

# From Movement to Transitivity: The Role of Hippocampal Parallel Maps in Configural Learning

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## SYNOPSIS

Whether spatial learning is a special case of configural or relational learning, or whether abstract principles evolved from the concrete need to navigate in space, is a question of long-standing debate. The parallel map theory of hippocampal function offers a resolution of the debate by redefining 'spatial learning' as two parallel, geometric processes, Euclidean metric and topological. Moreover, these processes are subserved by independent hippocampal subfields that underlie two ways of representing space, the bearing and the sketch map. It is possible that configural and relational learning, like spatial learning, should also be distinguished in this way. Transitive inference, requiring the construction of a value gradient, could be analyzed as a Euclidean metric problem. In contrast, transverse patterning could be seen as a topological analysis of the relationships among discrete objects. If this interpretation is correct, lesions to the primary bearing map structure (dentate gyrus) should impair transitivity while lesions to the primary sketch map structure (CA1) should impair transverse patterning and similar topological tasks. Recent results from diverse species and tasks lend support to these predictions, suggesting that the hippocampus not only creates parallel maps but uses these maps to solve more abstract configural or relational problems.

## KEY WORDS

cognitive map, evolution, relational, transitive inference, transverse patterning

## INTRODUCTION

Somehow the hippocampus allows the vertebrate brain to orient itself in external space, updating new exploratory forays and carrying around a reference value for future detours and shortcuts. Somehow it does this without an obvious topographic code in the spatial pattern of firing, and somehow this ability is related to episodic memory /6/. Did this remarkable ability to associate things (whether real or abstract), flexibly rearrange and encode the new relationships evolve from the need for spatial orientation? Or was orienting in space a new application for a recently evolved, flexible cognitive tool?

The parallel map theory of hippocampal function, a new model derived from ethological principles of spatial orientation and based on the evolutionary history of the medial pallium, attempts to address these questions /21,22/. What had been lacking in the literature on the behavioral neuroscience of the hippocampus was an understanding of spatial learning in the context of vertebrate evolution. Following in the footsteps of ethologists, such as Kramer and Wallraff /45/, the parallel map theory defined two ways that learning could be 'spatial': orienting to vectors (stimuli with magnitude and direction) and orienting within arrays of objects. The theory also proposed that the hippocampus processes these data separately into the 'bearing map' (mediated by the dentate gyrus [DG]) and the 'sketch map' (mediated by the CA1 subfield of Ammon's horn). The parallel map theory thus provided a framework for two types of geometries - Euclidean metric and topological - to

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be integrated by the hippocampal formation (HPF). Because the two systems rely on different classes of inputs (vector or scalar), the theory predicts that hippocampal subfields are differentially activated by exploration using these two classes of cues. For example, the bearing map is constructed from graded stimuli with magnitude and direction; i.e., where the magnitude of the relevant parameter (size, loudness, color, chemical concentration, temperature, altitude) changes predictably with the direction of self-movement. Such graded stimuli provide the axes of the bearing map Cartesian grid (Fig. 1A), which then acts as a scaffolding, allowing the integration of multiple sketch maps (Fig. 1B) to the underlying bearing map, creating the integrated map (Fig. 1C). In contrast to the permanent directional axes provided by the bearing map, the sketch map is an ephemeral representation, created for the permanent encoding of objects upon the bearing map scaffold. An individual sketch map is a snapshot of the objects in a local area; the panoramic view from a single vantage point where the objects in the array are individually encoded and hence no one object is necessary for the retrieval of the map. The nature of sketch maps is thus more topological than Euclidean metric; it is not the absolute distance that distinguishes one object or one sketch map from the other but the unique spatial relationship among objects. Because topology determines order in which objects are encountered (not necessarily the distance between them), temporal order would be an emergent property of sketch map encoding. Finally, for species such as homing pigeons, 'super' sketch maps, established by high aerial flight, may vie with the bearing map as a tool for long-distance navigation. We have reviewed different levels of experimental evidence for the parallel hippocampus maps elsewhere /21,22/.

