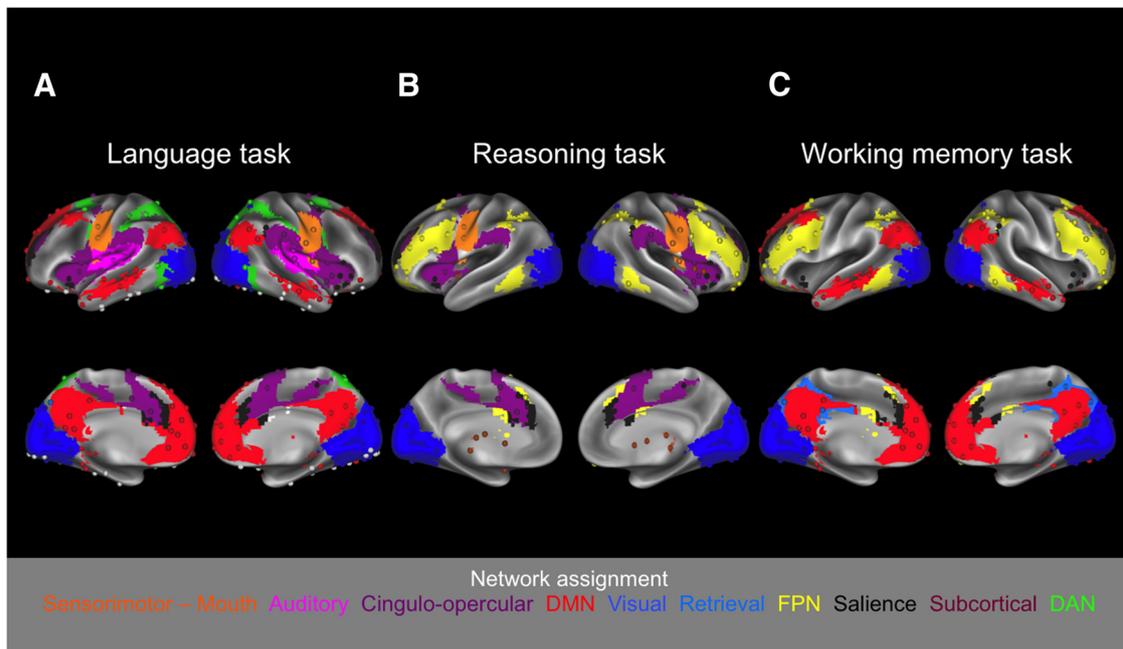


Figure 3. FC reconfiguration efficiency in specific networks is related to task performance across three tasks. We repeated the tests for FC reconfiguration efficiency correlations with task performance, but for each network separately. Colored networks indicate that the degree of efficiency for each node in the network to the rest of the nodes in the brain is correlated with performance on the language task (A), the reasoning task (B), and the working memory task (C).

ture. Specifically, it could be that either: (1) high performers perform well because their rest FC structure is preconfigured for a given task such that it does not need to be changed much or (2) high performers perform well because their task FC structure is optimized for efficiency, requiring less substantial changes to achieve equal or better task performance. The first possibility predicts that rest FC drives the FC update efficiency effects, whereas the second possibility predicts that task FC drives these effects.

To test these possibilities, we compared the rest FC structure of each individual with the mean task FC structure of the remaining 99 participants and calculated the correlation between this similarity measure and task performance. There was a significant correlation between this measure of similarity and task performance for the language task ($r = 0.22$, corrected $p = 0.037$), but there was not a significant correlation for the reasoning task ($r = 0.19$, corrected $p = 0.06$) or the working memory task ($r = 0.16$, corrected $p = 0.126$). We used a similar approach to compare each individual's task FC structure with the mean rest FC structure of the remaining 99 participants. We then correlated this similarity measure with task performance and found a significant correlation for the language task ($r = 0.27$, corrected $p = 0.018$) and the reasoning task ($r = 0.3$, corrected $p = 0.01$), but not for the working memory task ($r = 0.15$, corrected $p = 0.136$). Although the correlation was significant for some tasks and not others, the magnitude of the correlations for both analyses were in a similar range, suggesting that neither one was disproportionately contributing to the relationship between FC reconfiguration efficiency and task performance. Together, these results suggest that the similarity between rest and task FC patterns are driving the relationship between FC reconfiguration efficiency and task performance, not a change in either task or rest FC alone.

