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Trends in Neurosciences

Review

A Unifying Account of Angular Gyrus Contributions to Episodic and Semantic Cognition

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The angular gyrus (AG) region of lateral parietal cortex has been implicated in a wide variety of tasks and functions, generating numerous influential theories. However, these theories largely fail to explain why so many apparently distinct cognitive activities implicate common parietal structures. We propose a unifying model, based on a set of central principles, to account for coalescences of cognitive task activations across AG. To illustrate the proposed framework, we show how these principles account for findings from studies of episodic and semantic memory that have independently implicated the same AG regions but thus far been considered from largely domain-specific perspectives. We conclude that AG computations, as part of a wider lateral parietal system, enable the online dynamic buffering of multisensory spatiotemporally extended representations.

Highlights

The function of the lateral parietal cortex (LPC) has a long history of interest in neuropsychology and is gaining increasingly rapid investigation with advances in neuroimaging techniques.

The angular gyrus (AG) region of LPC in particular has been implicated in a myriad of cognitive domains, yet an accepted cross-domain synthesis has proven elusive.

Here, we propose a unifying account of AG function that can explain the findings from two highly related, yet independently researched cognitive domains: episodic memory and semantic memory.

We conclude that the AG enables the online dynamic buffering of multisensory spatiotemporally extended representations.

The Multitask-Multibrain-Region Challenge

One of the principal aims of cognitive neuroscience is to explain how underlying neural processes give rise to cognitive functions and dysfunctions. Cognitive neuropsychology, neuroimaging, and other neuroscience approaches typically explore one domain (e.g., memory or language) and seek to determine which brain regions are important and how their function changes with respect to core task-related factors. When considering this commonly-used approach, a rapidly evolving challenge emerges: if we look beyond the literature relating to each behavioural domain, it becomes apparent that many brain regions are common to multiple behavioural domains, implying that there is no simple one-to-one mapping between each domain and any single underlying brain region. In contrast, each cognitive behaviour maps onto a network of brain regions and, in reverse, each brain area plays a role in a variety of different cognitive domains. Broadly speaking, there are two contrastive approaches to this complex task-brain mapping conundrum. The first, which might be termed 'neuromarquetry' [1], assumes that functions/tasks are supported by a series of discrete, neighbouring subregions. Under this hypothesis, behaviour-brain mappings look complex because of the tight packing of functions into a brain region, yet are more one-to-one when considered at a finer spatial resolution. An alternative, the 'primary systems hypothesis' [2–7], observes that cognitive tasks and activities are likely to be supported by variable combinations of more generalised neurocognitive computations and that these 'primary systems' will be called upon by multiple tasks. Under this view, the coalescence of task-related brain activity or dysfunctions in neuropsychological patients with respect to the same brain region, may reflect the shared neurocomputation that the tasks call upon.

This multitask-multibrain-region challenge repeats across many brain regions and for a myriad of tasks, a complete description of which is beyond the scope of this brief review. Instead, we have selected a pertinent and prominent worked example: the lateral parietal cortex (LPC). Within the LPC, we focus primarily on the angular gyrus (AG) and its purported contributions to episodic and

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semantic memory. Like other tertiary association regions, the LPC has been implicated in a wide variety of tasks and functions [1,8,9]. We focus here upon AG contributions to episodic and semantic memory because: (i) there are considerable bodies of functional neuroimaging and neuropsychology literature on both topics, (ii) there are matured domain-specific theories and proposals about the AG in each domain, yet (iii) these literatures have tended to remain isolated from each other, despite being centred on two forms of long-term declarative memory and implicating the same LPC regions (although see recent reviews [10,11]). Accordingly, these theories (and those for other cognitive domains) largely fail to unify the myriad of cognitive activities that implicate certain common LPC structures.

In this review, we examine potential roles of AG in episodic and semantic memory, considering each body of literature in turn and pointing out some pitfalls that must be circumvented to more readily understand implications of the data. We propose a unifying model, based on a set of central principles, to account for the variety of cognitive tasks that activate the parietal cortex. We illustrate how these central principles might account for the findings from cognitive neuroscience studies of episodic and semantic memory. For clarity, we will define our anatomical labelling here. The LPC is a heterogeneous region with multiple graded subregions (Box 1). Whereas some of the observations and proposals we identify may well apply more broadly across these LPC regions, in this review we focus principally upon the episodic and semantic memory data implicating AG and differentiate between its dorsal subregion (PGa), that borders with the intraparietal sulcus (IPS), and the more ventral AG (PGp). According to our proposed model, AG, as part of a wider LPC system, operates as an online, dynamic, multisensory buffer that,