#### REDUNDANCY AND INTEGRATION

The power of hippocampal processing is the manner by which the bearing and sketch maps combine to create the emergent integrated map. This map can combine the extrapolatory power of bearing map vectors with the specificity and detail of relationships among objects in the sketch map.

Wielding both maps together, a bird or mammal can determine the shortest route between two objects in areas that had not been previously joined by common exploratory pathways. Connecting the disconnected sketch maps, by virtue of their encoding to the bearing map scaffold, is the function of CA3 /21,22/ and indeed is the 'pattern completion' function discussed by others /28/.

It has long been recognized that the three best-studied hippocampal subfields (DG, CA3, CA1) have different computational properties by virtue of their neural architecture /18,42/. The parallel map theory offers a functional and phylogenetic framework for the mechanics of these differences - why each function is found in each subfield, based on its evolutionary history. Another implication of this theory is that these three subfields each constructs a different type of map: DG (bearing map), calculating a grid from intersecting vectors (Fig. 1A); CA1 (sketch map), calculating the relative position of objects (Fig. 1B); and CA3, integrating the vector and scalar information in the integrated map (Fig. 1C). If the three maps (Fig. 1: bearing, sketch and integrated) make fundamentally different calculations, then evolutionary specialization arising from these subfields should show computational homology, at least at the level of function. For example, these functions could be: bearing map/DG: extrapolation of graded stimuli; sketch map/CA1: topology of object-defining stimuli; integrated map/CA3: aligning topological and Euclidean metric maps via extrapolation and pattern completion.

Of these, the ability to calculate one's current position by the rate of change of a graded stimulus, and using this rate to project the distance required to reach the source, might be considered the ancestral mapping function. All mobile animals may orient in space using simple movement rules to exploit the graded nature of stimuli in the physical world. An animal can use a taxis, for example, whether photo-, chemo- or other modality, to move up or down an intensity gradient, detecting the magnitude and the direction of a constructed vector of intensity /13/. In contrast, representing the topology of objects in an array requires both image-forming sensory structures and considerable working memory /13/. Finally, the integration and extrapolation between non-contiguous arrays in order to

