Trends in Cognitive Sciences

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Opinion

Process-Specific Alliances (PSAs) in Cognitive Neuroscience

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Most cognitive neuroscience theories have focused on the functions of individual brain regions, but cognitive abilities depend also on functional interactions among multiple regions. Many recent studies on these interactions have examined large-scale, resting-state networks, but these networks are difficult to link to theories about specific cognitive processes. Cognitive theories are easier to link to the mini-networks we call process specific alliances (PSAs). A PSA is a small team of brain regions that rapidly assemble to mediate a cognitive process in response to task demands but quickly disassemble when the process is no longer needed. We compare PSAs to resting-state networks and to other connectivity-based, task-related networks, and we characterize the advantages and disadvantages of each type of network.

Highlights

Process-specific alliances (PSAs) constitute small groups of active brain regions that functionally interact to carry out a process in the service of a larger task.

PSAs rapidly assemble and disassemble in accordance with task demands, and the same brain regions are involved in different PSAs during different tasks.

PSAs provide a flexible, theoretical framework for characterizing how the brain carries out cognition without succumbing to naïve reductionism or strict localizationism.

PSAs offer important advantages and disadvantages relative to resting-state networks and connectivity-based, task-related whole-brain networks.

Overview of Networks in Cognitive Neuroscience

Most cognitive neuroscience studies using functional neuroimaging have focused on the contributions of specific brain regions during particular cognitive tasks. However, carrying out cognitive tasks depends not only on individual segregated brain regions but also on their interactions with one another. **Functional magnetic resonance imaging (fMRI)** (see Glossary) can be used to study these interactions via **functional connectivity (fCon)**, which typically refers to correlated brain activity across time or trials. Since the 1990s, one fCon approach has been to identify 'mini-networks' of two or three brain regions assumed to mediate a specific cognitive process during the task of interest. In parallel, there has been considerable interest since the early 2000s in **resting-state networks (RSNs)**, such as the **default mode network (DMN)** [1,2]. More recently, several studies have investigated large-scale **connectivity-based, task-related networks (cTRNs**; Box 1). In this article, we focus primarily on mini-networks that we call **process-specific alliances (PSAs)**, which are typically comprised of two or three interacting regions [3,4]. PSAs are essential for cognitive neuroscience because they permit straightforward, component-based mechanistic hypotheses based on the available knowledge about the functional profiles of individual brain regions and the individual cognitive processes mediating behavioral tasks. The article has three main sections. First, we define PSAs, identify the three criteria for characterizing them, and provide examples. Second, we compare PSAs to RSNs and cTRNs, noting their respective advantages and disadvantages. Finally, we suggest a possible approach for linking PSAs and cTRNs.

Process-Specific Alliances

We define a PSA as a small 'team' of brain regions that rapidly assemble to mediate a cognitive process in response to task demands but quickly disassemble when the process is no longer needed [3,4]. As indicated by the term 'alliance', PSAs are flexible, temporary, and opportunistic. The same brain region can form different PSAs with multiple different regions to support distinct (but related) processes during different tasks. For example, a prefrontal cortex (PFC) region might form a PSA with visual cortex (VisCtx) to mediate attentional modulation of visual

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Box 1. Task-Related Networks (cTRNs) and Graph Theory

We use the term cTRN to refer to the set of functional connections between brain regions in the functional network observed during a cognitive task or in some condition. Thus, cTRNs should not be confused with the discrete set of regions significantly activated (compared to a control) during a cognitive task. Although the discrete set of regions showing significant activation effects is sometimes called a 'network', without subsequent functional connectivity analyses, it is unclear if the regions are actually connected to each other. In fact, there is evidence that significantly activated regions differ from those regions that are functionally connected during cognitive tasks [32], and that the identified functional connections between regions that do not exhibit significant activations may still be closely related to cognitive performance and behavior [95].

Network science and the formalisms of **graph theory** offer a framework and a comprehensive set of tools to describe how any network, including cTRNs, is organized [86]. All graphs that model real-world networks are comprised of differentiable elements of the system (nodes) and pairwise relationships between those elements (edges). Connectivity matrices, or matrices in which both rows and columns are labeled by an ordered list of elements (nodes), represent the full set of nodes and connections in a network [86]. In task-related functional brain networks, nodes (i.e., brain regions) must be delineated and edges (i.e., functional connections) must be measured prior to characterizing the topological properties of the system using graph theoretic measures. Of course, the topological properties of RSNs can be investigated in a similar fashion, by first delineating brain regions and then by measuring functional connectivity between brain regions. In practice, graph theoretic network analyses have been conducted by delineating nodes from all brain space with a detectable signal, but they have also been conducted by identifying only some subset of *a priori* identified regions [96]. After all nodes and edges have been identified in any given cTRN, graph theoretic metrics can be used to characterize the topological properties of the system.

processing, and then the same region might form a PSA with the striatum to mediate attentional control of motor performance. This PFC region would have a similar control role in both PSAs, but the nature of the control process would be somewhat different because the contents (representations) controlled are different (visual vs. motor). To offer a metaphor, an accountant in a large corporation may form one PSA with an employee in the payroll department to process annual bonuses and a different PSA with an employee in the billing department to calculate quarterly sales. Each of these teams assemble to solve a particular task (annual bonuses, quarterly sales) and disassemble when the task is complete.

PSAs can vary widely in the number of their components, but PSAs that have been identified in practice typically consist of two or three brain regions, as illustrated by Figure 1A. We focus on two- and three-region PSAs for ease of explication. For example, a two-region PSA could involve one region passing information to another (e.g., V1 to V2) or one region controlling another (e.g., PFC upregulating visual cortex activity during top-down visual attention). An example of a three-region PSA would be Region X controlling the flow of information between Regions Y and Z (e.g., PFC modulating the flow of information from visual cortex to the amygdala). Importantly, the number of brain regions (and the particular pattern of functional connections between them) comprising any given PSA depends on what the task requires. Although larger PSAs likely exist, they might be decomposable into smaller PSAs. For example, what appears to be a four-region PSA might be better described as overlapping three-region and two-region PSAs (Figure 1B, left). Conversely, when subregions with different fCon profiles are identified, a single PSA may be subdivided into different PSAs (Figure 1B, right).

This latter scenario raises the following question: what is the optimal level of PSA granularity? This question does not have a single, context-independent answer. We tend to favor a hierarchical view [5] in which the functions of subregions tend to be related to (but are not necessarily always related to) the functions of the broader region that subsumes them. For example, much of the prefrontal cortex has a general control function during many different tasks, but the inferior frontal gyrus (IFG) is thought to perform a control function during some tasks specific to object representations, and the left anterior IFG is thought to perform a control

Glossary

Connectivity-based, task-related networks (cTRNs): the full set of functional connections, and the manner in which those connections are organized topologically, between brain regions during particular cognitive tasks.
Default mode network (DMN): a subset of brain regions that tend to be strongly functionally interconnected during rest and some tasks, typically comprised of the posterior cingulate cortex, the precuneus, the medial prefrontal cortex, the angular gyrus, and other regions.
Functional connectivity (fCon): statistical dependencies, or correlations, between spatially remote neurophysiological events.
Functional magnetic resonance imaging (fMRI): brain imaging tool used to acquire spatially precise measurements of activity across much of the brain every 1–2 s. fMRI measures the blood oxygenation level-dependent response, which serves as a proxy for the metabolic activity of neurons in a particular piece of brain tissue.
Graph theory: a branch of mathematics concerned with the study of graphs, which are structures commonly consisting of units called 'nodes' and links called 'edges'.
Process-specific alliances (PSAs): 'mini-networks' in the brain typically comprised of two or three regions that are assumed to mediate a specific cognitive process during some task of interest.
Resting-state networks (RSNs): sets of brain regions that tend to be functionally connected while individuals are resting in the scanner in a task-free state.
Salience network: a set of brain regions that tend to be strongly functionally interconnected during rest and during some tasks, typically comprised of the anterior insula, the dorsal anterior cingulate cortex, the amygdala, the ventral striatum, the substantia nigra/ventral tegmental area, and other regions.

