

discovery of clades that are perhaps subtly different in their disease-causing properties and their modes of transmission [13]. Also, recognizing taxa at the ecotype level could be useful in vaccine development [18] and in industrial biotechnology [13]. In addition, the broad definition of bacterial species has led to innumerable errors in population genetics, where parameters are estimated assuming that all local members of a species taxon are part of the same population [18]. Finally, perhaps the greatest cost of broad-brush species taxonomy is inflicted upon the field of systematics itself. When a systematist discovers a bacterial group and sees that it can fit into one species taxon, the traditions of systematics provide no motivation to further explore the ecologically distinct clades within the species. The research in systematics is then impoverished by a standard of detail that leaves much of a clade's diversity uncharacterized.

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Parahippocampal Cortex: Translating Vision into Space

Two recent imaging studies have shed new light on information representation in human parahippocampal cortex. Despite their different approaches, the two studies both support the view that this brain region represents space at an elementary level.

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Perceiving our local environment is one of the most crucial functions of the brain. The surrounding space is encoded initially in a first-person perspective; this 'egocentric' representation is transformed to encode relations between the viewer and external space. The latter, 'allocentric' representation is stored as an internally driven map-like guide

that allows us to manipulate and navigate in the world. The parahippocampal cortex, located in the medial temporal lobe, has been consistently identified in humans in supporting orientation and navigation. In a seminal study, Epstein and Kanwisher [1] showed that parahippocampal cortex preferentially responds to scene stimuli, rather than single non-scene stimuli like objects or faces; it is particularly concerned with layout-defining spatial

properties of scenes, including geometric features such as walls [2]. Spatial scenes are complex stimuli and the extent to which precise features are encoded by parahippocampal cortex is still unclear.

Two recent studies [3,4] provide new insights into how the parahippocampal cortex represents space. Both studies used functional magnetic resonance imaging (fMRI) in humans to test findings from different model systems of spatial processing (vision and spatial cognition). Mullally and Maguire [3] show that simply imagining objects against a blank background activates the parahippocampal cortex, but critically only for those objects where participants have a strong feeling of surrounding space. Kravitz et al. [4] report that, during the perceptual judgement of real-world scenes, the

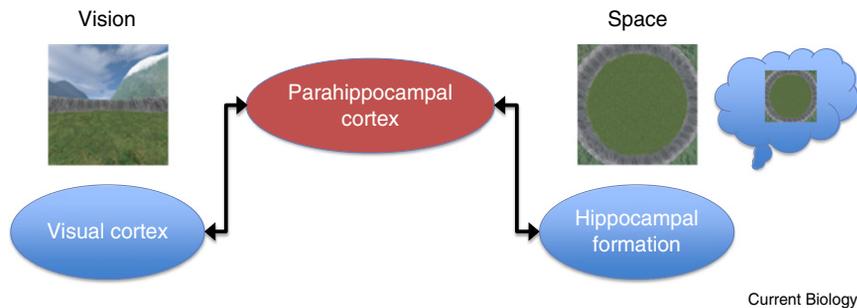


Figure 1. Hypothetical roles of the visual cortex and hippocampal formation in processing a visual scene, in this example a virtual mountain environment.

The visual system maintains an externally driven egocentric view of the environment, while the spatial representation system maintains an internal allocentric map and imagined perception of the same environment. This visuospatial information gathered about the environment is fed to the parahippocampal cortex, where it is integrated with information from the hippocampal formation's spatial representation system to create a hypothesized integrated sense of space. (Images of the virtual environment reproduced with permission from [20].)

parahippocampal cortex is selectively responsive to the spatial properties of the scene, but neither contextual nor categorical aspects.

Mullally and Maguire [3] introduce a new concept in the field of spatial cognition by defining local space as a means to identify types of representations encoded in the parahippocampal cortex. Independent ratings of large sets of items from a separate behavioural study were subsequently employed in the fMRI study, in which objects were separated into two classes: either space-defining or space-ambiguous. Space-defining objects evoked a stronger sense of surrounding space than did the space-ambiguous objects; in other words, it is easier to maintain representations of first-person perspectives within the confines of the object and its surrounding space. During the scan, participants heard short verbal descriptions of these objects; they then had to imagine one of these objects against a blank background for each trial. The parahippocampal cortex was selectively activated for the space-defining, but not the space-ambiguous objects.

The effect was not due to the specific presentation format, rather it was also found when participants viewed pictures of the objects. This result is consistent with evidence that objects that provide navigationally relevant information are represented in the parahippocampal cortex [5]. Interestingly, space-defining objects were consistently rated as bigger and less portable than space-ambiguous

objects, and these two factors strongly contributed to the specific activation of the parahippocampal cortex. Might more general spatial, but also non-spatial, contextual associations co-activated by the objects explain the effect in parahippocampal cortex as has been suggested previously [6]? The results of a series of analyses by Mullally and Maguire [3] indicate that this is unlikely. Additionally, a recent report shows that the parahippocampal cortex can support a visually independent internal representation of scenes perceived haptically in healthy and even blind participants [7]. Together, these findings indicate that the parahippocampal cortex supports an internally maintained map of spatial layout, independent of the externally driven first-person or egocentric perception of scene stimuli, which parallels other recent observations in the medial temporal lobe [8,9].

