Focus Article

Resting-state functional connectivity MRI reveals active processes central to cognition

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Analysis of spontaneously correlated low-frequency activity fluctuations across the brain using functional magnetic resonance imaging (MRI)—commonly referred to as resting-state functional connectivity (RSFC) MRI—was initially seen as a useful tool for mapping functional-anatomic networks in the living human brain, characterizing brain changes and differences in clinical populations, and studying comparative anatomy across species. However, little was known about the potential relevance of RSFC to cognitive processes. Indeed, there has been considerable controversy and debate as to the utility of studying the resting-state in cognitive neuroscience. However, recent work has shown that RSFC, rather than merely reflecting passive or epiphenomenal activity within underlying functional-anatomic networks, reveals important dynamic processes that play an active role in cognition. RSFC has been associated with individual differences in a number of behavioral and cognitive domains, including perception, language, learning and memory, and the organization of conceptual knowledge. In this article, we review and integrate the latest research demonstrating that RSFC is functionally relevant to human behavior and higher-level cognition, and propose a hypothesis regarding its mechanism of action on functional network dynamics and cognition. We conclude that RSFC MRI will be an invaluable tool for future discovery of the fundamental neurocognitive interactions that underlie cognition. © 2014 John Wiley & Sons, Ltd.

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INTRODUCTION

Since its inception, the majority of cognitive neuroscience research using functional magnetic resonance imaging (fMRI) has examined neural correlates of cognition by focusing on relatively small fluctuations of activity associated with explicit experimental conditions. This modest 'task-evoked' activity occurs in the context of a substantial amount of variance caused by the brain's spontaneous low-frequency activity fluctuations that persist across cognitive states. What has traditionally been seen as noise, however, contains a substantial amount of structure. In examining these activity fluctuations, one can detect and dissociate functional-anatomic networks by quantifying how activity in these brain regions is correlated in time.[1] In the first study to examine patterns of spontaneous fMRI signal correlations, Biswal et al.[2] demonstrated that these seemingly random intrinsic fluctuations are not random, but rather, they are spontaneously temporally coupled within functional-anatomic brain networks: Activity in motor cortex was correlated with the extended motor system.[2]

Since the introduction of 'resting-state functional connectivity' (RSFC) MRI, a multitude of 'resting-state' or 'intrinsic connectivity' networks have been identified that are spatially congruent

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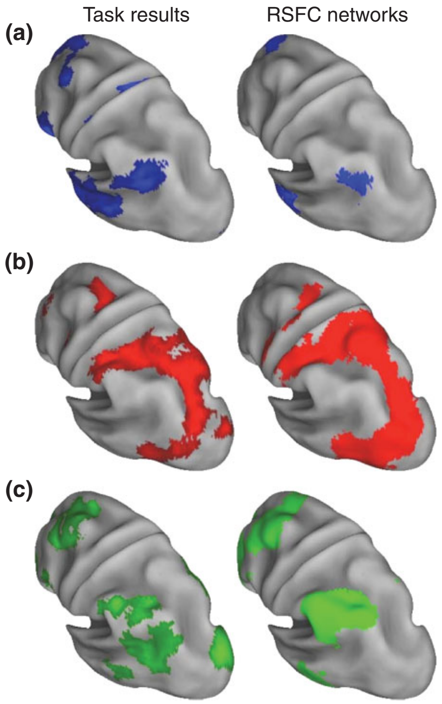

FIGURE 1 | Congruence of task-evoked and resting-state functional connectivity (RSFC) networks. Left lateral parietal lobe activity for (a) autobiographical planning, (b) visuospatial planning, and (c) activity common to these two planning tasks (left); and the (a) default, (b) dorsal attention, and (c) frontoparietal control RSFC networks (right). (a) Posterior inferior parietal lobule activity in autobiographical planning subsumes the posterior inferior parietal lobule cluster in the default resting-state network. (b) Visuospatial planning engaged the same superior parietal lobule to MT+ arc seen in the posterior portion of the dorsal attention network. (C) The two planning tasks commonly engaged a dorsal segment of the anterior extent of the inferior parietal lobule, part of the frontoparietal control network. (Reprinted with permission from Ref 8. Copyright 2010 Elsevier Ltd)