Box 1. Functional Heterogeneity of Lateral Parietal Cortex

The wider LPC (as depicted in Figures 1 and 2) is a structurally and functionally heterogeneous region, with multiple cytoarchitectonic subdivisions [92]. There appear to be two primary axes of variation; a dorsal versus ventral distinction, and an anterior versus posterior distinction. The dorsal inferior parietal lobe (dIPL) forms part of a frontoparietal system, whereas the ventral inferior parietal lobe (vIPL) connects with a distributed set of regions associated with the default mode network or saliency network [68,93–99]. In terms of function, dIPL forms part of a domain-general frontoparietal multiple demand network engaged by tasks that require a relatively high degree of executive control, including working memory, numerical calculation, and top-down attention [100]. By contrast, within vIPL, supramarginal gyrus is mostly associated with tasks involving phonological processes, theory of mind, and bottom-up attention [1]. There is disagreement in the literature as to whether functional boundaries within these brain structures are graded or sharply fractionated in nature, with some functional connectivity evidence supporting a 'fractionated' account [101], whereas other studies observe graded functional changes and shifts in cytoarchitecture [92,102,103].

It is possible that a wide variety of cognitive activities can draw from shared underlying machinery, with distinctions in emergent functions arising from graded variation in connectivity. Even if the local buffering computation is the same throughout the LPC, the types and forms of information being buffered will reflect the inputs and outputs to each subregion [28–30]. Applying this generalised hypothesis to LPC provides a potential explanation for the contrastive (and sometimes anticorrelated) expressed characteristics of various subregions. Specifically, dIPL is structurally connected to frontal executive processing areas [93,104]. Most notions of executive control and attention require the action of selection/manipulation processes on internally buffered information (akin to a working memory system), which might be reflected in prefrontal regions sending top-down signals to dIPL, as demonstrated in primate electrophysiological studies [105]. In contrast, without the direct influence of prefrontal goal-directed cognition, the vIPL will act more like a 'slave' buffer, whereby information is accumulated and maintained throughout a sequential activity. In addition to the emergent dorsal–ventral connectivity/functional differences, there are known anterior–posterior variations within the vIPL and it is possible that these subdivisions also emerge from differential connectivity to separate networks for language, memory, visuospatial processing, etc. [93,102,104]. A dorsal–ventral subdivision can be observed within AG itself. Specifically, dorsal AG (PGa)/lateral bank of intraparietal sulcus (IPS) serves a distinctive function to the ventral AG (central PGp), which is commonly associated with the default mode network. Indeed, dorsal and ventral AG show opposing effect of task difficulty in semantic and visuospatial tasks; dorsal areas show a greater response when difficulty is increased, whereas ventral AG shows the inverse pattern, stronger deactivation for harder tasks [7], as discussed in the main text. Dorsal and ventral AG also play distinct roles in episodic memory tasks: dorsal AG/IPS acts as a 'mnemonic accumulator' that guides episodic decisions, or as a 'familiarity signal' [106], whereas ventral AG is (positively) engaged by episodic recollection [107,108].

through experience, becomes sensitive to the sequential spatiotemporal structure of an event or behaviour that unfolds over time.

Identifying Principles of LPC Function

We focus here on three central principles. These notions link to a somewhat broader framework (the parietal unified connectivity-biased computation model [1,7,12]) and previous seminal proposals [8,13], which have taken a cross-domain perspective upon the AG (and wider LPC) and attempted to distil what generalised neurocomputations might be supported by this region and its long-range connectivity [9]. The first principle is that there are two orthogonal types of representations or statistical structures that can be extracted from our time-extended, multimodal experiences and behaviours [1,2,14,15]. If we integrate multimodal information over time, situations, and events, then we can extract stable representations for experienced verbal and nonverbal items that generalise across exemplars, irrespective of the situation or moment. This is one definition of 'coherent' semantic concepts and has been associated with the anterior temporal lobe (ATL) and the end of the ventral pathways within the temporal lobe [16–18]. In a complementary, orthogonal manner, we can also integrate multimodal experiences over items, resulting in generalisable representations about order, space, number, etc. Such spatiotemporal structures are typically invariant to the elements that go into them, examples being location or number that are invariant to the items being located or counted. These types of representation have classically been associated with parietal and frontal regions along the 'dorsal' pathways. Note that the input to both pathways is the same, time-extended, multimodal information, but the outcomes are mathematically orthogonal to each other (this is analogous to single value decomposition, which generates two orthogonal similarity matrices; when applied to language texts, for example, as they are in latent semantic analysis, then the output includes an item/word similarity matrix and a paragraph/time-chunk similarity matrix [19,20]).