Kravitz *et al.* [4] combined fMRI with multivoxel pattern analysis and a sparse, event-related design, which allowed for evaluation of the structure of neural representations for each single stimulus without averaging across stimuli. In the scanner, participants witnessed images of real-world scenes taken from different categories, such as cities or beaches. The images were categorised in two ways: they were either manmade or natural; and they showed either an open or enclosed space (defined by the presence or absence of spatial boundaries, such as walls or trees). The relative distance between the viewer and the nearest objects also

varied across images. Performing separate analyses on early visual cortex and parahippocampal voxels, the authors calculated the correlation between the pattern of activity for each possible pair of scenes. This revealed a region-specific similarity structure [10], which allowed the authors to look at how well the brain can categorize across and also discriminate between scenes. They found that there was only weak evidence for a grouping effect with regard to the category of scenes. Interestingly, they observed a grouping of scenes along the dimension of expanse (open *versus* closed) in the parahippocampal cortex, whereas early visual cortex representations mainly reflected relative distance.

How do these specific representational structures relate to behaviour? Kravitz *et al.* [4] observed a close correspondence between the selective, expanse-related grouping effect in parahippocampal cortex and an independent behavioural similarity rating of scenes along the expanse dimension (and a complementary brain-behaviour relationship for early visual cortex and the distance factor, respectively). These findings provide an interesting link between spatial processing in the medial temporal lobe and visual areas traditionally associated with the dorsal, or 'where', stream of the visual processing pathway [11,12].

These complementary studies [3,4] give rise to a common question. Kravitz *et al.* [4] used fMRI to look at how the parahippocampal cortex transforms first-person (external) visual information into well-defined spatial features. Conversely, Mullally and Maguire [3] looked at how hippocampal areas associated with imagining scenes may function at a more basic level in the parahippocampal cortex. These different approaches raise the exciting possibility of looking at both perceptual and cognitive inputs to the parahippocampal region as an integrative area, or 'translator', between respective visuospatial and spatial representational systems [13] (Figure 1). The parahippocampal region's role as a translator towards integrating information from these two systems can clearly be seen in its anatomy. The parahippocampal cortex in humans corresponds

approximately to postrhinal cortex in rats and areas TF and TH in non-human primates [14]. It receives strong projections from visual cortex (and cortical association areas) and in turn provides a dominant input into entorhinal cortex but projects also directly to the subiculum and the hippocampal subfield CA1 [14].

The parahippocampal cortex thus lies at the interface between the spatial representational system in the hippocampal formation and the visual system (Figure 1), which makes it an ideal candidate to integrate external visual and internal spatial signals. Notably, the interaction between incoming sensory information and stored spatial representations has a cellular correlate. Single cells in the rat brain signal an animal's allocentric position in the local environment, suggestive of an internal cognitive map [15]. Two recently discovered cell types might be of particular relevance here: boundary-vector cells in the subiculum [16] and border cells in entorhinal cortex (and to a small extent also in the vicinity of postrhinal cortex) [17]. Interestingly, they were found in the two regions which receive direct input from postrhinal cortex. These cells encode the animal's position relative to geometric features in the environment, like walls and corners. The functionality of these cells could relate to observations in the two fMRI studies that the space-defining object effect in the parahippocampal cortex is driven by lower portability and greater size, [3] and also the finding that parahippocampal cortex activity reflects expanse (whether it is open or closed) of scenes [4] (see also [2,18]).

An interesting avenue for future research will be the investigation of how mechanisms of scene perception previously measured between the parahippocampal cortex and high-order visual areas in human and non-human primates — particularly the 'what' versus 'where' pathways [11] — correspond to findings in targeted electrode studies of rodents, human neuropsychology and neuroimaging studies implicating the hippocampal formation during active spatial exploration and spatial introspection [8,9,13,15,19,20].

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Evolution of Development: Diversified Dorsoventral Patterning

Patterning of the dorsoventral axis by graded BMP signaling is conserved in the evolution of animals. However, this system has also proven to be highly adaptable, as is now highlighted by its short-range function in the leech *Helobdella*.

Ethan Bier

BMPs and their antagonists establish the embryonic dorsoventral axis in

many bilaterian groups, including chordates, cephalochordates [1], echinoderms [2], ecdysozoans, such as arthropods [3–5], and

lophotrochozoans, such as annelids [6–8] (Figure 1). Indeed, the localized deployment of BMP patterning components predates the emergence of bilaterians, as embryos of several species of the radially symmetric cnidarians display asymmetric expression of these genes [9]. Although this is a matter of ongoing debate, graded BMP signaling appears to have been co-opted during axis formation in a basal bilaterian to determine the relative locations of a neuroectodermal domain giving rise