Spatial and temporal cognitive mapping: a neural network approach

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Tolman suggested that cognitive behavior is purposive and can be described in terms of how different goals are pursued. When pursuing these goals, animals and humans display a remarkable adaptability, which is the result of the combination of a goal-seeking mechanism and a cognitive map. Whereas the goal-seeking mechanism permits the animal to seek different goals, adopting alternative behavioral strategies that are independent of any set of responses, the cognitive map allows the integration of multiple independent pieces of knowledge. Although the concept of cognitive mapping has been mostly applied to spatial mapping, we describe how both spatial and temporal cognitive maps can be mechanistically implemented in terms of recurrent associative networks which store either the adjacency of spatial locations or the contiguity of temporal events. The reinjected predictions of spatial locations or temporal events in the network can be conceptualized as images and their sequences conceptualized as the process of imagining. The combination of goal-seeking systems and cognitive maps permits the description of problem solving tasks in terms of the sequence of subgoals (a plan) to be pursued to reach the goal. Whereas the hippocampus might play a major role in the storage of both spatial and temporal cognitive maps in association cortex, the frontal cortex might participate in goal-seeking tasks, decision making and planning.

M ore than 60 years ago, Tolman[1] suggested that cognitive behavior is purposive and can be described in terms of how different goals are pursued. When pursuing these goals, animals and humans display a remarkable adaptability, which is the result of the combination of a goal-seeking mechanism and a cognitive map. Whereas the goal-seeking mechanism allows the animal to seek different goals, adopting alternative behavioral strategies that are independent of any set of responses, cognitive maps allow the integration, through a reasoning process called inference, of multiple independent pieces of knowledge. Although the concept of cognitive mapping has been mostly applied to spatial mapping, this article shows how similar principles might also apply to temporal mapping and how both spatial and temporal mapping seem to share some common neurophysiological bases.

Spatial cognitive maps

Some spatial tasks involving navigation between non-adjacent locations (such as latent learning and detour problems) require the combination of multiple independent pieces of in- formation about spatially adjacent places through inference and can therefore be solved through the use of cognitive maps. For instance, in latent learning, animals are exposed to a maze without being rewarded at the goal box and, when a reward is later presented, animals demonstrate knowledge of the spatial arrangement of the maze, which remains 'latent' until the re- ward is introduced[2]. In a detour problem in a maze, animals are alternately forced to take one of three different paths to reach the goal[3]. The shortest and intermediate paths share a common place that is absent from the longest path. When tested, animals take the shortest path to the goal. Upon dis- covering that a block has been placed in the common sec- tion of the shortest and intermediate paths, animals take the longest path instead of the intermediate path, thereby dem- onstrating their knowledge that the blocked section belongs to both the shortest and intermediate paths[3].

According to Tolman[1], animals acquire an expectancy that the performance of response R1 in a situation S1 will be followed by a change to situation S2 (S1–R1–S2 expectancy). Tolman hypothesized that a large number of local expectancies

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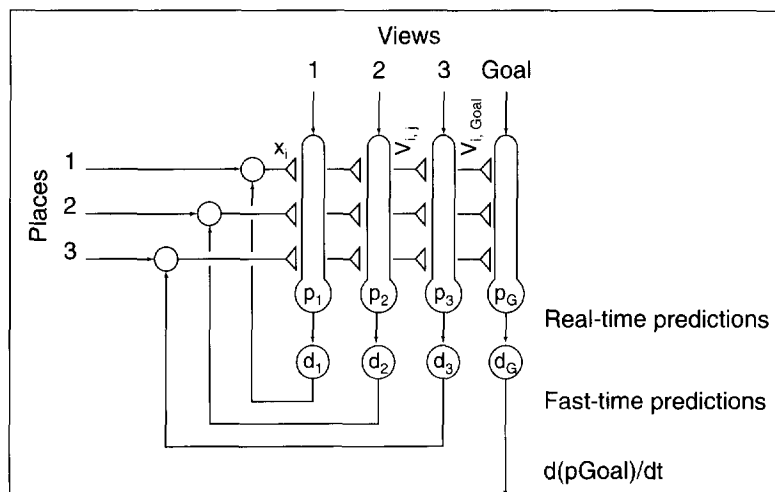
Fig. 1 Cognitive mapping and maze navigation. Neural network that associates Place representations x_i, with View representations Y_j. $V_{i,j}$, long-term memory of Place-View associations. $V_{i,Goal}$, Long-term memory of Place-Goal associations. The first derivatives of the aggregate predictions of View j, p_j, are fed back into the representation of Place j. d_j. Neurons computing first derivatives of the real-time predictions to provide fast-time predictions. As explained in Ref. 7, the use of first derivatives prevents the potential acquisition of spurious Place-View associations. Fast-time predictions of the Goal [d(pGOAL)/dt] for each alternative next place are stored into a working memory (not shown). By comparing the values stored in working memory, the goal-seeking mechanism decides which of all the possible next places is the best predictor of the Goal and moves into it. Arrows, fixed excitatory connections; open triangles, variable excitatory connections.