High-performer rest FC may be preconfigured into a task-general FC configuration

The relationship between FC reconfiguration efficiency and task performance is driven by the similarity between rest and task FC patterns, not exclusively by differences in either rest or task FC patterns. In particular, we were interested in exploring the portion of the variance driven by rest FC patterns. Differences in rest FC might indicate that high-performing individuals possess a rest FC structure that is preconfigured or more similar to the FC structure required for performing different tasks.

How could it be possible for rest FC to be preconfigured for such a range of tasks as we tested and possibly others? Previous studies have identified a “task-general” FC structure—task FC changes from rest that were present across a variety of diverse tasks (Cole et al., 2014a). We hypothesized that higher-performing individuals may have a rest FC structure that is more similar to this task-general FC configuration. This would likely lead to the ability to more quickly and efficiently switch FC patterns into an architecture conducive to performing a task regardless of what that task might be.

We first identified a “task-general” FC structure for each individual as described previously (Cole et al., 2014a). Briefly, we used the first principal component using each task FC matrix as an input for each individual. Importantly, we excluded the task that was later used to correlate with behavioral performance, removing circularity from the analysis. Note that all seven tasks were used for calculating the task-general FC structure (rather than just the three with normally distributed accuracy scores). Then, for each of the three main tasks of interest, we calculated the similarity between each individual's rest FC structure and their task-general FC structure (Fig. 4A). These similarity scores were then correlated with behavioral performance. We found that the similarity between rest FC

