

Minimal model of strategy switching in the plus-maze navigation task

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Abstract. Prefrontal cortex (PFC) has been implicated in the ability to switch behavioral strategies in response to changes in reward contingencies. A recent experimental study has shown that separate subpopulations of neurons in the prefrontal cortex were activated when rats switched between allocentric place strategies and egocentric response strategies in the plus maze. In this paper we propose a simple neural-network model of strategy switching, in which the learning of the two strategies as well as learning to select between those strategies is governed by the same temporal-difference (TD) learning algorithm. We show that the model reproduces the experimental data on both behavioral and neural levels. On the basis of our results we derive testable prediction concerning a spatial dynamics of the phasic dopamine signal in the PFC, which is thought to encode reward-prediction error in the TD-learning theory.

1 Introduction

The ability to switch between different navigational strategies for reaching the goal is crucial for adaptive spatial behavior. Large body of animal studies suggest a large variety of navigational strategies, which depend on sensory input of different modalities [1]. Existing lines of experimental research focus on (*i*) how the different strategies are implemented in the brain and what memory systems support them [2–5]; and (*ii*) what is the mechanism of selection between different strategies and corresponding memory systems during ongoing behavior [6–8]. In particular, a series of animal studies in the plus maze (Fig. 1A) provided an insight into the role of hippocampus (HPC), dorsolateral striatum (DLS) and prefrontal cortex (PFC) in learning the tasks in which changing reward contingency forced the animals to use either a place strategy or a response strategy. In the plus maze, the place strategies can be defined as approaching a particular place associated with reward, e.g. the end of the East arm in the case of strategy 'go East' (Fig. 1C). The response strategies can be defined as making a particular egocentric turn at the center, e.g. 'turn left' strategy (Fig. 1D). Note that if animals start their trial in the North position, both strategies lead to the same

location. In contrast, the two strategies lead to different locations if the starting position is South, permitting the dissociation between the two strategies.

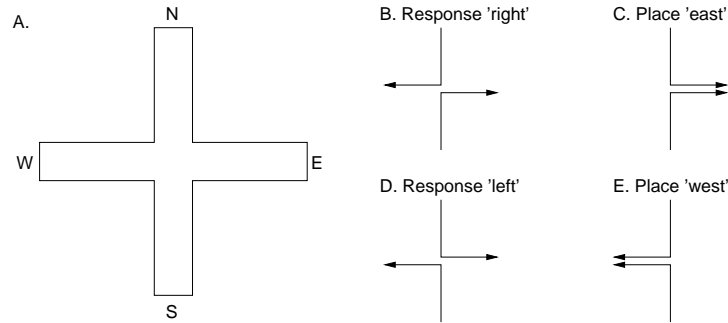


Fig. 1. Experimental setup in the plus-maze task [8]. A. Plus maze. B-E. Learning tasks testing response strategies (B,D) and place strategies (C,E). In (B,C) and (D,E) lower paths are consistent, while upper paths are inconsistent.

Experimental studies in the plus maze have shown that rats with inactivated HPC were strongly biased towards response strategies, while they were biased towards place strategies when DLS was inactivated [4, 5]. In other experimental environments a double dissociation between HPC and DLS has been demonstrated in place-learning and response-learning tasks, respectively [2, 3]. Moreover, recent electrophysiological recordings of PFC neurons while rats were navigating in the plus maze have demonstrated that different neuronal populations were active depending on which strategy is currently in use [8]. When rats had learned that the correct strategy was a place-based one, a subpopulation of neurons were highly active. When the reward contingency changed so that the response-based behavior was the only valid strategy, another subpopulation became active, while neurons in the first subpopulation became silent. In addition to being a suitable experimental setup for studying strategy learning and switching, the plus maze is also attractive from the modeling point of view. This is because the analysis of strategy switching and its neural correlates can be performed at a well defined location (the cross point) where behavior is crucial for successful performance (in contrast to, e.g., water maze where no such location can be identified).

The experimental data reviewed above suggest a two-level hierarchical organization of spatial behavior in the plus maze. On the first level, different neuronal networks (located in e.g. HPC or DLS) learn corresponding navigational strategies taking a particular sensory modality as an input. On the second level, a neural network (located in the PFC) learns to choose which strategy is more successful and gives the control of the behavior to that strategy [9]. In a simple way, a behavioral strategy can be considered as a rule that determines which of

the available motor actions should be performed when a particular sensory input is observed. Similarly, the strategy switching can be described as the choice of one of the available strategies, given the sensory input. From a theoretical point of view, these two learning tasks are identical, assuming that available motor actions (first level) or available strategies (second level) are encoded by the activities of neural populations.