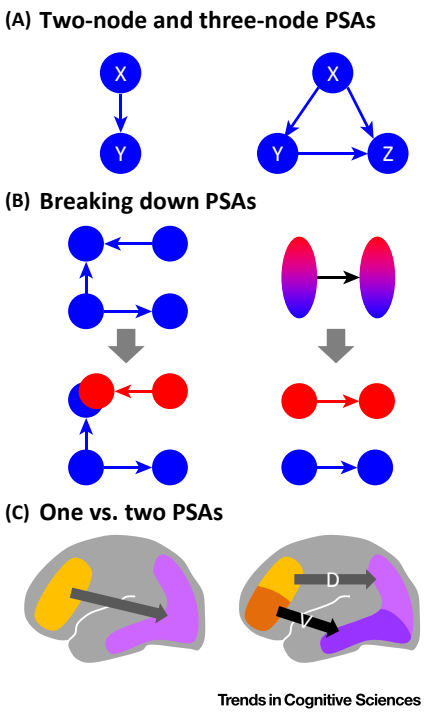

Figure 1. (A) Two- and three-node process-specific alliances (PSAs). (B) Left, PSAs with more than three regions can often be decomposed into multiple PSAs. Right, a two-region PSA with different functional subregions can also be decomposed into multiple PSAs. (C) According to a hierarchical view, the cognitive functions of subregions (e.g., IFG) tend to be related to the general function of the broader region (e.g., PFC). Depending on the level of abstraction, the same interaction may be described as one PSA or two PSAs.

function related to object meaning during other tasks [6]. Similarly, the visual cortex is involved in vision generally, with the ventral visual pathway preferentially implicated in object vision, and the fusiform face area (FFA) in vision of a particular type of object (faces) [7]. Note that this hierarchical view does not require a strict commitment to one-to-one mapping between structure and function in the brain, given that the functions subserved by many brain regions appear to be context-specific. At the same time, however, if one-to-one mapping of structure to function is discovered, the hierarchical view remains compatible with this possibility. It is worth noting that although we favor a hierarchical view, PSAs are compatible with non-hierarchical views such as those advocating sharp functional distinctions between immediately neighboring brain regions.

Generally speaking, we suggest that broad functions are carried out in large areas of cortex. Such functions, however, are realized by neural computations commonly carried out on a much smaller scale over relatively circumscribed regions of the brain. One can conceive of these circumscribed regions as existing at the bottom of a hierarchy whose computations contribute to the broader general function, such as control for prefrontal cortex, or high-level vision for inferior temporal cortex. These subregions mediate primarily one computation, but this computation is different depending on the PSA. For example, the FFA may be one subregion, and different parts of the FFA may perform the same computation, possibly enabling holistic representation, but with respect to different material – faces with regard to one subregion and different complex objects in another subregion. This differential coupling of computation and material supports a different process underlying each PSA. Thus, although a subregion

may typically mediate one computation, this computation contributes to a different process in each PSA.

As with individual brain regions, it is possible to characterize the functions of PSAs at different levels of abstraction. For example, one can describe a PSA between PFC and visual cortex (VisCtx) as responsible for mediating top-down visual attention during one task (Figure 1C, left), but this PSA could be split into a dorsal PSA for spatial top-down attention during some tasks and a ventral PSA for object top-down attention during other tasks (Figure 1C, right) [8]. Both levels of description are valid, and the optimal level of description should depend on the particular question(s) being investigated by the researcher.

Given this flexibility in defining PSAs, it is important to provide some criteria for determining when to use this term. We propose three requirements for calling a small group of regions a PSA. Requirement 1 specifies that every PSA region should be linked to the broader cognitive process attributed to the PSA. Using cognitive neuroscience methods, one must show that the disruption of any PSA regions (damage, transcranial magnetic stimulation [TMS], drugs, etc.) impairs the process mediated by the PSA, and/or that task-related activity in every PSA region is associated with successful process performance (e.g., with event-related fMRI).

Requirement 2 specifies that PSA regions should perform a suboperation of the process attributed to the PSA. These suboperations are assumed to be different but complementary. For example, if a region is assumed to perform a basic computation and to then feed that information to another region that performs a more complex computation (e.g., V1–V2 PSA), then the two suboperations complement each other.

Requirement 3 specifies that PSA regions should interact during successful deployment of the process attributed to the PSA. The existence of a direct white-matter connection indicates that two regions are capable of interacting directly, and resting-state fCon indicates that the regions do interact in some contexts (we take resting-state to just be another kind of task that recruits certain brain regions and implicates certain functional connections for certain purposes). However, the critical requirement is that the two regions functionally interact while the process is performed (task-related) and that this interaction contributes to successful performance (success-related). Importantly, it is not necessary that an identifiable direct structural connection exists between two brain regions to form a PSA, because those regions might be indirectly structurally connected, or there might be a direct structural connection that is undetectable with current technologies. It is, however, more likely that two brain regions are forming a PSA during a task if there is an identifiable direct structural connection between them. These three PSA requirements are made more concrete in the examples in the next section.

Examples of PSAs

Reviewing the vast fCon literature is beyond the scope of the current article. Instead, we provide a few examples of PSAs that meet the three requirements. To illustrate the point that the same Region A may form a PSA with Region B during one task and with Region C during another task, we provide examples of pairs of PSAs sharing one particular brain region in different contexts. Because they share a brain region, there are similarities between the processes performed by the PSAs in each pair. It is worth noting that PSAs that seem to overlap (e.g., AB PSA and AC PSA) may turn out to be non-overlapping, if it is discovered that the shared region consists of two subregions with dissociable functions (e.g., A_1 vs. A_2), each participating in a different PSA (e.g., A_1–B PSA and A_2–C PSA). Thus, in some of the examples below, the pairs

of overlapping PSAs may turn out to be non-overlapping. For ease of explication, all examples below are for two-region PSAs.

PSAs during Semantic Processing and Emotion Regulation

As is the case with other frontal regions, left ventrolateral PFC (LVLPFC) is part of multiple PSAs mediating control processes during different cognitive tasks. For example, LVLPFC is part of PSAs involving language comprehension and reappraisal-based emotion regulation. During language comprehension, LVLPFC forms a PSA with left middle temporal gyrus (LMTG), which is assumed to mediate semantic processing [9]. Consistent with Requirement 1, both regions are strongly associated with semantic processing [9,10] (Figure 2A, left). For example, TMS of LVLPFC [11] and lesions of LMTG [12] have been shown to impair word comprehension. Meeting Requirement 2, the contributions of both regions are thought to be complementary: LVLPFC is hypothesized to mediate control operations [6], while LMTG processes and/or stores semantic representations [12–14]. Finally, meeting Requirement 3, LVLPFC and LMTG are not only structurally connected by direct white-matter tracts [15] and functionally connected during rest [15,16], but, critically, they also display task-related fCon during tasks requiring semantic processing, including sentence comprehension [17] and semantic judgments [16].