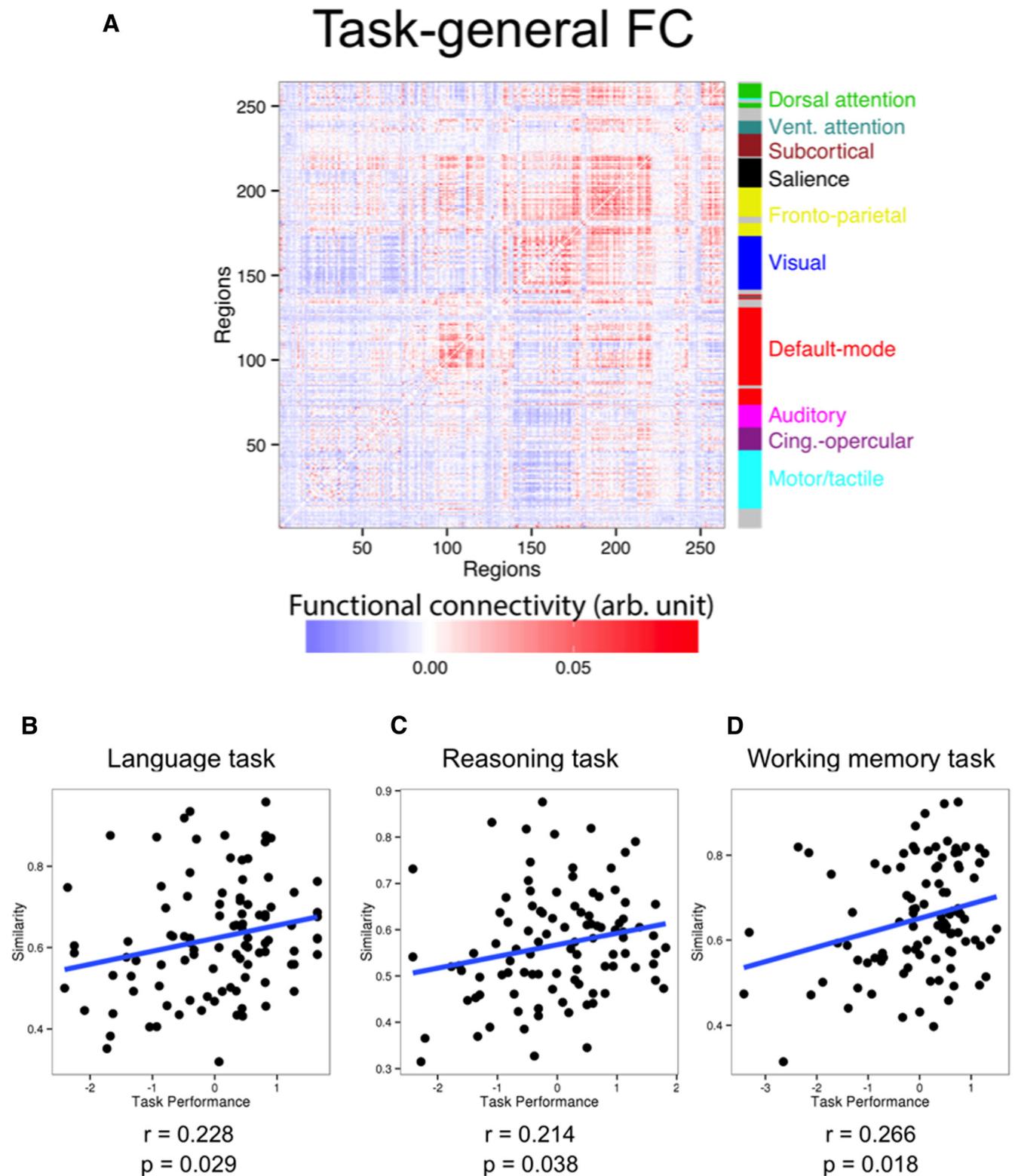


Figure 4. Rest FC is “preconfigured” to switch into a task-general structure in high-performing individuals. *A*, Visualization of the task-general network. The figure depicts changes in FC from rest common to all seven tasks. This matrix would appear to be quite similar to the rest FC matrix if this subtraction was not performed. Note, however, that the task-general FC matrix without the rest FC matrix subtracted was used for analysis. Similarity between rest FC and task-general FC structure is correlated with performance on the language task (*B*), the reasoning task (*C*), and the working memory task (*D*).

and task-general FC was correlated with behavioral performance for the language task ($r = 0.228$, corrected $p = 0.029$; Fig. 4*B*), the reasoning task ($r = 0.214$, corrected $p = 0.038$; Fig. 4*C*), and the working memory task ($r = 0.266$, corrected

$p = 0.018$; Fig. 4*D*). This suggests that higher-performing individuals have more efficient FC updates because their rest/intrinsic FC is already closer to a “task-general” configuration before the onset of task performance.

Efficient FC reconfiguration is related to general intelligence

We have shown that more efficient FC reconfiguration is related to better performance on three diverse behavioral tasks. Building on this, we hypothesized that FC update efficiency is related to general cognitive ability. We began to test this possibility more directly using the Penn's Progressive Matrices (PMAT) (Bilker et al., 2012), a measure of fluid intelligence (Prabhakaran et al., 1997). Fluid intelligence reflects general cognitive ability (Gottfredson and Saklofske, 2009), especially as it relates to cognitive control (Cole et al., 2012a; Diamond, 2013). As expected, similarity measures between task and rest FC for each of the three tasks were significantly positively correlated with PMAT scores (language task: $r = 0.208$, corrected $p = 0.045$; reasoning task: $r = 0.263$, corrected $p = 0.018$; working memory task: $r = 0.292$, corrected $p = 0.012$). Consistent with fluid intelligence reflecting general cognitive ability, the fluid intelligence scores were significantly positively correlated with behavioral performance on each of the three tasks (language task: $r = 0.286$, $p = 0.004$; reasoning task: $r = 0.467$, $p < 0.001$; working memory task: $r = 0.35$, $p < 0.001$). These findings suggest that efficient updates in FC configuration may be a hallmark of individuals with higher levels of fluid intelligence.