Here we were interested to see how far we can go in explaining the behavioral and neural data by suggesting the learning algorithm is identical on both levels. The learning algorithm we use is a standard temporal-difference (TD) learning rule called Q-learning [10]. At the core of TD-learning algorithms is the minimization of a so-called reward-prediction error which is proposed to be coded by the phasic activity of dopaminergic (DA) neurons in the ventral tegmental area (VTA) [11]. We have analyzed the learning dynamics of the reward-prediction error in our model and compared the error propagation on the two levels. Our results suggest that a two-level organization of behavioral control with TD-learning on each level is compatible with principal experimental results [4, 8]. In addition, our model generated testable predictions concerning differences in DA signaling between HPC and PFC.

2 Model

Our neural network model of navigation consists of three interconnected subnetworks responsible for response strategy, place strategy and strategy selection, respectively (Fig. 2). The response-strategy subnetwork learns egocentric movements such as, e.g., turning left, while the place-strategy subnetwork learns to enter a particular arm. The strategy-selection network learns to choose which strategy will take control of behavior on each time step. In our model, the three subnetworks functionally correspond to different neural structures in the rat brain that are implicated in spatial learning. Namely, the response subnetwork corresponds to the DLS, the place network corresponds to the HPC, while the selection network corresponds to the PFC.

Each of the three subnetworks has the same simple architecture of a single-layer perceptron in which learning occurs according to a TD learning rule. The input layer encodes sensory input to the network, while the output layer represents actions that this network generates. The subnetworks are hierarchically organized in two levels: the two subnetworks of the lower level learn the place and response strategies, while a single subnetwork of the upper level (strategy selection network) learns to select which of the two subnetworks of the lower level will take control over behavior. The selection is assumed to occur by inhibiting the motor output of the non-winner strategy. Below we describe the inputs, outputs, and learning in the different subnetworks.

2.1 Place learning

Place strategy was implemented as follows. Input to the network was represented by the activities of N_{pc} place cells with Gaussian spatial receptive fields, centers

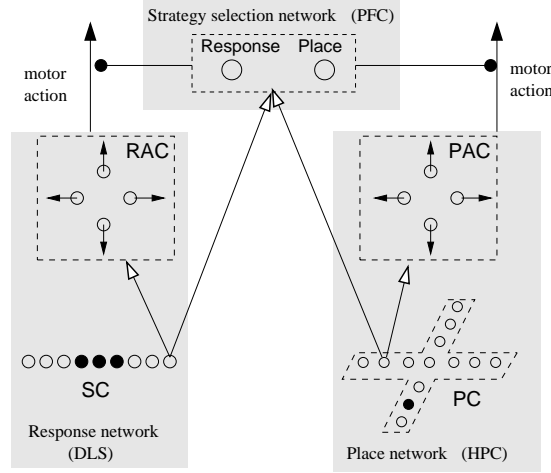


Fig. 2. The architecture of the model. SC – sensory cells, PC – place cells, RAC – response-action cells, PAC – place-action cells. Open (filled) circles denote inactive (active) cells; the large open arrows denote all to all feed-forward projections between corresponding neural structures; the large filled arrows denote motor output of the model; small filled arrows denote preferred direction of the action cells in these structures; ball-arrows denote inhibition.

of which were distributed uniformly over the environment. More precisely, the activity of place cell j was calculated as $r_j^P = \exp(-d_j^2/2\sigma^2)$, where σ is the width of animal in the maze and the center of the j -th receptive field. Place cells projected to place-action cells a_i^P with weights w_{ij}^P . Four place-action cells coded for movements in allocentric directions East, West, North and South. Activities of the place-action cells were calculated according to Eq. 1, and the weights were updated using Eq. 2 on each time step. An allocentric movement, proposed to be performed on the next time step by the place strategy, was chosen on the basis of response-action cell activities according to Eq. 4 on each time step.

