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Perspective

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A tripartite view of the posterior cingulate cortex

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Abstract

The posterior cingulate cortex (PCC) is one of the least understood regions of the cerebral cortex. By contrast, the anterior cingulate cortex has been the subject of intensive investigation in humans and model animal systems, leading to detailed behavioural and computational theoretical accounts of its function. The time is right for similar progress to be made in the PCC given its unique anatomical and physiological properties and demonstrably important contributions to higher cognitive functions and brain diseases. Here, we describe recent progress in understanding the PCC, with a focus on convergent findings across species and techniques that lay a foundation for establishing a formal theoretical account of its functions. Based on this converging evidence, we propose that the broader PCC region contains three major subregions — the dorsal PCC, ventral PCC and retrosplenial cortex — that respectively support the integration of executive, mnemonic and spatial processing systems. This tripartite subregional view reconciles inconsistencies in prior unitary theories of PCC function and offers promising new avenues for progress.

Sections

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Introduction

The posterior cingulate cortex (PCC) is one of the most poorly understood regions of the cerebrum[1–3]. In general, the PCC has not received the consistent empirical and theoretical research attention given to other neocortical regions such as the anterior cingulate cortex (ACC)[4,5]. However, this comparative absence of knowledge has not arisen because the PCC lacks interesting properties or has failed to capture the interest of neuroscientists. Anatomically, the PCC is a large cortical expanse (with an unfolded size of approximately 18 cm^2 in humans[6]) and serves as a central connectivity hub for many large-scale brain networks[7]. Physiologically, it is a site of peak metabolic activity within the neocortex[8]. The PCC is also acknowledged as critically important in the development of neurodegenerative and psychiatric diseases[1] (Box 1) and appears to be especially implicated in the progression of Alzheimer disease[9–11]. Functionally, the PCC has been implicated in many domains, including memory, learning, navigation, decision-making, emotion, creativity and executive control[1]. Despite these myriad points of interest, focused efforts to study the PCC have been limited, leaving us with a poor understanding of the region and its unique role in health and disease.

Box 1

PCC and disease

The posterior cingulate cortex (PCC) has been implicated in a wide range of neurological and psychiatric disorders, as reviewed previously[1,6]. In brief, the PCC is a site of prominent, early hypometabolism in Alzheimer disease[9]. In autism spectrum disorders, its hypometabolism and abnormal functional connectivity have been related to social impairments[241–243]. The cingulum bundle, which is a major carrier of PCC (and other cingulate) fibres, displays reduced tract integrity in schizophrenia[244,245]. Finally, studies of major depressive disorder frequently implicate the PCC in particular, and the default mode network (of which the PCC is a part) more broadly, as being overactive and hyper-connected in the disordered state[246,247].

At present, most studies of PCC abnormality do not explicitly use the tripartite dorsal PCC (dPCC)–ventral PCC (vPCC)–retrosplenial cortex framework that we have described here. Indeed, areas of pathology often span two or three of these subregions. Nevertheless, there are some studies for which disease-related pathology in the PCC appears to be more confined to one subregion or another. For example, rumination in major depressive disorder is associated with enhanced activity in what we here term the dPCC relative to controls[248]. Deep brain stimulation of the subgenual cingulate for depression appears to decrease activity in an area corresponding to the vPCC[249]. While it is possible that these studies point to different roles for the dPCC versus the vPCC in the pathology and treatment of depression, it is difficult to make such judgments without direct comparisons across the three divisions within a study. Nevertheless, given the frequent identification of the PCC in studies of brain disease, consideration of its organization may prove useful in dissociating the cognitive impairments resulting from distinct subregional pathophysiology[132].

Multiple factors may account for the overall lack of focus on the PCC. First, it is noteworthy that a consensus on the basic anatomical definition and nomenclature for the PCC is lacking[12]. Second, there is currently no central theory as to its specific function that can serve as a focal point to motivate research or as the fulcrum of debates that drive questions, answers and scholarly progress; theory can drive new research into a brain area, as was the case, for example, with ACC and cognitive control[4,5,13–15]. Third, there is no single cognitive function for which the PCC is proposed to be the central and causal locus, yet such proposed functions can propel and organize new focus a brain area. Finally, there are unique empirical challenges that have restricted study of the PCC owing to its distinct anatomy and physiology. Most importantly, focal damage to the PCC is rare, meaning that the neuropsychological foundation of classic case studies that are common to many other brain structures[16] are limited for the PCC.

These challenges notwithstanding, there remains a sizable body of convergent empirical research on the PCC, which is ripe for integrative theorizing. The goal of the present Perspective is to synthesize such work and render a new framework for studying the PCC. In short, we will argue that past literature on the PCC can be reconciled with a tripartite approach (three subdivisions) to understanding its structure and functions. Although much work is needed to adjudicate on our proposed tripartite view, particularly regarding the retrosplenial cortex (RSC), we argue that this approach will aid in the development of new, testable theories of PCC function, reconciling prior discrepancies in the literature, and provides a foundation for progress in understanding this important brain structure.

PCC anatomy

PCC gross anatomy

The cingulate (derived from the Latin word for girdle) is the cortical tissue that surrounds and borders the full length of the corpus callosum on the medial surface of the brain[17]. Therefore, the cingulate cortex includes the callosal sulcus, cingulate gyrus and cingulate sulcus. In primates, the PCC is differentiable from and caudal to the ACC and the mid-cingulate cortex (MCC) and extends posteriorly around the splenium of the corpus callosum[6,17] (Fig. 1).

While lacking consistent and overt sulcal boundaries, the rostral border between the PCC and MCC is approximately demarcated by the medial aspect of the central sulcus, whereas its caudal border occurs at the convergence of the parahippocampal gyrus and parieto-occipital sulcus. As the PCC follows the curvature of the splenium, its dorsal borders are approximated by the marginal ramus of the cingulate sulcus, superiorly, and the arc of the splenial sulcus, posteriorly[6,12] (Fig. 1). The splenial sulcus also serves as a gross anatomical boundary with the related but distinct precuneus (area 7m; see below). Within the PCC gyrus, particularly in humans, several shallow or tertiary sulci have been noted[12,17]. A recent large-scale analysis of PCC sulcal morphology suggests that one of these tertiary sulci in particular, the infra-marginal sulcus, is a common morphological feature in humans and some non-human primates (NHPs)[12]. In addition, the infra-marginal sulcus may serve as a useful anatomical landmark in humans as it is observed to be both consistently posterior (by approximately 0.5–1 cm) to delineations of the PCC–MCC boundary[12,17,18] and often superior to the isthmus[19] of the corpus callosum (Fig. 1a).

PCC architecture

Although we use the term PCC, the posterior or caudal portion of the cingulate cortex has historically been associated with two differing nomenclatures. In some cases, the term PCC includes the posterior

cingulate gyrus (area 23), splenial sulcus (area 31; also termed the subparietal (or PCC) sulcus[20]) and the RSC (areas 29 and 30)[21–25]. In other cases, the term PCC excludes the RSC, which occupies the callosal sulcus in primates[6,17,26] (Box 2). However, using this narrower definition, there is no single term that then describes the entire caudal aspect of the cingulate region. Thus, in this Perspective, we will use PCC as a general term for this larger cingulate region, including areas 29, 30, 23 and 31 (ref.[6]). Importantly, the PCC is distinct from but functionally related to the precuneus[27], which is not cingulate cortex (although often these terms are used synonymously in the literature). Together, the PCC (as defined here) and the precuneus form the posterior medial cortex (PMC)[28]. In this Perspective, we anchor our focus specifically on the PCC but note the importance of also understanding the role of the precuneus within the PMC region[27,29–32].

Importantly, as emphasized below, there appear to be structural and functional differences between the dorsal and ventral aspects of areas 23 and 31 in the human brain[17,33–35]. Thus, based on convergent anatomical evidence from studies of cytoarchitecture and connectivity as well as function (discussed below), we propose that the primate PCC is best thought of as consisting of three key subregions (Fig. 1a,b): the RSC (areas 29 and 30), the ventral PCC (vPCC; the ventral and posterior portion of areas 23 and 31) and the dorsal PCC (dPCC; the dorsal and anterior portion of areas 23 and 31). Figure 1b shows equivalent regions in NHPs. The RSC resides chiefly within the callosal sulcus and its rostral to caudal extent aligns with the anterior boundary of the dPCC and the inferior boundary of the vPCC (Fig. 1 and Box 2). An approximate division of the posterior cingulate gyrus indicates that two-thirds of it comprises the dPCC and one-third the vPCC (with the dPCC–vPCC boundary being proximal to the start of the ventral branch of the splenial sulcus in humans; Fig. 1a). We emphasize that these subregional divisions have been proposed previously and are consistent with contemporary anatomical demarcation[33,34,36–38]. However, most studies investigating PCC function do not incorporate these formal distinctions or do so using alternative borders. Throughout this Perspective, when feasible, we will attempt to interpret prior results with these divisions in mind rather than the original designations of the authors.

Receptor architecture can also allow us to differentiate between the subregions of the PCC as well as to distinguish the PCC from the ACC (although it is not entirely clear how these divisions should be interpreted functionally). For example, the dPCC contains higher densities of $GABA_B$ receptors, muscarinic M_3 receptors, and serotoninergic $5\text{-}HT_{1A}$ receptors and a lower density of M_1 receptors compared to the vPCC[39]. In addition, the PCC has greater acetylcholine receptor binding densities than the ACC[39,40].

