

## Feature Review

# Cognitive contributions of the ventral parietal cortex: an integrative theoretical account

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**Although ventral parietal cortex (VPC) activations can be found in a variety of cognitive domains, these activations have been typically attributed to cognitive operations specific to each domain. In this article, we propose a hypothesis that can account for VPC activations across all the cognitive domains reviewed. We first review VPC activations in the domains of perceptual and motor reorienting, episodic memory retrieval, language and number processing, theory of mind, and episodic memory encoding. Then, we consider the localization of VPC activations across domains and conclude that they are largely overlapping with some differences around the edges. Finally, we assess how well four different hypotheses of VPC function can explain findings in various domains and conclude that a bottom-up attention hypothesis provides the most complete and parsimonious account.**

## Introduction

Recently, the cognitive functions of ventral parietal cortex (VPC), which is comprised of the supramarginal gyrus (SMG) and the angular gyrus (AG), have become the focus of intense research interest and lively theoretical debate. The research interest has been stimulated by the ubiquity of VPC activations in functional neuroimaging studies in a variety of cognitive domains, including perceptual and motor reorienting, episodic memory retrieval, language and number processing, and social cognition. Indicative of this interest, a recent symposium at a major cognitive neuroscience conference was devoted to the functions of a single VPC subregion\*. The theoretical debate reflects the difficulty of explaining how VPC can play a role in very dissimilar tasks, from reorienting to simple visual targets and actions to remembering personal events, understanding language and performing mental calculations, and attributing beliefs to other people. Cognitive neuroscientists have generated very different hypotheses about the functions of VPC depending on the specific tasks investigated, and it is

uncertain if a single global function could explain VPC contributions to so many different tasks.

When cognitive neuroscientists try to explain why a broad brain region is recruited by different cognitive tasks, they usually adopt one of two theoretical positions. One position, which may be called the ‘fractionation view’, is that the different tasks engage distinct subregions within the broad area, with each subregion mediating very different cognitive processes. According to this view, the idea that the different tasks engage the same region is only an illusion, which is dispelled by careful demarcation of the subregions engaged by each task. An alternative position, which can be termed the ‘overarching view’, argues that, although functional subdivisions within the broad brain region do in fact exist, the differences are more graded, because each subregion mediates a different aspect of the global cognitive function supported by the broad region. The debate between fractionation and overarching views has occurred for several brain regions, with the lateral prefrontal cortex being a clear example. Whereas some authors have emphasized differences in function between various lateral prefrontal subregions (e.g., ventrolateral vs. dorsolateral [1,2]; anterior vs. posterior ventrolateral [3,4]), others have proposed that all lateral prefrontal subregions contribute to different aspects of an executive control function [5,6]. For other brain regions, most researchers support an overarching view. For example, most cognitive neuroscientists today believe that ventral occipito-temporal regions play a general role in visual processing, while at the same time acknowledge that within this broad area, different subregions are specialized in processing faces, scenes, faces, etc. [7] Put another way, most overarching views focus on the general function of the region [8], whereas the fractionation view focuses on differences in the nature of representations [9].

Currently, a debate between fractionation and overarching views involves theories of VPC function. Whereas some researchers have emphasized sharp functional differences between anterior (SMG) and posterior (AG) VPC subregions [10,11], others have proposed a global function for all VPC subregions [12]. In the current article, we review functional neuroimaging evidence regarding VPC activations in vari-

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### Box 1. The effects of VPC lesions

Reports of cognitive disturbances following VPC lesions date to the turn of the 20<sup>th</sup> century [110]. Among the symptoms that have been noted in the past century are disorders of attention, action (apraxia), language and reading, mathematical calculations, body schema, spatial orientation and construction, short-term or working memory, and intentionality and theory of mind [111–114]. The most prominent attention disorder associated with VPC lesions is hemi-spatial neglect, which is characterized by defective detection of events and impaired exploratory activities in the contralesional part of space. The frame of reference of neglect can be extra-personal or peri-personal, within egocentric or object-based frames of reference [115–117]. The source of the neglect is attributed, in part, to an inability to disengage attention automatically from the intact region and direct it to the contralesional side [102,103,118]. However, other evidence suggests that neglect is typically accompanied by other spatial and non-spatial attentional deficits that affect both sides of space [112]. An even more debilitating attentional disorder caused by bilateral parietal lesions is Balint-Holmes' syndrome, which includes an inability to perceive and report more than one object at a time, and even to bind the features of an object together [111]. Ideomotor apraxia (an impairment in imitating gestures, pantomiming tool use and making meaningful gestures to command) can occur after left inferior parietal lesions, especially if the gestures require a series of sequential movements [33]. Gerstmann's syndrome [119] is yet another visuomotor syndrome consisting of a tetrad of symptoms: finger agnosia (the inability to recognize, name, and select individual fingers of both hands), left-right disorientation, agraphia (impaired writing), and acalculia (impaired mathematical calculation and symbol recoding and manipulation [120]). Although this syndrome is typically associated with left AG damage [121], the heterogeneous deficits may not reflect the function of this region and could be caused by the damage of white matter fibers passing through AG [122].

VPC lesions have been also associated with reading [123,124], working memory [111,125], and reasoning disorders [126]. Among

reading disorders, left AG damage has been associated with some forms of developmental dyslexia [127–129]. Although attention directly plays a part in some types of acalculia [130] and dyslexia [131], there is reason to believe that it does so indirectly in many other forms of these disorders via short short-term or working-memory (WM), both of which are intimately tied to attention (see below). WM deficits have been reported following AG lesions, with verbal and spatial short-term memory being impaired following damage to the left and right side, respectively [125,132,133]. Although these deficits were initially attributed to impaired phonological or visuospatial WM buffers [114,134], more recently they have been linked to impaired attention whose operation is needed to activate and sustain the long-term memory representations that constitute the contents of WM [135–137]. Finally, VPC lesions have been associated with deficits in reasoning about one's own and others' mental states, such as thoughts, intentions, and beliefs, or ToM [81,90,113]. Although reading and reasoning involve some mechanisms that are different, the deficits following VPC lesions may share an impairment in WM which arises from deficient attention-mediated processing [138] that, as we noted, is necessary to activate and sustain the contents of WM.

In addition to the difficulty of finding a common explanation to account for the variety of functions associated with VPC lesions, one also has to overcome the discouraging evidence that each of the elements of the syndromes described above tend not to cohere with one another. Thus, different aspects of Gerstmann's and Balint's syndrome are as likely to occur independently of one another [122,139,140] as together [122,141]. The same applies to the different manifestations of hemi-neglect [116], and to different aspects of ToM [81,90]. As noted above, the heterogeneity of symptoms may reflect the disconnection of regions outside VPC rather than VPC functions per se [122]. Nonetheless, a deficit in bottom-up attention could contribute to several of these disorders, as well as to memory difficulties following VPC damage, as reviewed in the main text.

ous cognitive domains. After reviewing this evidence, we consider the issue of localization across VPC subregions, and finally turn to different overarching accounts of VPC function.

### Functional neuroimaging of VPC function

This section reviews functional neuroimaging evidence of VPC activations in various cognitive domains (for a brief summary on lesion evidence regarding VPC function, see Box 1). We focus on five cognitive domains: (i) perceptual and motor reorienting, (ii) episodic memory retrieval, (iii) language and number processing, (iv) theory of mind, and (v) episodic memory encoding. Although VPC activations are also found in other domains, these domains were selected because they represent areas where VPC is assumed to be one of the core regions mediating the function in question, and specific hypotheses regarding VPC function have been advanced. Given the complexity of these domains, we focus only on the most typical paradigms and contrasts yielding VPC activations within each domain (Table 1) and mention only a few representative studies for each of them. Our goal is to show a broad pattern across domains (the 'big picture') rather than to explain the complexity of activation patterns within each domain.

### Perceptual and motor reorienting

Functional neuroimaging studies that have linked the VPC to perceptual reorienting have used mainly two tasks, the 'Posner' task and the oddball task. Although VPC activations during these tasks are usually bilateral and occur in

both SMG and AG, most studies highlight the right temporo-parietal junction or TPJ (for VPC anatomy, see Box 2). In a typical Posner task, a central cue indicates whether a target stimulus is likely to occur on the left or the right of the screen, and the target occurs in the expected (valid) location in the majority of the trials. Whereas dorsal parietal cortex (DPC) activity is greater during the cue period, VPC activity is greater during the target period [13]. Moreover, target-related VPC activity tends to be greater for invalid than valid trials (e.g., Figure 1a) [14–17], consistent with a reorienting of attention when expectations are violated [18,19]. In a typical oddball paradigm, subjects process a long series of identical stimuli ('standards') intermixed with a few (e.g., 10%) deviant stimuli ('oddballs'), which attract reflexive attention [20–27]. Compared to standard stimuli, oddball stimuli elicit VPC activity bilaterally (e.g., Figure 1b). This occurs only when the oddballs are somehow relevant to the main task, indicating that the effect is not merely due to novelty or saliency [28,29]. In sum, functional neuroimaging studies of Posner and oddball tasks have strongly linked VPC to reorienting attention to locations or stimuli that are not part of the focus of attention, but are nonetheless related to the task at hand.