2.2 Response learning

In the response strategy network, input cells were N_{sc} sensory cells that coded for the presence of walls around the simulated rat. All sensory cells were divided into four subpopulations coding for the space in front of the rat, left from the rat, right from the rat and behind the rat, respectively. Presence or absence of a wall at a specified egocentric direction from the rat (and hence the ability to move in this direction) was encoded by setting activities r_j^{sc} of the corresponding sensory cells to 0 or 1, respectively. Sensory cells projected to response-action cells a_i^R with weights w_{ij}^R . Four response-action cells coded for movements in egocentric directions Forward, Leftward, Rightward and Backward. Activities of the response-action cells were calculated according to Eq. 1, and weights were

updated using Eq. 2 on each time step. An egocentric movement, proposed to be performed on the next time step by the place strategy, was chosen on the basis of response-action cell activities according to Eq. 4 on each time step.

2.3 Strategy-selection learning

In the strategy selection network, input was represented by the combined activities of $N_{pc} + N_{sc}$ input cells from place and response strategy networks. An intuition for this particular choice of input is the following: given all available information at the current state, the selection network decides which strategy should be chosen to take control over behavior. Input cells projected to strategy-selective (action) cells a_i^S with weights w_{ij}^S . Two strategy-selective cells coded for place and response strategies, respectively. Activities of the strategy-selective cells were calculated according to Eq. 1, and the weights were updated using Eq. 2 on each time step. One of the strategies (the winner strategy) was selected on the basis of activities of the strategy-selective cells according to Eq. 4 on each time step. The next movement actually performed by the simulated rat was the one proposed by the winner strategy.

2.4 Experimental setup and simulation procedure

All simulations were performed in a simulated plus-maze environment (Fig. 1A) with length L between the ends of the opposite arms (in arbitrary units, see all parameter values in Table 1). All results were averaged over 100 simulated rats. The noise in the model comes from (i) pseudo-random choice in starting position and (ii) stochastic action choice, see Section 2.5 below.

At the start of a trial, each simulated rat was put in one of the starting positions (either N or S in Fig. 1A) and allowed to reach one of the goal arms (either E or W in Fig. 1A). Starting positions were chosen in a pseudo random order, while the goal position on each trial was chosen depending on the reward contingency (see Fig. 1B). For example, if the task was ‘response right’ and the starting position was S, then the goal position was set to be E. If a simulated rat started from position S (N), the entrance to northern (southern) arm from the center was blocked.

The simulated rats were tested in either strategy switches or strategy reversals. During strategy switches, different simulated rats were first trained in either place or response task (see Fig. 1B). After 200 trials of training the task was changed to the task of the other type (if it was a response task in the first phase, it changed to a place task for the second phase, and vice versa). During strategy reversals, the first phase of training was the same as during strategy switches; however, in the second phase the task was of the same type but with a different reward contingency (if it was, e.g., a ‘response left’ task in the first phase, it changed to ‘response right’ for the second phase).

Upon reaching the goal arm, the rat was given reward $R_t = R$ (see Eq. 3 below and Table 1) and a new trial started. All other actions resulted in $R_t = 0$.

An attempt to backtrack, or reaching the arm opposite to the goal arm resulted in starting a new trial (backtracks were not counted as trials).

2.5 Learning equations

Basic learning equations implemented a standard Q-learning algorithm [10] in which states and actions were encoded in the firing rates of activities of artificial neurons [12,13]. More precisely, a state s_t at time t was represented by the activities of input units $r_i^{\text{state}}(t)$, which projected via connections with weights w_{ij} to action units with activities r_i^{action} :

$$r_i^{\text{action}}(t) = \sum_j w_{ij} r_j^{\text{state}}(t) \quad (1)$$

Each action unit i represented an action a_i available in the state s_t . Activity of an action cell (Eq. 1) was interpreted as the Q-value $Q(s_t, a_t)$ of performing action a_t at state s_t . In the present notation, symbol a_i denotes i -th action available at the current state, while a_t denotes the action actually chosen at time t from the available actions, thus $\forall t \exists i : a_t = a_i$.

During learning, weights w_{ij} were adjusted on each time step according to a TD-learning rule:

$$\Delta w_{ij}(t) = \eta \delta(t) e_{ij}(t) \quad (2)$$

where η is the learning rate,

$$\delta(t) = R_t + \gamma Q^*(s_t, a_t) - Q(s_{t-1}, a_{t-1}) \quad (3)$$

is the reward prediction error and $e_{ij}(t)$ is the eligibility trace that represents the memory of past actions. The eligibility trace of a synapse [10] was increased each time the synapse had participated in generating a movement, i.e. $e_{ij}(t+1) = e_{ij}(t) + r_j^{\text{state}}$ if action a_i was performed at time t . All eligibility traces decayed with time according to $e_{ij}(t+1) = \gamma \lambda e_{ij}(t)$, where $0 < \gamma, \lambda < 1$. In Eq. 3, $Q^*(s_t, a_t) = \max_i Q(s_t, a_i)$ is the Q-value of the optimal action at state s_t .

