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The posterior parietal cortex and non-spatial cognition

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Abstract

The primate posterior parietal cortex (PPC) processes information related to environmental physical space. The human PPC has apparently expanded not only in size but also in its functional range to encompass certain abstract and higher-order conceptual spaces. In this report, we review various forms of non-spatial representation in the PPC. These forms are presented roughly in order of the level of abstraction of the 'objects' and pseudo-spatial relations represented. Also, we consider mechanisms that could have enabled the hominid PPC to establish such representations. Lastly, we offer a general principle to unify the newer forms of representation with the original functions of the PPC.

Introduction and context

When asked to give an account of his creative process, Albert Einstein reported that language played virtually no role in his thought process. 'The psychical entities which seem to serve as elements in thought ... are, in my case, of visual and some of muscular type' [1]. *When Einstein's brain was examined postmortem, it was noted that among other irregularities, the inferior parietal lobe was significantly larger than normal* [2].

The posterior parietal cortex (PPC) plays a central role in multisensory integration [3] and environmental-spatial cognition [4]. Many recent human imaging (and also some monkey neurophysiology) studies demonstrate that the PPC additionally supports various forms of high-order non-spatial cognition that are not necessarily directly related to physical space itself. For example, while the superior parietal lobule (SPL) tends to process spatial information in a conventional way, the inferior parietal lobule (IPL) is often credited with non-spatial cognition. Debate exists on the comparative anatomy of the primate PPC (Figure 1). The IPL is said to be evolutionarily new and uniquely expanded in humans and the monkey PPC is said to correspond to the human SPL [5,6], but there is another view that the monkey PPC possesses functional homologues of both regions [7,8]. If the latter view is correct, neuroscientists should be able to identify precursory mechanisms of non-spatial information processing in non-human primates. Indeed, when monkeys were trained to acquire tool use – a high-order behavior they rarely exhibit naturally – PPC expansion was observed at both microscopic [9] and macroscopic [10] scales.

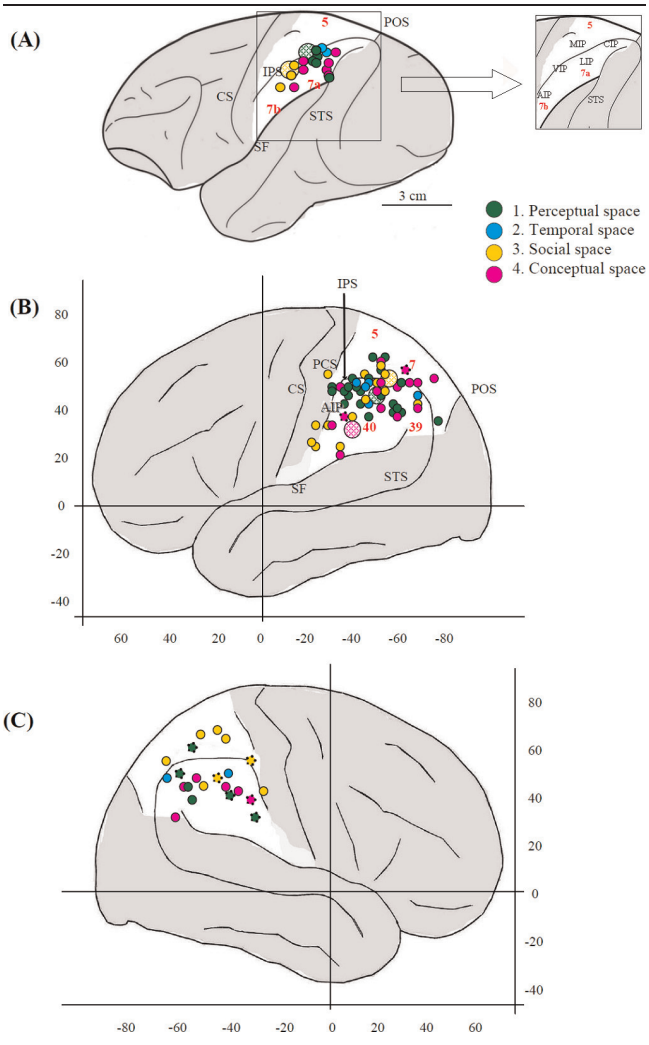
The following section reviews various recently reported forms of non-spatial representation in the PPC. They are ordered roughly in terms of the level of abstraction of the 'objects' and pseudo-spatial relations represented (Figure 2). The last section considers potential mechanisms that could have enabled the hominid PPC to establish such representations and hypothesizes a general principle to unify these newer forms of representation with the PPC's original functions.