During emotion regulation, LVLPFC is part of a PSA with the amygdala, particularly during reappraisal [18,19]. Consistent with Requirement 1, LVLPFC and the amygdala are both associated with emotion regulation via reappraisal [19,20]. Fulfilling Requirement 2, these two regions are assumed to mediate complementary processes during reappraisal-based

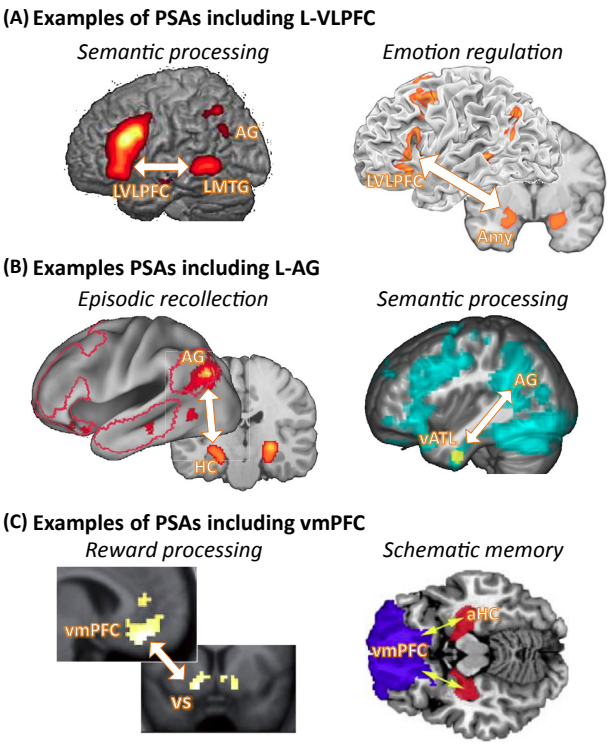

Figure 2. Examples of Process-Specific Alliances (PSAs) in Different Cognitive Domains. (A) Examples of PSAs including LVLPFC. The left panel shows regions typically activated (activation likelihood estimate [ALE] meta-analysis) during language comprehension tasks involving controlled semantic processing [9], and the right panel shows regions typically activated during emotion regulation conditions involving reappraisal [20]. (B) Examples of PSAs including left AG. The left panel display regions usually activated (ALE) during episodic memory retrieval tasks involving recollection [94], and the right panel shows the results of a study of semantic processing that placed a seed in vATL and found fCon with AG [35]. (C) Examples of PSAs including vmPFC. The left panel shows the results of a study [52] that identified vmPFC and VS during processing of monetary rewards. The right panel displays the results of a study in which functional connectivity between vmPFC–aHC during encoding was stronger for schema-consistent than schema-inconsistent information [63].

emotional regulation: the amygdala is thought to generate emotional responses to emotional stimuli, whereas LVLPFC is assumed to dampen amygdala responses by reinterpreting emotional stimuli [19]. Finally, meeting Requirement 3, LVLPFC and the amygdala are anatomically connected by the uncinate fasciculus (via ventromedial PFC [vmPFC]) and show fCon during emotional regulation tasks [21,22] (Figure 2A, right).

In sum, LVLPFC serves a control function in both PSAs, but the specific control operations differ: during language comprehension, LVLPFC controls semantic processing of representations stored in or processed by LMTG, whereas during emotional regulation, LVLPFC controls the semantic reinterpretation of emotional stimuli, dampening amygdala responses. This arrangement is typical of PSAs: the general function of a region is similar, but the specific operations performed vary depending on the PSA. Thus, PSAs allow us to concurrently consider both the functions of individual regions and the functions of brain networks, bridging two approaches that often have traditionally been investigated separately in cognitive neuroscience. Importantly, while the PSA formed between LVLPFC and LMTG is present during language comprehension, this PSA disassembles during emotion regulation because it is not necessary for carrying out emotion regulation. And while the PSA formed between LVLPFC and the amygdala is present during emotion regulation, this PSA disassembles during language processing because it is not necessary for carrying out language processing. This kind of transient and dynamic functional reorganization to subserve different task demands is also characteristic of the examples that follow.

PSAs during Episodic Recollection and Semantic Processing

The angular gyrus (AG) has been identified as a brain region implicated in diverse areas of research, including: social cognition, number processing, episodic memory retrieval, and semantic processing [5,23]. Below are examples of PSAs involving AG during episodic retrieval and semantic processing. During episodic retrieval, the AG forms a PSA with the hippocampus (HC), particularly during vivid retrieval or recollection (Figure 2B, left). Fulfilling Requirement 1, both AG and HC are strongly associated with recollection [24–26]. Satisfying Requirement 2, these regions are assumed to play complementary roles during recollection: HC is thought to mediate the recovery of memory details and AG to process the recovered details. The specific role of AG in processing recovered memory details is supported by the effects of AG lesions, which do not impair memory retrieval *per se* but the ability of reporting retrieved memories [27]. Consistent with the notion that PSAs assemble to mediate a process and then rapidly disassemble, AG activity during recognition memory lasts only a few hundred milliseconds (e.g., 300–600 ms after stimulus), as indicated by the parietal old–new event-related potential effect [28]. Finally, meeting Requirement 3, AG and HC are not only structurally connected [29,30] and coactive during rest [31], but, critically, they show task-related fCon during recollection [32–34].

Like LVLPFC, left AG plays an important role in semantic processing [10,35]. During this process, left AG forms PSAs not only with LMTG but also with the ventral anterior temporal lobes (vATL). Fulfilling Requirement 1, both AG and vATL have been associated with semantic processing [14,35,36], and meeting Requirement 2, these regions are assumed to have complementary roles during semantic processing: vATL is thought to store or process integrated/abstract semantic representations [37], and AG to mediate combinatorial semantic processing [14]. Finally, consistent with Requirement 3, AG and vATL are structurally connected, and, importantly, they display task-related fCon during semantic processing [36]. For instance, one study found significant fCon during a semantic task between a vATL seed and left AG (Figure 2B, right) [35].

In sum, both in the PSA with the HC and in the PSA with vATL, AG supports the processing of representations. The specific form of processing mediated by AG is a topic of debate. In the episodic memory retrieval literature, the role of AG has been attributed to bottom-up attention to episodic memory representations [26,38] and to binding [39] or maintaining [40] integrated episodic representations. In the language/semantic memory literature, the function of AG has been attributed to processes such as fluent conceptual combination [10], integration of semantic information into context [14], and combinatorial semantics [41]. There is consensus that AG plays a role in processing memory representations, episodic or semantic, but its specific role is disputed. Consistent with this representational account of AG function, multivariate pattern analyses can distinguish classes of stimuli in this region [42–45]. This research provides an example of how comparing overlapping PSAs across tasks, such as AG–HC during episodic retrieval and AG–vATL during semantic processing, can help constrain theories about the function(s) of the shared region.

PSAs during Reward/Value Processing and Schematic Memory

vmPFC is a multifaceted region that is involved in many different task domains, including: reward processing, value-based decision making, emotion, social cognition, and memory [4,46–48]. We focus here on the roles of vmPFC in reward processing and schematic memory. During reward/value processing, vmPFC forms a PSA with the ventral striatum (VS) (Figure 2C, left). Fulfilling Requirement 1, both vmPFC and VS are strongly associated with reward processing [49], and satisfying Requirement 2, these regions are assumed to play complementary roles during reward processing: VS has been linked to the anticipation or prediction of reward and vmPFC, which is assumed to modulate VS, is associated with processing value representations [50–52]. Finally, meeting Requirement 3, vmPFC and VS are not only structurally connected [53,54] and coactive during rest [55,56], but, critically, they also show task-related fCon during reward processing [57].