The second linked principle is that the local neurocomputation in this region provides the basis for online, dynamic, multisensory buffering that, through experience, becomes sensitive to the sequential spatiotemporal structure of an event or behaviour that unfolds over time (i.e., as a by-product of buffering, it can extract the item-invariant representations of order, location, number, etc. noted earlier). The local computation is domain-general, acting on any modality (as well as multimodal combinations) of spatiotemporal input. This kind of domain-general computation is important because time-extended verbal (e.g., speech) and nonverbal behaviours (e.g., sequential object use) necessitate precise synchronisation of planned actions with data about the current state of the internal and external worlds [21,22]. This information, however, arrives through different internal and external input channels and is ephemeral, necessitating a multimodal convergent buffer or hub [23,24]. A number of prominent parallel distributed processing (PDP) computational models have shown that the addition of recurrent feedback loops allows a model to 'buffer' verbal or nonverbal spatiotemporal input (Elman nets: [25]) in support of time-extended verbal and nonverbal behaviours [2,21,26]. Furthermore, in these types of model, repeated buffering can lead to long-term statistical learning and thus, by buffering time-, context-, and space-varying inputs, it is possible for systems to become sensitive to content-invariant structures/schemata (indeed, the extraction of information by PDP models can be formally related to single value decomposition [27]).

The third principle is that the 'expressed' task contribution of AG, and wider LPC areas, will be influenced by their long-range connections. Thus, even on an assumption that the local buffering computation might be the same throughout the LPC, the types and forms of information being buffered will reflect the inputs and outputs to each subregion (Box 1). This tenet is observed in various implemented computational models, which have shown that the involvement of a processing unit to each cognitive activity is moulded both by its local computation and its connectivity to different input/output information sources (cf. 'connectivity-constrained cognition: C3' [28–30]). Thus, even in a situation where the local unit computation is exactly the same, the contribution to different cognitive tasks can vary in a graded way across a layer of such units (taken to be analogous to a cortical region); units with equivalent connection to multiple inputs/outputs have a domain-general character, whereas units with stronger connection to a subset of inputs/outputs will become more domain-specific in nature [i.e., becoming tuned towards the domain(s) for which those particular input/outputs are critical].

Episodic Memory

Compared with the storied history of research examining the role of the parietal cortex in domains such as visuospatial attention and visuomotor abilities [31,32], investigation of a putative role in episodic memory is a relatively recent development. Damage to medial parietal regions has been known for some time to result in amnesia [33,34], but virtually no studies of episodic memory following LPC lesions were published in the 20th century. Patients with such lesions typically did not forget appointments with their neurologist, tended to be oriented in time and place, and could usually remember the names of objects shown to them a few minutes before. As such, they did not appear to be amnesic and neurologists understandably focused on the patients' more debilitating cognitive deficits. However, advances in functional neuroimaging have led to a growing realisation that the AG makes an important contribution to episodic memory, resulting in an explosion of research over the last decade or so that has sought to understand what role the region might play (Figure 1).

Research in this area was stimulated by a review of functional neuroimaging studies [35], which highlighted how left LPC responses, in particular centred on AG (mainly the PGp subregion), are closely linked with processes contributing to successful retrieval [36]. A further common finding was greater activation in AG when memory tasks involve retrieval of the context in which stimuli were previously encountered, suggesting a particular importance for conscious recollection [37]. AG appears not to contribute to successful encoding, often exhibiting deactivation [38,39], but a number of meta-analyses have confirmed the prevalence of parietal activity in the episodic retrieval fMRI literature, identifying that AG regions may be more consistently activated during recollection than regions traditionally considered critical for episodic memory, such as the medial temporal lobes [40,41].

On the basis of such findings, a number of suggestions have been made as to the functional contribution that AG might make to episodic memory. One influential review considered three possible hypotheses [35]: that AG may be involved in the allocation of attention towards aspects of mnemonic representations (a view subsequently expanded on by others [42]; Box 2), that activity in AG regions may reflect a memory strength signal that can be used to guide behavioural responses [43], or that AG acts as a temporary storage buffer in which information retrieved from long-term memory can be maintained online [44,45]. It was noted that the data available at the time appeared to be partly, but not completely, explained by each of these hypotheses [35]. Subsequent findings from neuroimaging research, and from studies involving neuropsychological and neurostimulation-induced brain lesions, have led to the development of further theories, all of which account for some aspects of the data but fall short of accommodating the full range of findings from episodic memory research, or indeed from the numerous other cognitive domains to which AG appears to contribute. These theories do, however, converge on a number of common fundamental principles, namely that the computations undertaken by AG result in dynamic, multimodal, consciously accessible representations that integrate features of events that unfold over time.