Major recent advances

1. Perceptual space

The PPC is implicated in three-dimensional (3D) object recognition, processing of number and quantity, attention, and memory. The intraparietal sulcus (IPS) and anterior intraparietal area are activated when concrete 3D objects are recognized, explored, imagined, and

Figure 1. Comparison of substructures (unshaded) of monkey and human posterior parietal cortex (PPC)



(A) monkey PPC; **(B)** human left PPC; **(C)** human right PPC. Results of meta-analysis (based on the references listed in Figure 2) of cortical areas responsible for non-spatial cognition are superimposed. Data points in monkeys are projected onto the left hemisphere (because no particular laterality has been claimed), whereas those in human subjects are illustrated independently for each hemisphere (being biased toward the left hemisphere). Large and dashed symbols indicate areas estimated from reviews and original papers, respectively, in which coordinates were not clearly specified. Arabic numerals indicate Brodmann areas (40: supramarginal gyrus; 39: angular gyrus). The subdivisions of the PPC were referred from the original sources. AIP, anterior intraparietal area; CIP, caudal intraparietal area; CS, central sulcus; IPS, intraparietal sulcus; LIP, lateral intraparietal area; MIP, medial intraparietal area; PCS, post central sulcus; POS, parieto-occipital sulcus; SF, sylvian fissure; STS, superior temporal sulcus; VIP, ventral intraparietal area.

constructed [11,12]. Discerning continuous quantity recruits the anterior IPS [13] while discrete number processing recruits the bilateral IPS [14-16], forming a mental number line [17] and mental arithmetic [18]. Sustained attention to spatial locations recruits the area between the right IPS and the IPL [19]. The lateral intraparietal area responds to various features of the stimulus shape [20-25]. Angular gyrus and temporo-parietal junction (TPJ) activity is related to stimulus saliency detection and control [26,27]. The left and right posterior TPJ are active while processing global and local information, respectively [28]. The bilateral IPS supports episodic and semantic memory [29]. The PPC may play a critical role in working memory [30-33], although this region can also be active during tasks requiring no working memory [34]. Thus, the PPC's apparent role in working memory may reflect a broader function, such as temporally transferring information from present to future (see 'Temporal space' section).