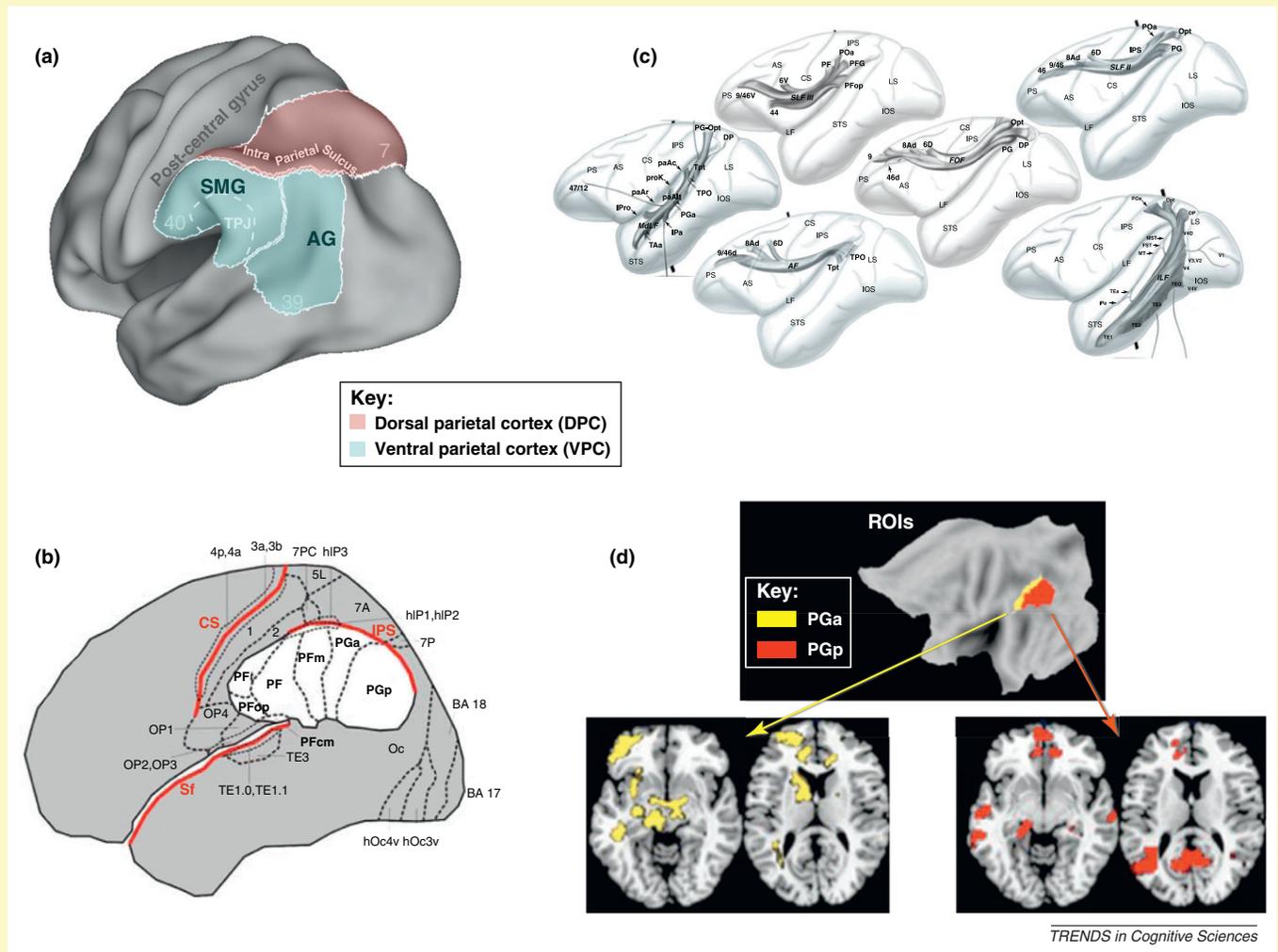
The VPC, particularly the left supramarginal gyrus, is also activated by a motor version of the Posner task, in which a cue indicates which finger must be used to respond to a subsequent target [30]. Transcranial magnetic stimulation (TMS) of this region interferes with participants' ability to redirect the motor action when the target is

### Box 2. VPC anatomy and connectivity

As illustrated in Figure 1a, VPC (also known as inferior parietal lobule – IPL) is a region ventral to the intra-parietal sulcus (IPS) and anterior to post-central gyrus. VPC is comprised of the supramarginal gyrus (SMG) and the angular gyrus (AG). The imprecise term temporo-parietal junction (TPJ) usually refers to an SMG area around the end of the Sylvian fissure, but it has been applied to activations in AG and in the superior temporal gyrus. AG largely corresponds to Brodmann Area (BA) 39, and SMG, to BA 40. Cytoarchitectonically (see Figure 1b), the AG can be subdivided into anterior area PGa and posterior area PGp,

whereas the SMG can be subdivided into at least five different areas [142,143].

The VPC has direct anatomical connections with most frontal and temporal lobe regions (see Figure 1c) [144]. Functional connectivity differs for various VPC subregions. For example, a recent resting-state fMRI study found that the PGa is more strongly connected with the basal ganglia and ventrolateral prefrontal cortex, whereas the PGp is more strongly connected with the hippocampus and posterior cingulate (see Figure 1d) [145].

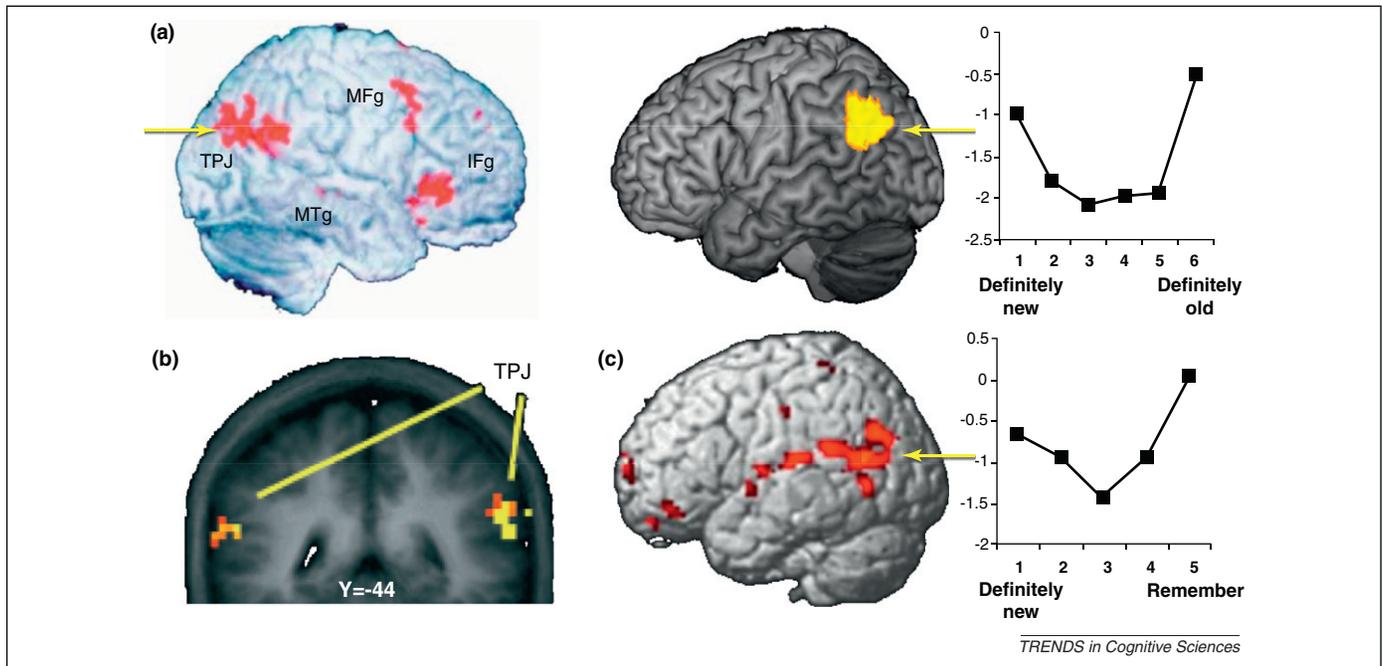


**Figure 1.** (a) The VPC is comprised of the SMG (BA 40) and the AG (BA 39). (b) The AG can be subdivided into areas PGa and PG, and the SMG into areas PFop, PFT, PF, PFm, and PFcm. Reproduced, with permission, from [143]. (c) The VPC is connected to the frontal lobes via the superior longitudinal (SFL), fronto-occipital (FOF), and arcuate (AC) fasciculi, and to the temporal lobes via the middle (MdlF) and inferior (ILF) longitudinal fasciculi. Reproduced, with permission, from [144]. (d) The PGa is more strongly connected with regions such as the ventrolateral prefrontal cortex, whereas the PGp is more strongly connected with the hippocampus and other regions. Reproduced, with permission, from [147].

invalid [31]. This effect may be interpreted as a deficit in disengaging motor attention [32]. This idea fits with evidence that errors in ideomotor apraxia following VPC lesions [33] tend to be greater for tasks that require a sequence of movements [34,35], and hence involve rapid reorienting of motor attention. Impairments in tool use may also reflect a deficit in redirecting attention from a typical reach to a tool-appropriate reach [32]. Consistent with the role of VPC in reorienting motor attention, a study found that VPC stimulation in awake patients undergoing surgery led to a sense of having acted, although no action was detected [36].