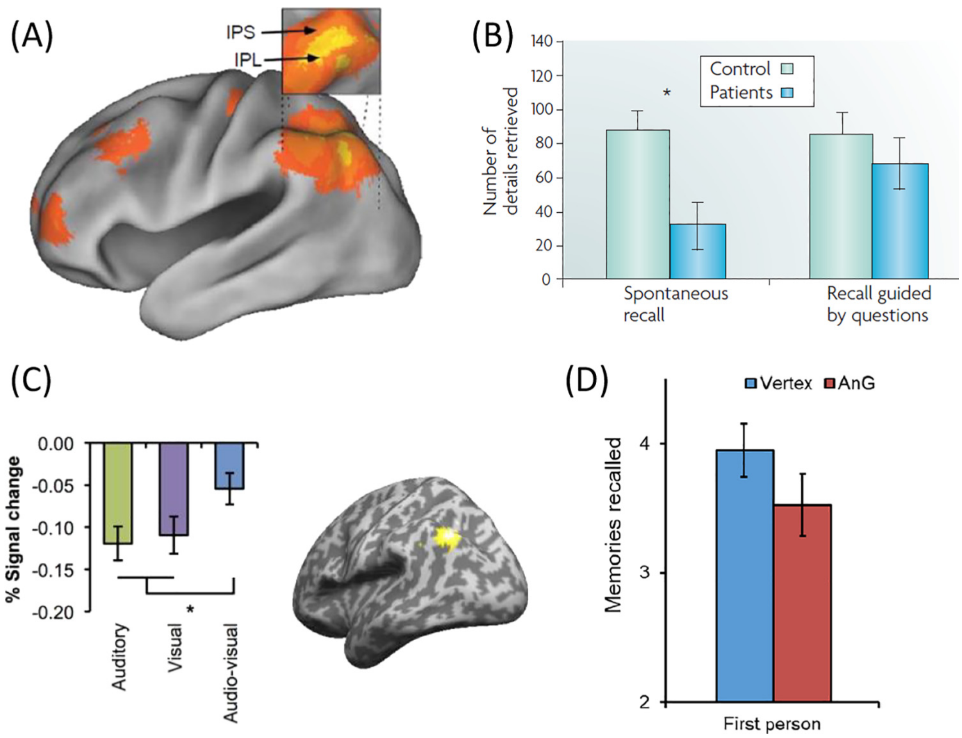

Figure 1. Role of Angular Gyrus (AG) in Episodic Memory May Be to Enable the Subjective Experience of Remembering. The results in (A) highlight consistent lateral parietal cortex (LPC) activity in neuroimaging studies of episodic retrieval, particularly around inferior parietal lobe (IPL) regions such as the AG (from [35]). (B) Results from a study testing autobiographical memory in patients with bilateral IPL lesions (from [46]). The patients were impaired when freely recalling events from their lifetimes but their memory was unimpaired when answering specific questions about the events. Several studies have identified that AG is sensitive to retrieval of multimodal episodic memories. The results shown in (C) are one example, finding that AG exhibits greater activity during retrieval of integrated audio-visual compared with unimodal information (from [54]). Another feature of IPL function may be in integrating retrieved episodic features within an egocentric perspective. Data shown in (D) illustrate how disrupting AG with brain stimulation results in fewer autobiographical memories being reported as experienced from a first-person perspective (from [47]). Together these results converge on the notion that AG computations drive the online, dynamic buffering of multisensory spatiotemporally extended representations that can enable the subjective experience of remembering past events. The asterisk in (B) and (C) denotes significant differences. Abbreviation: IPS, intraparietal sulcus.