In the memory domain, vmPFC forms a PSA with the anterior hippocampus (aHC) to support schematic relational memory. In keeping with Requirement 1, both vmPFC and aHC are associated with schematic memory [4,47], and fulfilling Requirement 2, these regions are thought to mediate complementary functions during schematic memory: aHC is assumed to store global context representations, and vmPFC operates on those representations by linking them to stored knowledge (schemas) [4]. When vmPFC is damaged, patients exhibit confabulation symptoms, in which they experience the present and re-experience the past through the lens of distorted and misapplied schemas. Finally, satisfying Requirement 3, these regions are structurally connected (via the uncinate fasciculus) [58,59], coactivate during rest [60], and, most importantly, show task-related fCon [61,62]. For example, there is evidence that vmPFC–aHC connectivity during encoding tends to be greater for schema-consistent than schema-inconsistent information [63–65].

Comparing PSAs, cTRNs, and RSNs

Table 1 and Figure 3 compare PSAs to cTRNs and RSNs. Table 1 lists some examples, features, and relative advantages of each. An example of a cTRN is the thresholded connectivity matrix representing all significant functional connections between all brain regions of interest during an episodic memory retrieval task. From this thresholded connectivity matrix, the topology of the cTRN can be described at nodal (e.g., the HC operating as a more central, influential region for the convergence and joint processing of distributed information to facilitate remembering), subnetwork (e.g., the pattern of connections maintained by many MTL nodes during episodic retrieval), and global (e.g., the capacity for efficient communication across the entire network during episodic retrieval) levels using graph theoretic metrics. Examples of RSNs

Table 1. Summary of PSA, cTRN, and RSN Features[a]

	PSAs	cTRNs	RSNs
Examples	PFC–VisCtx in top-down attention HC–AG during episodic retrieval	Many areas during attention task Many areas during retrieval task	DMN Salience network
Number of regions	Two or three typically	Many	Many
Identification	Data-driven and hypothesis-driven: success-related activity, fCon, converging evidence, neuroscience and cognitive theories	Data-driven but theory-inspired: fCon during a task assumed to be responsible for certain cognitive processes	Data-driven: fCon among a set of brain regions during rest
Overlap with other networks of the same kind	Some overlap between PSA components across tasks	Some overlap between connections and topological properties across tasks	RSN components traditionally non-overlapping during rest
PSA advantages			
Link to cognitive theory	Strong	If subdivided into modules or communities	Difficult
Component-based explanation of neurocognitive processes	Strong	If subdivided into modules or communities	Difficult
cTRN advantages			
Holistic network view	Worst	Best	Better
Linking entire network organization to behavior	Worse (not whole network)	Best (whole-network, within-participants)	Better (whole-network but only across-participants)
RSN advantages			
Simplicity of fMRI paradigms	Most complex	More complex	Simplest
Exploratory research	Worse	Better	Best

[a]Abbreviations: cTRN, connectivity-based, task-related network; DMN, default mode network; fCon, functional connectivity; fMRI, functional magnetic resonance imaging; HC–AG, hippocampus–amygdala; PFC–VisCtx, prefrontal cortex–visual cortex; PSA, process-specific alliance; RSN, resting-state network.

include the DMN [2,66] and the **salience network** [67]. The DMN and salience networks are commonly characterized as particular groups of regions that tend to exhibit more similar activity amongst each other over time during resting-state than they do with other brain regions in the network. Whereas PSAs typically consist of two or three regions, cTRNs and RSNs typically consist of many regions– if not all brain regions with detectable signal – and their connections.

Identification

PSAs are identified using functional neuroimaging (process-related, success-related activity, and fCon) and other methods (e.g., lesions, electrophysiology) combined with theories about regional functions (e.g., modeling) and task component processes (cognitive theory). For example, the PFC–VisCtx PSA is based on evidence that task-related fCon between these regions is associated with successful top-down visual attention, on neuropsychological data that PFC damage impairs control processes, and on electrophysiology findings showing that VisCtx neuronal activity is modulated by attention, all combined with cognitive attention models [8,68,69]. In contrast, a cTRN is just the set of functional connections between brain regions in the network during a cognitive task or condition (e.g., 'episodic retrieval network'). Investigations into the topology of cTRNs can be driven by cognitive neuroscience theories [70,71], or they can be more data-driven and exploratory. Finally, RSNs are groups of regions showing greater similarities in measured signal over time amongst each other than with other regions during resting-state, and they are typically identified using data-driven methods.

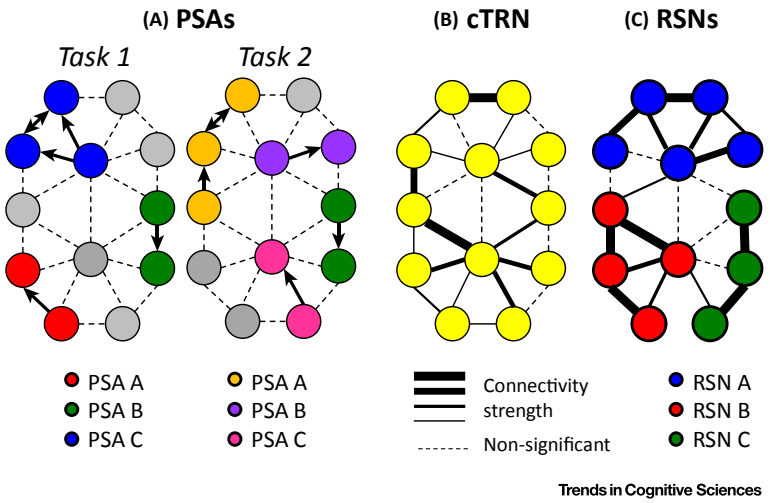

Figure 3. Diagrams Illustrating Three Types of Networks. (A) Process-specific alliances (PSA), (B) a connectivity-based, task-related network (cTRN), and (C) resting-state networks (RSNs). In PSAs, the same brain region can participate in different PSAs depending on the task. In this cTRN, the network is thresholded and weighted. The RSNs represented have similar patterns of activation over time such that brain regions within each RSN maintain stronger functional connections with each other than they do with the other brain regions in different RSNs.

Average Duration

As noted, PSA regions assemble to mediate a cognitive process and disassemble when the process is no longer required. Thus, a PSA lasts only as long as the cognitive process is required, which is typically brief. For example, the involvement of parietal regions during episodic recollection (see AG–HC PSA above) lasts only a few hundred milliseconds during typical laboratory recognition paradigms [72,73]. Transience is a key property of PSAs, and this property could even be considered a fourth criterion for defining PSAs. cTRNs are usually associated with a whole cognitive task (e.g., all working memory trials) or conditions defined by a group of trials (e.g., successful working memory trials), but they can be also created for a segment of trials (e.g., delay period of working memory trials). So, like PSAs, they can also be relatively short in duration. Finally, RSNs have traditionally been assumed to be relatively fixed over time and present during diverse cognitive tasks, during rest, and even during sleep [74]. However, recent work has suggested that there might be transient, dynamic changes in functional connectivity and functional network organization even during rest, and that these changes might be cognitively meaningful [75,76]. The extent to which RSNs are fixed over time is currently controversial in the literature. Nevertheless, because we take resting-state to just be another kind of task that recruits certain brain regions and implicates certain functional connections for certain purposes, in our view the active regions and functional connections necessary for an individual to be in resting-state will remain for the duration that an individual is in resting-state.