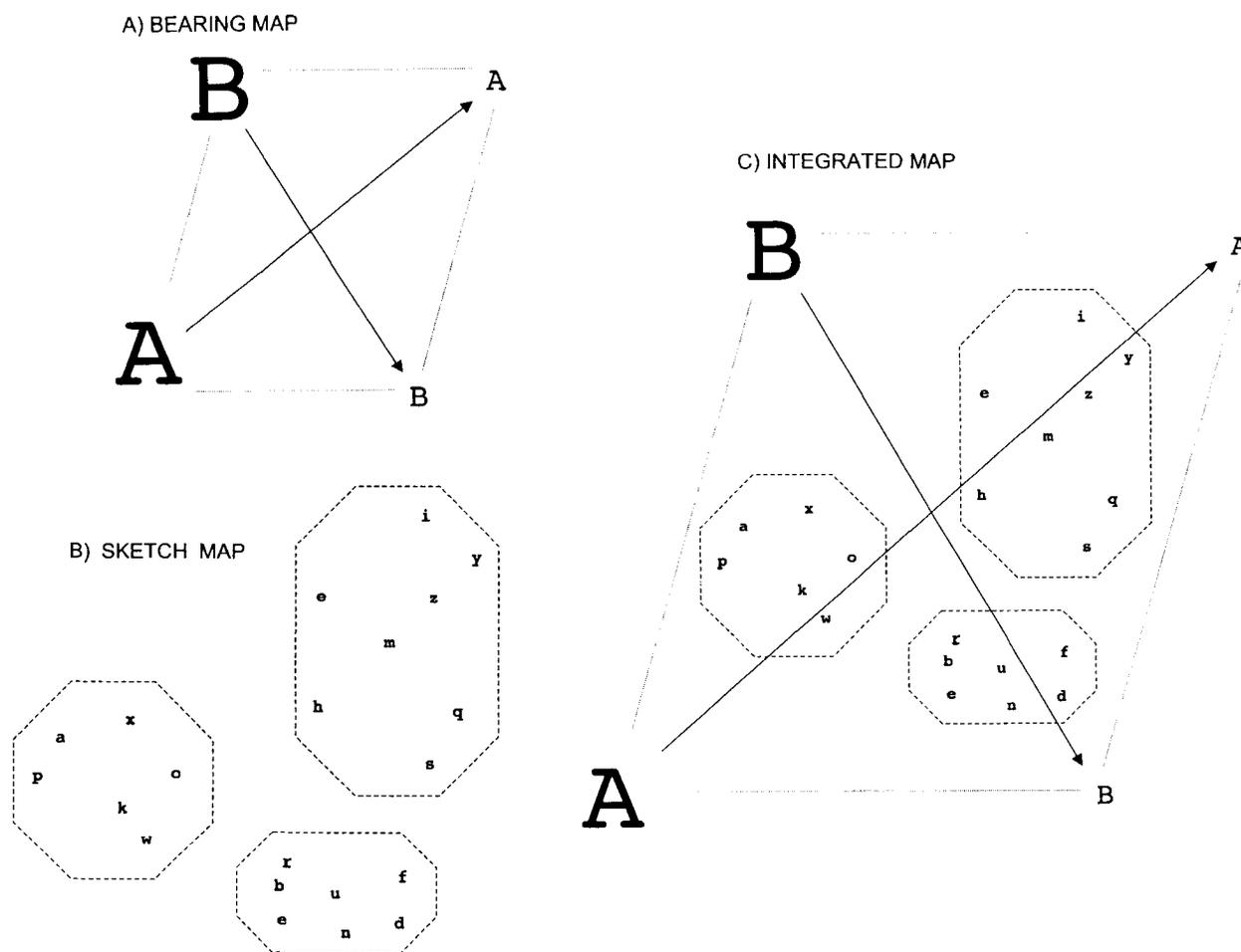


Fig. 1: Parallel map theory. **A)** Bearing map. Directional cues indicated by capital letters; size of letter indicates intensity of stimulus. Arrow indicates direction of gradient. **B)** Sketch maps. Positional cues indicated by lower case letters. **C)** Integrated map. See text for explanation.

make a novel shortcut appears to be an ability found to date only in birds and mammals /14,40/.

#### THE ESSENTIAL HIPPOCAMPAL CALCULATION: SPATIAL, WORKING OR CONFIGURAL LEARNING

What the parallel maps have in common, however, is the encoding of stimuli that are perceived either simultaneously or within the window of working memory. Spatial data (whether points experienced as one moves up a gradient or objects perceived in relation to each other) can be bridged via working memory, to hold multiple stimuli and their locations simultaneously in mind.

For this reason, following the publication of O'Keefe's and Nadel's "The Hippocampus as a Cognitive Map" /29/, the relative importance of spatial versus working memory as the primary function of the HPF was a source of great debate, eventually settled by Olton, who concluded the hippocampus is involved in both activities /31/. The working/spatial memory debate, however, was almost immediately replaced by a new challenge from Rudy, Sutherland and colleagues /1,36,38/ and later Eichenbaum and colleagues /8,15/. Rather than working memory, a different kind of general learning was proposed: configural or relational learning, respectively. This type of learning has had

many definitions, but for present purposes, I will rely on the following definition by McDonald: “an association comprising more than one distinguishable cue. Both the configural cue and the individual cues that it includes can be used independently as information about the situation in which they are found. That is, the meaning or significance of the individual cues is different when they occur alone and when they occur as part of the configural cue. According to Sutherland’s and Rudy’s theory, configural cues represent both spatial and nonspatial information. This is because spatial information is made up of a series of configural associations relating the individual locations within any environment. Thus spatial maps are a special, complex case of configural learning.” /24/.