Finally, we note that obtaining detailed cytoarchitectural data is empirically challenging and results in few targeted studies for any brain region, of which the PCC is no exception. As contemporary methods of studying cortical cytoarchitecture progress, particularly in the human brain, it will be important to see how the demarcations employed here are supported or further refined. For example, efforts such as the Julich–Brain Atlas[41], which has yet to report on the PCC, will provide an important test of the tripartite framework outlined here by, for example, determining the cytoarchitectural demarcation of human RSC areas 29 and 30 (Box 2).

PCC connectivity

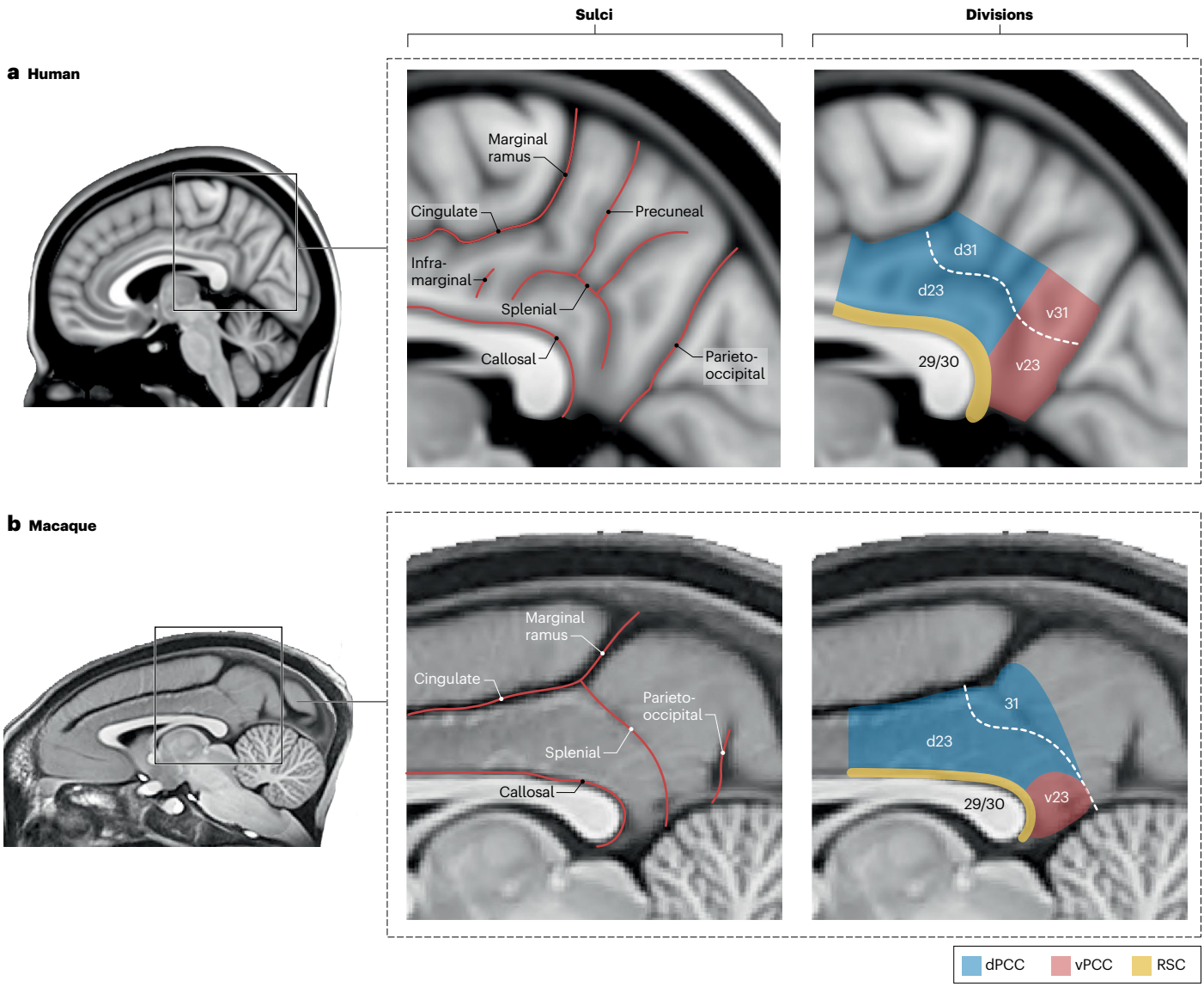
Broadly speaking, the PCC connects with regions involved in memory, emotion and executive control. However, tracer injection studies in NHPs have made it clear that the three subregions of the PCC have different connectivity profiles (although with substantial overlap). Regarding thalamic projections, the dPCC preferentially receives inputs from the posterolateral nucleus (associated with somatosensory information), the central nucleus (associated with basal ganglia feedback), the mediodorsal nucleus (which also connects heavily with the prefrontal cortex (PFC)), the ventral anterior nucleus (strongly associated with basal ganglia connectivity), the ventral lateral nucleus (associated with motor functions)[33], and the limbic-associated anterior dorsal, anterior ventral and anterior medial nuclei[28]. The vPCC preferentially receives input from the anterior medial nucleus (a limbic nucleus associated with memory) and the pulvinar and lateral dorsal nuclei (associated with memory)[33]. The RSC preferentially receives inputs from the anterior thalamic nuclei (strongly associated with limbic circuitry, including the hippocampus) and the medial pulvinar nucleus[33]. The majority of these PCC–thalamic projections are reciprocal[28,33].

Regarding cortical projections, the entire PCC connects with the dorsolateral PFC, ACC, lateral parietal lobe, temporal pole and entorhinal cortex[28,42]. However, there are also connections that differentiate these subregions, both quantitatively and qualitatively. Relative to the rest of the PCC, the vPCC receives fewer projections from the PFC and also receives more projections from the temporal cortex (not including the hippocampus) than does the dPCC. The RSC, relative to the vPCC and dPCC, receives more input from the hippocampus, parahippocampal cortex and dorsolateral PFC[26,43,44]. The RSC does not directly connect with the precuneus, whereas the vPCC and dPCC do so reciprocally[28]. Whether any parts of the PCC connect with cortical sensory areas is difficult to know given the inconsistent literature. Parvizi et al.[28] noted an absence of connections between the PCC and primary sensory areas. However, Morecraft et al.[45] reported connectivity between the PCC (mainly dPCC) and a variety of sensory areas, including the primary somatosensory cortex, area V3, medial superior temporal area and auditory association cortex.

Together, the connectivity of the PCC supports our tripartite view of the region. That is, the dPCC is more intimately coupled with frontal regions, whereas the vPCC is more intimately connected with both frontal and temporal lobe regions. By contrast, the RSC is particularly innervated by connections from the medial temporal lobe. While these data are derived from NHPs, tractography in the human brain also supports distinct dorsal and ventral pathway convergence within the PCC[46]. These connectivity profiles help to set a foundation for putative functional roles for these subregions, discussed below.

Comparative issues

As detailed above, the human and NHP PCC show a high level of anatomical homology (Fig. 1). The situation is more complex when considering a homologous PCC region in rodents. The traditional neuroanatomical view holds that there is no homologue of areas 23 or 31 in rodents[47] based on a specific cytoarchitectural feature of primate versus rodent PCC tissue. In primates, areas 23 and 31 can be differentiated from areas 29 and 30 by the number of layer IV stellate cells that they contain, which is higher in areas 23 and 31 (ref.[48]). Rodents do not possess an area with this larger number of layer IV stellate cells, and therefore may lack an equivalent of primate areas 23 and 31 (refs.[47,48]). However, rodents have a large retrosplenial region (areas 29 and 30) occupying much of the posterior medial surface[2,47]. Thus, within our tripartite division, rodents only possess the RSC and lack vPCC and dPCC homologues. However, PCC homologies have not received the attention that ACC homologies have (largely because ACC homologies are considered in the broader context of the PFC, which is the subject of extensive study), and thus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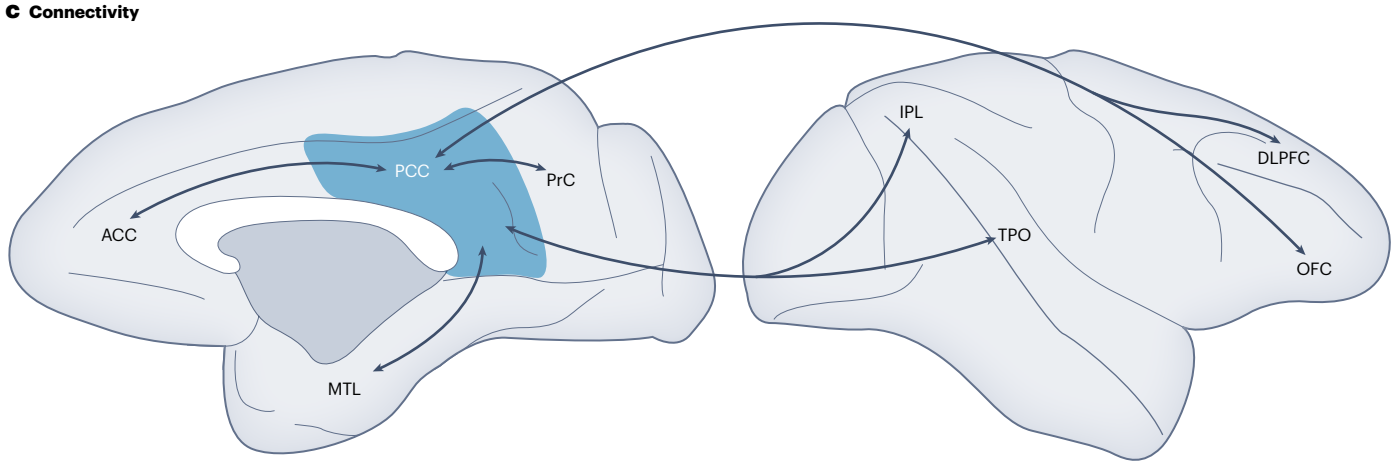
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Fig. 1 | Comparative anatomy of the PCC. a,**b**, Anatomy of the posterior cingulate cortex (PCC) is shown for the human (part **a**) and non-human primate (macaque; part **b**). Focusing on the posteromedial region of the brain, major sulci are shown for both species (red lines), along with the homologous cytoarchitectural regions. Based on data from refs.[27,181], the anatomical locations of the dorsal PCC (dPCC; d23/d31), ventral PCC (vPCC; v23/v31) and retrosplenial cortex (RSC; 29/30) are shown. The dashed white line indicates the cytoarchitectural division between area 23 and area 31. Note that area 31 occupies more restricted territory in the macaque than in the human, where it extends caudally and ventrally into the vPCC[239]. In addition, there is a small amount of ectocallosal cingulate cortex present in human area 26 (not shown) that does not occur in the macaque. **c**, Schematic of the shared reciprocal connectivity between both the dPCC and vPCC and other brain structures based on tract tracer studies in the macaque (part **b**; data from refs.[28,42–44]). ACC, anterior cingulate cortex; DLPFC, dorso-lateral prefrontal cortex; IPL, inferior parietal lobule; MTL, medial temporal lobe; OFC, orbito-frontal cortex; PrC, precuneus; TPO, temporal-parietal-occipital area.