can be combined into a cognitive map. When seeking a reward in a maze, organisms compare the expectancies evoked by alternative paths, and approach the path that elicits the largest expectancy of the appetitive goal. Milner[4], Deutsch[5] and Hampson[6] proposed systems capable of writing and reading cognitive maps to control the animal's navigation towards the goal in a maze.

Schmajuk and Thieme[7] (see also Refs 8 and 9) presented a real-time, biologically plausible neural network approach to purposive behavior and cognitive mapping. The system is composed of a goal-seeking system and a cognitive system, the latter being shown in Fig. 1. The goal-seeking mechanism displays exploratory behavior until either the goal is found or an adequate expectancy (or prediction) of the goal is generated by the cognitive system.

The cognitive system is implemented by a heteroassociative recursive network[10] (see Box 1). Two types of inputs
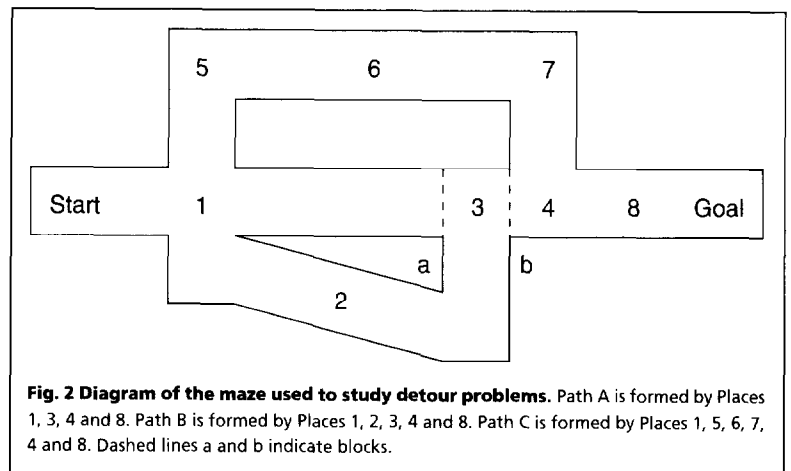
Box 1. Associative networks

Kohonen[a] classified associative networks into autoassociative and heteroassociative. Autoassociative networks are those in which the input pattern is associated with itself in such a way that the whole pattern is retrievable on the basis of an arbitrary fragment of it. Heteroassociative networks are those in which two different input patterns are associated in such a way that one of the patterns is retrievable on the basis of an arbitrary fragment of the other. Recurrent networks are networks in which the outputs either constitute additional inputs or are reinjected to the inputs of the network.

Reference
a Kohonen, T. (1977) *Associative Memory. A System-Theoretical Approach*, Springer-Verlag

are considered: Places and Views. Places refer to discernable regions in the maze: Several authors have offered models that describe how place representations can be built based on environmental stimuli[11–14]. Views refer to the sights of places as seen from another place. Place i in a maze is assumed to give rise to a short-term memory trace, x_i. Place trace x_i may become associated with the views of other places to form long-term associations $V_{i,j}$ between Place i and View j. When the animal is at Place i and perceives View j, $V_{i,j}$ increases. When the animal is at Place i and cannot perceive View j, $V_{i,j}$ decreases. Each time the animal is in Place i, $V_{i,i}$ associations generate real-time predictions of Views j to be seen from Place i. If there is a mismatch between the actual and the predicted view, $V_{i,j}$ is readjusted to reflect the maze configuration. The cognitive map built by the network is a topological map, that is, it represents only the adjacency, but not the exact distance or direction, of places.