Outcomes of different actions at different states need to be explored in order to learn action values. Exploration was ensured by choosing actions stochastically in each state using softmax algorithm, i.e. the probability of choosing action a_i at time t was calculated according to

$$p(a_t = a_i) = \exp(\beta a_i) / \sum_i \exp(\beta a_i) \quad (4)$$

with β as a constant parameter. We also tested ϵ -greedy criterion for action selection, in which an optimal action is chosen with probability $1-\epsilon$ and a random action is chosen otherwise. Results were similar to those reported here (we used $\epsilon = 0.1$).

Maze length L	7.0
Size of input populations N_{pc}, N_{ac}	13
Q-learning parameters γ, λ	0.9
Reward for reaching the goal R	10.0
Learning rate η	0.05
Softmax parameter β (selection network/strategy networks)	1.0 / 4.0
Place field width σ	0.4

Table 1. Model parameters.

3 Results

3.1 Learning switches and reversals

Learning performance was estimated by calculating a mean number of failures across training trials, for strategy switches and for reversals (Fig. 3). An outcome of a trial was defined as a failure if the simulated rat reached the arm opposite to the goal arm at the end of the trial, and a success when the rewarded arm was reached. Criterion of 80% of correct trials in the last 40 trials [8] was reached within less than 100 trials for switches and reversals (red solid lines in Fig. 3), similarly to rats. For the purposes of subsequent analysis, we defined a ‘before’ phase as the period between the trial in which the criterion was reached for the first time and the trial where task contingencies changed; an ‘after’ phase corresponded to the period after the trial when the criterion was reached after the contingency change and until the end of training (see Fig. 3A).

3.2 Activity of modeled prefrontal neurons during behavior

Next, we analyzed the activity of strategy-selective neurons during behavior. The focus was on the activity at the choice point of the simulated maze, since only at this position a difference in the activities is crucial for successful performance. During switches from a response to a place strategy, the response-strategy neuron was significantly more active than the place-strategy neuron during ‘before’ phase, while the activity pattern reversed during the ‘after’ phase (Fig. 4A). In the model, this is a consequence of the fact that for a reward contingency corresponding to response strategy, place strategy is able to correctly predict reward only in approximately half of the trials. Conversely, when the contingency corresponds to the place strategy, reward predictability of the response strategy is only about half of that of the place strategy. The activity of the strategy selective neurons in our model resembled the persistently changing cells recorded by Rich & Shapiro (2009) [8] ($\approx 24\%$ of all cells recorded from PFC during strategy switches). Persistently changing cells were defined as cells that fired at significantly different rates during the ‘before’ and ‘after’ phases.

The advantage of the experimental setup used by Rich & Shapiro (2009) is that the selectivity of neural activity to a particular strategy can be dissociated from the selectivity to other behavioral variables. To clarify this idea,