Overlap with Other Networks of the Same Kind

As noted before, the same brain region can be part of several PSAs mediating different processes, which means there is substantial overlap between different PSAs during different tasks. For example, a PFC region may interact with VisCtx to support top-down attention at one time, but with the amygdala to support emotion regulation at another time. The cTRN for one task can also partially overlap with the cTRN for other tasks. Or, a PFC region may perform a control function by interacting with certain brain regions during one task, and that same PFC

region may perform another control function by interacting with other brain regions during a different task [77,78]. These overlaps often involve similar kinds of interactions between pairs of regions mediating a particular process (e.g., frontoparietal interactions mediating top-down attention), which can be described as a PSA, but the overlap might also involve topological properties characterizing the overall organization of the system. Moreover, cTRNs may often be comprised of overlapping communities of densely interconnected brain regions at different levels of the spatial hierarchy, so there is growing interest in developing methods that allow for characterizing network structure when brain regions belong to multiple communities simultaneously during a task or across different tasks [79,80]. These overlapping communities are also thought to be dynamic and transient in nature [81]. Finally, RSNs are identified using data-driven analyses, which are used to identify subsets of brain regions that exhibit similarities in measured signal over time. While different RSNs are typically not thought to be overlapping, the number of RSNs that researchers have identified is, to a certain extent, arbitrary depending upon the particular methods used (e.g., from 7 to 17 networks [82]). Thus, the same region can be assigned to different RSNs depending on the total number of networks that a researcher identifies. Regardless, it is still customary to assume that each brain region 'belongs' to one RSN (e.g., PCC belongs to the DMN). Nevertheless, as with cTRNs, it is now possible to conceptualize and investigate RSNs as overlapping communities of densely interconnected brain regions [80].

Localization of Function

In the history of neuropsychology, strict localizationists have assumed that the brain is a modular machine in which cognitive processes are performed by individual brain regions, which always perform the same process [83]. The strict localizationist position is compatible with a variant of a hierarchical view, but it does not necessitate adopting a hierarchical view. In contrast, equipotentialists have argued that cognitive processes are distributed over the brain, with individual regions having no particular specialization, rendering this view decidedly not hierarchical.

PSAs represent a more moderate position between strict localization of cognitive processes and holistic distributive cognitive processing. Although each region is assumed to mediate a relatively narrow function, the specific operations performed also depend on functional interactions with other regions. Returning to the metaphor, the accountant uses related skills when processing bonuses with the payroll employee and when calculating sales with the billing employee, but the specific calculations she performs differ in the two tasks. Thus, although the functions of different regions can be specified, the actual computations can only be understood in the specific context of each PSA. In other words, our view is largely localizationist at the level of the broad functions ascribed to relatively large brain regions but our view is not localizationist about the specific computations performed by these regions, which vary depending on the task and the nature of the network as a whole. (However, we do not strictly necessitate that these broad functions are the only possible functions ever carried out by these relatively large brain regions.) In this way, PSAs differ from other recent attempts to develop frameworks of neurocognitive functioning occupying middle ground between strict localizationism and more holistic distributed processing [84,85]. Under these other frameworks, for many complex cognitive tasks, the system as a whole is not decomposable into individual parts (i.e., brain regions) carrying out component processes that can be described in the language of cognitive psychology. Instead, cognition just is the product of the abstract pattern of the functional connections that exist between many brain regions; but for PSAs, the component processes subserved by individual brain regions and the processes carried out by their interactions are individually necessary and jointly sufficient for achieving cognition during many tasks. For any given cognitive task, it is still possible to characterize the component

parts of PSAs within the larger system, even if the interactions between component parts are what make more complex processes possible.

In RSNs, in contrast, functions are typically attributed to a large set of spatially disparate brain regions (e.g., what the DMN does). The contributions of individual regions within that set are typically left unspecified. In cTRNs, some individual regions are assumed to play specific roles in mediating certain processes, but region-specific theories in cTRNs typically involve references to how a region is situated within the larger network (i.e., how the region directly and/or indirectly interacts with other brain regions in the larger network). What a region does is dependent upon how that region interacts with disparate other regions directly and/or indirectly. When nodal graph theoretic analyses are implemented, cTRNs can make more explicit characterizations about the functions of specific regions, but those functions will be described in reference to how the node is embedded within the larger network [70,71].

PSA Advantages

A key advantage of PSAs is their direct link to cognitive theory and their ability to offer component-based explanations of neurocognitive processes, drawing directly from the language used in cognitive psychology. More specifically, PSAs are based on the cognitive psychology approach of explaining cognitive tasks in terms of processing phases, each consisting of operations acting on representations. Thus, for PSAs, there is a natural flow from cognitive hypotheses, to cognitive neuroscience hypotheses, to functional neuroimaging predictions. In contrast, it is less clear that the topological properties of networks explain cognitive processes and performance in a way that closely accords with theories from cognitive psychology, unless the entire network is subdivided into PSAs or network modules (by dividing the entire cTRN into functional communities, or modules, it is possible to ascribe functions to those network modules with cognitive terms). Finally, some RSNs have been associated with particular cognitive processes (e.g., frontoparietal control network), but all brain regions and connections within such large RSNs may not be necessary for achieving any given cognitive process.

A related advantage of PSAs is that they provide a straightforward means of decomposing a system into component parts by characterizing a specific structure's role during a task in contributing to the overall function of the system. In contrast with PSAs, it is difficult to characterize component parts of cTRNs using the language of cognitive psychology unless the cTRN is (partially) decomposed into PSAs or into consistently identified network modules. One can say that the dozen regions interconnected in a particular way during an episodic retrieval task are involved in episodic retrieval, but without a hypothesis about what each region does and how it affects each of the other regions, a component-based mechanistic account of neurocognitive processing is difficult (if not impossible) to achieve. Finally, RSNs are the farthest from component-based explanation in cognitive neuroscience, as they are only defined as regions that tend to be functionally related during rest. The specific contributions of each region during tasks and the flow of information and control across regions during tasks are left largely unspecified. For example, although there is general agreement that the main components of the DMN are the posterior cingulate cortex (PCC) and the medial prefrontal cortex (mPFC), there are no accepted theories about the specific contribution of each of these regions or how they are related to each other during any given task (e.g., PCC acting on MPFC, or vice versa).

cTRN Advantages

The key strength of cTRNs is that they can take into account all functional connections (the whole network) associated with a cognitive state or task simultaneously (e.g., episodic memory retrieval, visual search). Then, the patterns of connections can then be described using graph

metrics [86]. In other words, they provide the 'big picture' of complex patterns of interactions that can, in theory, include all brain regions and functional connections with a detectable signal. PSAs provide a clear description of the functions of certain subsets of the larger cTRN, but they do not provide this full picture. Another advantage of cTRNs is that, when using event-related designs, researchers can link the network topology to behavior directly within participants. For example, separate cTRNs could be constructed for each participant for successful and unsuccessful trials, respectively, during an episodic memory retrieval task [71]. Then, the topological properties of those two networks can be quantitatively compared using graph theoretic metrics. In contrast, properties of RSNs can only be indirectly related to behavior across participants. PSAs do not provide information about whole-network topology.