Although LPC lesions do not result in amnesia, memory is not entirely unaffected. Two patients with bilateral parietal damage were reported to be impaired at freely recalling autobiographical memories, although their memories for the events tested appeared to be preserved when their recall was cued by specific questions [46]. This deficit in the free, but not cued, recall of autobiographical memories has been replicated by subsequent brain stimulation studies that have disrupted LPC function [47,48] and found to be specific to free recall of autobiographical memories, with free recall of previously studied word-pairs, or word-definition pairs, unaffected [47,49,50]. The retrieval of autobiographical and word-pair memories differs, in that the former often involves the subjective experience of remembering multifaceted events that take place over a sequence of phases, combining features that may be of several modalities and recalled from a first-person point-of-view [51–53]. Accordingly, AG has been found to be differentially sensitive to the retrieval of multimodal spatiotemporal memories compared with those involving only a single sensory modality [54–57] and to integrate these features within an egocentric perspective [47,58], in a way that is characteristic of true episodic memory [59].

Box 2. Attention Models

Dorsal versus Ventral Parietal Cortex

The current review focuses on the contribution of LPC to episodic and semantic memory, but a discussion of parietal function cannot be complete without a mention of the attention literature. One seminal attention model [13] proposed that LPC is divided into dorsal and ventral areas, which participate in top-down versus bottom-up/stimulus-driven attention, respectively. According to this model, the stimulus-driven network acts as an alerting system, or 'circuit breaker', for top-down processing. Some kind of dorsal–ventral LPC distinction is broadly recognised across investigations and theories of many different cognitive domains. For instance, dIPL/IPS forms a key region of the executive processing network responding more strongly to difficult decisions or task demands across diverse domains and task types [6,7,100]. The ventral LPC is involved in bottom-up/stimulus-driven and automatic task components [1,8]. Greater AG activation is associated with faster reaction times [109] and is more sensitive to automated than executively demanding tasks (e.g., numerical fact retrieval versus numerical calculation, or making semantic decisions on concrete versus abstract words) [1]. Indeed, there is also a dorsal–ventral distinction within the episodic memory literature, whereby 'recollection' is associated with AG responses and 'familiarity' with the IPS [35].

Attention in the Ventral Parietal Cortex

In some of the first attempts to unify explanations of LPC function across cognitive domains, it was proposed that the bottom-up attention system is not only automatically captured by salient external stimuli (e.g., a loud noise) but also salient internal information, such as when an episodic memory is triggered and readily 'pops' into awareness [42]. Much evidence supports the view that ventral LPC plays an attentional role in episodic memory [8], although other findings question predictions of this model. For example, neuropsychology and neurostimulation studies targeting ventral LPC report no disproportionate impairments in episodic memory tasks that involve attentional manipulations [47,50,61,110]). Although attention and memory can both be associated with bilateral LPC activity, episodic retrieval effects are typically observed in the left AG, whereas attentional reorientation is generally associated with the more anterior temporoparietal junction area in the right hemisphere [1,111,112]. This implies that there may be a separation of cognitive functions both within and across the left and right ventral LPC.

One question is what the adaptive value might be of the kind of dynamic, consciously accessible mnemonic representation that AG appears to be involved in constructing. One possibility is that subjective experience (also called 'autonoetic awareness' [59]) allows individuals to reflect on the content of their memories, to integrate those memories with prior semantic knowledge, and to make judgments about the things they remember. Consistent with this view, although patients with parietal lesions perform well on many tests of episodic memory, their accurate recollections are associated with reduced confidence [60,61] and fewer 'remember' responses on remember/know tasks [49,62]. Functional imaging experiments have found AG activity to be sensitive to qualitative characteristics of retrieved memories, such as their rated vividness, confidence, and precision [55,63,64]. Thus, it may be that this region contributes to episodic memory by enabling the online, dynamic buffering of multisensory spatiotemporally extended representations that are accessible to conscious assessment and evaluation by other, primarily prefrontally mediated, brain networks responsible for monitoring and decision making [65–67]. The flexible coordination of such whole-brain networks that involve prefrontal, medial temporal, and parietal cortices, appears to be important for promoting successful recollection and the adaptive benefits that can be gained by reflecting on our memories and using them to guide subsequent behaviour [68–70].

Semantic Memory

The association of the lateral parietal area with semantic processing has a long history. Henry Head [71] was one of the first to document that temporoparietal damage leads to a form of semantic impairment known as semantic aphasia. Intriguingly for our consideration of the contribution of LPC to episodic and semantic memory, Head also noted that these same patients had difficulty in relating their personal autobiographical history (perhaps prefiguring the findings of others [46], see earlier). Later, it was proposed that the AG is a 'semantic hub' that stores multimodal semantic information based on neuropsychological evidence of semantic impairment without other aphasic symptoms after AG damage [72,73]. Several large-scale, functional neuroimaging meta-analyses have shown that the ventral AG (in the PGp subregion) reliably exhibits differential activation levels with respect to semantic contrasts, such as words versus non-words, or concrete versus abstract words [74,75]. It is also possible that the AG semantic hub theory could be extended to explain AG engagement in the construction and expression of autobiographical and episodic memories in that many of the constituents are semantic in nature [76]. Similar recent proposals include that common AG activation for semantic and episodic tasks reflect the 'reinstatement' of conceptual processing necessary during episodic retrieval [11], or the convergence of multimodal representations [10].