We next assessed whether efficient FC reconfiguration was related to general intelligence. General intelligence is a broader construct than fluid intelligence because it is composed of both fluid intelligence (novel/flexible processing; e.g., solving a novel kind of problem) and crystallized intelligence (learned/stereotyped processing; e.g., vocabulary knowledge) (Cattell, 1963a). We estimated general intelligence by considering scores on multiple measures of cognition using factor analysis. We included scores from tests of episodic memory (NIH Toolbox Picture Sequence Memory Test), executive function and cognitive flexibility (NIH Toolbox Dimensional Change Card Sort Test), fluid intelligence (PMAT), language and vocabulary comprehension (NIH Toolbox Picture Vocabulary Test), verbal episodic memory (Penn Word Memory Test), and working memory (NIH Toolbox List Sorting Working Memory Test). We aggregated these six scores using principal component analysis. The first component (explaining 29.4% of the variance) was used as an estimate of general intelligence. As expected, general intelligence was significantly positively correlated with FC update efficiency for all three tasks (language task: $r = 0.38$, corrected $p = 0.002$; reasoning task: $r = 0.29$, corrected $p = 0.01$; working memory: $r = 0.23$, corrected $p = 0.02$) (Fig. 5). This suggests FC reconfiguration efficiency is even more broadly related to cognitive ability than fluid intelligence.

We next tested whether a general metric of reconfiguration efficiency (across multiple tasks) was related to general intelligence. This involved aggregating reconfiguration efficiency scores from the language, reasoning, and working memory tasks using principal component analysis. The first component (explaining 76% of the variance) was used as a measure of general

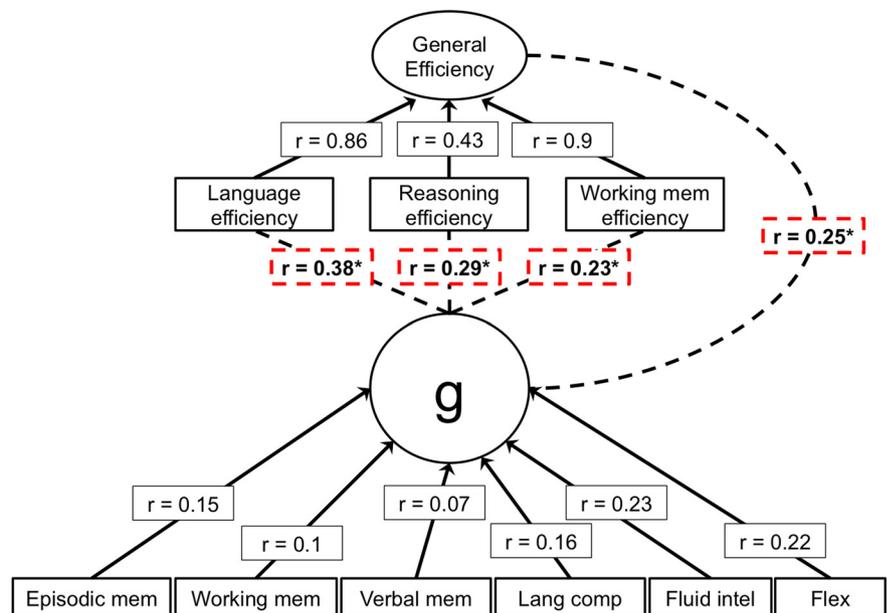


Figure 5. FC reconfiguration efficiency is related to general intelligence. A measure of general intelligence (g) was calculated for each individual based on six different measures of cognition (solid boxes at bottom). A measure of general efficiency was calculated for each individual based on reconfiguration efficiency scores from three tasks (solid boxes in middle). Correlation values inside solid boxes indicate the strength of the relationship between each measure and the first component from PCA. Efficiency measures for each of the three tasks (solid boxes in middle) were correlated with g (dashed boxes in middle). General efficiency is correlated with general intelligence (dashed box at right). Asterisks note significant correlations ($p < 0.05$) between efficiency and g . Note that results were similar when including all seven tasks (not just the three tasks that had well distributed accuracy scores).

efficiency. As expected, this measure was positively correlated with general intelligence ($r = 0.25$, corrected $p = 0.02$). This suggests that general FC reconfiguration efficiency is related to general intelligence.

We next ran the same analysis, but instead of including only three tasks, we included all seven tasks (emotion, gambling, language, motor, reasoning, social, and working memory). We were able to include all tasks because, unlike our other analyses, this analysis did not require the use of behavioral accuracies (which were poorly distributed for four of the tasks). We aggregated the seven efficiency scores using principal component analysis. The first component explained 62% of the variance. This measure of general efficiency was also positively correlated with general intelligence, as expected ($r = 0.28$, corrected $p = 0.017$). This suggests that FC reconfiguration efficiency is even more generally related to general intelligence than the three primary tasks investigated here.