with well-established functionally dissociable brain networks evoked during various cognitive tasks[3–9] (see Figure 1). The appeal of RSFC MRI is its relatively simple technique—the acquisition of a brief dataset while participants rest quietly or perform a minimally demanding task (e.g., visually fixating on a centrally located cross) in the MRI scanner—which can be used across a broad range of experimental and clinical populations due to its minimal behavioral demands. Furthermore, there is remarkable persistence and stability of RSFC patterns across individuals during a variety of rest states,[4,10,11] task states,[12–15] sleep,[16–18] under anesthesia,[19–21] as well as in the human fetus,[22] babies,[23] and even across species.[24–26] Thus, RSFC was initially seen as a potentially useful tool for mapping functional-anatomic networks in the living human brain, characterizing brain changes and differences across development and in clinical populations, and studying comparative anatomy across species. These applications have been well described in a number of recent reviews.[1,27–31] Little was known, however, about the potential relevance of this spontaneous activity to cognitive processes. In this article, we review and integrate a growing body of evidence that RSFC reveals brain activity associated with processes that play an active and dynamic functional role in cognition. We argue that RSFC reveals processes central to individual differences and cognition, including perception, language, learning and memory, and the organization of conceptual knowledge. Finally, we conclude with a hypothesis regarding the mechanism of action of RSFC on functional brain network dynamics and cognition.

RSFC PREDICTS INDIVIDUAL DIFFERENCES IN BEHAVIOR AND COGNITION

Soon after its introduction, some speculated that RSFC might reflect processes involved in the maintenance or stabilization of neuroanatomical networks, memory consolidation, and preparation for future behavior,[32–34] though there was no evidence to support this. To substantiate these ideas, an association between behavior or cognition and measures of RSFC among functionally relevant brain regions would need to be demonstrated. Several studies have now shown that individual differences in the strength of RSFC within functional networks predict behavior and cognitive performance in a variety of domains.

A number of studies have shown that individual differences in behavior and personality can be correlated with RSFC strength across brain regions. Seeley et al.[35] observed dissociable correlations between RSFC and individual differences in cognition and emotion: Connectivity within the executive control network was correlated with performance on an executive task and self-reported anxiety was correlated with connectivity in the salience network. The Big Five personality domains have also been predicted by dissociable patterns of RSFC among specific brain regions.[36] Yang et al.[37] more recently observed that the propensity for one to spontaneously relate personal memories to those of another individual predicted medial temporal lobe connectivity within the default network. Using network graph analysis, van den Heuvel et al.[38] demonstrated that intelligence quotient was positively correlated with small-worldness, a graph analytic measure of network architecture efficiency. A recent study demonstrated more generally that regions of highest variability of

RSFC across individuals coincided with those regions identified in a meta-analysis as predicting individual differences in cognitive domains.[39] Many new studies linking individual differences with RSFC architecture of the brain are likely to emerge.

Meaningful associations have been observed between task performance and RSFC. Hampson et al.,[40] found that performance on a working memory task was associated with the magnitude of RSFC between medial prefrontal cortex and posterior cingulate. Kelley et al.[41] found that the magnitude of the anti-phase relationship between the default and dorsal attention networks at rest was associated with variability of performance on the Flanker task. A study by Koyama et al.[42] demonstrated that the strength of RSFC between critical language processing regions at rest predicted reading competence in both adults and children. In addition, adults showed stronger RSFC between Wernicke's and Broca's areas than children. These results show a clear association between the strength of coupling at rest and performance, and suggest that functionally relevant RSFC increases over the course of development as skill is acquired. Similarly, Zhu et al.[43] showed that increased RSFC between two critical nodes of the face-processing network—the fusiform face area (FFA) and the occipital face area (OFA)—predicted performance across a variety of face-processing tasks, including recognition of familiar faces, perceptual discrimination of novel faces, and holistic face processing. This effect was specific to faces and unrelated to similar tasks involving the processing of objects, such as recognition of familiar objects, perception of global form or global motion, and global processing of visual stimuli. This study demonstrates the specificity of the correspondence between functionally relevant patterns of RSFC within a particular network and performance in a particular cognitive domain.[43]

RSFC may also be a marker of individual differences in learning capacity. A study by Baldassarre et al.[44] demonstrated that individual differences in RSFC among retinotopically defined visual quadrants (ventral and dorsal in the left and right hemispheres) predicted performance on a visual perceptual task and the propensity to improve with training. A composite performance measure of pre-training performance and skill acquisition—'task fitness'—was correlated with pre-training RSFC among heterotopic (dorsal to ventral within and across hemispheres) visual regions. Interestingly, task fitness was not associated with RSFC among homotopic (ventral to ventral or dorsal to dorsal across hemispheres) or within local (within quadrant) visual regions (Figure 2,[45]). Furthermore, the strength of RSFC between visuotopic cortex and cortical regions associated with top-down attentional control was negatively correlated with task-fitness (Figure 2).