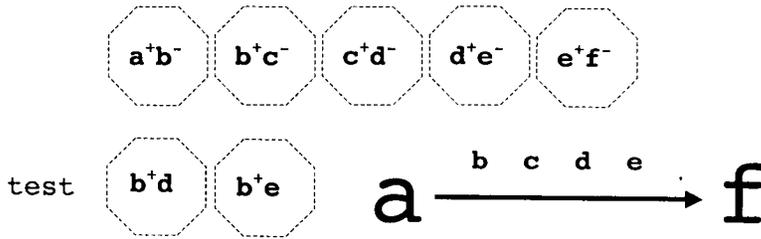
Another possibility, of course, is that configural/relational learning evolved as a type of spatial learning. For example, if the sketch map evolved as a new way of encoding simultaneous (or near-simultaneously perceived) stimuli, the spatial quality of this map is in its topology and not in the distance between objects. Because many researchers consider spatial as synonymous with Euclidean metric, non-metric spatial geometries, such as topology, are described as ‘non-spatial’ /35/. A classic example of such a topological problem is the transverse patterning problem:  $a^+b^-$ ,  $b^+c^-$ ,  $c^+a^-$ , where one stimulus in a set of two predicts the pattern of reinforcement. The arrangement of the cues in this problem is shown in Figure 2C. It is not a problem that can be solved by a gradient; in fact, setting up a transitivity problem in which the last premise pair is linked to the first premise pair severely impairs a laboratory rat’s ability to make the transitive inference /34/. This result, among others derived from studies of children /3,20/ and adult humans /10/, suggested that premise pairs are ordered and encoded metrically on a linear gradient of value (Fig. 2A, B). Such a gradient could be used to order objects that differ in value, e.g., best to worst. Instead of calculating a gradient from discrete samples, ordered in one dimension such as intensity, one could calculate a gradient as a series of objects of known value. As an example, an olfactory gradient must be sampled with discrete sniffs; these could be used to construct a continuous gradient through extrapolation between samples or as a

gradient of samples ordered by intensity. Therefore ordering discrete objects (Fig. 2A, stimuli A-F) or successive samples may require essentially the same calculation. In both cases, what is constructed is both order and distance, whether the stimulus to be encoded is a sample from a gradient or is itself a separate, discrete stimulus. The result is a Euclidean linear representation of value. Such a representation differs fundamentally from the analysis of relative position that characterizes the topology of discrete objects (e.g., Fig. 1B).