Despite the long-standing prominence of the semantic hub hypothesis and the robustness of one line of neuroimaging data, there are several important caveats and apparent contradictions. First, in terms of the neuropsychological evidence, patients with semantic aphasia do not appear to have lost semantic representations but rather have dysfunction in the flexible use and manipulation of semantic information [77]. Second, in revisiting a seminal case study [73] from a contemporary viewpoint, it is striking that the patient's anoxia-induced damage was not isolated to the AG but encompassed multiple areas, including prefrontal cortex, and was particularly severe in the lateral and ventral ATL, bilaterally, all areas known to be crucial for representing and manipulating conceptual knowledge [16].

There are also important caveats to the neuroimaging evidence, which varies dramatically depending on the imaging contrast used. Specifically, the vast majority of tasks based on word/non-word or concrete/abstract comparisons tend to involve a contrast of an easier versus more difficult task. When studies use different contrasts then ventral AG activation is often missing. For instance, no ventral AG activation was found in a meta-analysis of semantic versus non-semantic tasks [78] or in a study specifically directed to examine semantic involvement in AG processing, which instead found stronger activation for tongue movements than meaningful speech [79]. It is, in fact, possible that the reliable differences found for concrete/abstract or word/non-word contrasts represent difficulty-related deactivations in the ventral AG [1,7]. For example, a recent investigation that directly manipulated task difficulty for both a semantic and a non-semantic visuospatial task found a main effect of task difficulty (easy versus hard) in the ventral AG but no semantic versus non-semantic difference [7]. Finally, and compellingly, the classic pattern of differential activation associated with the contrast of words versus non-words or concrete versus abstract processing, can be flipped by reversing the difficulty of the task or the stimuli [80,81].

A second important issue when considering the neuroimaging literature on the AG is that it is important to take into account the polarity of activation relative to a resting baseline [1,12]. It is, of course, always difficult to interpret 'rest', which could involve spontaneous language and semantic processing [82]; however, if we consider the pattern of AG activation and deactivations across tasks, then clear differences emerge. First, as noted earlier for both semantic and non-semantic tasks (e.g., judgements of word meaning, episodic encoding, visuospatial decisions), the ventral AG deactivates; indeed, the ventral AG forms a core part of the default mode network [83], which is not true of other brain regions known to be involved in semantic representation (e.g., the ATL shows activation for semantic tasks over rest but deactivation with non-semantic tasks) [7,12]. The ventral AG, however, is most commonly engaged positively in studies that examine episodic memory retrieval, as described earlier [35,84].

Taken together, these neuropsychological and functional neuroimaging data challenge the classical notion that the AG supports semantic representation *per se* (see Figure 2 for summary of the alternative interpretations of the 'semantic' ATL versus AG hubs). The current literature involves investigation of at least two alternative hypotheses. One proposal has reformulated the classical semantic AG hypothesis to suggest, instead, that the AG might support 'event-semantic'