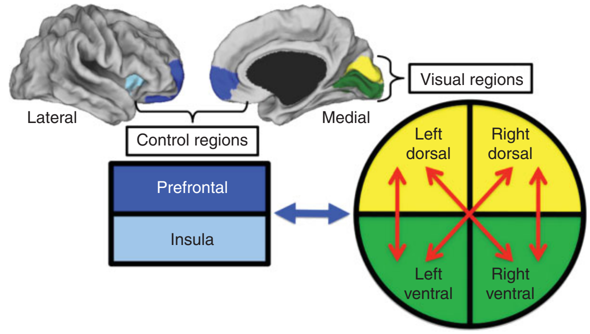

FIGURE 2 | Resting-state functional connectivity (RSFC) of visual regions predicts visual perceptual performance. Individual differences in pre-training RSFC predicted task fitness. Colored regions projected onto the lateral and medial cortical surfaces approximate visual (yellow, dorsal; green, ventral) and control (dark blue, prefrontal cortex; light blue, insula) regions. Task fitness was positively correlated with pre-training RSFC (red arrows) between heterotopic (i.e., dorsal to ventral within and across hemispheres) but not homotopic (ventral to ventral and dorsal to dorsal across hemispheres) or local (within visual quadrant) visual regions. Conversely, task fitness was negatively correlated with pre-training RSFC (blue arrow) between visual regions and both prefrontal and insular areas involved in cognitive control. (Reprinted with permission from Ref 45. Copyright 2012 National Academy of Sciences)

RSFC has been used extensively in attempts to characterize and quantify brain differences associated with various clinical disorders.[31,46] There have been rising concerns, however, that several technical artifacts, including head motion and physiological noise, can be confounds across experimental or clinical populations. These issues complicate the interpretation of direct comparisons between groups.[29,47–51] More effective methods for RSFC MRI data collection and processing to overcome these technical issues are in constant development (e.g., Ref 49, 52–56). One convincing approach is to demonstrate an association between RSFC differences in clinical populations and independent measures of behavior or symptomology. Wang et al.[57] found that RSFC between the hippocampus and posterior cingulate in older adults was correlated with neuropsychological tests of episodic memory but not with performance in non-memory domains. Using novel preprocessing techniques to minimize or control for the effects of motion and physiological artifacts, Gotts et al.[58] demonstrated that individuals with Autism Spectrum Disorders, which are defined in part by impairments of social and communication abilities, show a 'fractionation of the social brain'. They reported reduced RSFC between brain regions involved in affective aspects of social processing and those that support language and sensorimotor processes. Importantly, this same selective pattern of brain regions showed a correlation between RSFC and an independent behavioral measure of social symptom severity. Thus, Gotts et al.[58] convincingly demonstrated that RSFC can be used to reveal abnormal brain organization underlying this developmental cognitive disorder.

The studies reviewed heretofore demonstrate that RSFC MRI reveals not only that spontaneous fluctuations of activity are coordinated within dissociable functional anatomic networks but also that the strength of this coupling has functional relevance to cognition. Typically, stronger RSFC within particular domain-relevant networks is associated with better performance in the respective cognitive domain that engages those network regions during task performance. At least one study has also shown that more complex network properties, as measured with network graph analysis, are likely associated with cognitive performance as well[38]—a promising approach for future discovery.[59,60]

RSFC IS MODULATED BY PREVIOUS EXPERIENCE, WHICH IMPACTS FUTURE COGNITIVE PERFORMANCE

In the previous section, we reviewed the evidence that the strength of RSFC within functional anatomic networks is related to individual differences in personality, behavior, and cognition. These observations, however, leave unresolved the question of whether the observed differences reflect hardwired, genetically determined factors or are plastic and experience-dependent to some degree. To substantiate the hypothesis that RSFC reflects processes that play a dynamic functional role in learning and memory, one must demonstrate that RSFC can be modulated by prior experience in a sustained way. A number of studies have demonstrated substantial correspondence between patterns of RSFC and measures of anatomical connectivity,[61] reflecting both monosynaptic and polysynaptic connections, indicating that RSFC is constrained to a large extent by anatomy (e.g., Ref 62, 63) However, numerous recent studies have now shown that RSFC does not exclusively reveal static anatomical connectivity. Rather, some portion of the variance in spontaneous fluctuations is malleable on short timescales, is related to ongoing or recent experience, and predicts learning and memory.