According to Tolman[1], when reaching a choice-point in a maze, animals display what is referred to as vicarious-trial-and-error (VTE) behavior, that is, the orienting to the different alternative pathways. For Tolman, this active sampling of alternative pathways leads to the generation and comparison of expectations before reaching a decision about which course to take. Schmajuk and Thieme[7] approximated VTE behavior by assuming that, before making 'their mind up', animals briefly attend to the views y_i of all the alternative next places i linked to the place that they are currently occupying. These brief inspections of views y_i result in fast, short and relatively weak activation of their corresponding place traces, x_i. In turn, place traces x_i activate cells y_j in proportion to their $V_{i,j}$ connections. Therefore, view cells, y_j, are activated by fast-changing signals proportional to $x_i V_{i,j}$, that are recurrently reinjected into x_i through cells d_j. In Konorski's[15] terms, whereas activation of x_j by the environmental inputs is experienced as the perception of Place j, activation of x_j by d_j is experienced as an 'image' of Place j. Subsequently, x_i activates y_k, y_k activates x_k, and so forth, spreading the activation over the network. Because activation spreads decrementally (proportional to the magnitude of a reinjection constant that is less than one), the output of cell d_G decreases as the distance (measured as the number of interposed places) of the alternative next Place i to the Goal increases. The sequence of reinjected images can be conceptualized as the process of imagining. As the animal examines all the alternative next views, the output of cell d_G for each alternative next place is stored into a working memory. By comparing the values stored in the working memory, the goal-seeking mechanism decides which of all the possible next places is the best predictor of the Goal and moves into it.

Schmajuk and Thieme[7] showed that the network successfully describes latent learning and detour behavior in rats. Figure 2 shows a diagram of the maze with three pathways (A, B and C) that Tolman and Honzik[3] used to analyze how rats solve a detour problem. Path A is the shortest, Path B is the next shortest and Path C is the longest. During preliminary training, rats are alternately forced to take Paths A, B and C, by introducing blocks in different segments of the maze. During testing, a block is placed in the common section of Paths A and B (Block b between Places 3 and 4,

in Fig. 2), thereby obstructing both paths. In Tolman and Honzik's experiment, most rats, after backing out of Path A, take the longest path, Path C, instead of the second shortest path, Path B.

Figure 3 illustrates how internal navigation in the cognitive map of the maze occurs in fast-time, that is, it proceeds at a faster pace than the real movement through the maze. The upper pan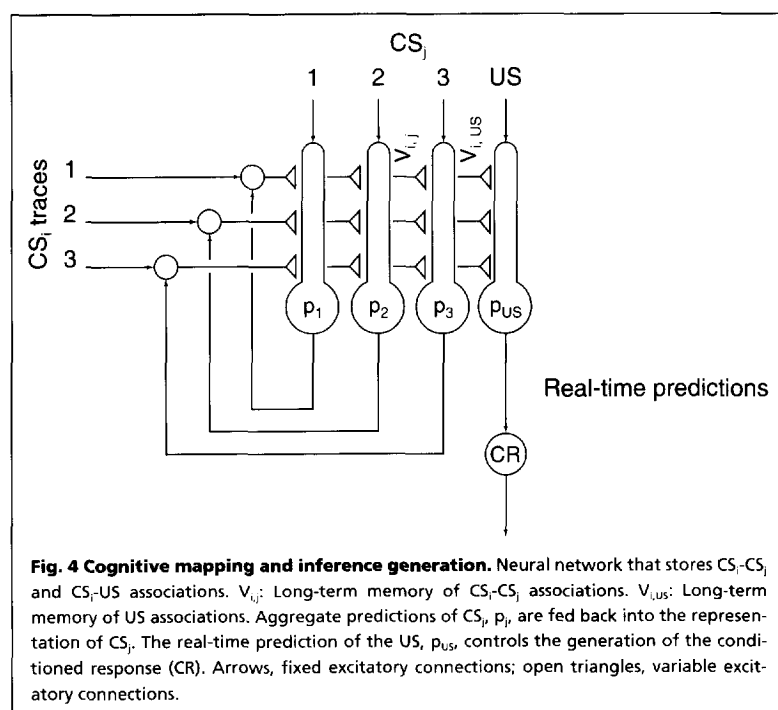el in Fig. 3 shows a real-time simulation of the activity of neurons representing different maze views when the animal briefly moves from Place 1 into Places 2, 3 and 5, before Block b is introduced. The upper panel in Fig. 3 shows that Place 3 evokes the strongest representation of the Goal and, therefore, it becomes a subgoal that will be entered by the animal. The lower panel in Fig. 3 shows a real-time simulation of the activity of the nodes representing different maze views when the animal briefly moves from Place 1 into Places 2, 3 and 5, after finding Block b. The lower panel in Fig. 3 shows that after Block b is introduced, Place 5 elicits the strongest representation of the Goal and, therefore, it becomes a subgoal that will be en-