remain largely unclear (see refs.[49–51]). It is for these reasons that we have focused this Perspective on the primate brain.

PCC function

In reviewing the functions of the PCC, we use PCC as a general regional term, as defined above, or when discussing data for which further anatomical precision is not possible. Otherwise, we employ the distinctions of dPCC, vPCC and RSC whenever appropriate. Importantly, we note that, unlike many other brain regions, the PCC lacks the canonical lesion studies that often serve to orient a field as to the putative core or unique function of an area[16]. The PCC is among the most densely vascularized regions of the brain[52,53] and receives a dual blood supply from the posterior and middle cerebral arteries, greatly reducing the rate of ischaemic stroke (for comparison, ischaemic stroke in the neighbouring precuneus accounts for less than 1% of cases[54]). In addition, the anatomical location of the PCC limits the occurrence of focal lesions and, when cases of insult do affect the PCC, they typically incorporate major pathways, like the cingulum bundle or corpus callosum[55], complicating functional interpretation. Therefore, we note a general paucity of causal studies of PCC function but do acknowledge key examples within the context of specific sections below. Finally, as discussed in Box 2, the demarcation of the RSC, particularly in humans, varies widely in the literature. Contemporary anatomical findings differ greatly from the common translations of Brodmann's maps[56], presenting a serious challenge when interpreting the literature. In light of this, and given several recent reviews[57–59], we provide only a limited discussion of RSC function.

Neuroimaging studies of the PCC

Early neuroimaging studies repeatedly observed that the PCC was one of several brain regions showing consistent reductions or 'deactivations' in haemodynamic measures of activity across a wide range of attention-demanding tasks[60]. Conversely, the PCC and the precuneus were routinely observed as regions of peak blood flow and metabolism during resting or non-task states[61]. Together, these findings established the PCC as a common node within a unique network of brain regions showing high basal levels of haemodynamic activity that is greatly reduced during many forms of cognitive effort — now commonly referred to as the default mode network (DMN)[61–63]. This peculiar 'task-negative' property of the PCC and precuneus led them to be referred to collectively as the 'medial mystery parietal area'[64]. As to what function this paradoxical suppression of activity during 'cognition' served, it was initially speculated that "the PCC and adjacent precuneus can be posited as a tonically active region of the brain that may continuously gather information about the world around, and possibly within, us"[61]. The PCC was viewed as a region supporting a type of surveillance of ongoing cognitive processes that is transiently suspended by tasks with high attentional demand[31]. A rapidly growing contemporary literature has further examined these links between ongoing spontaneous thought and the DMN[65–67].

Following this early work, the functional MRI (fMRI) literature has examined PCC function primarily as part of studying the DMN or the larger PMC region. However, although deactivation within the PCC during attention-demanding tasks has been widely replicated[68], a large literature now demonstrates that many task-evoked cognitive states reliably produce increased haemodynamic activity within the PCC, consistent with early positron emission tomography (PET) observations[69–72]. In particular, PCC haemodynamic activation occurs during tasks relying on episodic memory, spatial navigation, self-referential cognition or other types of higher-order, abstract thought related to contextual and semantic processing[73–75]. Indeed, the role of the PCC in episodic memory is characterized by its opposing directionality of responses at different stages of memory processing[76]: PCC activity is typically suppressed during episodic memory encoding and enhanced during episodic memory retrieval. During encoding, PCC deactivation is greater for items more likely to be subsequently remembered[77–79]. Likewise, PCC activity is more enhanced during successful episodic memory retrieval across a variety of stimulus types[80–84]. Building on early observations, PCC activation has generally been framed as occurring under conditions that require 'internal' or 'self-referential' focus, and PCC deactivation as occurring under conditions that require 'external' or 'non-self-referential' focus[85]. More specific theories have implicated PCC activation in spatial and environmental processing (such as scene construction[75,86]), abstract associative processing (such as contextual or semantic processing[74]) and, more recently, reinforcement learning[87]. It is important to again note that such accounts are often not specific to the PCC and its subregions but rather incorporate the PCC as a key node of the DMN or larger posterior medial or 'midline' regions. However, subsequent progress in brain network parcellation, together with targeted cognitive paradigms, have further detailed the network memberships and putative functions of the human PCC.

Brain networks and PCC subdivisions

Using patterns of correlated blood oxygen level-dependent (BOLD) fMRI activity during resting states together with network statistics, researchers have made great progress in identifying distinct large-scale networks in the human brain[88–91] that often recapitulate patterns of fMRI activity evoked during task performance[92,93] and are believed to reflect the putative network architecture of functional brain circuits[94,95]. While early network neuroscience studies incorporated the entire PCC within a larger PMC 'node' (Fig. 2a), more recent work has indicated a heterogeneous subregional organization[96]. When directly comparing whole-brain patterns of correlated resting-state activity between the vPCC and dPCC, a clear division emerges. The dPCC is regularly coupled with frontoparietal or executive control networks, whereas the vPCC

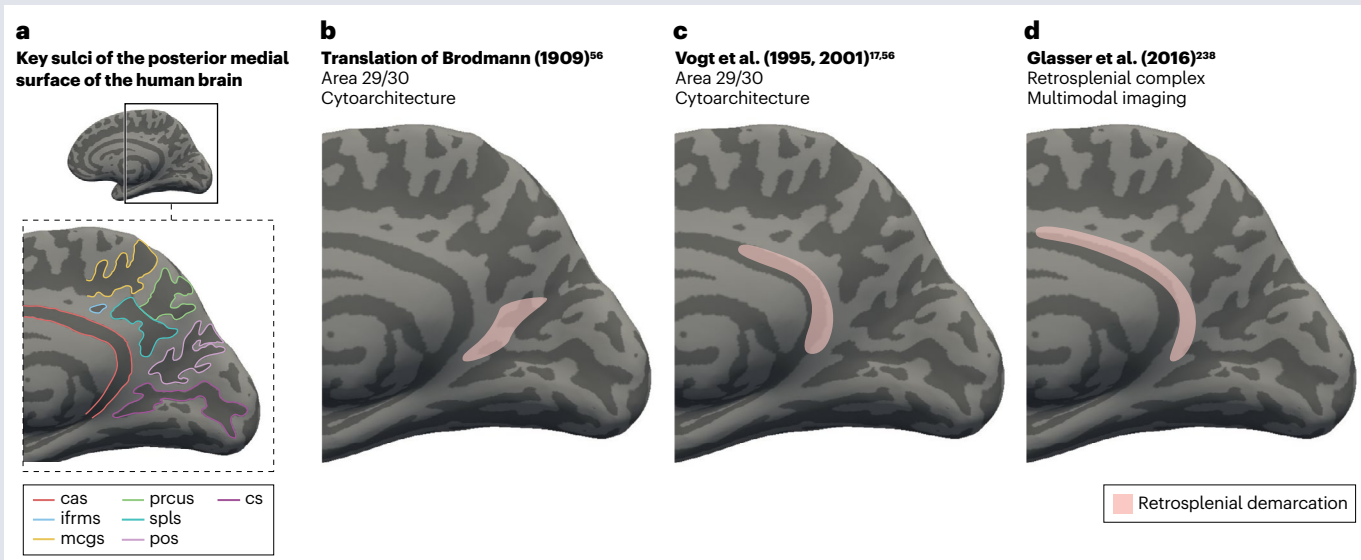
Box 2

Demarcation of the RSC

Historically, the retrosplenial cortex (RSC; areas 29 and 30) has been a neglected region of study[2] but, in recent years, it has become a key focus in the fields of learning, memory and navigation[57,59,250]. However, debate surrounds the appropriate demarcation of the RSC in relation to gross anatomy (see the figure, part **a**), particularly in the primate brain when comparing contemporary studies of cytoarchitecture with the earlier work of Brodmann (see the figure, part **b**).