Perhaps the first study to report that patterns of RSFC are modulated by previous experience demonstrated that, relative to a pre-task rest period, RSFC was strengthened between several brain regions following a blocked language task.[64] Subsequent studies replicated this basic effect of recent experience on RSFC, reporting more robust and functionally selective results.[65–72] For example, Albert et al.[65] reported pre- versus post-task RSFC differences in visuomotor and cerebellar regions following a motor learning task. Grigg and Grady[70] found greater spatial and temporal variance in the RSFC of the default network following task. Lewis et al.[67] demonstrated particularly striking specificity of RSFC changes, where following several days of intense training on a visual perception task constrained to a single visual quadrant, RSFC changed significantly between frontal-parietal areas involved in the control of spatial attention and only the trained visual quadrant. Stevens et al.[68] reported that repeated experience with different categories of visual information (faces vs scenes) caused frontal networks to couple differentially with category-preferential ventral occipitotemporal cortex regions [FFA vs parahippocampal place area (PPA), respectively] during subsequent periods of rest. Subsequent studies have replicated and extended these findings, showing increased spontaneous coupling in functionally relevant brain regions or networks following an associative encoding task,[69] a motor task,[71] and a working memory task.[72]

On the basis of these studies, there is now substantial evidence that RSFC is modulated by recent experience in task-relevant brain regions and networks. Furthermore, these effects show a striking degree of functional and spatial specificity, as demonstrated by altered connectivity of category-preferential regions[68] and even a single retinotopically defined visual quadrant.[67] One question that remains, however, is whether modulation of RSFC by prior experience is an epiphenomenon, occurring automatically within regions or networks previously engaged by task performance, akin to a passive 'echo' or 'ripple effect' (e.g., Ref 73) or whether such modulation plays a functional and/or causal role in cognition. A handful of studies have now demonstrated that the degree of experience-dependent modulation of RSFC in task-relevant brain regions or networks predicts subsequent performance.

The first study to report that task-dependent modulation of RSFC has an impact on subsequent performance was that of Lewis et al.[67] reviewed above, which involved perceptual learning. Relative to a pre-training rest period, RSFC revealed increased negative correlation of activity between a frontal-parietal attention network and only the trained visual quadrant during a post-training rest period. Importantly, the degree of this altered coupling during

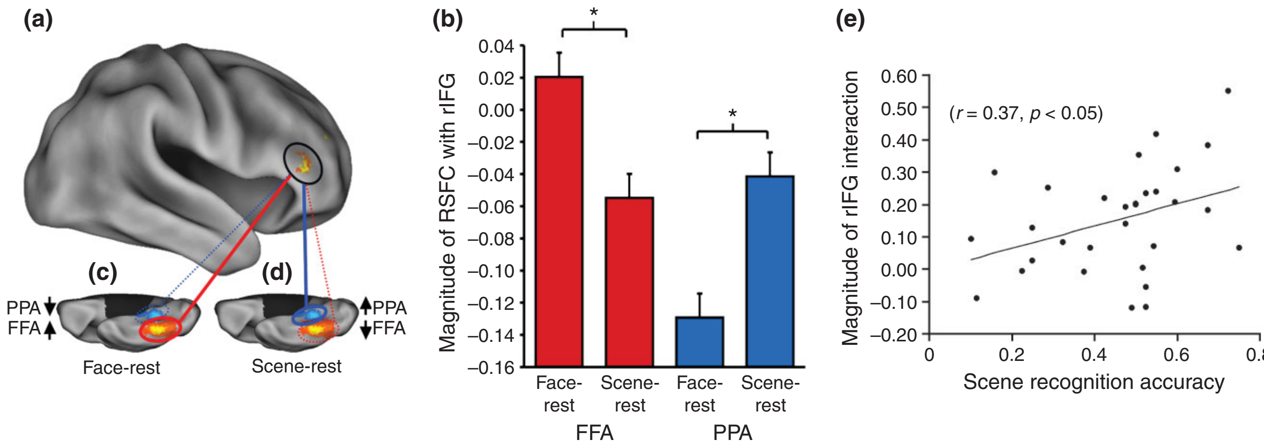

FIGURE 3 | Resting-state functional connectivity (RSFC) is modulated by previous task, which predicts future memory. (a) Region in the right inferior frontal gyrus (rIFG; circled) involved in both face- and scene-processing showed a task by region of interest (ROI) interaction for RSFC with the fusiform face area (FFA) and parahippocampal place area (PPA) ROIs (b) Paired samples comparisons revealed a significant simple effect of task on subsequent RSFC between rIFG and both the FFA and PPA. (c) RSFC with the FFA increased during rest after a face-task ('face-rest') relative to after a scene-task ('scene-rest'); conversely, (d) RSFC with the PPA increased during scene-rest relative to face-rest. Red and blue lines indicate RSFC with the FFA and PPA, respectively; solid lines and dotted lines indicate increased RSFC and decreased RSFC, respectively. (e) Modulation of the RSFC of the rIFG with category-preferential visual regions during rest predicts subsequent memory. Across all participants, the magnitude of the interaction in rIFG was significantly correlated with subsequent recognition accuracy for scenes. (Reprinted with permission from Ref 68. Copyright 2010 Oxford University Press)

rest predicted subsequent performance on the learned perceptual task (i.e., shape identification in a single visual quadrant) across individuals.