Fig. 2 Diagram of the maze used to study detour problems. Path A is formed by Places 1, 3, 4 and 8. Path B is formed by Places 1, 2, 3, 4 and 8. Path C is formed by Places 1, 5, 6, 7, 4 and 8. Dashed lines a and b indicate blocks.

tered by the animal. It is important to notice that the network generates the sequence in which different places in the maze are interconnected independently of the sequence in which these places were originally visited.

Fig. 3 Imagining the maze with a cognitive map. Simulation of the fast predictions of the goal, generated by the network illustrated in Fig. 1, after glimpses at the Views of alternative next Places 2, 3 and 5 from Place 1 before and after introducing Block b. **(A)** Network activity before introducing Block b. **(B)** Network activity after introducing Block b. Left-hand panels: glimpses at View 2. Central panels: glimpses at View 3. Right-hand panels: glimpses at View 5. Notice that the glimpses at View 3 generate the strongest prediction of the Goal (Place 9) before Block b is introduced, and glimpses at View 5 generate the strongest prediction of the Goal (Place 9) after Block b is introduced. In order to maximize display clarity, scales for each activity trace are different in every case, except for the Goal (Place 9). Goal activity is scaled to its maximum value for glimpses at View 3 in (A) and for glimpses at View 5 in (B).

Fig. 4 Cognitive mapping and inference generation. Neural network that stores CS_i-CS_j and CS_i-US associations. $V_{i,j}$: Long-term memory of CS_i-CS_j associations. $V_{i,US}$: Long-term memory of US associations. Aggregate predictions of CS_j, p_j, are fed back into the representation of CS_j. The real-time prediction of the US, p_{US}, controls the generation of the conditioned response (CR). Arrows, fixed excitatory connections; open triangles, variable excitatory connections.

Interestingly, Hampson[6] suggested that by identifying different locations in a maze with different states in a problem (e.g. the Tower of Hanoi), networks capable of maze navigation are also capable of problem solving[7].

Temporal cognitive maps
In addition to spatial navigation, some tasks, involving relationships between temporally noncontiguous events such as sensory preconditioning, second-order conditioning and transitivity, require the combination of multiple independent temporally contiguous pieces of information through inference and might also be solved through the use of cognitive maps. For instance, in sensory preconditioning[16], two conditioned stimuli (CSs), CS_A and CS_B, are paired together in the absence of the unconditioned stimulus (US). In a second phase, CS_B is paired with the US. Finally, when CS_A is presented alone, it generates a conditioned response (CR). In second-order conditioning[17], a CS, CS_B, is paired with the US. In a second phase, CS_A and CS_B are paired together in the absence of the US. Finally, when CS_A is presented alone, it generates a CR. In a transitivity task, when CS_A is presented CS_B is reinforced, and when CS_X is presented CS_Y is reinforced. In addition, when CS_B is presented CS_C is reinforced, and when CS_Y is presented CS_Z is reinforced. When CS_A is presented in a test trial, animals chose stimulus CS_C over CS_Z, but CS_Z over CS_C when CS_X is presented[18].