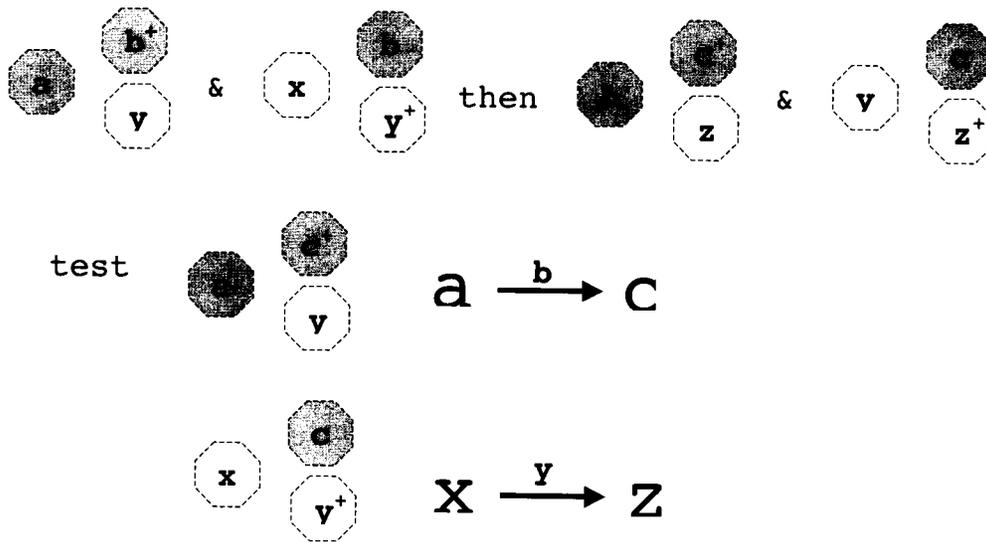
The input into this map of relative value must come, as does most information, through some form of conditioning. There has been an ongoing debate on the nature of configural learning: Is transitive inference spatial or can it be derived from conditioning principles, without recourse to spatial learning assumptions? Recently, Rudy and colleagues have brought the two sides of this debate much closer with a new body of theoretical and empirical work /16,43/. What they propose is a reformulation of the value transfer theory of transitivity, as originally proposed /44/. In the value transfer explanation of transitive inference (Fig. 2A), the animal learns  $a^+b^-$ . Based on conditioning theories, however, the value of b, having been established in the context of a, is never independent of a, regardless of the actual reinforcement history of b. The association of a’s value can therefore affect the value assigned to b, as value ‘bleeds’ from a to b or vice versa /26/. Thus if  $a^+b^-$  learning is followed by the new associations ( $b^+$  and c), the value of c has already been predetermined by its relationship to b, which has an existing relationship with a. As has been argued eloquently by Rescorla, conditioning is a complex, flexible and cognitive process and the value of stimuli is often colored by the context in which they previously appeared /33/.

An example of a value gradient would be transitivity, measured by the ability of an animal to make a transitive inference (TI): if  $A > B$  and  $B > C$ , then  $A > C$ . The ability to show this type of reasoning in non-humans was first demonstrated in the squirrel monkey /25/ but since then has been shown in a number of mammalian and avian species (Table 1). If the reinforcement history of one item in a premise pair influences the other item in that pair, then it will also influence performance in

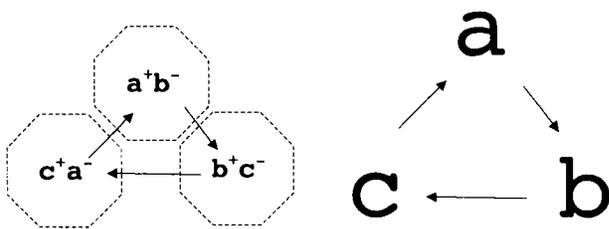
A) TRANSITIVE INFERENCE 1-series problem



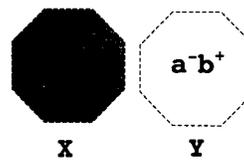
B) TRANSITIVE INFERENCE 2-series problem



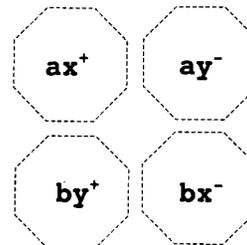
C) TRANSVERSE PATTERNING



E) CONDITIONAL CONTEXT



F) BICONDITIONAL CONTEXT



D) NEGATIVE PATTERNING

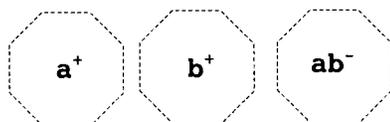


Fig. 2: Configural learning tasks. A) Transitive inference, single-series problem. B) Transitive inference, two-series problem: shading demarcates the two series (ABC, XYZ). C) Transverse patterning. D) Negative patterning. E) Conditional context. F) Biconditional context.