Although some studies have identified consistency in functional connectivity patterns between RSNs and cTRNs [87], many other studies have now shown that there is significant, meaningful,

Box 2. Linking PSAs to cTRNs

A significant challenge facing cognitive neuroscience is describing and explaining the relationship between component-based mechanistic accounts of PSA operations and the 'big picture' of the more abstract architectures of large-scale networks provided by cTRNs and RSNs. One speculative idea we propose is that PSAs predominantly link network modules in cTRNs. Modules are groups of nodes (brain regions) that are more densely interconnected among themselves than with other nodes in the larger cTRN [97,98]. For example, Figure I depicts a simulated example of a cTRN with three modules: green, orange, and blue. Each network module is thought to dynamically and transiently assemble as a function of task demands, and each network module remains interconnected with all other network modules through direct and indirect intermodule connections [97,99].

Each component of a PSA might typically serve as a member of a different network module within the larger cTRN during some task. For example, Figure I shows four hypothetical PSAs, three of them operating as intermodule connections. In this way, the PSAs represent the critically important brain regions carrying out certain processes within network modules necessary to achieve the task, and the functional interactions between PSA nodes within different network modules might facilitate the more complex process characterizing the entire PSA. For example, Geib and colleagues (2017) showed that during successful memory retrieval, the hippocampus was part of one module with other MTL regions, and dorsal superior PFC was part of a separate module with other PFC and posterior parietal regions [71]. Despite being assigned to different modules, the hippocampus formed a significantly stronger functional connection with the dorsal superior PFC during successful relative to unsuccessful memory retrieval, providing some partial evidence for the presence of a PSA. These two nodes might be the critical nodes within their respective modules for carrying out task-specific processes and the more complex process characterizing the entire PSA via their functional interactions.

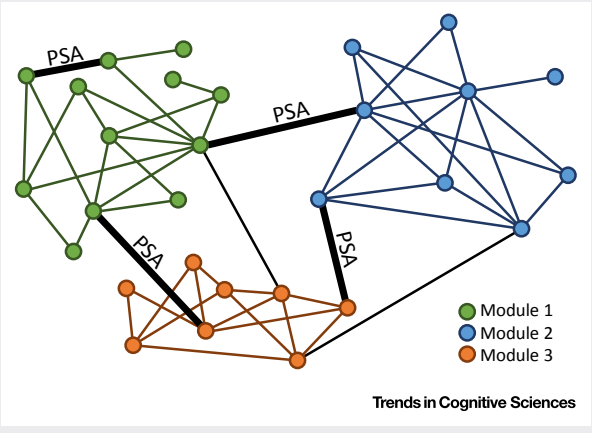

Figure I. PSAs Might Disproportionately Link Different Modules within a cTRN.

and predictable reorganization of functional connections from rest to various tasks [88–93]. These changes in functional connectivity occur for (i) specific, individual connections; (ii) topological properties of specific network nodes embedded within the network; (iii) topological properties subnetworks; and (iv) topological properties of the entire brain network. In this way, cTRNs provide different, unique pieces of information about how cognition is subserved in the brain that cannot be captured from RSNs alone.

RSN Advantages

The main advantages of RSNs compared to other network types is that they are relatively easy to identify and useful for exploratory research. RSNs can be identified in a single resting-state scan, during which no response is required of the participant, which is one reason for their popularity in clinical neuroimaging research. Identifying cTRNs is more demanding because a cognitive task is required, which typically entails longer scans, the presentation of stimuli, recording of behavioral responses, etc. Identifying PSAs is even more complex because researchers need a sufficient number of experimental conditions to isolate the cognitive processes of interest. Because of scanning simplicity and data-driven identification, RSNs are ideal for exploratory research: without a preexisting hypothesis based on cognitive theory, one can compare two groups of participants (e.g., healthy older adults versus Alzheimer's disease patients) and look for differences in RSN properties. Although most RSN studies are data-driven, they can also be hypothesis-driven once a function is assigned to a RSN. In contrast, studies investigating cTRNs require theories justifying the selection of tasks and control conditions. Finally, PSAs are not well-suited for exploratory research because they require hypotheses about the functions of specific brain regions and the particular cognitive process they are assumed to mediate.

Concluding Remarks

In sum, RSNs, cTRNs, and PSAs have different strengths and weaknesses. Whereas RSNs offer unique advantages for clinical and exploratory studies, PSAs are better for basic, hypothesis-driven cognitive neuroscience studies. cTRNs occupy an intermediate position and are able to take into account more information relevant for carrying out the task. RSNs, cTRNs, and PSAs have traditionally been investigated in parallel for very different purposes. A central challenge facing the field (see Outstanding Questions) is to better understand how these different kinds of networks are related to each other (or not) in different contexts, especially for cTRNs and PSAs (Box 2).

Outstanding Questions

How exactly are PSAs, cTRNs, and RSNs all related to one another?

To what extent do RSNs identified during resting-state constrain or predict the functional connectivity patterns of PSAs and cTRNs during diverse tasks? In other words, what exactly does the investigation of PSAs and cTRNs offer above and beyond resting-state analyses?

During different cognitive tasks, how do the properties of PSAs change in development, aging, and disease?

What exactly is the relationship between activity and functional connectivity during different cognitive tasks?

When there is no direct structural pathway between any two PSA components, how do indirect connections between PSA components help PSAs to achieve their functions?

Do different people use different PSAs to achieve the exact same function? For the same cognitive task, how much consistency and stability is there in PSA recruitment across people?

References

1. Gusnard, D.A. *et al.* (2001) Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proc. Natl. Acad. Sci. U. S. A.* 98, 4259–4264
2. Gusnard, D.A. and Raichle, M.E. (2001) Searching for a baseline: functional imaging and the resting human brain. *Nat. Rev. Neurosci.* 2, 635–694
3. Cabeza, R. and Moscovitch, M. (2013) Memory systems, processing modes, and components: functional neuroimaging evidence. *Perspect. Psychol. Sci.* 8, 49–55
4. Moscovitch, M. *et al.* (2016) Episodic memory and beyond: the hippocampus and neocortex in transformation. *Annu. Rev. Psychol.* 67, 105–134
5. Cabeza, R. *et al.* (2012) Cognitive contributions of the ventral parietal cortex: an integrative theoretical account. *Trends Cogn. Sci.* 16, 338–352
6. Badre, D. and Wagner, A.D. (2007) Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia* 45, 2883–2901
7. Grill-Spector, K. and Weiner, K.S. (2014) The functional architecture of the ventral temporal cortex and its role in categorization. *Nat. Rev. Neurosci.* 15, 536–548
8. Paneri, S. and Gregoriou, G.G. (2017) Top-down control of visual attention by the prefrontal cortex. Functional specialization and long-range interactions. *Front. Neurosci.* 11, 16
9. Noonan, K.A. *et al.* (2013) Going beyond inferior prefrontal involvement in semantic control: evidence for the additional contribution of dorsal angular gyrus and posterior middle temporal cortex. *J. Cogn. Neurosci.* 25, 1824–1850
10. Binder, J.R. *et al.* (2009) Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* 19, 2767–2796
11. Hoffman, P. *et al.* (2010) Ventrolateral prefrontal cortex plays an executive regulation role in comprehension of abstract words: convergent neuropsychological and repetitive TMS evidence. *J. Neurosci.* 30, 15450–15456