Stevens et al.[68] first demonstrated that modulation of RSFC plays a role in memory consolidation and predicts subsequent explicit memory. Frontal networks coupled more strongly with either the FFA or the PPA during rest periods following either a face- or scene-processing task, respectively. Critically, the degree of this category-specific modulation of RSFC was correlated with subsequent memory for the images previously viewed, as indexed by performance on a recognition memory test (Figure 3). Tambini et al.[69] reported complementary results, where the magnitude of increased coupling between the hippocampus and a portion of the lateral occipital complex during rest following an associative encoding task predicted subsequent associative memory. Finally, a recent study reported that performance during a working memory task (reaction time on an N-back task) predicted RSFC strength in a post-task rest period.[72]

The earlier studies reviewed above provide compelling evidence that the strength of RSFC within functionally relevant brain regions or networks is related to individual differences and cognitive performance across several domains. Furthermore, RSFC can be modulated by prior experience. The latter studies reviewed provide initial evidence that the degree of experience-dependent modulation of RSFC predicts future performance in these cognitive domains. To date, these effects have been shown for both perceptual learning[67] and explicit memory.[68,69] Prior to the emergence of anatomical changes, RSFC changes may also be associated with the lasting impact of task-evoked activity changes associated with training.[74,75] Future work will likely elucidate the dynamics of these processes further, in terms of the magnitude, specificity, and temporal dynamics of RSFC-behavior interactions in these and other cognitive domains.

RSFC PLAYS A ROLE IN CORTICAL SPECIALIZATION AND THE ORGANIZATION OF CONCEPTUAL KNOWLEDGE

An important aspect of development that impacts the acquisition of perceptual skills and cognitive abilities is functional specialization across topographically organized regions of the cortex. For example, hemispheric functional asymmetry may reflect specialization that underlies improvements in cognitive abilities over the course of evolution, development, and skill acquisition.[76–79] As an example of the interrelation between skill acquisition and hemispheric asymmetry, there is evidence of a correlation between the acquisition of reading competence and the emergence of left versus right lateralization of word-