### Episodic memory retrieval

Episodic memory retrieval tasks, such as old/new recognition memory tasks, consistently activate the VPC [37]. These activations are usually bilateral, but are more frequent in the left VPC, consistent with the verbal nature of the stimuli typically employed in these studies. The activations tend to increase as a function of recollection and confidence [12,38–40]. The involvement of VPC in recollection (rich, vivid memories) has been demonstrated with both subjective measures, such as the remember-know procedure, and objective measures, such as source memory [12,38–41]. Interestingly, compared to low-confidence



**Figure 1.** Examples of VPC activations during perceptual reorienting and episodic retrieval. (a) Invalid > valid trials in a Posner task. Reproduced, with permission, from [14]. (b) Relevant > irrelevant distractors in an oddball task. Reproduced, with permission, from [30]. (c) Confidence during recognition memory. Top panel reproduced, with permission, from [43]; bottom panel reproduced, with permission, from [44].

responses, the VPC shows greater activity not only for high-confidence ‘old’ responses, but also for high-confidence ‘new’ responses [12,42–44]. Thus, when VPC activity is plotted as a function of perceived oldness (from ‘definitely new’ to ‘definitely old’ responses), it shows a clear U-function (Figure 1c). This U-function suggests that VPC activity tracks the relevance of recognition responses or cues rather than memory recovery *per se*. Consistent with this idea, recent evidence suggest that VPC tracks the violation of expectations during retrieval [45,46]. Whereas VPC activity is greater when memory recovery is high (recollection, high confidence, etc.), dorsal parietal cortex (DPC) activity is greater when recovery is low (familiarity, low confidence, etc.). Based on this and other dissociations, we have proposed an ‘Attention to Memory’ (AtoM) model [12,39,47], whereby VPC and DPC mediate bottom-up and top-down attention, respectively, during episodic retrieval (Box 3).

### Language and number processing

In language studies, VPC activations are frequently found during word and sentence comprehension. Regarding word comprehension, a recent meta-analysis [48] identified VPC as one of the regions most strongly associated with semantic processing of spoken and written words, including contrasts such as words vs. nonwords [49–51], familiar vs. unfamiliar people names [52,53], semantically related vs. unrelated words [54,55], and semantic vs. non-semantic tasks [56,57]. Although researchers in this domain usually emphasize the left AG, the results of the meta-analysis (Figure 2a) clearly shows that VPC activations are bilateral and occur in both the AG and the SMG. Regarding sentence comprehension, VPC is also activated while reading or hearing sentences compared to lists of random words or pseudowords [58–60]. Several studies found that VPC

activity was greater for sentences with semantic violations than for normal sentences [61–63]. This effect may reflect the demands of retrieving semantic knowledge or the demands of processing discourse for coherence. To investigate these two explanations, one study [63] compared normal vs. anomalous sentences (e.g., ‘With lights you can see more/less at night.’) that were preceded either by a standard context or by an unusual context that explained the anomaly (e.g., ‘Lamp posts block the night sky. This is sad for astronomers.’). As illustrated in Figure 2b, the VPC showed greater activity for anomalous than for normal sentences in the standard context, but the opposite pattern in the unusual context, suggesting that VPC activity tracks discourse incoherence rather than knowledge retrieval *per se*.

In the related domain of number processing, VPC activations also tend to be bilateral (e.g., Figure 2c), but again researchers emphasize the role of the left AG. In general, VPC activations are found in conditions that require the retrieval of numerical facts [64]. For example, VPC activity is greater for exact (e.g.,  $4 + 5 \rightarrow$  select correct: 9 or 7) than approximate (e.g.,  $4 + 5 \rightarrow$  select closer: 8 or 3) calculations [65,66]. Also, VPC activity is greater for problems whose answer is stored in memory, including multiplying single digits [67,68], adding single digits up to a total of 10 [66], and comparing small numbers [69]. Moreover, the VPC shows greater activity when participants solve previously trained than untrained multiplications problems (e.g.,  $14 \times 7 = 98$ ) [70] or when they report using retrieval rather calculation strategies [71]. All these findings are consistent with numerical fact retrieval.

### Theory of mind

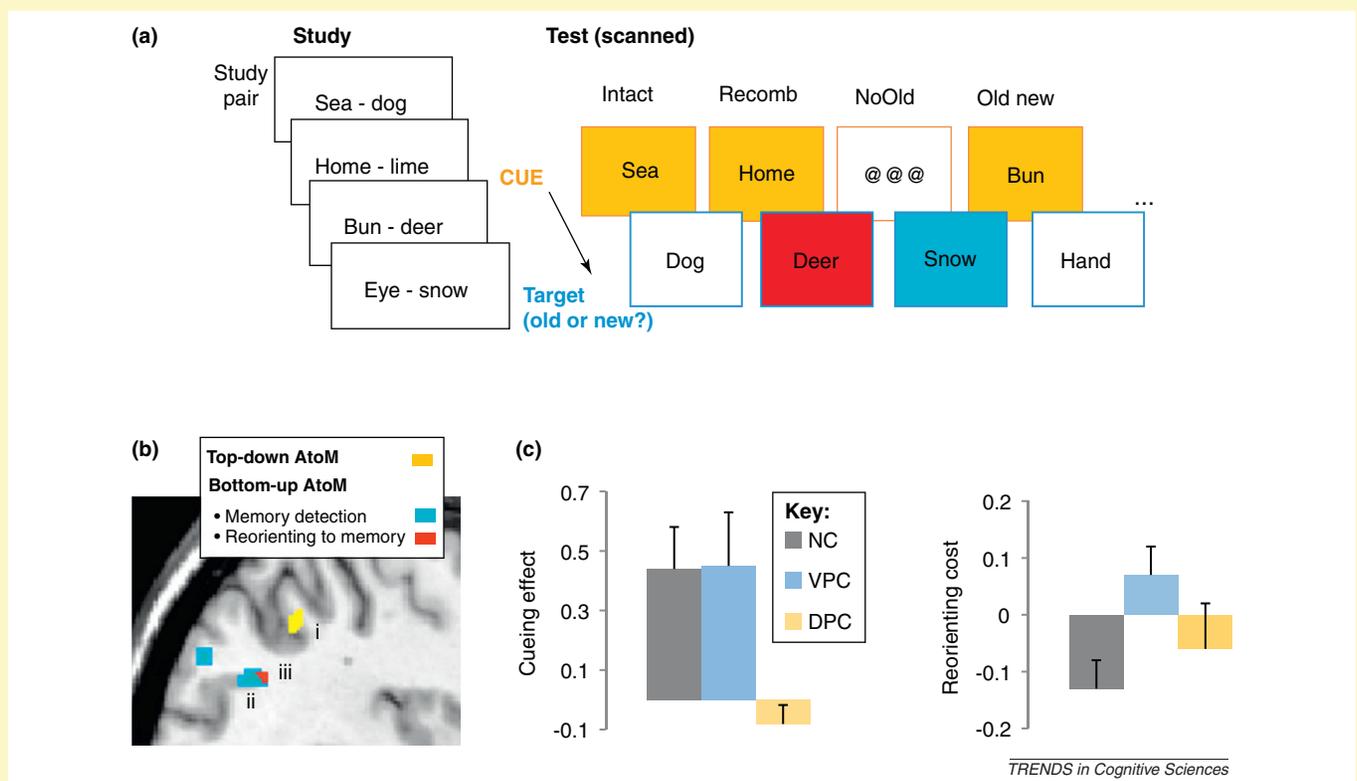
Theory of mind (ToM) refers to the ability to think about mental states in oneself and other people, including

### Box 3. The AtoM model

The Attention-to-Memory (AtoM) model was formulated to explain the contribution of DPC and VPC to episodic memory retrieval [12,38–40]. The AtoM model makes an explicit distinction between the mnemonic roles of DPC and VPC based on the differential roles these regions play in attention. According to a prominent model [102], the DPC mediates endogenous attention, which enables selection of stimuli based on internal goals, whereas the VPC mediates exogenous attention, which enables detection of relevant stimuli when attention is not directly focused on them. According to the AtoM hypothesis, the DPC and VPC serve analogous attention roles in memory retrieval: the DPC mediates the allocation of attention to memory retrieval operations (top-down AtoM), whereas the VPC mediates the bottom-up capture of attention by salient memory contents (bottom-up AtoM). Consistently, processing in DPC is prominent when memory retrieval loads heavily on top-down attention (e.g., strategic retrieval operations), whereas processing in VPC is prominent when the recovered memory is salient and therefore captures attention bottom-up (e.g., recollection) [12,38–41]. Moreover, PPC patients may be unable to retrieve and re-experience

relevant memory contents spontaneously (bottom-up), in the face of a generally preserved ability to access memory contents if adequately probed (top-down) [104,105,107,146].