**TABLE 1**  
Pattern of results of configural tasks in five species

Species	Task	Version	Lesion	Result	Reference no.
Rat	NP	Go/no-go; visual	HP	Impaired	/36/
Rat	NP	Lever press; visual	HP	Facilitated	/17/
Rat	NP	Lever press; visual	HP	No effect of lesion	/9/
Rat	TI	2-series; scented sand	HP	Impaired	/5/
Rat	NP CD BC	Lever press; visual	FF or HP	HP impaired NP, BC FF - no effect	/24/
Rat	TI	1-series (A-E); scented sand	FF or retroEC	Impaired	/11/
Rat	TVP	ABC; scented sand	FF or periEC	Impaired	/12/
Rat	TVP	ABC; touch-screen visuals	FF	Facilitated	/7/
Rat	TI	1-series (A-F); scented sand	–	Correct BE, not BD	/43/
Mouse	TVP	ABC; scented sand	CA1- NMDA	Impaired	/35/
Mouse	TI	2-series; scented sand	Aging	Impaired	/30/
Rhesus monkey	TI	2-series; visual (cookies)	EC	Impaired	/4/
Pigeon	TI	1-series (A-E); visual	–	Correct BD inference	/44/
Pigeon	TI	2-series; visual	HP	No effect of lesion	/37/
Human	TI	2-series; visual	–	HP activation	/32/
Human	TI	1-series (A-E); visual	–	Anterior HP activation	/19/

BC = biconditional discrimination; CD = conditional discrimination; EC = entorhinal cortex; FF = fimbria-fornix; HP = hippocampus; NP = negative patterning; TI = transitive inference; TVP = transverse patterning. Rat, pigeon and mouse are common laboratory strains.

unrewarded probe tests. In most tests of transitivity in non-humans, a five-item list is used and the test for transitivity is anchored upon choosing B over D when that novel pair is presented (Table 1). When the series length is increased from five to six, however, an interesting situation develops. Now several internal pairs can be used to measure transitivity, such as BD and BE. In this case, value transfer predicts that rats should choose B in the presence of E but not in the presence of D. This

result is not predicted by any other model of transitive inference, yet this is exactly the result obtained with the laboratory rat (Table 1) (/43/). Frank *et al.* have presented a computational model for this result that computes how conditioning with simple stimuli can lead to the construction of a graded relationship among them; in their words, a 'gradient of associative strength' /16/.

Such a gradient is functionally identical to the idea of a spatial relationship. Just as the rat cannot

solve the transitive inference problem when premises are trained in a circular space /34/ so can pigeons not solve the transitive inference problem in an explicit test of the value transfer theory when two serial problems are linked end to end, essentially forming a circular, and hence nonsensical, gradient /44/. If, however, two logical series are linked one to the other, forming a series of greater length, then monkeys can extrapolate from one to the other, solving TI problems not only within but between such logical series, despite learning them in isolated pairs /41/.

#### ROLE OF THE PARALLEL MAPS IN CONFIGURAL LEARNING

Based on Rudy and colleagues' model of value transfer /16,43/, one could make the argument that value transfer underlies the construction of spatial gradients and hence is the link from conditioning to spatial representation. The bearing map, for example, might use value transfer as a mechanism to construct spatial vectors. This has two important implications for the understanding of spatial learning. First, transitive inference should be mediated by the bearing map, in particular the dentate gyrus - a conclusion reached independently by Frank *et al.* /16/, based on their computational model. Second, it means that non-metric configural problems should not be mediated by the dentate gyrus. Instead, interpreting configural learning in light of the parallel map theory leads to a dissociation of two classes of configural problems, linear problems, such as transitive inference (Fig. 2A,B), and topological problems, such as transverse patterning (Fig. 2C-E). Lesions of specific hippocampal subfields should therefore differentially affect these two classes of configural problems. Lesions of bearing map components (dentate gyrus or fimbria-fornix /22/) should impair transitive inference but not transverse patterning. Lesions of the major sketch map component, CA1, should impair transverse patterning but not transitive inference. These predictions could be tested by examining the effects of different lesions on tasks that should be dependent on the bearing map (transitive inference, 1- and 2-series versions) or on the sketch map (transverse patterning, negative

patterning and biconditional discrimination). Table 1 summarizes the major studies by task, lesion and species, while the tasks used in Table 1 are shown in schematic form for comparison in Figure 2. The effects of lesions on these classes of configural learning are summarized below.