Several workers have developed neural network models that describe cognitive mapping in classical conditioning[19–23]. Figure 4 shows a neural architecture that implements a cognitive map consisting of CS-CS and CS-US associations stored in a recurrent network[10]. The outputs of the cognitive map system are the aggregate predictions of the CSs or the US (p_1, p_2, p_3 and p_{US}). Aggregate predictions p_j represent the expected magnitude of a CS or the US based upon all the CSs with a trace active at a certain time. As in the case of the spatial cognitive map, predictions are inferred by reinjecting the predictions p_1 and p_2 into the

traces of their corresponding CS_j. As in the case of spatial maps, because activation spreads decrementally, the output of cell p_{US} decreases as the time interval (measured as the number of interposed CSs) between CS_i and the US increases. This recurrent property allows the network to describe sensory preconditioning, second-order conditioning and transitivity. As mentioned, whereas the activation of a trace of CS_i by the stimulus is experienced as a perception, activation of the trace by pi is experienced as an 'image' of CS_i.

Computer simulations, shown in Fig. 5, demonstrate that a network proposed by Buhusi and Schmajuk[23], which incorporates the architecture described in Fig. 4, successfully describes sensory preconditioning, transitivity and symmetry. In terms of the network, sensory preconditioning is described as follows. During CS_A–CS_B trials $V_{A,B}$ association increases and during CS_B reinforced trials $V_{B,US}$ association grows. When CS_A (never presented with the US before) is presented by itself in a test trial, it activates the prediction of CS_B, B_B, which in turn activates prediction of the US. Transitivity is described as follows. During CS_A–CS_B trials, $V_{A,B}$ associations increase and during CS_B–CS_C trials, $V_{B,C}$ associations increase and $V_{C,US}$ associations grow during CS_C reinforced trials. When CS_A (never presented with the US before) is presented by itself in a test trial, it activates the prediction of CS_B, B_B, which in turn activates prediction of CS_C, B_C, which in turn activates the $V_{C,US}$ association, thereby generating a prediction of the US. Based on this prediction, the goal-seeking system will choose C over Z when A is presented. Finally, symmetry (the ability to associate paired elements presented in the reverse of training order) is simply the result of the simultaneous increase in $V_{B,A}$ and $V_{A,B}$ associations.

The neurophysiological bases of cognitive mapping
Starting with the seminal work of O'Keefe and Nadel[24], several theories have proposed that the hippocampus functions as a spatial cognitive map[25–27]. Whereas some of the theories (Muller, Stead and Pach[28]) suggest that the hippocampus codes the distance between places, a view similar to that proposed by Schmajuk and Thieme[7,8], other models incorporate the notion that responses are also coded in the hippocampus (McNaughton and Nadel[29]). Interestingly, O'Keefe and Nadel[24] suggested that whereas the human right hippocampus stores spatial cognitive maps, the left hippocampus stores maps which provide semantic deep structures for language (a temporal map in our terminology).

Different cells in the hippocampus seem to code information related to spatial cognitive mapping (such as representations of places, the prediction of places, views, goals, directions and 'imagined' navigation) and temporal cognitive mapping (such as the prediction of CSs). Some hippocampal pyramidal cells show place fields – they are maximally activated at different spatial locations as the rat moves through the environment[30]. Some evidence (Muller and Kubie[31], but see Deadwyler, Breese and Hampson[32]) suggests that, instead of reflecting the current place occupied by the animal, place cells might actually predict the future position on a 100 ms time scale. In addition to place representations and predictions, some hippocampal neurons have view fields, that is, they fire when monkeys look at certain parts of space[33]. The activity of some pyramidal cells

might also represent goals, as they become active when rats orient toward or approach significant cues or places[34–36], but see also O'Keefe and Speakman[37]. Interestingly, some cells in the postsubicular area of the hippocampal formation represent head directions and fire when the animal's head points in a particular direction[38,39]. Finally, hippocampal cells that display temporally correlated activity (that is, have overlapping place fields) during open field behavior show enhanced temporal correlations during slow-wave sleep[40], a result reminiscent of the imagined navigation displayed in Fig. 3. In addition to the overwhelming information related to spatial cognitive mapping, some reports hint that cells in the hippocampus might also code information related to temporal cognitive mapping: some hippocampal cells increase their activity during paired CS_A–CS_B presentations in a sensory preconditioning paradigm[41].