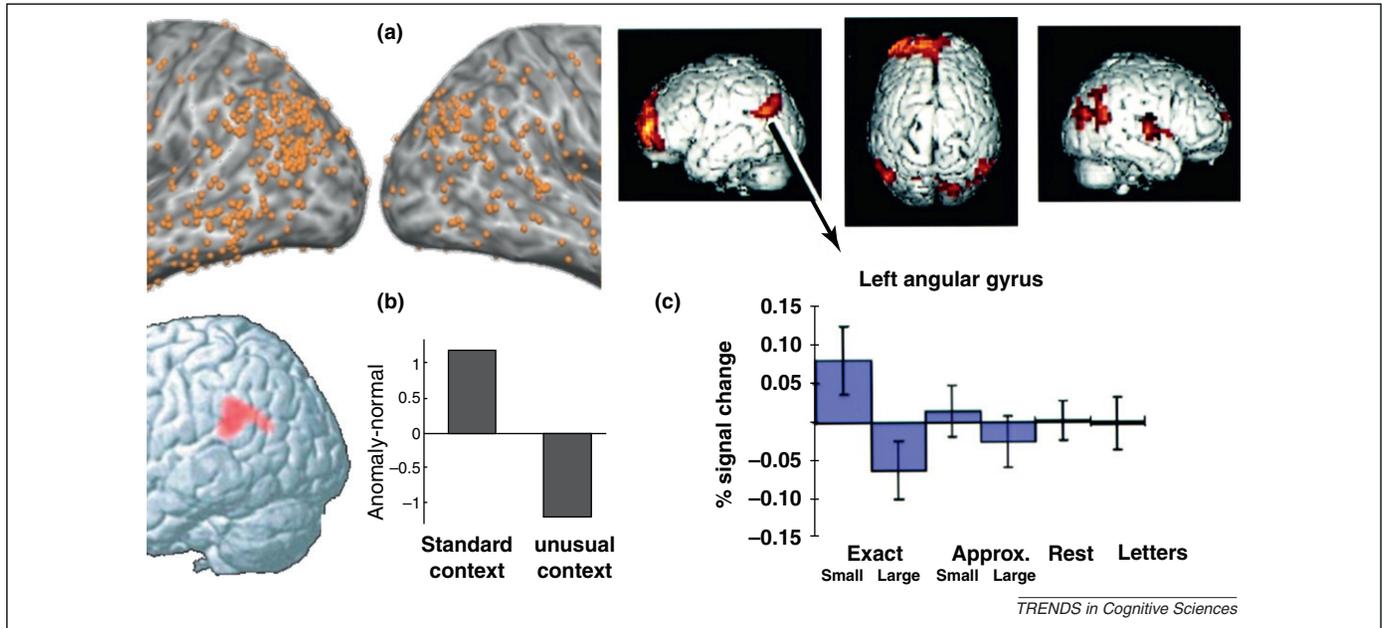
Using fMRI, Ciaramelli and collaborators [46] dissociated the functional profile of DPC and VPC in episodic memory within a single, Posner-like, recognition memory paradigm. Participants studied word pairs and then detected studied (target) words among new words. In some conditions, a studied word cued the upcoming target word, facilitating recognition performance (Figure 1a). The left DPC (i) was engaged when participants searched for anticipated memory targets upon presentation of memory cues, whereas left VPC mediated target detection on noncued (ii) and invalidly cued trials (iii) (Figure 1b). These results mirror closely those obtained in the perceptual domain [13]. These findings were confirmed in a small sample of patients with lesions limited to VPC and DPC. DPC patients did not show a normal advantage in the validly cued compared to the non-cued condition, whereas patients with VPC lesions had problems detecting memory probes that violated mnemonic expectations (Figure 1c).



**Figure 1.** (a) Example trials of the Posner-like recognition memory paradigm. (b) The left DPC (i) is associated with top-down attention to memory during cued recognition decisions; the left VPC is associated with (bottom-up) detection of non-cued (ii) and invalidly cued (iii) memory targets. (c) Damage to the DPC causes a reduction of the cueing effect; damage to the VPC causes an increase in the reorienting cost after invalid cues. Reproduced, with permission, from [46].

thoughts and beliefs. Functional neuroimaging studies have investigated ToM using a variety of stimuli, including stories [72–76], cartoons [77–79], and animations [73,80]. VPC activations are very frequent during ToM tasks, particularly when using stories [81]. ToM stories usually involve ‘false beliefs’ [73–77] as in the classic Sally-Anne story: ‘Sally put her ball in a basket and left the room. While Sally was away, Anne moved the ball from the basket to a box. When Sally came back, did she look for her ball in the basket or in the box?’ Answering this question correctly requires inferring Sally’s mental state, which is the false belief that the ball is in place

where she left it. As a control condition, several studies [74–76,82] have used ‘false photograph’ stories such as the following: ‘A photograph was taken of an apple hanging on a tree branch. While the photograph was being developed, strong wind blew the apple to the ground. Did the developed photograph show the apple on the branch or on the ground?’ The false belief vs. false photograph contrast, which has been called a ‘ToM localizer’, typically yields activations in bilateral VPC regions, including both the AG and SMG. However, these activations are often labeled TPJ and the right hemisphere is emphasized [83,84].



**Figure 2.** Examples of VPC activations during language and numerical processing. (a) Meta-analysis of semantic processing during word comprehension. Reproduced, with permission, from [48]. (b) VPC activity increases with discourse incoherence. Reproduced, with permission, from [63]. (c) VPC activity is greater for exact than approximate number calculation. Reproduced, with permission, from [66].

### Episodic memory encoding

Whereas in all the domains above, VPC activations are generally associated with successful performance, in the episodic encoding domain they are associated with failed performance. In contrast with the medial temporal lobe and ventrolateral prefrontal cortex, which typically show greater activity for subsequently remembered than forgotten items (subsequent memory effect – SME) [85], the VPC usually shows greater activity for subsequently forgotten than remembered items (reverse SME) [86,87]. Interestingly, the VPC regions showing reverse SME effects during encoding overlap with the ones showing memory success effects during retrieval. As illustrated in Figure 3, across five different experiments involving a variety of stimuli [88], the same VPC regions associated with memory failure during encoding (subsequently forgotten > remembered) were associated with memory success during retrieval (remembered > forgotten). This finding of an ‘encoding-retrieval flip’ markedly constrains possible accounts of VPC function, because it implies that VPC mediates a cognitive process that is beneficial for perceptual/motor reorienting, episodic memory retrieval, language/number processing, and ToM, but detrimental for episodic memory encoding. As discussed later, few cognitive processes can fulfill both requirements.