A likely contributing factor to this confusion are the differences in the organization of the RSC in the rodent and primate. Unlike primates, rodents lack a posterior cingulate cortex (PCC; areas 23/31), with much of the posterior medial surface being composed of the RSC[2,47]. By contrast, in non-human primates, where the PCC is present, the RSC forms an arc around the splenium of the corpus callosum, being restricted to the callosal sulcus and typically not extending to the medial surface[26,35,38,239]. The human RSC shows a highly similar organization, with the possible exception of area 30, which may partially extend out of the callosal sulcus and onto the most ventral aspect of the medial surface (termed the isthmus) where the posterior cingulate gyrus transitions into the parahippocampal gyrus (see refs.[17,56,251,252] and see the figure parts **a** and **c**). In descriptive terms, the primate RSC is a thin region forming a 'C-shaped' arc around the splenium, primarily reflecting the anterior sulcal rim of the posterior cingulate gyrus. This 'perisplenial' anatomy contrasts with the commonly depicted maps of Brodmann, in which the RSC is restricted to a posteroventral region, comprising much of the medial gyral surface posteriorly between the callosal and postero-occipital sulci (see the figure, part **b**). However, it has long been noted that this demarcation is likely due to a misrepresentation of Brodmann's original findings[56,251]. While modern anatomical work shows subtle distinctions in the medial surface extent of area 30 (refs.[26,35,38]), no extant findings recapitulate common interpretations of the RSC derived from Brodmann. As presciently noted by Vogt et al.[56]: "... Brodmann's map understates the rostral extent of retrosplenial cortex, overstates its caudoventral extent, and abridges the caudomedial extent of area 23". We note that part **b** of the figure shows area 29/30 as previously translated from Brodmann's drawings[56] and as incorporated into a common neuroimaging cytoarchitecture atlas[253]. Therefore, we echo prior suggestions to utilize the convergent findings of modern anatomical studies in the human and non-human primate, noted above, over translations of Brodmann's maps for the RSC[56,251,254]. Ongoing work to develop improved probabilistic maps of human cytoarchitecture will provide important updates and corrections in this regard[41].

It is important to note that this anatomical demarcation of the primate RSC does not affect the consistency or veracity of functional studies. Rather, it represents progress in understanding the functional neuroanatomy of the posteromedial region and allows for better terminological and comparative consensus. Consequently, some but not all prior observations previously ascribed to the RSC in the primate may be better credited to the ventral PCC. Indeed, such a scenario has been documented in human studies of spatial scene processing, where consideration of anatomy has motived progress in determining that previously reported 'RSC' activations do not fall within areas 29 or 30 but rather within proximal regions of the ventral PCC and the parieto-occipital sulcus[141,142,255]. In a similar fashion, the underappreciated arcing rostral extent of the RSC is consistent with recent multi-modal cortical parcellations that show a perisplenial organization[238] (see the figure, part **d**). The figure shows schematic representations of three historic descriptions of the demarcation of the RSC. cas, callosal sulcus; cs, calcarine sulcus; ifrms, inframarginal sulcus; mcgs, marginal ramus cingulate sulcus; pos, parieto-occipital sulcus; prcus, precuneal sulcus; spls, splenial sulcus.



is more strongly connected to the DMN[97–99] (Fig. 2a). In addition, the vPCC (often reported as RSC) is routinely coupled with a memory or association network that includes the medial temporal lobe and inferior parietal lobule[91,100]. Using complementary approaches, large-scale meta-analyses of task-based coactivations have also reported that the dPCC, vPCC and RSC can be functionally dissociated[37,96,101]. Together, these data provide compelling links to the tripartite anatomical divisions of the PCC.

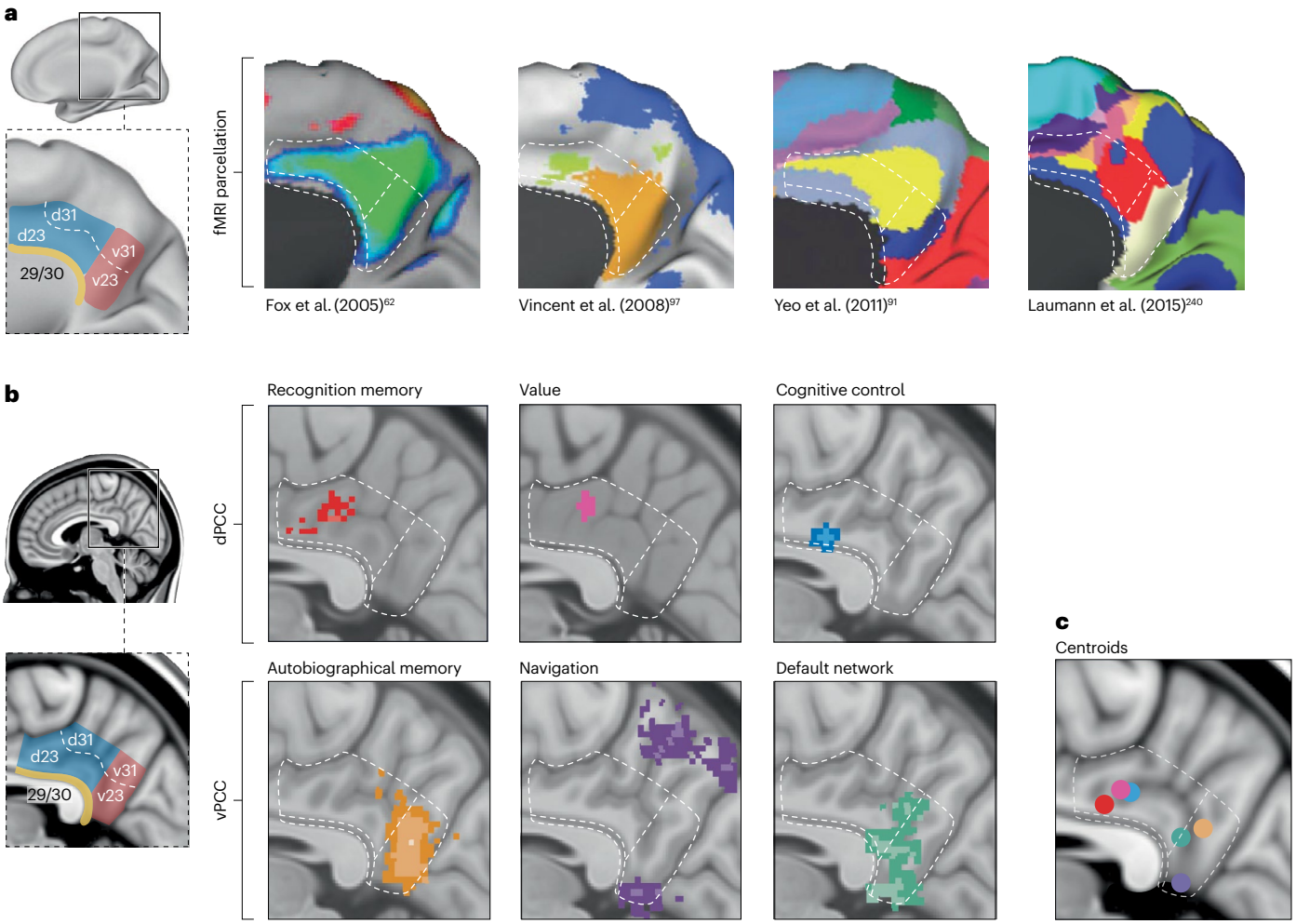


Fig. 2 | Functional neuroimaging of the PCC. a, Progress in network identification and parcellation of the posterior cingulate cortex (PCC). An inflated cortical surface is shown with approximate cytoarchitectural boundaries indicated (left panel). In 2005, the PCC was identified through functional imaging as part of a singular posterior medial cortex component of the default mode network (DMN). Green regions reflect a negative correlation (that is, deactivation) with brain regions that are activated during goal-directed attention[62]. Subsequent connectivity analysis conducted in 2008 dissociated the DMN (shown in orange) from a cognitive control-related network (shown in green) within the dorsal PCC (dPCC)[97] when focusing on these specific networks. In 2011, a large-sample group connectivity analysis that considered the entire brain further divided the PCC (here, blue/grey regions are part of the cognitive control network, yellow regions are part of the DMN and dark blue regions are part of a temporo-parietal memory network)[91]. Finally, more recent (2015) large sampling of an individual (same person scanned multiple times) revealed more fine grained parcellations within the PCC[240] (here, distinct colours reflect putatively distinct areas and shared colours reflect members of the same putative network). Approximate cytoarchitectural boundaries are overlaid (white dashed line). The areal parcellations based on functional MRI (fMRI) show some correspondence and divergence from these putative architectural boundaries, differing in terms of where and how the dorsal and ventral divisions occur and whether or not a retrosplenical cortex perisplenial parcel is identified. Multiple analytical factors will influence the number and location of functional parcel boundaries. **b**, The left panel shows an anatomical scan of the human brain, highlighting the posteromedial region. PCC cytoarchitecture is shown in the inset panel (see also Fig. 1). The right panels show the results of term-based meta-analyses of neuroimaging studies derived from the Neurosynth platform. The images show thresholded z-scores from Neurosynth's meta-analytic 'association test' for each term, with lighter colours representing higher values. Details of the method used to create these images are provided in the Supplementary Information. The terms 'recognition memory', 'value' and 'cognitive control' (top row) are associated with reports of activation within the dPCC. In contrast, meta-analytic term associations for 'autobiographical memory', 'navigation' and 'default network' (bottom row) are associated with reports of activation within the ventral PCC (vPCC). These images highlight the dissociation of PCC subregions across episodic memory tasks, related cognitive domains and brain networks discussed in this Perspective. **c**, Image shows the centroids of each meta-analysis association map in part **b**. Part **a**, second panel from the left, is adapted with permission from ref.[62]. Part **a**, third panel from the left, is adapted with permission from ref.[97]. Part **a**, fourth panel from the left, is adapted with permission from ref.[91]. Part **a**, right panel, is adapted with permission from ref.[240].