Discussion

Task performance is correlated with FC reconfiguration efficiency

We found that task FC pattern update efficiency has a surprisingly general relationship with task performance. Our analyses culminated in extracting a general factor for task FC reconfiguration efficiency, which was robustly correlated with a general factor for intelligence. Critically, these relationships were all positive. This suggests that more efficient FC pattern updates may be a factor supporting higher general intelligence.

Previous studies support the possibility that intelligence is related to efficient neural processing. For instance, individuals with higher intelligence scores show less metabolic activity in the brain during task performance (Haier et al., 1988). Here, we expand on these results by finding that the efficiency of FC recon-

figuration between rest and task-oriented brain states is positively correlated with intelligence. These results suggest that the neural efficiency hypothesis not only applies to stimulus-evoked BOLD responses and to updates from rest FC architecture, but also to the efficiency by which functional connection patterns are reconfigured in response to different task demands.

Note that a recent article questioned the utility of the concept of efficiency in cognitive neuroscience (Poldrack, 2015). It was suggested that interpreting reduced fMRI activation levels in higher-performing individuals as efficiency does not provide an adequate mechanistic explanation for the observed phenomenon. However, Poldrack also acknowledged that identifying potential efficiency effects is a good starting place for more mechanistic explanations in the future. It will be important for future work to assess more directly whether this network reconfiguration process is a large-scale network mechanism underlying the activation efficiencies seen in other studies.

There were two possible outcomes for how FC updates could have been related to behavior: either larger or smaller FC changes could have been associated with better performance. The more straightforward possibility may have been that larger changes are more helpful for behavioral performance. This outcome also would have been consistent with findings from attention-deficit/hyperactivity disorder (ADHD), in which patients have an inability to suppress default mode network activity during tasks that demand attention and smaller changes in brain activity between rest and task produce worse behavioral outcomes (Sonuga-Barke and Castellanos, 2007; Castellanos et al., 2008; Uddin et al., 2008). Given the strength of this logic, as well as the results with ADHD, we expect that our observed FC update efficiency effect is superimposed on an alternative distraction-based effect. As an extreme example, a subject who simply does not perform a task at all (i.e., remains in a resting state) would undoubtedly show poor performance along with high FC similarity to resting state. It will be important for future work to investigate the possibility of dissociating these two effects.

We conducted a series of follow-up analyses to test the robustness of the observed FC update efficiency effect. We found that the general stability of FC architecture (measured across two rest scans) over time was not related to task performance. However, there is evidence that FC fluctuates over time (Bassett et al., 2011; Zalesky et al., 2014; Betzel et al., 2016a). It is possible that there are important changes in FC on a smaller temporal scale and that our approach is not sensitive to these more transient FC states. Previous studies have found that the degree of flexibility on this shorter temporal scale is related to behavioral performance and mood (Braun et al., 2015; Betzel et al., 2016b).

We were also concerned that the results could have been driven by peculiarities of the resting state rather than a truly intrinsic brain network organization. We used an alternative measure of intrinsic FC (across-task mean) and found that the FC update efficiency with this estimate of intrinsic FC correlated with task performance. This result suggests high-performing individuals have an intrinsic (i.e., context-independent) FC structure that is well tuned to enter into a variety of task FC configurations.

FC reconfiguration efficiency is at least partially network specific across distinct tasks

We found that FC reconfiguration efficiency between specific networks and the rest of the brain are significantly correlated with performance. Efficiency of some networks was related to performance of specific tasks, whereas other networks were important

across multiple tasks. For instance, salience and visual network efficiency were significantly correlated with performance on all three tasks. Efficiency in the salience network may reflect the ability to integrate and process multimodal information important for guiding behavior across a variety of task demands. Efficiency in the visual network was correlated with performance on all three tasks. Both the reasoning and the working memory task involved visual stimuli. In the language task, the stimuli were auditory, but several studies have found that the visual system can be activated by visualizing stimuli presented in other modalities (Le Bihan et al., 1993; D'Esposito et al., 1997). An additional possibility is that a general arousal response drives pupil dilation (Bradley et al., 2008), increasing visual stimulation such that sympathetic activity is reflected in the visual network. It will be important for future work to investigate the role of visual network responses during auditory tasks, especially in the context of visual network update efficiency and its relationship to task performance.