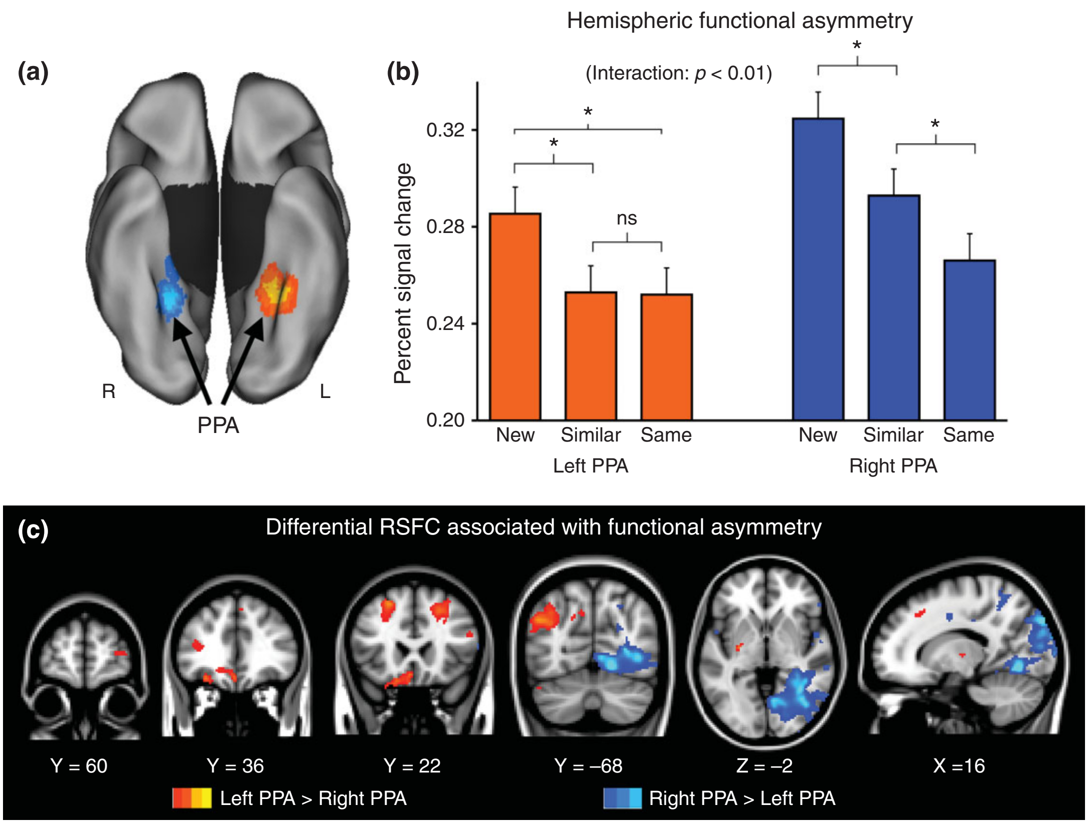

FIGURE 4 | Hemispheric functional asymmetry of the parahippocampal place area (PPA) is associated with differential resting-state functional connectivity (RSFC). (a) Independently localized right (blue) and left (orange/yellow) PPA. (b) Percent signal change relative to fixation baseline for scenes in three repetition priming test conditions (repeated SAME, repeated SIMILAR, and NEW): A significant hemisphere by test condition interaction indicates hemispheric asymmetry of repetition suppression. Form-specific perceptual processing in the right PPA is indicated by a graded repetition suppression effect, with a lower response for SIMILAR than NEW scenes and for SAME than SIMILAR scenes. Conversely, form-abstract processing in the left PPA is indicated by equivalent suppression of the response for SIMILAR and SAME scenes relative to NEW scenes. (c) Whole-brain RSFC analyses confirm hemispheric asymmetry of PPA connectivity, with differential RSFC of the right (blue scale) versus left (yellow/orange scale) PPA. The right PPA showed differentially higher correlations with primarily visual perceptual brain regions. The left PPA showed differentially higher correlations with regions primarily involved in abstract/conceptual processes. (Reprinted with permission from Ref 83. Copyright 2012 Oxford University Press)

versus face-processing, respectively, in lateral fusiform cortex.[80] One hypothesis is that functional specialization of a particular cortical region occurs by virtue of its privileged connectivity with other functionally relevant brain regions.[81–83] Stevens et al.[83] tested this hypothesis directly using RSFC MRI. A number of studies have demonstrated consistent hemispheric asymmetry of form-specificity—e.g., for visual processing of entities such as objects and faces in ventral occipitotemporal cortex—with more form-specific/perceptual processing in the right hemisphere and more form-abstract/conceptual processing in the left hemisphere.[78,84–92] However, little was known about brain organization underlying this specialization. Stevens et al.[83] demonstrated that this dissociation across hemispheres extends to the processing of complex visual scenes within the PPA—a region specialized for visual scene processing[93]—with form-specific processing in the right PPA versus form-abstract processing in the left PPA (Figure 4(a) and (b)). Using RSFC, the authors demonstrated that this functional dissociation was associated with differentially stronger RSFC of the right versus left PPA with posterior visual processing regions versus higher-order conceptual processing brain regions, respectively (Figure 4(c)). This study provides evidence that cortical specialization is associated with differential connectivity with other distributed brain regions that store and/or process functionally relevant information.

Several studies have used RSFC to investigate the nature of hemispheric functional specialization on a broader scale.[94–96] Liu et al.[94] used RSFC to demonstrate that independent factors control hemispheric asymmetry for distinct brain systems—those involved in language and internal thought (default network) were left lateralized, while those involved in vision and attention were right lateralized. A recent study by Gotts et al.[95] provided compelling evidence that hemispheric asymmetry is beneficial for cognitive functioning. Using RSFC, they demonstrated that the left hemisphere shows a relative bias for intra-hemispheric interaction, particularly for regions involved in language and fine motor control, while right hemisphere regions involved in visuospatial and attentional processing show a bias for inter-hemispheric integration. Importantly, these measures of lateralization within distinct systems selectively predicted behavioral measures of verbal and visuospatial ability, respectively.[95] A recent study by Wang et al.[96] used RSFC to investigate the relationship between cerebellar and cerebral hemispheric asymmetry, and showed that the degree of cerebellar functional asymmetry was correlated with cerebral asymmetry, and further, predicted cerebral lateralization during an active language task.