Interestingly, because region CA3 in the hippocampus seems to be organized as a recurrent associative network, such as those depicted in Figs 1 and 4, some theories[27,29,42,43] assumed that this region is involved in the storage and retrieval of sequences of events. In contrast, Buhusi and Schmajuk[23] suggested that the recurrent feedback in the networks is implemented through a non-local circuit that involves neocortex, hippocampus and thalamus.

As an alternative to the view that the hippocampus stores spatial cognitive maps, Schmajuk and colleagues[8,13,21] suggested that the hippocampus participates in both spatial and temporal cognitive mapping. The hippocampus would (a) compute spatio–temporal predictions of future events (what, when and where events will occur) and (b) modulate neocortical storage of information critical for both spatial and temporal cognitive mapping, such as Place representations, Place-View associations and CS-CS associations, and computes the predictions of places, CSs and USs. This view is supported by computer simulations showing that models that incorporate recurrent architectures[8,21–23] correctly describe the deleterious effects of hippocampal lesions in spatial cognitive mapping (e.g., place learning[44], latent learning[45] and detour learning[46]) and temporal cognitive mapping (e.g., sensory preconditioning[41,47] and transitivity[18]).

In addition to hippocampal participation in cognitive mapping, Schmajuk et al.[8] suggested that the frontal cortex is involved in the generation of fast-time predictions and the examination of the predicted consequences associated with each possible alternative pathway (goal-seeking function). According to Fuster[48], such prospective function is essential for the organization of purposive behavior by the frontal cortex. Interestingly, the nucleus accumbens might combine cortical and hippocampal information to control spatial navigation[49].