Since the first fMRI-based network analyses, an incredible amount of progress has been made in refining putative network boundaries and then utilizing these networks as a lens for exploring functional neuroanatomy[102]. Recently, researchers have been able to harness a combination of high-resolution functional imaging techniques (such as 7 T fMRI) with precision neuroimaging protocols (where the same individual is repeatedly scanned over many sessions at high spatial resolution) to estimate functional networks not from a group average but from individuals themselves[103,104]. Such approaches have recapitulated the main results from group parcellation maps and have found that the dPCC, vPCC and RSC are most often members of dissociable functional networks[105,106]. In addition, they have shown a degree of topographic variability, which promotes further use of such precision methods within the PCC. Thus, these more contemporary neuroimaging studies of putative functional brain networks, like the anatomical studies described above, support a tripartite division of the PCC. Importantly, we acknowledge that, as a haemodynamic-based measurement (that is, one sensitive to vascular organization), fMRI parcellations may not perfectly recapitulate cytoarchitectural boundaries. By considering these network divisions and specifically focusing on PCC activation profiles, the putative functions of PCC subregions start to emerge.

PCC subregions and episodic memory. Consistent with its anatomical connections with the medial temporal lobe, the PCC has been regularly implicated in episodic memory by neuroimaging studies[80,83,107,108], in which its activity increases with subjective memory strength and detail of retrieved stimuli. Such findings have motivated consideration of the PCC as a key node in a larger medial temporal lobe–neocortical memory system[30,108,109]. Within these extended memory system theories, the PCC is thought to be part of a memory retrieval or elaboration network that represents the context or gist associated with previous experience[109]. Indeed, in the limited number of case studies reporting on PCC damage, the reported deficits relate to 'retrosplenial' or 'topographic' amnesia, where spatial memory is particularly impaired[110–112], highlighting the association between the PCC and episodic and spatial memory behaviour[113]. However, the unique contribution of the PCC to episodic memory is still poorly understood. We believe that consideration of subregions may help delineate the functional roles of the PCC. For example, the locus of the encoding–retrieval response flip within the PCC, noted above, differs between PCC subregions depending on the mnemonic task conditions being contrasted (see ref.[114]). Thus, extant data already highlight unique subregional effects within the PCC during different kinds of memory retrieval behaviour.

To study episodic memory, researchers often use autobiographical recall tasks, wherein individuals freely recollect details of real-world experiences. While these tasks are ecologically valid, they are challenging to implement, and it is difficult to verify subjective reports. Therefore, researchers often prefer more controlled item-recognition tasks, wherein individuals are presented with lists of stimuli (such as images) and, after some delay (of varying durations), are asked which stimuli they recognize from the studied list (that is, whether a stimulus presented is old/studied or new/unstudied). Interestingly, these two types of retrieval tasks tend to produce strikingly different patterns of activity, which may be best explained by a subregional account of the PCC. While activity in the vPCC increases during autobiographical retrieval and recall, activity in the dPCC is related to performing item-recognition tasks[115,116] (Fig. 2b and Supplementary Information). This distinct pattern of PCC responses persists even when the same stimuli are employed to probe both tasks[117]. Given that the dPCC shows activation in response to item-recognition decisions[118] but often not to autobiographical recall[116], what role does it perform during item recognition? The dPCC has been implicated in tasks that involve balancing attention between internal/mnemonic and external/perceptual sources[119], and is responsive to the familiarity of a stimulus even outside of overt memory contexts[114,120]; it has also been implicated in long-term memory-guided attention[121]. This suggests that the dPCC serves as a bridge between mnemonic and control processes. Furthermore, it is interesting to note that, while visuo-spatially relevant mnemonic processes (such as recalling details about your favourite park growing up) are associated with vPCC activity, visuo-spatially relevant control processes (like using environmental cues to decide where to allocate attention) have been associated with dPCC activity[122,123].

What factors account for the task–region functional dissociation within the PCC? Closer examination of previous results reveals that levels of BOLD activity within the vPCC can be directly linked to effortful memory retrieval[76]. Additionally, the vPCC has been implicated as part of a semantic processing network[74,124,125] as well as in the representation of details about the self and others[126–128]. Further insight may be found by looking outside of the PCC and towards distributed neocortical regions implicated in mnemonic processing. The distinct activation patterns observed in the vPCC versus dPCC mirror the relative contributions of the two dissociable cortical–hippocampal memory systems that are proposed by the PMAT framework[109]. The PMAT framework specifies a network of brain regions with a posterior medial (PM) core, including the parahippocampal cortex, PCC, RSC and precuneus, that also extends to the ventral medial prefrontal cortex and angular gyrus. This PM network is involved in representing spatial and contextual memory features as well as egocentric information, and is crucial for autobiographical and episodic memory retrieval[129]. Conversely, the anterior temporal (AT) network, including the perirhinal cortex, amygdala, anterior ventral temporal and lateral orbitofrontal cortices, is involved in item recognition and associative memory and may be essential for assigning significance or value to stimuli. The response profile and intrinsic connectivity of the vPCC described above strongly implicates the region in the PM network, while the dPCC more aptly aligns with the AT network[130,131].

Alternatively, according to the 'integrative memory model' of recollection and familiarity, the dPCC is closely connected with frontoparietal control regions responsible for generating and evaluating familiarity signals, while the vPCC is more strongly linked to memory association and representational processes that underlie recollection. In this framework, the RSC is also considered an important connectivity hub but thought to have critical involvement in mnemonic reinstatement[132]. Finally, it has also been suggested that the differential functional response and connectivity profiles of the dPCC and vPCC may link the subregions to mnemonic concepts that have been proposed as primary axes of retrieval processes such as allocentric processing versus egocentric processing[133–136], the degree to which a memory has undergone consolidation[137,138], or the degree to which control is necessary for memory search or post-retrieval monitoring[116,139,140].

The dichotomies common to these theories raise the question of whether the activity observed in the dPCC during recognition tasks is best viewed strictly through a mnemonic lens[114] or whether there are alternative accounts that may help better isolate dPCC function and the dissociation with the vPCC. We return to this topic later, when we review compelling literature from the fields of decision-making and cognitive control that also routinely identifies dPCC activation, shedding light on the activity observed during mnemonic decisions.

PCC subregions and visuo-spatial processing. Given the clear implication of the PCC in episodic memory, it is not surprising that, like the medial temporal lobe, it has also been associated with visuo-spatial processing[134]. In particular, substantial literature across species has focused specifically on the role of the RSC in scene perception and navigational coding. Detailed discussion of this literature is beyond our current scope and this topic has been previously reviewed (see refs.[2,59,141]). However, it is noteworthy that this literature raises important issues regarding the anatomical and functional definitions of the RSC, particularly in the human brain[141,142] (Box 2).

Related to these observations is a growing literature which indicates distinctions between PCC subregions in their visual coding for places and people (both common attributes of episodic memory). For example, several recent fMRI studies have directly compared responses within the PMC region to place and face stimuli and reported that the vPCC, extending into the parieto-occipital sulcus (referred to as the medial place area), is selectively responsive to place stimuli. By contrast, a region of the dPCC centred around the splenial sulcus is selectively responsive to face stimuli[143–146]. When comparing perceptual versus mnemonic processing of place and face items, there is some evidence of overlapping regional responses to these conditions within the PCC[144]. However, there may also be a systematic anterior perception-to-memory shift in functional responses particularly to place stimulus conditions[147,148]. Further work is needed to understand these data as the PCC has historically not been routinely implicated in higher-order visual category selectivity[149,150]. Interestingly, putative place and face 'areas' of the PCC display particularly strong responses during perception of personally familiar stimuli when compared to unfamiliar stimuli[143,145], implicating a memory facet to these responses. It will be important to further understand the nature of these visual/semantic category responses and how they relate to the PCC memory retrieval processes detailed above.