12. Dronkers, N.F. *et al.* (2004) Lesion analysis of the brain areas involved in language comprehension. *Cognition* 92, 145–177
13. Thompson-Schill, S.L. *et al.* (1999) Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron* 23, 513–522
14. Lau, E.F. *et al.* (2008) A cortical network for semantics: (de) constructing the N400. *Nat. Rev. Neurosci.* 9, 920–933
15. Turken, A. and Dronkers, N. (2011) The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analyses. *Front. Syst. Neurosci.* 5, 1
16. Davey, J. *et al.* (2016) Exploring the role of the posterior middle temporal gyrus in semantic cognition: integration of anterior temporal lobe with executive processes. *Neuroimage* 137, 165–177
17. Hartwigsen, G. *et al.* (2017) Integration demands modulate effective connectivity in a fronto-temporal network for contextual sentence integration. *Neuroimage* 147, 812–824
18. Ochsner, K.N. and Gross, J.J. (2007) The neural architecture of emotional regulation. In *The Handbook of Emotion Regulation* (Gross, J.J. and Buck, R., eds), pp. 87–109, Guilford Press
19. Ochsner, K.N. *et al.* (2012) Functional imaging studies of emotion regulation: a synthetic review and evolving model of the cognitive control of emotion. *Ann. N. Y. Acad. Sci.* 1251, E1–E24
20. Buhle, J.T. *et al.* (2014) Cognitive reappraisal of emotion: a meta-analysis of human neuroimaging studies. *Cereb. Cortex* 24, 2981–2990
21. Leshikar, E.D. and Duarte, A. (2014) Medial prefrontal cortex supports source memory for self-referenced materials in young and older adults. *Cogn. Affect. Behav. Neurosci.* 14, 236–252
22. Duarte, A. *et al.* (2010) Age-related changes in neural activity associated with familiarity, recollection and false recognition. *Neurobiol. Aging* 31, 1814–1830
23. Davis, S.W. *et al.* (2018) Contributions of ventral parietal cortex to declarative memory. In *The Parietal Lobe* (Vallar, G. and Coslett, H.B., eds), pp. 525–554, Elsevier
24. Kim, H. (2014) Encoding and retrieval along the long axis of the hippocampus and their relationships with dorsal attention and default mode networks: The HERNET model. *Hippocampus* 25, 500–510
25. Vilberg, K.L. and Rugg, M.D. (2007) Dissociation of the neural correlates of recognition memory according to familiarity, recollection, and amount of recollected information. *Neuropsychologia* 45, 2216–2225
26. Cabeza, R. *et al.* (2008) The parietal cortex and episodic memory: an attentional account. *Nat. Rev. Neurosci.* 9, 613–625
27. Berryhill, M.E. *et al.* (2007) Parietal lobe and episodic memory: bilateral damage causes impaired free recall of autobiographical memory. *J. Neurosci.* 27, 14415–14423
28. Rugg, M.D. and Yonelinas, A.P. (2003) Human recognition memory: a cognitive neuroscience perspective. *Trends Cogn. Sci.* 7, 313–319
29. Clower, D.M. *et al.* (2001) The inferior parietal lobule is the target of output from the superior colliculus, hippocampus, and cerebellum. *J. Neurosci.* 21, 6283–6291
30. Uddin, L.Q. *et al.* (2010) Dissociable connectivity within human angular gyrus and intraparietal sulcus: evidence from functional and structural connectivity. *Cereb. Cortex* 20, 2636–2646
31. Vincent, J.L. *et al.* (2006) Coherent spontaneous activity identifies a hippocampal-parietal memory network. *J. Neurophysiol.* 96, 3517–3531
32. King, D.R. *et al.* (2015) Recollection-related increases in functional connectivity predict individual differences in memory accuracy. *J. Neurosci.* 35, 1763–1772
33. Daselaar, S.M. *et al.* (2006) Triple dissociation in the medial temporal lobes: recollection, familiarity, and novelty. *J. Neurophysiol.* 96, 1902–1911
34. Robin, J. *et al.* (2015) Functional connectivity of hippocampal and prefrontal networks during episodic and spatial memory based on real-world environments. *Hippocampus* 25, 81–93
35. Jackson, R.L. *et al.* (2016) The semantic network at work and rest: differential connectivity of anterior temporal lobe subregions. *J. Neurosci.* 36, 1490–1501
36. Rosselli, M. *et al.* (2015) Modelo de conectividad de la circunvolución angular en el lenguaje: meta-análisis de neuroimágenes funcionales. *Rev. Neurol.* 60, 495–503
37. Ralph, M.A.L. (2014) Neurocognitive insights on conceptual knowledge and its breakdown. *Philos. Trans. R. Soc. B Biol. Sci.* 369, 11
38. Ciaramelli, E. *et al.* (2008) Top-down and bottom-up attention to memory: a hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia* 46, 1828–1851
39. Shimamura, A.P. (2011) Episodic retrieval and the cortical binding of relational activity. *Cogn. Affect. Behav. Neurosci.* 11, 277–291
40. Vilberg, K.L. and Rugg, M.D. (2008) Memory retrieval and the parietal cortex: a review of evidence from a dual-process perspective. *Neuropsychologia* 46, 1787–1799
41. Price, A.R. *et al.* (2015) Converging evidence for the neuroanatomic basis of combinatorial semantics in the angular gyrus. *J. Neurosci.* 35, 3276–3284
42. Kuhl, B.A. *et al.* (2013) Dissociable neural mechanisms for goal-directed versus incidental memory reactivation. *J. Neurosci.* 33, 16099–16109
43. Kuhl, B.A. and Chun, M.M. (2014) Successful remembering elicits event-specific activity patterns in lateral parietal cortex. *J. Neurosci.* 34, 8051–8060
44. Leshinskaya, A. and Caramazza, A. (2015) Abstract categories of functions in anterior parietal lobe. *Neuropsychologia* 76, 27–40
45. Devereux, B.J. *et al.* (2013) Representational similarity analysis reveals commonalities and differences in the semantic processing of words and objects. *J. Neurosci.* 33, 18906–18916
46. Hiser, J. and Koenigs, M. (2018) The multifaceted role of ventromedial prefrontal cortex in emotion, decision-making, social cognition, and psychopathology. *Biol. Psychiatry* 83, 638–647
47. van Kesteren, M.T. *et al.* (2012) How schema and novelty augment memory formation. *Trends Neurosci.* 35, 211–219
48. Schneider, B. and Koenigs, M. (2017) Human lesion studies of ventromedial prefrontal cortex. *Neuropsychologia* 107, 84–93
49. Haber, S.N. and Knutson, B. (2010) The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology* 35, 4–26
50. Levy, D.J. and Glimcher, P.W. (2012) The root of all value: a neural common currency for choice. *Curr. Opin. Neurobiol.* 22, 1027–1038
51. Pujara, M.S. *et al.* (2016) Ventromedial prefrontal cortex damage is associated with decreased ventral striatum volume and response to reward. *J. Neurosci.* 36, 5047–5054
52. Lin, A. *et al.* (2011) Social and monetary reward learning engage overlapping neural substrates. *Soc. Cogn. Affect. Neurosci.* 7, 274–281
53. Haber, S.N. *et al.* (2006) Reward-related cortical inputs define a large striatal region in primates that interface with associative cortical connections, providing a substrate for incentive-based learning. *J. Neurosci.* 26, 8368–8376
54. Draganski, B. *et al.* (2008) Evidence for segregated and integrative connectivity patterns in the human basal ganglia. *J. Neurosci.* 28, 7143–7152
55. Di Martino, A. *et al.* (2008) Functional connectivity of human striatum: a resting state FMRI study. *Cereb. Cortex* 18, 2735–2747
56. Choi, E.Y. *et al.* (2012) The organization of the human striatum estimated by intrinsic functional connectivity. *J. Neurophysiol.* 108, 2242–2263
57. Cauda, F. *et al.* (2011) Functional connectivity and coactivation of the nucleus accumbens: a combined functional connectivity and structure-based meta-analysis. *J. Cogn. Neurosci.* 23, 2864–2877