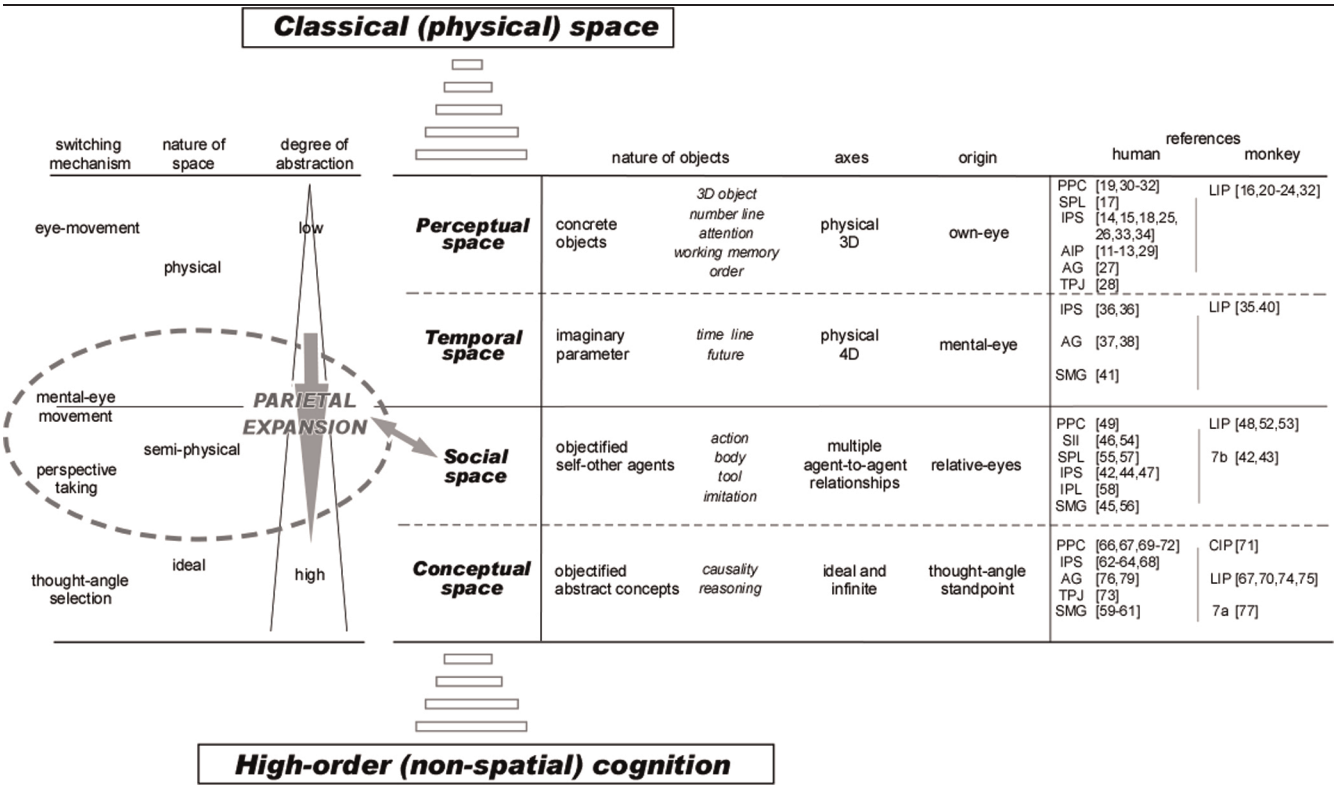
2. Temporal space

The PPC is implicated in temporal processing [35,36], time estimation, and future planning [37]. The TPJ plays a crucial role in temporal order judgment tasks [38] as well as in magnitude judgments about numbers [18]. The PPC supports time interval estimation and is active when estimating future object position [39,40]. In the PPC, events are processed in order and placed in a timeline [41].

3. Social space

The PPC processes some aspects of social space, including action understanding, tool use, and self-other relationships, thereby enabling imitation. The PPC is one of the brain areas showing mirror properties [42-44]. Gesture imitation activates the IPL and supramarginal gyrus (SMG) [45]. Imitation activates the left inferior parietal cortex more than observation does, regardless of first- or third-person perspective [46]. The human anterior IPS distinguishes between observed and executed movements [47], suggesting that PPC neurons have hierarchical properties for recognizing sameness or difference of kinematics, goals, and function of motion [48]. The PPC supports tool usage, an extension of the bodily self [49-52]. This faculty may require an implicit equivalence to be drawn between innate body parts and external objects. A proposed brain network subserving such body-part objectification includes the PPC [53]. The PPC supports the recognition and drawing of distinctions between agents [54,55]. Evaluations of physical

Figure 2. Hypothetical mechanisms of non-spatial representations processed by posterior parietal cortex as a function of abstractness



Left, hypothesized mechanism for increasing abstract levels of representations (see 'Future directions' section for details). Right, structure of various levels of abstract spaces (references for respective levels are listed in the far-right column). 3D, three-dimensional; 4D, four-dimensional; AG, angular gyrus; AIP, anterior intraparietal area; CIP, caudal intraparietal area; IPL, inferior parietal lobule; IPS, intraparietal sulcus; LIP, lateral intraparietal area; PPC, posterior parietal cortex; SII, secondary somatosensory cortex; SMG, supramarginal gyrus; SPL, superior parietal lobule; TPJ, temporo-parietal junction.

and social distance to others involve the superior and inferior PPC, respectively [56], in accordance with egocentric distance estimation by the parietal cortex [57]. Cooperative and competitive tasks recruit a common set of brain regions with competition activating the right inferior parietal lobe more strongly, reflecting the apparent contrast between self and others [58]. The PPC's facility with both concrete spatial cognition and self-other discrimination may have preadapted it to handle perspective transformation in social situations. This in turn could have laid the basis for further functional expansion into realms such as social categorization and, later in evolution, conceptual spaces [48].