PCC subregions in decision-making and cognitive control. While being routinely implicated in item-recognition memory, the dPCC is also consistently engaged in studies of decision-making (Fig. 2). However, the substantial human neuroimaging literature implicating the dPCC in decision-making has not been well integrated with the findings from memory studies. Early observations from neuroimaging showed that activity in the dPCC, together with other brain regions, was associated with gain (that is, a positive decision outcome)[151] and with the subjective value of economic decisions[152–154]. Unlike objective value, subjective value considers all factors that may influence valuation such as the delay in receiving a reward or the effort required (explaining, for example, the popular delay-discounting effect[152,155,156]). Activity in the dPCC, as well as its functional relationship with other regions, is sensitive to a number of contextual factors that influence subjective value such as the riskiness (the probability of a low-likelihood reward compared to a more likely option) of a stimulus leading to a reward[157] and how well the subjective value of a stimulus aligns with current task goals[158]. However, the subjective value of stimuli often correlates with other experimenter-controlled environmental factors such as the contextual predictability of receiving rewards. Indeed, many researchers have found that, rather than being involved in the processing of subjective values of individual stimuli, the dPCC is more likely involved in tracking environmental uncertainty or probability[159]. For example, activity in the dPCC has been found to correlate with decision-making variables such as context prediction errors (the mismatch between expectations and experienced events or outcomes)[160,161], uncertainty or riskiness of decisions[162–164], updating of values based on contextual information[165,166], and change points in context[167]. While the unique contributions of the dPCC to decision-making remain to be delineated, these findings suggest a role for the dPCC as a bridge linking local reward contingencies with broader contextual schemes, possibly relying on or operating upon memory retrieval processes.

Importantly, multiple meta-analyses have shown the striking consistency of dPCC engagement during decision-making[153,154,168], while responses within the vPCC and RSC are comparatively uncommon (however, see ref.[169]). More work will be needed to merge findings from the separate decision-making and memory literature[170] to better pinpoint the involvement of the dPCC. As detailed below, this executive role, specific to the dPCC, provides a compelling homology with NHP electrophysiology.

Electrophysiological studies of the PCC

Electrophysiology offers an important complement to neuroimaging studies. While human neuroimaging of the PCC has tended to focus on interrogating memory-related processes, electrophysiological work in NHPs has focused on decision-making and cognitive control[3,171–173] and, to some extent, on spatial encoding[174–176]. Thus, the two types of study have provided complementary information rather than direct cross-species replications (however, see ref.[177]). These apparent differences in research foci may suggest species differences in function as revealed by the two methods. However, we caution against this view; in fact, we believe that there is tentative evidence for functional homology across methods (and therefore species).

NHP single-unit studies. Early single-unit studies of the PCC in primates were motivated by the goal of understanding its relationship with the parietal cortex and, in particular, its role in spatial processing[173–176]. Because of the interest in the parietal cortex, these studies targeted the area with the strongest parietal connections (area CGp). As this region best approximates what we refer to as the dPCC (Fig. 3), we will herein use the term dPCC for this region. Recordings from the dPCC of the macaque have highlighted a host of coding attributes, including the capacity to encode spatial information, value, and other cognitive and mnemonic variables[3].

The studies that identified spatial coding in the PCC, broadly speaking, found evidence of coding of gaze direction and saccade target location; these responses did co-vary with reward size as do responses in many parietal regions. For example, neurons in the dPCC respond to targets that cue saccades and are active at the time of the saccades themselves[174–176]; these responses are modestly spatially selective, generally to contralateral cues and contraversive saccades. Some tentative evidence supports the hypothesis that spatial coding in the dPCC is allocentric[175], orienting objects in space relative to one another rather than relative to the self, which would make it hippocampal-like. More recent work in this domain has used novel paradigms, such as a moving platform, to probe the spatial repertoire of the dPCC and has shown stronger spatial selectivity in the dPCC than in the RSC[178]. These studies typically emphasize the importance of post-saccadic timing of dPCC responses[21], which suggests that the dPCC may be specifically selective for monitoring functions (that is, indicating important information in light of a recent action or decision)[171,179]. It is important to note that studies of the human dPCC have generally avoided these questions; therefore, these NHP studies provide a complementary source of information that broadens our understanding of the function of the dPCC and highlight key areas for comparative work in the

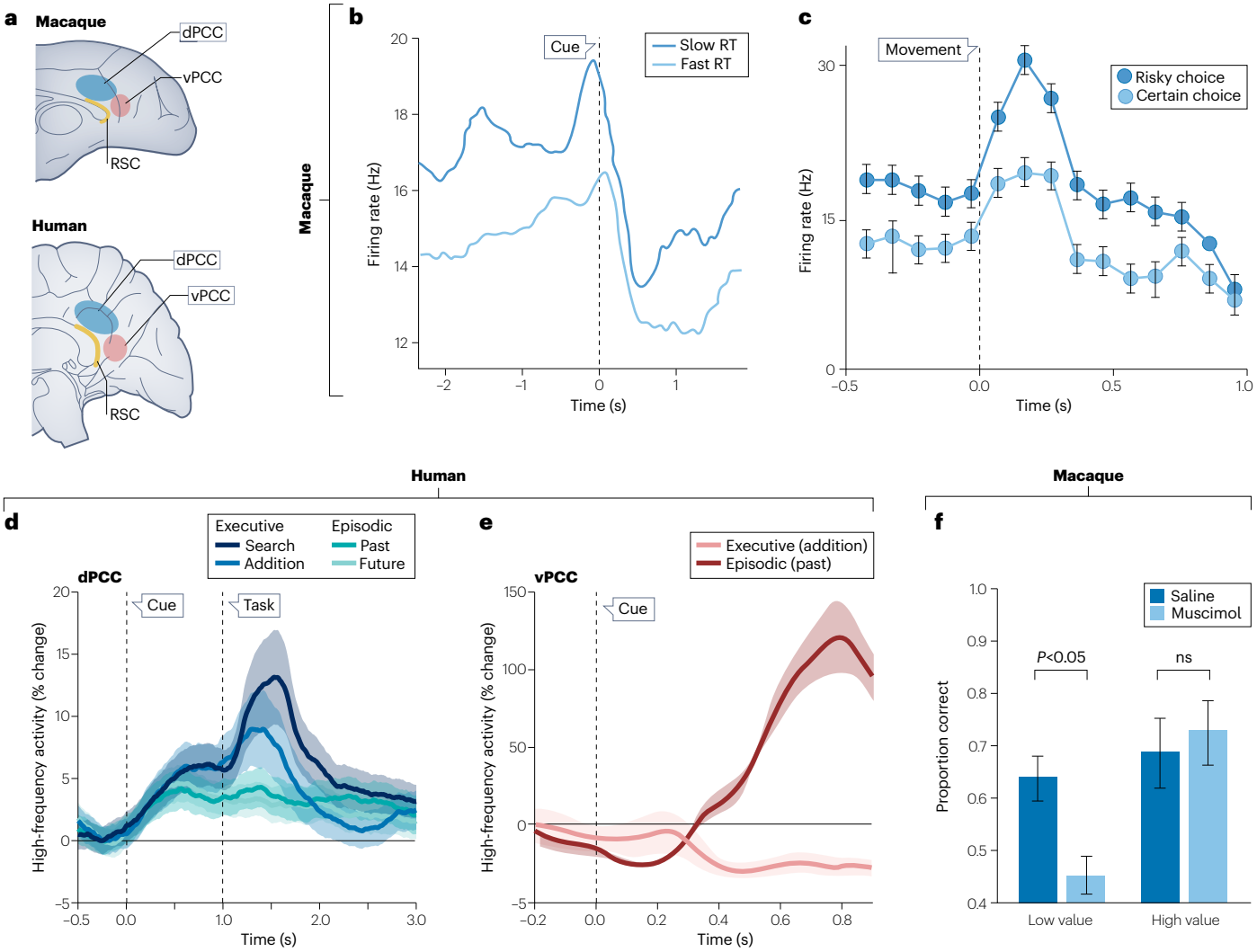


Fig. 3 | Electrophysiology of the PCC. a, Schematic of the proposed tripartite division of the posterior cingulate cortex (PCC) in the macaque and human, with sites of prior recordings indicated within boxes. **b**, Firing rates are suppressed in the macaque dorsal PCC (dPCC) during attentional task engagement[177]. In this figure, the average trial-aligned firing rates of a population of neurons in two macaques completing an attentional task (fixating on a visual target to detect a colour change) is shown; firing rate is systematically suppressed at the onset of attention (time 0 on the plot). Moreover, tonic firing rate is lower in task states that are associated with faster reaction times (RT), presumably reflecting greater task engagement[177,186]. **c**, Firing rates are enhanced after a saccadic decision in macaque dPCC. Firing rate increases are greater for more risky decisions[183]. **d**, Within human dPCC, high-frequency activity (amplitude in the 70–150 Hz range) is increased during the execution of executive tasks such as visual search (identifying a target rotated letter or number in an array of the same letter or number) and addition (adding five single-digit numbers). This increase is far greater than that observed during episodic tasks relating to past or future event scenarios[215]. **e**, By contrast, within ventral PCC (vPCC), high-frequency activity is suppressed during an executive task (addition) but is greatly increased during an episodic task in which individuals recalled past event scenarios[205,210]. **f**, Muscimol injections (which strongly inhibit local neural activity) to the dPCC in the macaque cause a reduction in the performance of a visually cued associative item learning task for low-value (small juice reward) but not high-value (large juice reward) decisions[191] (proportion correct reflects the number of correctly selected target items via saccade to one of two locations, based on a learned visual cue). ns, nonsignificant; RSC, retrosplenial cortex. Part **b** is adapted from ref.[186]. Part **c** is adapted from ref.[183]. Part **d** is adapted from ref.[215]. Part **e** is adapted from ref.[210]. Part **f** is adapted from ref.[191].

future. One intriguing point of potential homology in this domain is the cingulate sulcus visual area within the dPCC, which is associated with spatial and visuo-motor processing in both humans and NHPs[180].