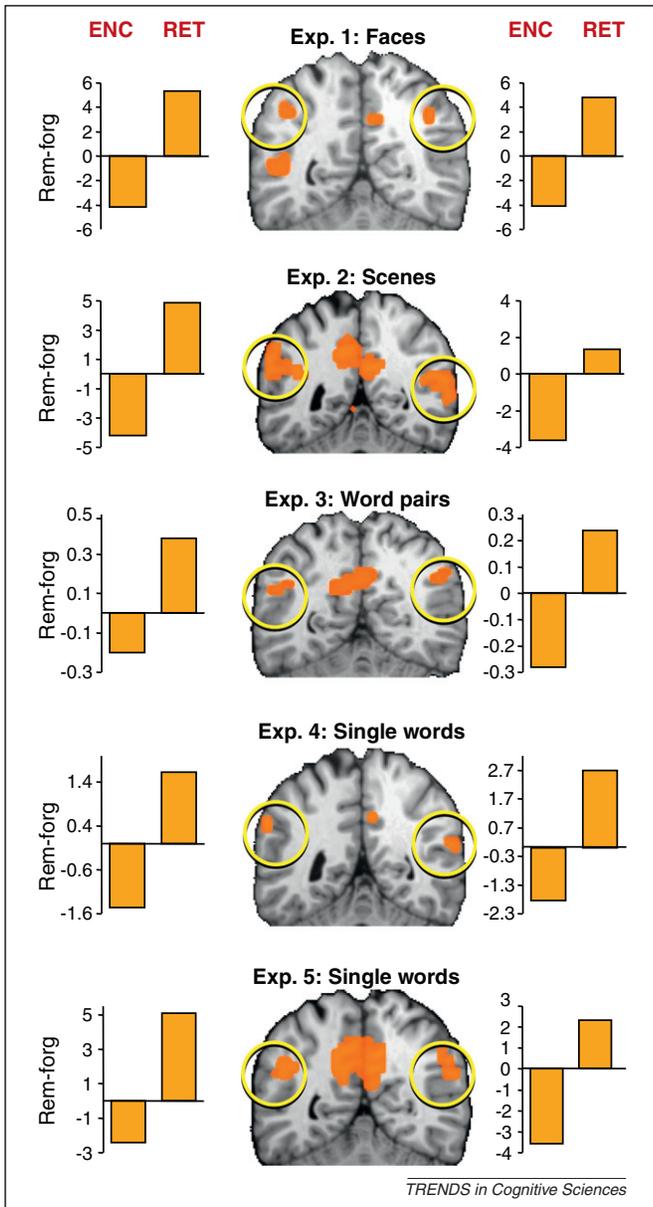
### Localization of VPC activations across cognitive domains

As noted previously, VPC activations in all the cognitive domains reviewed have been observed in both the left and right hemispheres and in both anterior and posterior VPC subregions. Despite this fact, discussions in most domains emphasize one hemisphere and one VPC subregion. The focus on a single hemisphere probably originated in the brain damage literature, which often underscored trends in lesion lateralization (e.g., neglect is more frequent after

right than left parietal damage). The focus on a single VPC subregion is partly due to the popularity of certain anatomical labels, such as TPJ and AG. For example, perceptual reorienting studies tend to label most VPC activations ‘TPJ’, even if they occur in posterior VPC (e.g., Figure 1a), whereas language/number processing studies tend to label most VPC activations ‘AG’, even if they extend into SMG (e.g., Figure 2b). We are not suggesting that the spatial distribution of VPC activations is identical across all cognitive domains. The spatial distributions of VPC activations in different domains are neither perfectly segregated nor perfectly overlapping; they are largely overlapping with some differences around the edges. The following sections provide two examples of this overlap-with-differences pattern and consider possible explanations.

### Examples of the overlap-with-differences pattern

One example of overlap with differences around the edges is between the domains of perceptual reorienting and episodic retrieval. A meta-analysis of left VPC activations in these two domains concluded that activation peaks were more anterior (SMG) for perceptual reorienting but more posterior (AG) for episodic retrieval [10]. To investigate this idea, a recent fMRI study compared VPC activations in these two domains within participants [89]. In the perceptual reorienting task, participants searched a stream of consonants on the screen and pressed a key when they detected a vowel (an oddball task), whereas in an episodic retrieval task, they searched their memory for previously studied word-chains and pressed a key when they detected the last word of a chain. Consistent with the AtoM model (Box 3), conjunction analyses showed that in both tasks the search phase activated the DPC whereas the detection phase activated the VPC (Figure 4a). The overlap in VPC was found within SMG (yellow region in Figure 4b), but, consistent with the aforementioned meta-analysis [10], VPC activations



**Figure 3.** Contrasts between retrieval and encoding in the same participants show that VPC is associated with retrieval success (remembered > forgotten) but with encoding failure (forgotten > remembered). Reproduced, with permission, from [88].

in the episodic retrieval task extended posteriorly towards the AG (green region in Figure 4b). As discussed later, functional connectivity of the overlapping (yellow) region varied according to the task (Figure 4c). In sum, the results of this study suggest that perceptual reorienting and episodic retrieval engage overlapping VPC regions with some differences around the edges.

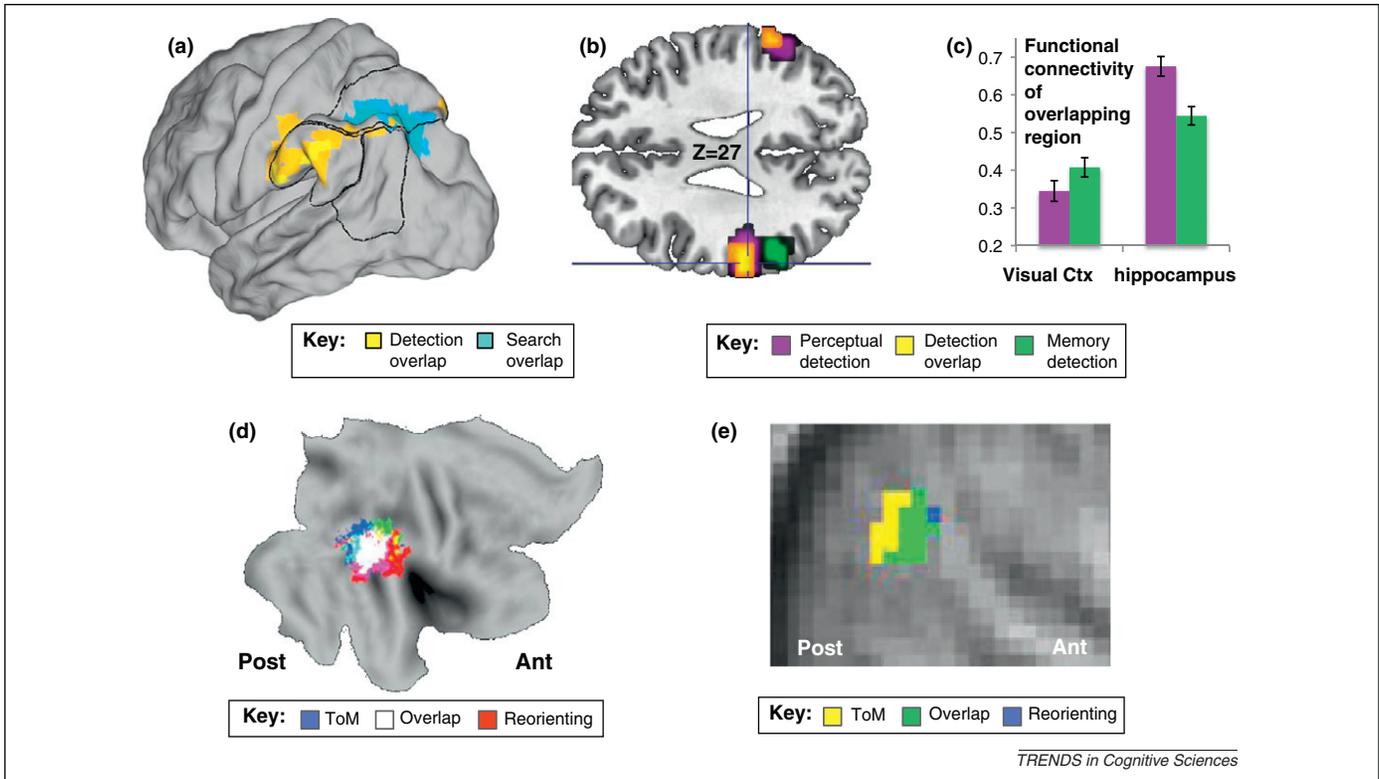
Another example involves the domains of perceptual reorienting and ToM. Even though VPC activations in these domains are typically bilateral and involve both the SMG and the AG, discussions of both domains tend to emphasize the role of the right TPJ. To investigate the distribution of activations in this region, Decety and Lamm [90] conducted a meta-analysis that included perceptual reorienting and ToM studies. Activations in these two domains largely overlapped within the SMG (in white in

Figure 4d), but from there reorienting activity extended anteriorly and ToM activity, posteriorly. A similar pattern was found by Mitchell [76] when he compared a ToM task (false belief vs. false photo stories) to a Posner task (invalid > valid trials) within participants: there was large overlap (in green in Figure 4e), and from there reorienting and ToM activity extended anteriorly and posteriorly, respectively. In another study comparing these two domains, the differences were more along a ventral-dorsal axis [91]. In sum, when VPC activations across domains are compared across studies [10,90] or within participants [76,89] the results consistently show large areas of overlap with some differences around the edges.