4. Conceptual space

Finally, the PPC appears to play a role in causal reasoning, mental object manipulation, attention switching, set shifting, and dimensional abstraction. In addition to the role of the PPC in tool usage (see 'Social space' section), different PPC areas support broad concepts such as the causal ramifications of using tools [51,59,60] and the logical structures of the gestures involved [50]. The SPL and SMG are differentially activated during rotations of visual and motor imagery, respectively [61]. Spatial scanning through mental imagery activated the precuneus, SPL, IPL, and IPS [62]. The PPC is responsible for mentally manipulating sequentially learned materials [63], whereas the mid-dorsolateral prefrontal cortex is responsible for monitoring the learned items [64]. PPC activation is also related to cognitive set shifting [65-70]. During a visual search with attention shifts, PPC neurons depend on a targeted dimension irrespective of the stimuli's spatial features [71]. PPC activation was diminished in elderly people in the solution-search phase of a set-shifting task [72]. Perspective taking [73] is one of the prominent qualitative distinctions between the attention-shifting abilities of humans and other primates [48]. PPC activity also correlates with abstract information at various levels and dimensions [74-77] and with modulation of the strength of the visual stimulus and motor planning [78]. The left parietal cortex is involved in the cortical rearranging of the relationship between semantic items in space [79].

Future directions

As outlined above and illustrated in Figure 2 (right), various kinds of non-spatial cognition can be grouped and ordered based on the levels of abstraction of the 'objects' and ideally defined spaces represented. Assumed coordinate systems for such 'spaces' are summarized here.

The pseudo-spatial nature of the high-order cognition supported by the PPC may derive from the essential characteristics of the objects represented but alternatively may derive from the nature of the PPC's pre-existing information-processing mechanisms, namely as a hub for multisensory integration and representing physical environmental space. The meta-analysis in Figure 1 illustrates that the PPC areas responsible for these novel forms of cognition are not necessarily clearly segregated, either in monkeys or humans, but does suggest a trend of gradual expansion toward the IPL as the level of abstraction proceeds. Thus, it seems that the PPC gradually incorporated high-order cognition as it expanded during hominid evolution while preserving its original principles of operation.

What is the explanation for this expansion of function? Here is a hypothesis involving mechanisms for 'selecting' and 'switching' between objects among different represented spaces: (a) in classical (physical) space, spatial attention toward concrete objects was typically expressed as eye movement; (b) when such attention needed to be sustained or when the attending content needed to be memorized, invisible 'time' was 'visualized' in the mind's eye, becoming a new virtual dimension in the PPC's existing suite of spatial coordinate systems; (c) once the PPC could visualize an invisible virtual entity, a similar objectification process could be extended further, enabling intentional perspective switching (Figure 2, left).

Acquiring representations of social space might have accelerated this process. Through objectification processes [53] and the development of 'virtual eyes' [48,73], flexible and mutually integrated representations of the bodily self, the analogous selves of others, and tools as equivalents of body parts (and *vice versa*) might have served as a bridge between concrete physical and abstract conceptual spaces. As the PPC expanded in both physical volume and range of function [9,10] (Figure 2, dashed circle), a positive feedback process (arrow) could have been established to achieve further human-specific forms of non-spatial conceptual cognition.

Thus, crucial components of human intelligence derive their character from the precursorial spatial cognition process of the PPC. Indeed, language is rife with spatial metaphors for abstract thoughts. Non-human primates possess the same precursorial parietal mechanisms as human ancestors; through training, their cognitive capacities can be artificially extended in the hominid/human direction. If correct, this hypothesis will be valuable in guiding the design of future experimental paradigms, in both animal and human studies, to elucidate the principles of parietal information processing.

Abbreviations

3D, three-dimensional; IPL, inferior parietal lobule; IPS, intraparietal sulcus; PPC, posterior parietal cortex; SMG, supramarginal gyrus; SPL, superior parietal lobule; TPJ, temporo-parietal junction.

Competing interests

The authors declare that they have no competing interests.

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