58. Von Der Heide, R.J. *et al.* (2013) Dissecting the uncinate fasciculus: disorders, controversies and a hypothesis. *Brain* 136, 1692–1707
59. Schmahmann, J.D. *et al.* (2007) Association fibre pathways of the brain: parallel observations from diffusion spectrum imaging and autoradiography. *Brain* 130, 630–653
60. Gerraty, R.T. *et al.* (2014) Transfer of learning relates to intrinsic connectivity between hippocampus, ventromedial prefrontal cortex, and large-scale networks. *J. Neurosci.* 34, 11297–11303
61. McCormick, C. *et al.* (2013) Functional and effective hippocampal–neocortical connectivity during construction and elaboration of autobiographical memory retrieval. *Cereb. Cortex* 25, 1297–1305
62. Robin, J. and Moscovitch, M. (2017) Details, gist and schema: hippocampal-neocortical interactions underlying recent and remote episodic and spatial memory. *Curr. Opin. Behav. Sci.* 17, 114–123
63. van Kesteren, M.T. *et al.* (2010) Persistent schema-dependent hippocampal-neocortical connectivity during memory encoding and postencoding rest in humans. *Proc. Natl. Acad. Sci. U. S. A.* 107, 7550–7555
64. Liu, Z.X. *et al.* (2017) Effects of prior-knowledge on brain activation and connectivity during associative memory encoding. *Cereb. Cortex* 27, 1991–2009
65. Bonasia, K. *et al.* (2018) Prior knowledge modulates the neural substrates of encoding and retrieving naturalistic events at short and long delays. *Neurobiol. Learn. Memory* 153, 26–39
66. Buckner, R.L. *et al.* (2008) The brain's default network: anatomy, function, and relevance to disease. *Ann. N. Y. Acad. Sci.* 1124, 1–38
67. Seeley, W.W. *et al.* (2007) Dissociable intrinsic connectivity networks for salience processing and executive control. *J. Neurosci.* 27, 2349–2356
68. Gazzaley, A. and Nobre, A.C. (2012) Top-down modulation: bridging selective attention and working memory. *Trends Cogn. Sci.* 16, 129–135
69. Bar, M. and Bubic, A. (2013) Top-down effects in visual perception. In *Oxford Handbook of Cognitive Neurosciences, vol. 1* (Ochsner, K. and Kosslyn, S.M., eds), pp. 60–73, Oxford University Press
70. Geib, B.R. *et al.* (2017) Hippocampal contributions to the large-scale episodic memory network predict vivid visual memories. *Cereb. Cortex* 27, 680–693
71. Geib, B.R. *et al.* (2017) From hippocampus to whole-brain: the role of integrative processing in episodic memory retrieval. *Hum. Brain Mapp.* 38, 2242–2259
72. Gonzalez, A. *et al.* (2015) Electrocorticography reveals the temporal dynamics of posterior parietal cortical activity during recognition memory decisions. *Proc. Natl. Acad. Sci. U. S. A.* 112, 11066–11071
73. Hoppstädter, M. *et al.* (2015) Simultaneous EEG–fMRI reveals brain networks underlying recognition memory ERP old/new effects. *Neuroimage* 116, 112–122
74. Rosazza, C. and Minati, L. (2011) Resting-state brain networks: literature review and clinical applications. *Neurol. Sci.* 32, 773–785
75. Khambhati, A.N. *et al.* (2017) Modeling and interpreting mesoscale network dynamics. *Neuroimage* Published online June 20, 2017. http://dx.doi.org/10.1016/j.neuroimage.2017.06.029
76. Hindriks, R. *et al.* (2016) Can sliding-window correlations reveal dynamic functional connectivity in resting-state fMRI? *Neuroimage* 127, 242–256
77. Cole, M.W. *et al.* (2013) Multi-task connectivity reveals flexible hubs for adaptive task control. *Nat. Neurosci.* 16, 1348
78. Cocchi, L. *et al.* (2013) Dynamic cooperation and competition between brain systems during cognitive control. *Trends Cogn. Sci.* 17, 493–501
79. Najafi, M. *et al.* (2016) Overlapping communities reveal rich structure in large-scale brain networks during rest and task conditions. *Neuroimage* 135, 92–106
80. Pessoa, L. (2018) Understanding emotion with brain networks. *Curr. Opin. Behav. Sci.* 19, 19–25
81. Pessoa, L. (2017) A network model of the emotional brain. *Trends Cogn. Sci.* 21, 357–371
82. Yeo, B.T.T. *et al.* (2011) The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *J. Neurophysiol.* 106, 1125–1165
83. Tizard, B. (1959) Theories of brain localization from Flourens to Lashley. *Med. History* 3, 132
84. Mill, R.D. *et al.* (2017) From connectome to cognition: the search for mechanism in human functional brain networks. *Neuroimage* 160, 124–139
85. Mišić, B. and Sporns, O. (2016) From regions to connections and networks: new bridges between brain and behavior. *Curr. Opin. Neurobiol.* 40, 1–7
86. Bullmore, E. and Sporns, O. (2009) Complex brain networks: graph theoretical analysis of structural and functional systems. *Nat. Rev. Neurosci.* 10, 186–198
87. Cole, M.W. *et al.* (2014) Intrinsic and task-evoked network architectures of the human brain. *Neuron* 83, 238–251
88. Cao, H. *et al.* (2014) Test–retest reliability of fMRI-based graph theoretical properties during working memory, emotion processing, and resting state. *Neuroimage* 84, 888–900
89. Fransson, P. (2006) How default is the default mode of brain function? Further evidence from intrinsic BOLD signal fluctuations. *Neuropsychologia* 44, 2836–2845
90. Hasson, U. *et al.* (2009) Task-dependent organization of brain regions active during rest. *Proc. Natl. Acad. Sci. U. S. A.* 106, 10841–10846
91. Kim, D. *et al.* (2017) A new modular brain organization of the BOLD signal during natural vision. *Cereb. Cortex* 1–17
92. Rzucidlo, J.K. *et al.* (2013) Stability of whole brain and regional network topology within and between resting and cognitive states. *PLoS One* 8, e70275
93. Stanley, M.L. *et al.* (2015) Changes in brain network efficiency and working memory performance in aging. *PLoS One* 10, e0123950
94. Kim, H. (2016) Default network activation during episodic and semantic memory retrieval: a selective meta-analytic comparison. *Neuropsychologia* 80, 35–46
95. Bellana, B. *et al.* (2017) Similarities and differences in the default mode network across rest, retrieval, and future imagining. *Hum. Brain Mapp.* 38, 1155–1171
96. Stanley, M.L. *et al.* (2013) Defining nodes in complex brain networks. *Front. Comput. Neurosci.* 7, 169
97. Newman, M.E. (2006) Modularity and community structure in networks. *Proc. Natl. Acad. Sci. U. S. A.* 103, 8577–8582
98. Sporns, O. and Betzel, R.F. (2016) Modular brain networks. *Ann. Rev. Psychol.* 67, 613–640
99. Telesford, Q.K. *et al.* (2016) Detection of functional brain network reconfiguration during task-driven cognitive states. *Neuroimage* 142, 198–210