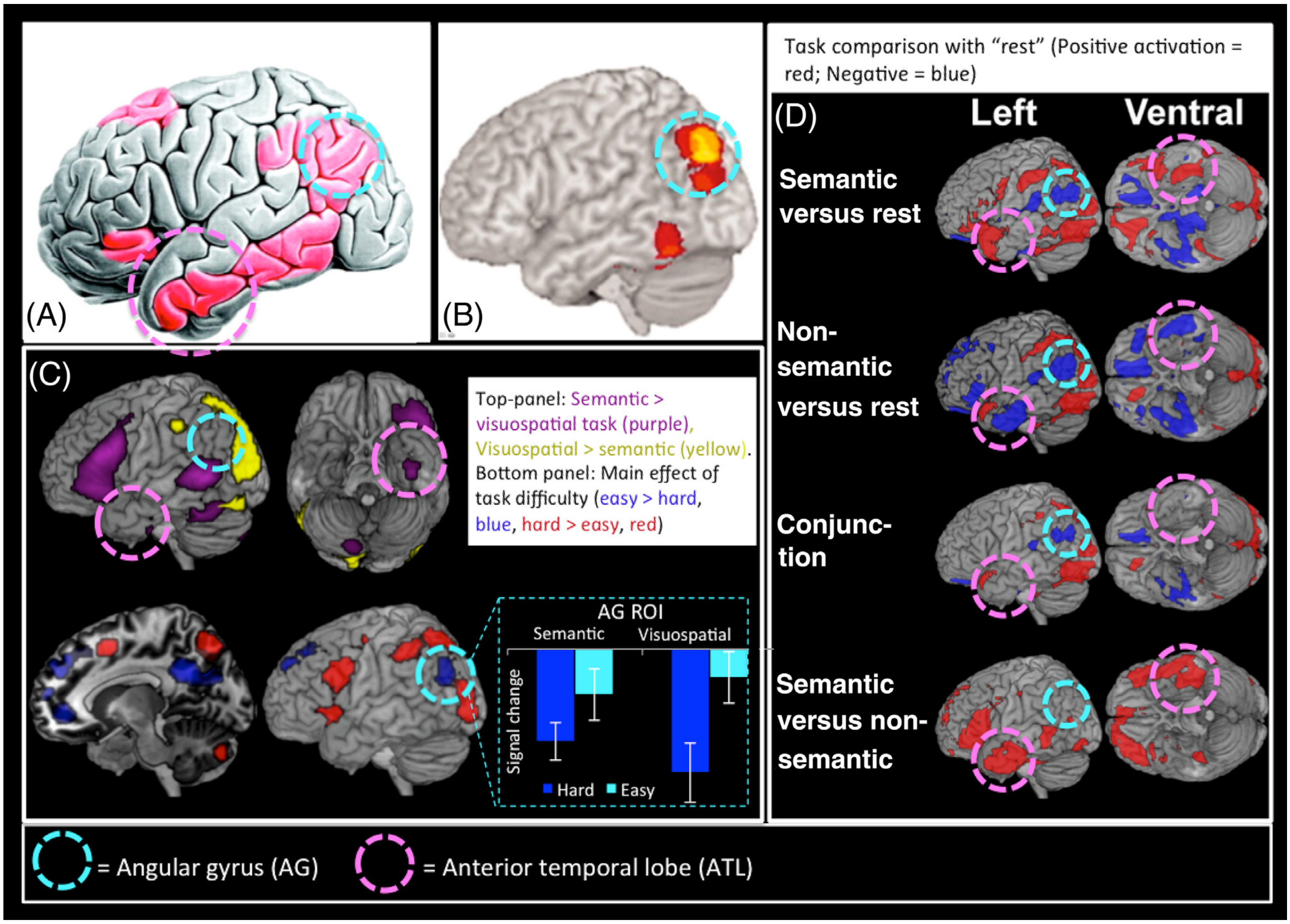

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Figure 2. Alternative Interpretations of the 'Semantic' Anterior Temporal Lobe (ATL) versus Angular Gyrus (AG) Hubs. The results from (A) and (B) have both been interpreted as strong evidence that the AG is a core semantic hub. Specifically, (A) shows the summary from a meta-analysis [74] that included studies using a semantic contrast (e.g., words versus non-words, concrete > abstract items). (B) Shows the results from a meta-analysis that contrasted concrete > abstract items (from [75]). Nevertheless, unlike areas such as the positively activated posterior inferior temporal gyrus (ITG), the results in the AG largely reflected differential levels of deactivation, which raises the alternative possibility that they result from differential difficulty rather than semantic representation. This is clearly illustrated in the results from (D) (from [12]). This study showed that, when contrasting tasks versus a resting baseline, the AG is consistently deactivated for both semantic studies > rest, and non-semantic tasks > rest (blue regions). Importantly, there is no difference in AG activity levels when directly comparing the semantic and non-semantic studies. This is quite unlike the core ATL semantic hub, which is positively activated for semantic tasks (red activation), but deactivated for non-semantic control tasks. It is important to realise that AG deactivation can, for many though not all tasks, vary in line with task or item difficulty. For instance, in common 'semantic' contrasts there is often a difficulty confound: in contrasts such as words > non-words, or concrete > abstract, the easier task is contrasted with the harder task. In fact, the results from these contrasts can be reversed by manipulating task/item difficulty to be in the opposite direction [80,81]. The importance of difficulty-related deactivations is demonstrated in (C). This study directly manipulated difficulty of semantic and visuospatial tasks. Again, when semantic > non-semantic contrasts are matched in task difficulty (purple regions) [7], the AG does not show a response (whereas other known semantic regions do respond, including the ATL). Strikingly, the AG shows a task difficulty effect, revealing the same easy > hard difference not only in semantic but also non-semantic, visuospatial decisions (blue areas). Abbreviations: ROI, region of interest.