Another highly reliable example of cortical specialization is the remarkably consistent category-related topographical organization of human ventral occipitotemporal cortex observed across individuals. For example, dissociable regions show preferential responses to faces (FFA[97]), scenes (PPA[93]), bodies [extrastriate body area (EBA)[98]], written words [visual word form area: (VWFA)[99]], tools, and animals (medial and lateral fusiform cortex, respectively[100]). If specialization is driven to some extent by connections with other distributed brain regions, then various category-related regions should show differential RSFC with other brain regions that are critical for storing and/or processing category-relevant properties.[81,82] Ongoing work has provided evidence to support this idea: Stevens et al.[101] demonstrated that across participants, functionally

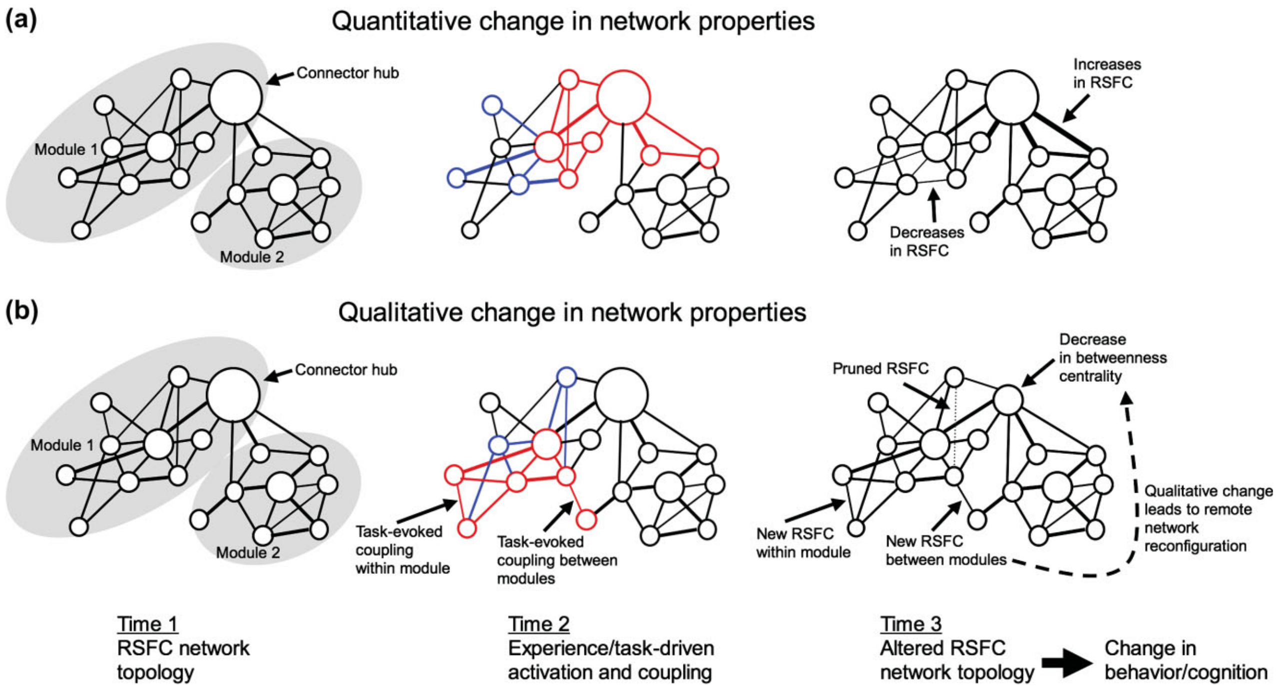

FIGURE 5 | Illustration of the proposed mechanism of action of resting-state functional connectivity (RSFC): experience-dependent modulation leads to sustained network changes that facilitate future performance. Time 1: the RSFC network is comprised of two modules (i.e., communities) with a single connector hub. Time 2: Experience causes task-driven activity and coupling between regions. Time 3: Sustained changes to the network may be either (a) Quantitative or (b) Qualitative. (a) Quantitative changes to the network at Time 3 reflect increases and/or decreases in the magnitude of RSFC among network nodes relative to Time 1, which may be associated with changes in task performance. (b) Qualitative changes in RSFC at Time 3 would reflect the pruning of RSFC or the addition of new RSFC among nodes relative to Time 1, both of which may be associated with changes in performance. Qualitative changes, however, may modify features of the network that are remote from the activity site. In the above example, new RSFC between modules reduces the importance of the connector hub, and causes a decrease in this node's 'betweenness centrality', a graph analytic measure of its contribution as an inter-module connector hub. These remote changes may also be associated with performance. We review evidence supporting experience dependent quantitative changes. At this point, it is unclear if experience produces qualitative changes in RSFC. Line weights signify RSFC magnitude. Red circles indicate an increase in activity; blue circles, a decrease in activity. Red lines indicate an increase in coupling; blue lines, a decrease in coupling. Dotted line indicates the former location of a pruned connection. Initial network topology derived from Ref 110.