#### THE BEARING MAP AND EUCLIDEAN METRIC TASKS

Because of the proposed anatomical basis of the parallel maps, lesions of the fimbria-fornix (FF) should have a proportionately greater impact on the bearing map than on the sketch map /22/. Therefore the FF lesion should selectively impair Euclidean metric tasks, such as 1- and 2-series transitive inference tasks (Fig. 2A,B) and have little effect on topological tasks (Fig. 2C,D,F). For example, Dusek *et al.* found that FF lesions impaired performance on the 1-series TI task in the rat, using olfactory stimuli /11/. The parallel map interpretation of this result is therefore that the metric task was impaired by a bearing map lesion. In a second study of the effect of lesions on configural tasks, McDonald *et al.* /24/ compared lesions of the FF and the hippocampus proper (HP) on three configural tasks, using visual and auditory stimuli: negative patterning (Fig. 2D), conditional context (Fig. 2E) and biconditional context (Fig. 2F). FF lesions had no effect on the first two tasks and facilitated performance on the biconditional context task. HP lesions, in contrast, impaired both negative patterning and biconditional context. These results support the parallel map interpretation of configural learning: impairment of the bearing map did not affect topological problem solving, which was only impaired by a combined lesion of the bearing map and sketch map (HP lesion).

It is difficult to assess the results of the remaining TI studies, however, because of the placement of lesions; the parallel map interpretation demands that the lesion is confined to a specific hippocampal subfield or component. For example, on the 2-series TI task, transitive judgments have been impaired by complete HP lesion in the rat /5/, by normal aging in the mouse /30/, and by complete entorhinal cortex lesions in the monkey /4/.

In contrast to these results from mammalian

species, there was no effect of lesion on transitive judgment on the 2-series task in the pigeon /37/. This result raises several interesting questions. First among them is the question of whether impairment by HP lesion only occurs when the task demands that stimuli be simultaneously processed, as suggested by McDonald *et al.* /24/. In this study, HP-lesioned rats were impaired on biconditional but not on conditional discrimination. The authors suggested that rats solved the conditional discrimination task with a non-hippocampal mechanism, i.e., by associating reward simply with context, either X or Y (Fig. 2E). In contrast, in the biconditional discrimination task (Fig. 2F), no one stimulus effectively predicted the outcome and hence pairs of stimuli had to be processed simultaneously.

If a hippocampal task must demand simultaneous processing of stimuli, then this may explain the lack of impairment in HP-lesioned pigeons (Fig. 2B). As a caveat, this important study is the first to examine the effect of brain lesions on configural learning in any non-mammalian species. The training procedure, however, may have differed subtly from that used in mammal studies, in the following way: the stimulus 'a' was followed by a choice ('b' or 'x') but did not simultaneously appear with them, as in the previous pigeon TI study of von Fersen *et al.* /44/, using the 1-series task (Fig. 2A; Table 1). Because stimuli were presented serially, this may have resulted in activation and solution by a different brain structure than the hippocampus and therefore this ability was left intact by later hippocampal lesions. An alternative hypothesis is that the inference was completed accurately using residual ventral hippocampal tissue. This would contradict the conclusion, however, by this group and other researchers that the dorsal hippocampal area in birds is homologous to the mammalian dentate gyrus /23,39/. But if the ventral area is homologous to the mammalian dentate gyrus and sufficient ventral tissue was spared, then this might explain why the bearing map was intact and hence why the birds showed no impairment in transitivity judgment. Granted this is not a terribly convincing argument, but it underscores the need for more comparative work with other vertebrate groups, particularly birds and reptiles, on the effect of HP lesions on configural learning.