Conclusion

Although the concept of cognitive mapping has been mostly applied to spatial mapping, this article shows that both spatial and temporal cognitive maps can be implemented in terms of recurrent associative networks which store either the adjacency of spatial locations or the contiguity of temporal events. These neural networks provide a mechanistic description of cognitive constructs such as inference generation, reasoning, thinking, imagining, plan-
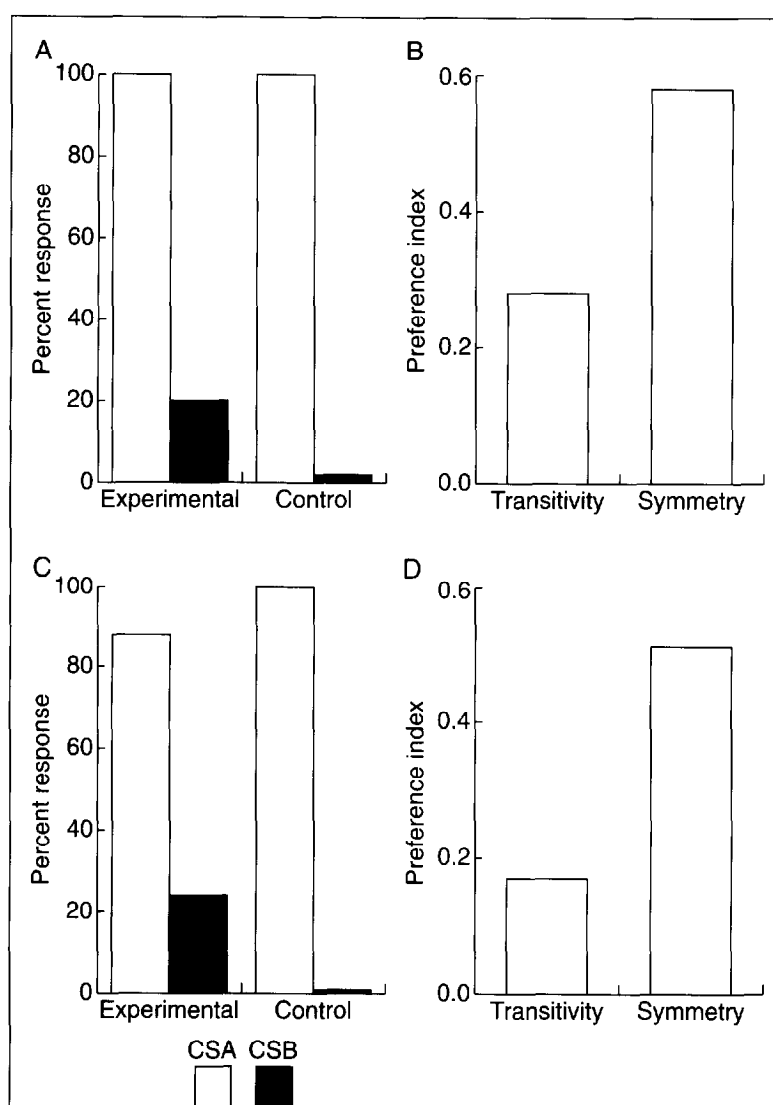
Fig. 5 Sensory preconditioning and transitive inferences. (A) Sensory preconditioning; data from Ref. 11. Percentage of conditioned responses elicited by CS_A and CS_B trials after non-reinforced CS_A-CS_B trials followed by reinforced CS_A trials (experimental group), or reinforced CS_A trials (control group). **(B)** Transitivity and symmetry; data from Ref. 13. Preference index calculated as $(X-Y)/(X+Y)$, where X is the time in the transitive (or symmetry) choice and Y is the time in the alternative choice. **(C)** Sensory preconditioning; Simulated peak CR amplitude elicited by CS_A and CS_B after 120 non-reinforced CS_A-CS_B trials followed by 120 reinforced CS_A trials (experimental group), or 120 context alone trials followed by 120 reinforced CS_A trials (control group). **(D)** Transitivity and symmetry; Simulated preference indexes $(X-Y)/(X+Y)$ for transitivity and symmetry tests after 150 trials of alternated reinforced CS_A-CS_B and CS_X-CS_Y trials and non-reinforced CS_A-CS_Y and CS_X-CS_B trials, followed by 150 trials of alternated reinforced CS_B-CS_C and CS_Y-CS_Z trials and non-reinforced CS_Y-CS_C and CS_B-CS_Z trials. For the transitivity test, X was computed as the average of the peak CR amplitudes elicited by CS_C following CS_A presentations and by CS_Z following CS_X presentations, Y was computed as the average of the peak CR amplitudes elicited by CS_Z following CS_A presentations and by CS_C following CS_X presentations. For the symmetry test, X was computed as the average of the peak CR amplitudes elicited by CS_B following CS_C presentations, and by CS_Y following CS_Z presentations, Y was computed as the average of the peak CR amplitudes elicited by CS_Y following CS_C presentations and by CS_B following CS_Z presentations. Simulated results were obtained with the model described by Buhusi and Schmajuk[23].

ning and problem solving. Whereas the hippocampus might play a major role in the storage of both spatial and temporal cognitive maps in association cortex, the frontal cortex might participate in goal-seeking tasks, decision-making and planning.

Outstanding questions

- Although progress has been made in our understanding of some of the theoretical aspects of cognitive mapping, how can these conceptual approaches be extended to eventually become closer to the reported behavioral and neurophysiological data?
- Should the place representations used in our models be created whenever an unfamiliar spatial location is visited?
- When in a novel environment, should a simulated animal explore novel locations (curiosity drive[50]) until the environment becomes familiar?
- What is the optimal number of places and connections to describe a given environment? That is, what is the optimal cognitive map that a model can build?
- How can a cognitive map represent, not only adjacency, but also the direction of places? Can a map representing place direction use covert responses to 'imagine' the views of the next alternative places instead of actually having to look at them?
- How can a temporal cognitive map represent not only contiguity, but also the time interval between events?
- What decision rules should be used so that decision time decreases, instead of remaining fixed, as knowledge of the environment increases and stronger predictions of the goal are generated?
- Because VTE behavior is slow when the number of alternative next places is large, can response-selection rules (turn right or left) replace VTE behavior when the maze is well learned[6]. Can these response-selection rules be disengaged and VTE behavior re-engaged when changes in the environment are detected?

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