defined category-related regions—left medial fusiform gyrus for tools, right lateral fusiform gyrus for animals, PPA for scenes, and FFA for faces—each show preferential RSFC with distributed cortical regions within category-relevant functional networks that process these respective categories of information: (1) reaching/grasping related regions in left lateral parietal cortex for tools[102]; (2) the EBA for animals; (3) the 'retrosplenial complex'[103] and 'occipital place area'[104] for scenes; and (4) the OFA and the posterior superior temporal sulcus for faces. Similarly, in other ongoing work, Stevens et al.[105] demonstrated that a region in the left occipitotemporal sulcus that shows a preferential response to written words (VWFA) has preferential RSFC with left lateralized language regions. Together, these results provide compelling evidence that the topographical organization of category-specialized regions depends, to some extent, on functionally specialized connectivity with other regions of the brain that store and/or process category-relevant properties.

CONCLUSION

When considering the evidence reviewed in this article, it is clear that much work is yet to be done to determine the nature of interactions between RSFC, large-scale brain organization, and cognition. For example, the extent to which this organization is constrained by predetermined or 'hard-wired' intrinsic networks versus more malleable configurations driven by an experience-dependent mechanism, is unknown. Understanding the non-stationary and other dynamic signals observable during resting-state MRI (e.g., Ref 106–108), as well as their relationship with cognition, poses an exciting avenue for future research. Furthermore, relating discoveries based on RSFC MRI, which gives a macroscopic view of brain interactivity at the level of whole networks and systems, to findings based on electrophysiological work that provides information on much finer spatial and temporal scales, will be necessary to fully understand the nature of these processes across different levels of analysis. While the evidence reviewed throughout this article demonstrates that patterns of RSFC are functionally relevant and experience-dependent to some degree, the strikingly consistent topographical organization of RSFC across individuals suggests that at some level, large-scale organization of this connectivity is at least partially constrained by genetic factors. We argue that RSFC MRI is an ideally suited method for investigating these important questions about the relevance of cognition to the functional organization of the brain. A general mechanism has been proposed by which RSFC might play a dynamic causal role in cognition, whereby cognitive performance is improved by experience-dependent modulation of RSFC.[67,83,109] We hypothesize that this occurs through a Hebbian-like mechanism, whereby a history of repeated co-activation of distributed brain regions engaged during task performance leads over time to selective increases and decreases in functional connectivity among local and distributed brain regions. This process facilitates the efficiency of future coupling among these regions, thus improving cognitive performance (Figure 5). In this article, we have reviewed evidence that such experience-driven changes are quantitative in nature, with stronger or weaker RSFC among nodes of existing networks resulting in individual differences and impacting future cognitive performance (Figure 5(a)). However, an intriguing additional possibility is that experience-driven changes to RSFC are qualitative in nature, resulting in more complex and higher-order changes to the functional network architecture, as measured by graph analytic techniques for example (Figure 5(b)). Future work will progress through the development of more sophisticated paradigms and more advanced approaches to characterizing and quantifying functional network properties. There is a wealth of evidence that anatomical specialization and variability play critical roles in the development, evolution, and individual differences of human cognitive functions (e.g., Ref 76, 111–114). While this growing body of work goes well beyond the scope of the current review, relating these findings to the RSFC MRI literature will ultimately be important for understanding how modulation of RSFC on shorter timescales might be relevant or causally related to the much slower anatomical changes associated with training, development, and evolution.

Since its introduction, RSFC has proven to be a powerful tool for mapping large-scale networks of the human brain.[1,29] However, its utility as a method of studying cognition has been less clear, and evidence has been slower to emerge. There has been controversy and debate within the literature on this very topic, with some who explicitly 'challenge the utility of studies of the resting state'.[115] In this article, we argue that studies of the resting-state, using RSFC MRI, have produced new and critical insight into the interrelationships between the brain and cognition. The evidence reviewed here demonstrates that (1) the strength of RSFC across functionally relevant brain regions and networks is correlated with individual differences in personality, behavior, and cognition; (2) RSFC is malleable on short timescales; it is modulated by ongoing and recent experience in functionally relevant brain regions and networks; (3) the degree of this experience-dependent modulation of RSFC predicts both learning capacity and future cognitive performance; finally, (4) cortical specialization and the organization of conceptual knowledge are associated with, if not to some extent driven by, preferential RSFC with distributed brain regions that process functionally relevant information. On the basis of these findings, we argue that RSFC MRI provides an invaluable tool for gaining new insight into the neurocognitive interactions that underlie cognition.

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