information and the ATL acts as a hub for other aspects of semantics [76]. Various forms of evidence have been used to support this emerging hypothesis, including combinatorial semantic tasks where readily combined adjective–noun or adjective–verb word pairs elicit stronger AG activation compared with less easily combined alternatives [85,86]. Like the prior AG general semantic view, this hypothesis offers an explanation for the involvement of AG in episodic retrieval by arguing that episodic memories necessitate event knowledge [76]. Challenges to this view include: (i) most of the combinatorial noun-phrase experiments are again based on contrasting an easy versus hard task condition, which as now known, can generate a difference in the ventral AG even for non-verbal, non-semantic activities [7]; and (ii) the multihub hypothesis does not appear to fit with the data from patients with semantic dementia, which arises from atrophy centred on the ATL bilaterally and not the AG, who have impoverished generalised semantic impairment, including reduced knowledge about events and social schema [87].

The second alternative hypothesis is that the AG does not support long-term stored information *per se* but rather is a multimodal online temporary buffer for external and internal information. Indeed, this hypothesis might be consistent with other proposals that AG acts a 'schematic-convergence zone' that binds information, if we assume that this binding is temporary [88]. An online buffer would seem to be a necessary neurocomputation for the construction of internal models of the world, reconstruction of autobiographical memories, or the envisioning of possible future events, and, perhaps, for the ongoing buffering of combinatorial meaning generated over a time-extended period [89–91]. All these processes would require the positive engagement of the AG, whereas the activation of semantic representations via the hub-and-spoke architecture does not require online buffering and thus the AG is not engaged or even deactivated. In cases when this form of AG buffering system is damaged, patients should find it difficult to construct detailed autobiographical memories and to complete other time-extended activities that all require an online internal buffering of recent stimuli and events.

Concluding Remarks

As siblings within the 'declarative' or 'explicit' family of long-term memory systems, episodic and semantic memory are defined by many shared features in addition to their essential differences. Despite the closeness of their taxonomic relationship, the cognitive and brain mechanisms of these two forms of memory have largely been investigated independently, leading to a proliferation of theories, which sometimes overlook that episodic and semantic memory (as well as a broader range of other non-memory cognitive activities) engage a number of the same brain areas and thus presumably share at least some underlying neurocomputations. One common brain area is AG, classically implicated in both episodic and semantic memory, as well as several other cognitive domains. Building on previous domain-specific theories of parietal function, we have here considered a unifying model that encompasses a set of common principles arising from cognitive neuroscience. This cross-domain synthesis proposes that AG, and wider LPC, computations support the online dynamic buffering that combines distinct forms of information, such as multiple sensory modalities or different spatiotemporal frameworks. Further work is required to understand the purpose and implications of such an integrative buffering function (see Outstanding Questions). Its uses might include the internal representation of the current external and internal state of the world, which would seem to be a necessary element for keeping track of time-extended events or activities. With respect to higher forms of human cognitive functions, the AG buffer may enable the conscious evaluation and exploration of the complex feature networks that comprise many of our autobiographical experiences and conceptual knowledge structures. Such in-depth and demanding cognitive processing may not be necessary for accomplishing many laboratory memory tasks, such as those that require the retrieval of a single episodic feature or semantic fact. But the capacity to flexibly and dynamically reflect on the content of our memories affords us the invaluable real-world ability to understand and learn from our experiences and use them to guide subsequent action in novel and creative ways that may be crucial for successful adaptive human behaviour.

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Outstanding Questions

What are the adaptive benefits of the proposed integrative buffering function of AG for behavioural domains beyond episodic and semantic memory?

To what extent can the functional distinctions that have been observed across AG subregions be explained by a single underlying function modulated by domain-specific alliances with other brain areas?

What is the functional significance of activation and deactivation patterns in AG that are seen in some behavioural domains but not others?

To what extent do the episodic memory confidence reductions demonstrated following lateral parietal lesions generalise to subjective judgments about other cognitive abilities?

Can therapeutic interventions targeting AG function be demonstrated to enhance components of episodic and semantic cognition?

Declaration of Interests

The authors declare no competing interests in relation to this work.

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