Showing closer links to the human findings detailed above, the NHP dPCC also plays a prominent role in decision-making, valuation and choice, a functionality it also shares with the parietal cortex[181,182]. Studies of value coding in the NHP dPCC have shown that dPCC neurons encode the values associated with completed saccades[171,173,179] and that their firing rates track the variance of risky offers (which varies with their subjective but not with their objective expected values[183]; Fig. 3). These findings are consistent with the idea that the dPCC is part of a set of regions whose activity varies with subjective value[168], often termed the

subjective value network[170], which may relate to its connections with the orbitofrontal cortex (among other reward structures)[184]. However, a subsequent study that carefully dissociated value (the preference for certain choices) from salience (the absolute difference between a choice outcome and baseline outcome) found that salience provided a better explanation for dPCC firing[172]. This may help to explain why this region only appears in certain human neuroimaging studies of subjective value, far fewer than do regions such as the ventral striatum and ventromedial PFC. As above, all of these studies targeted single-unit activity within the dPCC.

In one example of specific homology between NHPs and humans, neurons in the NHP dPCC show tonic deactivation as might be expected given the role of this area in the DMN[173]. For example, in a simple delayed saccade task (with or without a working memory component), tonic firing rate activity is reduced during the task period relative to the delay between trials[177] (Fig. 3). Indeed, during the more demanding active maintenance of information in working memory, the firing rate in the dPCC is further reduced[177]. These findings are reminiscent of the idea that dPCC activity reflects processes antagonistic to successful task performance as noted above[185]. In an environment with multiple interleaved tasks, dPCC activity is reduced following task switches[186], which are presumably more cognitively demanding trials; consistent with this idea, activity systematically increases with time (number of trials) since a task switch. Likewise, dPCC firing rates predict switch or change decisions in a bandit task (where a decision between exploiting a current and known option versus exploring other options must be made) and in a foraging task (where a decision is made between exploiting a current and depleting reward source versus spending time exploring in order to find a new reward source)[187,188]. As other studies have shown, inter-trial activity is not redundant – instead, it likely reflects a record of the outcome of the past trial and predicts (and even causes) upcoming adjustments in behaviour[171]. These results are of particular interest as they relate to a growing human neuroimaging literature indicating the PCC and precuneus as two of several cortical regions with long windows of temporal integration[189,190]. Thus, activity within the PCC at any given moment is influenced by a prior history of neural events that extends much further back in time than that observed in sensory cortices.

Beyond these findings, there is a paucity of work focused on learning and memory within the NHP PCC. However, one study has directly examined the neuronal correlates of memory formation within this region[191], and therefore provides a crucial bridge between the larger memory-focused human neuroimaging literature and NHP physiology. This particular study, which was inspired by conditional visuomotor learning tasks[192,193], found that dPCC neurons signal performance errors and that their activity is greatest around the time that the error occurs. While this result appears to be consistent with the idea that dPCC activity is inimical to learning, findings in which localized muscimol inactivation was used argue otherwise; paradoxically, inactivation of the dPCC reduced learning[191] (Fig. 3). These results suggest that dPCC activation is seen at the time that an error occurs in cognitively demanding situations because it is a consequence of processes implemented to reduce control errors. A role for this region in learning is also suggested by Pearson et al.[187] who reported enhanced tonic dPCC activity during explore trials (associated with greater learning), compared to exploit trials, in an explore–exploit task.

Just as they can be compared to findings of human neuroimaging studies of the dPCC, these electrophysiological findings in the PCC can be contextualized by comparing them with responses of neurons in the NHP dorsal ACC (dACC). Relative to the dPCC, neurons in the dACC tend to have much more task-related activity and much stronger task-evoked responses. For example, post-trial reward-encoding responses tend to last several seconds in the dPCC[171] and a few hundred milliseconds in the dACC[194]. Indeed, neurons in the dACC tend to respond to reward and then return to a pre-trial baseline within a few hundred milliseconds, whereas neurons in the dPCC remain modulated for several seconds, often lasting several trials. Neurons in the dACC appear to encode both the values of offers and their salience, whereas dPCC responses appear to be dominated by salience signals[4,172,195]. Both regions carry modest spatial information, although the selectivity appears to be sharper in the dACC than in the dPCC[186,196]. Both regions also display spiking modulation during arousal events that elicit activity in the locus coeruleus and drive pupil dilation[197]. Together, these results illustrate that there are clear differences between the areas but just as many (if not more) similarities, and raise the possibility of a broad trans-cingulate functional repertoire involving monitoring and adjustment functions.

Human electrophysiological studies. Non-invasive methodologies that are common in human neuroscience (such as electroencephalography and magnetoencephalography) are limited in their capacity to reliably isolate PCC-specific electrophysiological signals given the deep medial location of this region and its proximity to key sensorimotor regions[198]. Therefore, invasive recordings from the human brain, while rare, provide a critical opportunity to directly capture PCC electrophysiology. Such recordings are performed in patients with pharmaco-resistant epilepsy who are undergoing invasive monitoring for potential neurosurgical treatment[199]. This clinically motivated invasive monitoring involves the surgical insertion of subdural electrode arrays on the cortical surface (electrocorticography) and/or penetrating depth electrodes (stereo-encephalography) targeting deep cortical and subcortical structures.

Motivated primarily by observations from human neuroimaging, electrophysiological investigation of the human PCC has focused on its role as a member of the DMN[198]. Common to these studies (and others in the field) is a focus on changes in high-frequency activity (70–200 Hz) as a robust signature of local population spiking and associated synaptic events[200–204], which closely correlates with BOLD fMRI activity patterns[205]. Consistent with human neuroimaging, intracranial recordings from the human PCC have shown event-related suppression or deactivation of high-frequency activity during externally directed tasks such as target detection[206], visual search[207,208], mental calculation[209,210] and sustained attention[211] (Fig. 3). Also consistent with neuroimaging and NHP single-unit findings, greater high-frequency deactivation within the PCC correlates with improved task performance[208,210,211]. Such data provide an electrophysiological basis for the neuroimaging findings and reveal important temporal information. For example, event-related suppression of the PCC occurs relatively late (>300 ms) after event-related suppression in other nodes of the DMN (such as the lateral temporal cortex) but before others (such as the medial PFC[208]). In addition, high-frequency activity in the PCC displays deactivation after the engagement of the dorsal attention network (which includes the dorsolateral frontal and parietal cortices and typically occurs ~200 ms after trial onset[211,212]) as might be expected from a hub of the DMN. Task-related suppression of activity within the PCC is currently the only common electrophysiological finding between human and NHP studies.

Similar to the neuroimaging findings, while externally directed tasks induce PCC deactivation, a variety of internally directed cognitive

Glossary

Brodmann's maps
Maps of distinct cytoarchitectural areas in the human cerebral cortex created by Korbinian Brodmann in 1909.

Connectivity hub
A node within a network that is connected to many other nodes.

Episodic memory
Conscious memory for prior lived experiences and events in the recent and remote past.

Executive control
Higher level cognitive functions allowing and supporting the control of other cognitive processes.

Familiarity
Memory recognition that lacks conscious details of past items or events.

Recollection
Memory retrieval involving conscious details of past events.

Reinstatement
The reoccurrence of brain activity patterns associated with a prior stimulus or behaviour.

Resting-state activity
Spontaneous physiological brain activity during the absence of explicitly instructed task requirements.

Saccade
Rapid and short movements of the eyes to a new point of visual focus.

Self-referential cognition
Cognitive processes focused on consideration of or in relation to oneself.

Temporal receptive window
The length of time before a neural response during which sensory information may affect that response.

tasks result in increased high-frequency activity within the PCC, including shifts into resting non-task states and autobiographical memory retrieval[205,209,210,213] (Fig. 3). The latter responses typically have late onset (>300 ms) relative to task cues but are closely aligned with those of other DMN regions associated with memory retrieval[205]. In addition, high-frequency responses to autobiographical memory within the PCC are greater than those observed for similar semantic or personal judgements[205,213]. High-frequency increases in activity during autobiographical memory retrieval are larger, more reliable and shorter in onset latency within the vPCC than in the rest of the PCC when considering individual anatomy, consistent with neuroimaging findings[209,210]. However, high-frequency responses during autobiographical memory search can be observed throughout the PCC. Increased high-frequency activity within the dPCC is also observed for successful word-list free recall[214]. To date, there has been no systematic human intracranial PCC investigation specific to mnemonic decisions or decision-making in general. However, of note, non-mnemonic responses to more executive task conditions, such as task-switches or numerical processing, do produce increased high-frequency activity within the dPCC[213]. Most recently, this dissociation was directly examined via human intracranial recordings showing a clear selectivity for executive tasks (visual search and number addition) within dPCC recordings in contrast to vPCC recordings[215] (Fig. 3). These results were also supported at the single-unit level in the same study, where the majority of dPCC cells showed firing selectivity to only specific executive task conditions. These findings provide further functional evidence linking the dPCC to executive cognitive control brain networks[215].