### Explaining the overlap-with-differences pattern

How can this pattern of findings be explained? As mentioned in the introductory section, there are two different ways of conceptualizing the spatial distribution of cognitive functions across the subregions of a large area such as VPC. According to a fractionation view (Figure 5a), the region does not have a global function; instead, each of its subregions mediates a distinct – sometimes very different – function (subregion ‘a’ mediates process 6; subregion ‘b’ mediates process 14, etc.). Likewise, each subregion is assumed to be connected with a different network (e.g., subregion ‘a’ is connected to a ‘red’ network; subregion ‘b’, to a ‘blue’ network, and so forth). According to an overarching view (Figure 5b), in contrast, the broad region has a global function (e.g., function 7) and its various subregions mediate different aspects of the same function (e.g., subregion ‘a’ mediates process 7.1; subregion ‘b’, process 7.2, etc.). These various processes are dissociable by experimental manipulations and may appear to be very different on a concrete level. However, they can still be described as consistent with a global function for the entire region, described on more abstract levels. As suggested in the introduction, whereas the subregions may differ at the representation level, they all contribute to different aspects of the same function. Representational processes may be partly determined by variations in functional connectivity, but these variations are assumed to be graded rather than discrete, perhaps reflecting intermixed populations of neurons and their projections.

In general, the available functional neuroimaging evidence about VPC function fits better with the overarching than the fractionation view. The fractionation view cannot easily account for substantial overlap in VPC involvement across very different cognitive domains, such as attention, episodic retrieval, and ToM (Figure 4). In contrast, the overarching view can explain this overlap on the assumption that different cognitive domains engage different aspects of the same broad VPC function. One way of conceptualizing these different aspects is that they reflect the application of a similar cognitive operation to different kinds of information. For example, the overlap between perception and memory detection depicted in Figure 4a can be explained by assuming that VPC mediates a detection process that can be applied to perceptual information, as well as to memory information. Consistent with this idea, the overlapping VPC region showed stronger connectivity with visual cortex during a perception



**Figure 4.** VPC overlap across functions. (a) VPC overlap for perceptual and memory detection. Reproduced, with permission, from [89]. (b) In the same study, memory detection activity extends more posteriorly than memory detection. (c) Functional connectivity of the overlapping left VPC region (in yellow) with visual cortex was stronger during perception than memory, whereas functional connectivity with the hippocampus was stronger during memory than perception. (d) Meta-analysis showing overlap in right VPC activity for perceptual reorienting and ToM. Reproduced, with permission, from [90]. (e) Overlap between reorienting and ToM within participants. Reproduced, with permission, from [76].

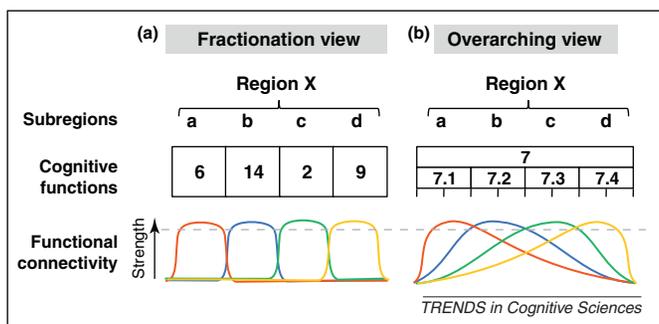
task, but stronger connectivity with the hippocampus during a memory task (Figure 4c). The overarching view can also explain differences around the edges under the assumption that the strength of VPC connectivity with different brain regions differs gradually across VPC subregions (Figure 5b). For example, if one assumes that connectivity with the hippocampus is stronger for posterior VPC regions (AG), the overarching view predicts that VPC activations extend more posteriorly during a memory than a perception task (Figure 4b), even if the VPC processes engaged by these tasks are very similar. The assumption that the localization of VPC activation varies according to functional connectivity can also explain why memory tasks that use words (which interact with a left-lateralized language network) tend to elicit stronger activations in the left VPC, whereas perceptual reorienting tasks that use

spatial information (which interacts with a right-lateralized spatial processing network) tend to elicit stronger activations in the right VPC. Even if the left and right VPC mediate similar cognitive operations, hemispheric asymmetries can be expected depending on other brain regions engaged by the task.

In sum, the overarching view fits very well with evidence of overlap with differences around the edges. This evidence suggests that the VPC has a global function, but different subregions apply this process to different types of information and goals, which vary according to functional connectivity. A similar idea has been previously proposed for frontal lobe subregions, which could mediate a general executive control function by applying it to different posterior regions depending on the task [5,8,92,93]. What global VPC function could explain the involvement of this region in perceptual/motor reorienting, episodic memory retrieval, language/number processing, and ToM tasks, as well as its association with encoding memory failure remains an open question. This is the topic of the next section.

**Hypotheses about a global VPC function**

The sections that follow discuss four hypotheses that were originally proposed to account for the contribution of a specific VPC subregion to a particular cognitive domain. Here, we assess whether these hypotheses could be expanded to account for VPC contributions to all the domains reviewed, namely perceptual/motor reorienting, episodic retrieval, ToM, language/number processing, and episodic encoding (Table 1).



**Figure 5.** Fractionated vs. overarching views of functional organization across hypothetical subregions 1-4 of hypothetical Region X.

**Table 1. Cognitive domains showing frequent VPC activations and hypotheses that could account for these activations**

| Cognitive Domain Paradigm           | Typical Contrasts                      | Semantic Retrieval Hypothesis | WM Maintenance Hypothesis | Multimodal Integration Hypothesis | Bottom-Up Attention Hypothesis |
|-------------------------------------|--|-------------------------------|---------------------------|-----------------------------------|--------------------------------|
| <b>Perceptual/Motor Reorienting</b> |  |                               |                           |                                   |                                |
| Posner task                         | Invalid > valid targets                | –                             | –                         | –                                 | +                              |
| Oddball task                        | Deviant > standard                     | –                             | –                         | –                                 | +                              |
| <b>Episodic Memory Retrieval</b>    |  |                               |                           |                                   |                                |
| Recollection                        | Recollection > familiarity             | +                             | +                         | ++                                | +                              |
| Recognition confidence              | High > low confidence ‘old’            | +                             | +                         | ++                                | +                              |
|                                     | High > low confidence ‘new’            | –                             | –                         | –                                 | +                              |
| <b>Language/Number Processing</b>   |  |                               |                           |                                   |                                |
| Word comprehension                  | Word > nonword/pseudoword              | ++                            | +                         | –                                 | +                              |
| Sentence comprehension              | Anomalous > standard                   | –+                            | +                         | –                                 | +                              |
| Mental calculation                  | Exact > approximate answer             | +                             | +                         | –                                 | +                              |
|                                     | Known answer vs. calculation           | +                             | –                         | –                                 | +                              |
| <b>Theory of mind (ToM)</b>         |  |                               |                           |                                   |                                |
| ToM stories                         | false belief story > false photo story | +                             | +                         | –                                 | +                              |
| <b>Episodic Memory Encoding</b>     |  |                               |                           |                                   |                                |
| Subsequent memory                   | Subsequent forgotten > remembered      | –                             | –                         | –                                 | +                              |

### The semantic retrieval hypothesis

According to Binder and collaborators [48], left AG activations during language comprehension reflect the recovery of semantic knowledge. Can this hypothesis account for VPC activations in other cognitive domains? The easiest extension of the semantic retrieval hypothesis is to the number processing domain, where left AG activations have already been attributed to the retrieval of a particular kind of semantic knowledge, namely numerical facts [64]. The semantic retrieval hypothesis could explain some motor reorienting findings, such as deficits in processing meaningful actions in ideomotor apraxia. The semantic retrieval hypothesis could also account for VPC activations during episodic memory retrieval under the assumption that episodic retrieval requires the retrieval of concepts. As noted by Binder and collaborators ‘to recall, for example, that “I played tennis last weekend” logically entails retrieval of the concepts “tennis”, “play” and “weekend”’ ([48], p. 2781). Finally, the semantic retrieval hypothesis can account for the involvement of VPC during ToM tasks, such as false belief stories, because these stories tend to require additional semantic processing in order to integrate different perspectives.

On the other hand, the semantic retrieval hypothesis does not fare as well in accounting for VPC activations in other domains (see minuses in Table 1). First, perceptual and motor reorienting studies involve the detection of meaningless sensory stimuli or the execution of meaningless movements, and hence, they require very little semantic processing. Second, ‘definitely new’ recognition memory trials (Figure 1c) do not seem to involve additional semantic retrieval. Third, as illustrated in Figure 2a, there is evidence that VPC activations during sentence comprehension track discourse incoherence rather than semantic retrieval per se [63]. Finally, given that semantic processing generally enhances encoding [94], the semantic retrieval hypothesis cannot easily explain why VPC activity is associated with encoding failure rather than success.