In contrast to these networks that were involved across tasks, auditory network efficiency was significantly correlated with performance on the language task (the only task with auditory stimuli) alone. This suggests that, as expected, efficiency in the auditory network is a particularly important factor for performance of auditory tasks. The FPN was somewhat specific in that it was not involved in the language task, but it was general in that its update efficiency was related to performance of the reasoning and the working memory tasks. Regions within the FPN have many connections to other regions (Cole et al., 2010) and this network is thought to play a major role in cognitive control processes (Cole and Schneider, 2007; Vincent et al., 2008; Cole et al., 2013b). These findings suggest that efficiency in the FPN is important for tasks requiring flexibility and increased cognitive control (reasoning and working memory) relative to less-demanding (Schneider and Shiffrin, 1977; Cole and Schneider, 2007) tasks such as listening to a story (as in the language task).

High-performing individuals possess a rest FC structure that is “preconfigured” to switch to a variety of possible task FC states

The relationship between reconfiguration efficiency and task performance could have two possible explanations. High performers could be doing well on a task because their rest FC is partially preconfigured to switch into that task FC configuration such that there is less reconfiguration necessary at the time of the switch. Alternatively, high performers could be doing well because their task FC structure is functionally effective with only a small amount of reconfiguration. The results suggest that the relationship between efficiency and task performance are driven by individual differences in both rest and task FC structure. Both explanations contribute to the observed FC similarity–performance correlations. The strong role for rest FC in driving this relationship, however, suggests that high performers have rest FC structures that are preconfigured for task-related reconfiguration. Therefore, high performers on a given task can be characterized as having a rest FC structure that is already closer in state space to that task's FC configuration.

In addition to such task-specific preconfiguration, high performers also appear to be driven by a general factor that is consistent across different tasks. We found that the similarity between rest FC configuration and a “task-general” FC configuration was related to performance for all three tasks of primary interest. This suggests that the distance between intrinsic FC and a “task-general” FC state contributes to performance on a variety

of tasks. Consistent with the possibility of a task-general factor, we found a general FC reconfiguration efficiency factor across all seven tasks that was related to performance (Fig. 5). The observed differences in rest FC structure could be due to an inherited trait or it could be the result of experience-based tuning of the system. Many studies have found experience-dependent changes in rest FC structure, demonstrating some plausibility for this task-driven mechanism (Stevens et al., 2010; Schultz et al., 2012; Sami et al., 2014).

More efficient FC reconfiguration is a feature of greater general intelligence

The primary observed effects were across three distinct cognitive domains (language, reasoning, and working memory). This was suggestive of an even broader factor. We next focused on fluid intelligence, a general cognitive ability supporting novel problem solving related to cognitive control (Kane et al., 2004; Cole et al., 2012b) and predictive of many real-life outcomes (Gottfredson, 1997; Gottfredson and Saklofske, 2009). We found that fluid intelligence was positively correlated with FC reconfiguration efficiency.

We further found that general intelligence (Gottfredson, 1997; Gottfredson and Saklofske, 2009) was also correlated with FC update efficiency. General intelligence consists of fluid intelligence and crystallized intelligence, an estimate of an individual's general knowledge (Cattell, 1963b). Previous studies have found a link between intelligence and graph theoretical measures of rest FC (van den Heuvel et al., 2009; Santarnecchi et al., 2014; Cole et al., 2015). The current study expands on these findings to suggest that the efficiency of FC reconfiguration is related to general intelligence. Furthermore, our findings suggest that there is a general FC reconfiguration efficiency factor common across tasks involving different cognitive, motor, and stimulus modality demands. It will be important for future research to further investigate the neural mechanisms underlying this general FC reconfiguration efficiency factor.

An important remaining question is whether the observed relationship between general intelligence and FC reconfiguration efficiency is fixed for each individual. Individuals are likely born with a possible range of general intelligence and their actual general intelligence within this range is determined by experience. It will be important for future studies to use interventions to identify ways of increasing FC reconfiguration efficiency, assessing whether this can shift an individual's general intelligence along this range.

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