Intracranial recordings have also shed light on lower-frequency oscillations within the PCC, which have a number of proposed roles in coordinating neural activity. For example, during rest, the intrinsic oscillatory activity of the PCC peaks in the theta band range (4–7 Hz), which is distinct from the oscillatory activity in neighbouring brain regions such as the occipital alpha rhythm (8–10 Hz)[216]. In addition, the phase of PCC theta oscillations exhibits cross-frequency coupling with high-frequency amplitude[216]. This intrinsic oscillatory activity is similar to that of the hippocampus and, potentially, the DMN more generally[217]. Indeed, theta synchronization between the vPCC and the medial temporal lobe cortex occurs prior to high-frequency activation within the vPCC during autobiographical memory retrieval[218] and item recall[214]. Such findings add further support to the hypothesis that the vPCC is intimately involved with the memory retrieval functions of the medial temporal lobe[30]. Additional support for this view comes from electrophysiological studies of resting state connectivity, focusing on slow (<1 Hz) fluctuations of high-frequency activity[219]: recordings within the PCC show close temporal coordination with distant recording sites specifically within DMN regions during resting non-task states[205,217,220].

Overall, these studies corroborate human fMRI findings suggesting a role for the PCC in episodic memory retrieval and recapitulate common physiological features of the DMN[198]. While suboptimal for spatially mapping neural responses, intracranial findings suggest a more complex functional organization across the PCC[213], which requires further examination. However, far less electrophysiological evidence of human PCC engagement during tasks of decision-making and cognitive control have been observed. This focus contrasts not only with the neuroimaging literature reviewed above but, importantly, with many of the extant findings from the NHP PCC. This raises a potentially challenging divergence of PCC electrophysiology between species. What factors may account for such differences? Primarily, it is noteworthy that far fewer human intracranial studies have focused specifically on economic decision-making paradigms, whereas NHP studies have not been able to disentangle memory effects – suggesting an absence of required experiments rather than findings. Secondly, NHP studies have chiefly focused on single-unit activity, while only one such study has been reported in the human PCC[215]. However, as noted above, within the context of task-induced PCC suppression, when comparable tasks and measurements (such as local field potential spectra) are considered, there is a striking similarity between NHP and human electrophysiology[177,198,205,210,215]. A third factor may lie in the subregional organization of the PCC. As noted above, work in the NHP has exclusively focused on the dPCC (sometimes referred to as area CGp), while human studies (where electrode targeting is clinically determined) has been more anatomically varied. Future studies would therefore greatly benefit from systematic electrophysiological investigation of non-mnemonic coding within the human dPCC via both standard recording methods and single-unit studies[215].

Invasive recordings in humans also allow for direct electrical stimulation of cortical tissue to probe the causal role of specific regions[199]. When considering studies reporting on large cohorts of clinical stimulations within the PCC, findings range from no reported subjective experiences or observed behavioural effects[221] to heterogeneous clinical symptoms, including somatosensory and motor responses as well as complex subjective experiences such as derealization (such as an 'out of body' experience)[222]. Given the proximity of the PCC to both primary motor (dorsal) and visual areas (ventral), it is likely that some reports of sensory motor effects reflect stimulation spread at the boundaries

of these brain areas[221,223]. However, smaller-sample case studies have also suggested that PCC stimulation disrupts conscious awareness. For example, stimulation of white matter fibres proximal to the dPCC, after resection of the region, can lead to altered consciousness and dissociation, reflected by a loss of task performance and subjective report[224,225]. These data have been interpreted as supporting a role for the PCC in regulating conscious awareness and its apparent importance for self-referential cognition. However, confounding clinical factors challenge this interpretation[226]. More recently, both focal stimulation and endogenous seizure events within the PCC, specifically area 31, produced subjective reports of altered states of self[227]. During seizure events beginning within the PCC, one individual remained conscious but experienced a dissociated sense of self along with altered egocentric spatial awareness. Similar subjective effects occurred when electrical stimulation was performed[227].

While these stimulation studies provide intriguing causal insight, again linking the PCC (and DMN) to self-referential processing, small sample sizes, limited controls and clinical factors must be considered when interpreting such findings. For example, focal epilepsy commonly produces localized seizure events that cause a transient loss of awareness and non-responsiveness. In addition, systematic quantification of specific behavioural deficits is also critical for inferring causal impact. While conducting such experiments is challenging, stimulation of the PCC during word-list encoding has been related to worse subsequent word recall. This stimulation also results in increased power of hippocampal gamma oscillations, the magnitude of which predicted reduced recall performance[228]. These data causally implicate the PCC in memory encoding via an improved approach to studying PCC stimulation while still requiring further replication[229]. Overall, there remains a dearth of well-controlled causal studies of human PCC function. Future studies are needed to examine behaviour modulation during task execution, with sufficient controls and sample sizes, particularly during mnemonic and decision-making paradigms across PCC subregions.

Conclusions and future directions

As reviewed above, anatomical and physiological data support the view of the PCC comprising at least three functional divisions. This tripartite parcellation provides clearer links between observations made across species and techniques and, in some cases, reconciles prior conflicting findings. In brief, the dPCC appears to be much more associated with executive and decision features across both mnemonic and non-mnemonic tasks. In contrast, the vPCC is more strongly associated with primarily mnemonic processes and environmental and contextual features. While the RSC has been associated with both spatial memory and navigation, its anatomical definition varies greatly in the literature (Box 2). Moreover, it seems likely that the focus on mnemonic versus decision-making functions in the human versus NHP literature is a 'spotlight effect' (that is, publications demonstrating a link between an anatomical region and a specific function beget more similar investigations) and reflects the relative concentration of NHP studies on the dPCC. Moving forward, it will therefore be critical that investigators account for PCC subregional organization. This is particularly important for better understanding the potentially distinct functions of the RSC, whose complex anatomy in the primate requires careful consideration.

While we have focused on the unique functions of PCC subregions, what can be said for their collective functional role? Do the three divisions have any common features? One possibility is that the PCC, as a whole, collectively serves the integration of internal information (non-sensory or post-sensory), which would naturally include mnemonic information (primarily vPCC) and uses that to influence ongoing learning and decisions (primarily dPCC). We can understand the PCC by analogy to the lateral parietal cortex (LPC), which supports the integration of sensory evidence towards action; the PCC similarly supports the integration of internal and mnemonic evidence (defined broadly) towards future actions and strategies (that is, mnemonic decisions). Given this distinction, it is not surprising that, while sensory data (and systems) operate on much more rapid time scales (present, very recent past/future), mnemonic data and the PCC operate on much longer time scales (present, remote past and distant future). This view accounts for much of the extant functional data and also links to emerging evidence about the nature of associative cortices in general, and the PCC in particular, suggesting that these regions have a long 'temporal receptive window' and integration timescale and are functionally and anatomically 'distant' from sensory processing within the cortical hierarchy[189,230–232].

Several important tests of our tripartite view remain to be confirmed, defining key avenues for future work. While the tripartite organization we highlight is directly motivated by extant anatomical data, such studies are challenging and few in number. Advances in mapping human cytoarchitecture will be important for refining the borders of the dPCC, vPCC and RSC[41]. Relatedly, advances in precision neuroimaging and connectivity will also be important to assess the degree to which functional neuroanatomy confirms, consolidates or further divides these subregions.

This progress recapitulates a strikingly similar discourse regarding the organization of the human LPC and the relationship between memory and attention[233–236], in which debate surrounded the degree of functional overlap between executive attentional processes and specific mnemonic processes within the LPC[234]. This debate motivated several efforts focused on establishing the functional neuroanatomy of the human LPC[236], which included careful consideration for how distinct memory processes may be dissociated across the LPC[114,233,237], adding to further parallels with the medial parietal cortex. We hope that a similar discourse will occur for the PCC. Specifically, targeted examination of the dPCC within the context of decision-making, as it relates to memory behaviour, is of great importance. Perhaps more important is focused study of the RSC through its full rostro-caudal extent. As recently remarked, the subtle morphology of the RSC may require specific adjustments to common methods of group analysis in neuroimaging[238]. We note that the RSC, as defined here, can be inadvertently excised from cortical surface reconstructions in neuroimaging data processing pipelines, which generally seek to exclude the corpus callosum and favour visualization of the lateral convexity (for example, cortical flat maps). These future efforts will help to further establish principles of functional organization within the PCC, which may differ greatly from those common to sensory cortices. Causal studies of function and connectivity in humans and NHPs, with comparable behavioural assays, will also provide much-needed data.

As noted in our introductory remarks, our understanding of the PCC is in stark contrast to that of the ACC. Therefore, it is hoped that, as was the case for the ACC, empirical progress will spur more formal computational theories of PCC function. Promising starting points would be the adaptation of existing models of memory and decision-making processes. Finally, consideration of PCC subregions within the context of disease progression is already under way[132] and will serve to test and update the tripartite view. As progress is made in understanding the,

to date elusive, functions of the PCC, important insights are likely to be made on the neural basis of higher-order cognitive functions that are particularly specialized in the primate and, in turn, may help to lessen the health impact of its aberrancy in disease.

Data availability

The Neurosynth data for the term-based meta-analyses shown in Fig. 2 are available at https://neurosynth.org/analyses/terms/.

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