### The working memory maintenance hypothesis

Within the episodic retrieval domain, VPC activations have been attributed to the maintenance of information within working memory (WM) [37]. This hypothesis can explain why VPC activity during episodic retrieval is greater for recollection-based and confident ‘old’ recognition trials, given that these trials involve greater information recovery and hence a greater WM load. Can the WM hypothesis account for VPC activations in other cognitive domains? In the motor reorienting domain, this hypothesis could account for neuropsychological evidence of apraxia in VPC patients, which could arise from deficits in manipulating information in WM [95]. The WM hypothesis could account for language and number processing findings by assuming that recovering semantic information (e.g., words > nonwords) increases WM load. However, semantic retrieval may also lead to chunking, which reduces WM load. Showing some advantage over the semantic retrieval hypothesis, the WM maintenance hypothesis could account for the role of VPC in addressing text incoherence (Figure 2b), which requires holding and comparing alternative interpretations within WM. For similar reasons, the WM maintenance hypothesis provides a good account for ToM findings, which require simultaneous consideration of alternative viewpoints.

However, the WM maintenance hypothesis has several weaknesses (see minuses in Table 1). First, perceptual and motor reorienting effects entail very little or no change in WM load. In the perceptual reorienting domain, it could be argued that invalid > valid and deviant > standard contrasts involve WM updating, but it is difficult to distinguish between WM updating and bottom-up attention, which is the focus of a different hypothesis. Second, high-confidence ‘new’ recognition responses are unlikely to involve much memory recovery and WM load. Third, when solving mathematical problems, mental calculation should load WM more, not less, than retrieving the answer from memory [71]. Finally, the WM maintenance hypothesis cannot easily explain encoding failure findings, unless

one argues that VPC activity reflects the maintenance of irrelevant information within WM.

#### *The multimodal integration hypothesis*

Episodic recollection is characterized by the recovery of multiple types of information, such as sensory, conceptual, and emotional aspects of the same event, and the role of the VPC has been attributed to the integration of these multimodal features. There are two versions of this multimodal integration hypothesis. According to the episodic buffer view [40], left AG activity reflects the maintenance of integrated multimodal information by the episodic buffer in Baddeley's WM model [96]. According to the cortical binding of relational activity (CoBRA) view [97], the left AG is a convergence zone that binds episodic features stored in disparate neocortical regions to promote consolidation of memories in neocortex. These two views have different assumptions and make different predictions, but we consider them here only in terms of their shared assumption regarding multimodal integration. In this regard, the main strength of both views is accounting for the involvement of VPC in episodic recollection, which – by definition – involves greater multimodal integration than familiarity. For the same reason, the multimodal integration hypothesis can explain very well why VPC activity increases with the amount of information recollected [40,98–100] and with confidence in 'old' responses (see Figure 1c). It can also be extended to account for the application of actions in tool use or to visuo-spatial targets.

Conversely, the multimodal integration hypothesis has difficulty accommodating phenomena that do not involve multimodal integration. First, within the episodic retrieval domain, this hypothesis cannot easily explain strong VPC activity for high-confidence 'new' responses, given that multimodal information recovery is minimal or null. One possible counterargument [97] is that rejecting nonstudied items involves remembering studied items. However, there is evidence that this 'recall-to-reject strategy' is unlikely during item recognition [101]. Second, perceptual and motor reorienting effects entail very little multimodal integration because most paradigms involve the same kind of information (e.g., spatial, finger movements). The same can be said about language and number processing findings. Third, although ToM stories require considering multiple points of view, these different viewpoints are all conceptual and do not necessarily involve different types of information. Finally, like the semantic retrieval and WM maintenance hypotheses, the multimodal integration hypothesis cannot explain why VPC activity is associated with encoding failure. The episodic buffer view predicts that maintaining integrated multimodal information in WM should be beneficial for encoding. According to CoBRA, the contribution of the VPC to binding of multimodal information occurs after encoding, and hence, the VPC is not expected to be associated with encoding success [97]. However, CoBRA cannot explain why VPC is associated with encoding failure.

#### *The bottom-up attention hypothesis*

According to Corbetta and Shulman's dual-attention model [102], a dorsal frontoparietal system that includes the DPC

mediates the selection of perceptual stimuli based on internal goals or expectations (endogenous, or goal-driven attention), whereas a ventral frontoparietal system that includes the VPC enables the detection of salient and behaviorally relevant stimuli in the environment, especially when they were previously unattended (exogenous, or stimulus-driven attention). This exogenous attention account of VPC explains very well evidence of VPC activations during perceptual and motor reorienting tasks but it cannot accommodate VPC activations during tasks without obvious environmental targets, including episodic retrieval, ToM, and language/number processing tasks.

However, this situation changes dramatically if one modifies this hypothesis so that it includes not only attention captured by environmental stimuli but also attention captured by internal (memory-based) information [12,39,47,103]. According to this bottom-up attention (BUA) hypothesis, VPC activity reflects the capture of bottom-up attention by information entering WM either from the senses or from long-term memory. A clear example of memory-triggered BUA is the startle response individuals may display when they suddenly remember that they forgot an important appointment. Most of the time, however, bottom-up capture of attention by incoming memories is more subtle and consists of a brief awareness that new episodic or semantic information entered WM. Unlike the exogenous attention hypothesis, the BUA hypothesis can accommodate not only the findings in the perceptual and motor reorienting domain, but all reviewed findings in the domains of episodic retrieval, language/number processing, and episodic encoding.

*Episodic retrieval.* The BUA hypothesis can explain VPC activations during episodic retrieval [12,39,47]. Given that recollected episodic details capture BUA, this hypothesis can easily explain why VPC activity is greater for recollection than for familiarity [40], increases with the amount of information recollected [40,98–100], and is stronger for high- than low-confidence 'old' responses [42–44]. Importantly, the BUA hypothesis is the only one of the four hypotheses considered that can explain why VPC activity is stronger for high- than low-confidence 'new' responses [43,44]. BUA is captured not only by rich memories, but also by salient retrieval cues, such as items that appear very novel in a recognition memory task. According to the BUA hypothesis, what drives VPC activity is the extent to which memories or retrieval cues capture attention, and in a recognition memory test both 'definitely old' and 'definitely new' items are the most salient relevant items. Thus, the BUA hypothesis provides a parsimonious account for the U-function in Figure 1c.

Although the current review is focused on functional neuroimaging evidence, it is worth noting that the BUA hypothesis can also explain subtle memory deficits in patients with VPC lesions. The BUA hypothesis predicts that VPC lesions should not impair memory per se but only the extent to which these memories capture BUA. Thus, VPC patients should have a deficit in spontaneously reporting memories (BUA), but they should be able to report them when guided by the memory task (top-down attention). This is exactly what the few studies available have shown. In one study, VPC patients spontaneously

reported fewer details in their autobiographical memories but they were able to provide the missing details when prompted by the experimenter [104]. Similarly, patients with VPC lesions subjectively rated their memories as impoverished but were able to recall source memory information when specifically questioned [105]. This is analogous to the neglect syndrome, which does not affect perception per se, but bottom-up attention to percepts. Accordingly, memory deficits in VPC patients may be described as memory neglect [12,47]. Simons and collaborators noted that VPC lesions reduce confidence in episodic memories and impair the subjective experience of recollection [106,107]. The BUA hypothesis can account for these effects and additionally explain many other findings outside the episodic retrieval domain.

*Language and number processing.* The BUA hypothesis can account for VPC activations during language and number processing in a way that is similar to that of episodic retrieval: when information from long-term memory enters WM, it captures BUA. For example, evidence of greater VPC activity for words than nonwords [49–51], for familiar than unfamiliar names of people [52,53], and for semantically related than unrelated words [54,55], is explained by the idea that retrieved semantic knowledge captures BUA. VPC activity is likely to be greater for semantic than nonsemantic tasks [56,57] if responses to the former are more immediate and hence effective in capturing BUA. The BUA hypothesis can also account for mental calculation findings: the VPC shows greater activity for problems with known than unknown answers [66–69] and for problems with exact than approximate answers [65,66], because a known, exact answer ‘pops’ into mind, capturing BUA. For the same reason, VPC activity is greater for retrieval than calculation strategies [71] and for trained than untrained problems [70].

Turning to sentences, the BUA hypothesis can explain greater VPC activity for sentences than random words [58–60], because access to the sentence meaning is likely to capture BUA more strongly. On the other hand, anomalous sentences activate VPC more than normal sentences [61–63], because BUA is captured by the violation of expectations (reorienting). The BUA hypothesis can also explain why this effect is reversed when the sentences are preceded by an unusual context explaining the anomalous sentence [63] (Figure 2b): in the unusual context, the normal sentence is the one that violates expectations and captures BUA more strongly. Alternatively, comprehending inconsistent sentences may require more attentional switches between the different units of the phrase.