## THE SKETCH MAP AND TOPOLOGICAL TASKS

Due to the convoluted shape of the HP, most lesion studies are more likely to remove dorsal than ventral hippocampal tissue, and this is known to affect function /26,27/. One might therefore predict that generic HP lesions would have a larger effect on sketch map function, and hence on topological tasks, than Euclidean metric tasks. Another difficulty arises from different lesions and different tasks often being used by different researchers. Perhaps for this reason, the results have been inconsistent: negative patterning (Fig. 2D) has been impaired /24,36/, facilitated /17/ and unaffected /9/ by HP lesion. Transverse patterning (Fig. 2C) has been both impaired /12/ and facilitated /7/ by FF lesion. This last result is particularly puzzling. The facilitation would be predicted by the parallel map interpretation: with only residual sketch map function, the rat would not attempt to order stimuli in a gradient and should therefore more easily solve the transverse patterning task. A possible factor in the difference between these studies (Bussey *et al.* /7/ and Dusek *et al.* /12/) may be the sensory modality of the stimuli: FF lesion impaired transverse patterning using olfactory stimuli /12/ but facilitated transverse patterning using visual stimuli /7/. Given the differential pattern of sensory input into ventral and dorsal hippocampus from olfactory and visual areas /2/, one interpretation is that the FF lesion has a more significant effect on olfactory than visually-mediated tasks. The FF lesion therefore impairs performance on an olfactory task, but in a task using visual stimuli, the impairment of the bearing map might facilitate the use of the sketch map, with its direct input from visual and cortical regions /22/, and hence facilitate transverse patterning. Clearly, more specific lesions are needed to test the hypothesis that transverse patterning is a topological problem, subserved by the CA1-mediated sketch map. One example of such a lesion is the impairment of CA1-NMDA receptors (see /22/ for discussion of long-term potentiation and plasticity of sketch and bearing maps). Such an impairment, using genetic manipulations, has been shown to impair transverse patterning, as predicted, in mice /35/.

Another test of the parallel map interpretation of configural learning could come through functional

imaging of human hippocampus during transitivity judgments. Because the hippocampus shows functional differentiation in both rodents and primates /27/, it may be possible to localize bearing map structure to anterior regions and sketch map function to posterior regions of the human hippocampus, based on the relative representation of DG and CA1 subfields in these areas. Euclidean metric problems, such as transitive inference, might be more likely to activate the anterior hippocampus while transverse patterning should activate dorsal and posterior areas. Recent imaging studies have reported results consistent with this prediction. Heckers *et al.* found selective activation in anterior hippocampus in the 1-series TI task /19/. Similarly, Preston *et al.* found anterior hippocampal activation during transitive judgments in the 2-series task /32/. The parallel map account of these results suggests that designing a study using TI and a topological task, such as transverse patterning, could produce a double dissociation of activation in anterior and posterior hippocampal regions. Moreover, given the pattern of facilitation of topological tasks with FF lesions, imaging studies might also reveal a pattern of inhibition of activity in anterior or posterior hippocampal regions, depending on the task being solved.

### CONCLUSIONS

Whether configural learning is a subset of spatial learning (or vice versa), the parallel map interpretation suggests that there is an interesting dichotomy in both types of learning. In both spatial and configural learning, stimuli may be ordered in gradients (i.e., Euclidean metric and value gradients) or topologically, where what is extracted is the abstract relationship among objects and not the distance between them. This metric–non-metric dichotomy was first explored in the parallel map theory of spatial orientation by Jacobs and Schenk /22/ but may also be a powerful tool for dissecting the role of the hippocampus in configural or relational learning. A review of the evidence to date suggests that there may be a similar taxonomy of Euclidean metric and topological problems, and that these could be subserved by the bearing and sketch map hippocampal components. The evi-

dence at this point is sketchy, with simply enough data to provide fuel for the framing of a new hypothesis. Such a hypothesis, however, based on the parallel map theory, would offer a novel framework within which to understand the controversial pattern of results collected over the past two decades in the area of configural and relational learning. If these diverse ways of learning spring from the same root, then a theory of hippocampal function, derived from two methods for spatial orientation, may shed light on two ways to reason.

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