*ToM.* As previously proposed by other authors [76,90,103], BUA could account for VPC activity during ToM tasks. Like anomalous sentences [61–63] and incoherent texts [63], false belief stories require processing information detected outside the main focus of attention. Consistent with the BUA account, ToM and perceptual reorienting tasks recruit overlapping VPC regions across different studies [90] and within participants [76]. Activations in neighboring regions [91] are also consistent with the BUA hypothesis because BUA is only one of several factors accounting for localization within parietal cortex. Other factors include the nature of the stimuli (e.g., verbal

vs. nonverbal, spatial vs. nonspatial) and the nature of the task. Hence, contrasts between dissimilar stimuli are likely to yield activations in different locations, even if the same process is involved.

*Encoding-retrieval flip.* The BUA hypothesis is the only one of the four hypotheses considered that can explain why VPC activity is associated with success during retrieval but with failure during encoding (Figure 3). During retrieval, successful performance requires disengaging attention from the retrieval cue and reorienting it towards a recovered memory. In typical encoding conditions, by contrast, items to be encoded are in the focus of attention and no reorienting of attention is required. In these conditions, attention reorienting usually reflects distraction by unrelated stimuli or thoughts, and hence, VPC activity tends to be associated with failure to encode target items. However, the BUA hypothesis predicts that if one measures subsequent memory for the items that captured BUA, then VPC activity should predict encoding success rather than failure [47].

### Summary

Among the hypotheses assessed, the BUA hypothesis appears to provide a more complete account of VPC activations across cognitive domains (Table 1). The semantic retrieval and WM buffer hypotheses provide generally good accounts of episodic retrieval, language/number processing, and ToM findings, but they cannot easily explain perceptual/motor reorienting and episodic encoding findings. The multimodal integration hypothesis appears limited mainly to recollection and high-confidence ‘old’ findings. In contrast, the BUA hypothesis can explain not only internal/conceptual findings in the domains of memory, language, and ToM, but also the external/perceptual finding in the perceptual/motor reorienting domain.

### Caveats about the BUA hypothesis

Although the BUA hypothesis provides an excellent account of VPC activations across cognitive domains (Table 1), it is important to consider several potential issues for this hypothesis.

First, a potential issue for any theory postulating a global VPC function is the fact that this region consists of several subregions with different cytoarchitectonic structure and connectivity (Box 2). This is not a problem for the BUA hypothesis, which acknowledges that the different VPC subregions mediate different domains. The BUA hypothesis does not propose that the domains mediated by different VPC subregions are identical; it only assumes that these different domains can be conceptualized as different aspects of BUA. They could mediate different BUA processes or the same BUA process applied to different types of input (e.g., mnemonic input from the medial temporal lobes or visual input from occipital cortex). Differences in cytoarchitectonic structure and connectivity among VPC subregions do not always imply sharp differences in cognitive operations. If this were the case, various ventral occipito-temporal subregions, which differ in both cytoarchitectonic structure and connectivity, could not be said to mediate different aspects of visual information processing, yet serve an overarching common visual function.

Second, a potential problem for the BUA hypothesis would be evidence of fMRI dissociations between anterior and posterior VPC subregions. As reviewed earlier, however, meta-analyses of fMRI data [10,90] do not show sharp dissociations between these subregions; they show overlap with differences around the edges. Overarching views such as the BUA hypothesis can easily account for differences around the edges. A recent fMRI study found a dissociation between anterior and posterior VPC regions for visual vs. memory search, respectively [11]. This finding could be accommodated by an overarching view, although it must be noted that in that particular study the paradigm focused on top-down rather than on bottom-up attention, and hence the results are not directly related to the BUA hypothesis.

Third, it has been argued that the AG and SMG mediate different functions because the AG is more likely than the SMG to show deactivations compared to the resting baseline and to form part of the default mode network [103]. We believe that knowing whether a region is activated or deactivated compared to the resting baseline would be informative about function only if one could specify the cognitive processes active during rest, but this is very difficult or impossible. If one assumes that rest involves retrieval from episodic memory, then the AG could be more involved in episodic retrieval than the SMG is. This idea is consistent with the results of meta-analyses [10], as well as with evidence that VPC activations extend more posteriorly for BUA to memory than for BUA to perception (Figure 4b). As noted earlier, this finding is not inconsistent with the BUA hypothesis, because the exact localization of BUA-related activations within VPC may reflect the informational input (e.g., medial temporal lobe vs. visual cortex).

Finally, one weakness of the BUA hypothesis is that direct evidence that VPC activations reflect BUA is strong for only some of the domains reviewed. At present, the link between VPC activity and BUA is very strong in the perceptual/motor reorienting domain [13] and moderately strong in the episodic retrieval domain [12,39]. In the other domains, the BUA hypothesis provides a convincing account of many reported VPC activations, but the hypothesis has not been tested directly. In the language and number processing domains, we have argued that, when information from long-term memory enters WM (e.g., word meanings, mathematical facts), it captures BUA. However, strong evidence would require directly manipulating BUA during language and mathematical tasks, which, to our knowledge, has not been done. Likewise, we proposed that the involvement of BUA in ToM reflects the reorientation of attention during false belief stores. Although this hypothesis is consistent with the overlap of ToM and perceptual reorienting activations across studies [90] and within participants [76] (see Figure 4d and 4e), direct evidence for the hypothesis is lacking. Similarly, although BUA can account for the encoding-retrieval flip by assuming that BUA is captured by irrelevant information during encoding but by recovered memories during retrieval, direct evidence for this hypothesis is not yet available.

In sum, whereas the main strength of the BUA hypothesis is that it can parsimoniously explain findings in many

different cognitive domains, the breadth of the hypothesis is also its main weakness. As noted by Walsh, who proposed an overarching theory of parietal cortex in terms of magnitude processing (which coincidentally is also called AtoM as our model in Box 3) [108], attentional theories are often too non-specific and malleable. We believe that these potential weaknesses can be mitigated by making the predictions that follow from it specific, as we have attempted in this review. Moreover, whatever weakness may remain is offset by the broad explanatory power of this hypothesis and its potential for integrating evidence from many cognitive domains.

### Concluding remarks

On a more general level, the BUA hypothesis emphasizes the role that attention plays across all domains. Although such domain-general roles are typically assigned to prefrontal cortex, the close relationship of regions of posterior parietal cortex with the prefrontal cortex suggests that they may share in such broadly applied functions. Closely linked to the prefrontal cortex, and lodged between the ventral perceptual stream and the dorsal action stream, the VPC is ideally situated to fulfill its function of capturing and sustaining activated representations in the service of thought, planning, and action. Specialization within the VPC does not reflect different functions, but rather the engagement of the same function, BUA, with respect to information from different domains whose input and output pathways are located, in a graded manner, in different regions of the VPC. For example, we noted that WM, which has been identified with functions of the prefrontal cortex, can itself be considered an outgrowth of the interaction of VPC-mediated attention with perceptual and long-term memory representations in different regions of the neocortex. It also seems reasonable to assume that a process such

### Box 4. Questions for future research

- Do cognitive deficits following VPC damage reflect the function of this region or the damage of white matter fibers passing through this region?
- In studying patients with lesions, the focus is usually on the most salient deficit. Would VPC lesions typically produce an ensemble of deficits associated with the functions identified in this article?
- Can transcranial magnetic stimulation (TMS) reproduce the variety of symptoms associated with VPC damage, as it has done in neglect motor reorienting?
- How do spatial and nonspatial aspects of VPC function relate to each other? Is it possible to manipulate the relative contribution of left and right VPC to Posner and oddball tasks by varying the nature of the stimuli (spatial vs. nonspatial, meaningful vs. meaningless)?
- If the VPC activations for tasks in different domains overlap, would these tasks interfere with each other when conducted concurrently? What determines which function would capture attention?
- How is multimodal integration in episodic memory [97] related to binding of features in perception [147]? Are the same VPC regions implicated?
- Is unintentional recovery of internally generated information associated with VPC activation as much as capture by external stimuli is?
- What is the time course of the interaction between VPC and the regions from which it receives input and towards which it directs output, such as the prefrontal cortex? Can these time courses predict the onset of conscious awareness?

as BUA would be applied to all domains, since cognitive flexibility demands a mechanism that allows unexpected, but relevant, information to capture attention. Without such a mechanism, once a goal-directed process is initiated, it could never be interrupted, no matter how important such unexpected information might be. As with all models, we expect that, as new evidence emerges, details of the model will change (Box 4). Nevertheless, we hope that its general principles will prove more resilient and continue to guide research on the role of attention in perception, cognition, and action. The fact that all these different processes recruit similar VPC regions cannot be coincidental. As pointed out by Cajal, ‘All natural arrangements, however capricious they may seem, have a function.’ ([109], cited in [108]).

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