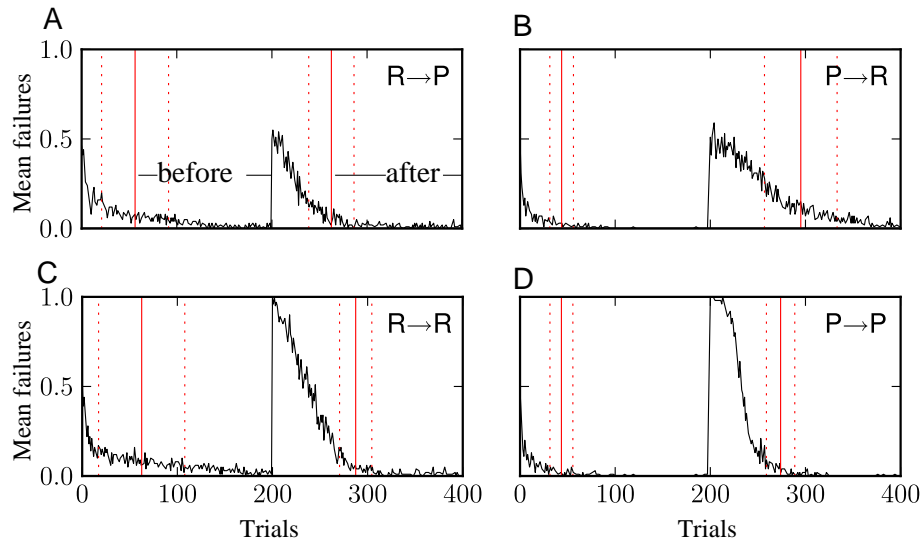


Fig. 3. Model performance during strategy switches (A,B) and reversals (C,D). Black lines show the mean number of failures as a function of trials. Red solid and dotted lines show mean trial number \pm SD at which the criterion was reached (see text).

consider all trials started in e.g., North position (see Fig. 1). When switching from, e.g., response strategy ‘turn left’ to place strategy ‘go east’, the ‘north-to-east’ path remains to be a valid (or *consistent*) path, in spite of being controlled by another strategy. In contrast, the ‘south-to-west’ path which was a valid path before the switch, becomes invalid (or *inconsistent*) after the switch. Therefore, in order to show that putative strategy-selective neurons respond specifically to strategy switches, but not to other behavioral and motor variables, one has to demonstrate that these neurons change their activity while the rat runs along the consistent path before and after the switch. This is true for strategy-selective cells in our model. In spite of the fact that on the consistent paths the simulated rats made the same turns before and after the switch, these turns were controlled by the response strategy before the switch and by the place strategy after the switch. The change in strategy is reflected by the corresponding change in the firing rate of strategy-selective cells in our model (Fig. 4B).

Conversely, putative strategy-selective neurons should fire with similar rates when strategy remains the same but behavior changes (e.g. when starting from the opposite arms of the maze). This is so in our model, as demonstrated by similar rates of response-strategy cell before the switch, when starting from different starting positions (Fig. 4C). The same is true for the place-strategy cell after the switch (Fig. 4D).

Finally, putative strategy-selective neurons should be sensitive to changes in strategy, but not to changes in reward contingency when the strategy remains the

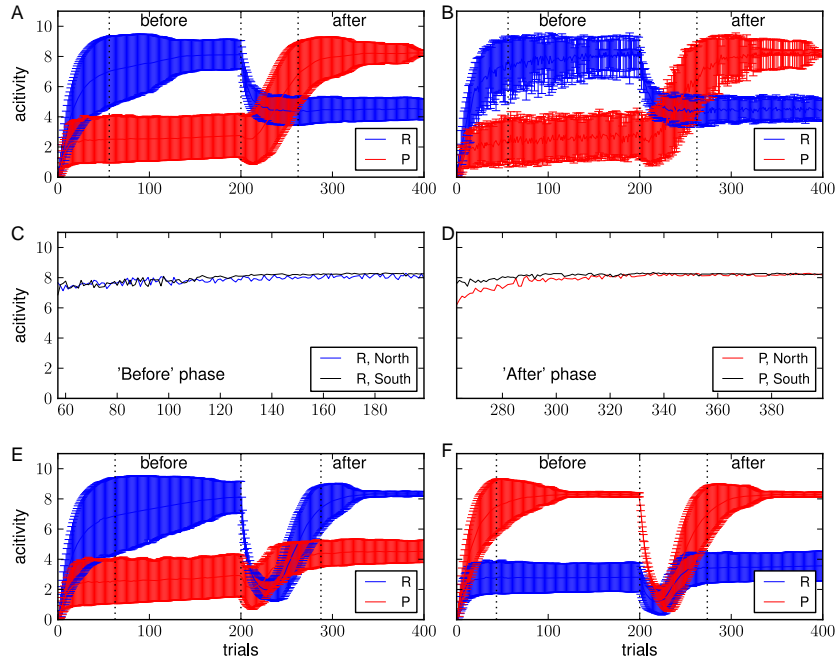


Fig. 4. Activity of the response-strategy (blue) and place-strategy (red) cells during switches (A-D) and reversals (E,F). A. Cell activity during reversal from response ('left') to place ('east') task. B. The same data as in A, but only successful trials from position N are shown (i.e., only for consistent paths). C,D. Activity of the response-strategy neuron during the 'before' phase (C) and of the place strategy neuron during the 'after' phase (D). The neural activities are grouped according to starting positions. E,F. Cell activity during response (E) and place (F) reversal.

same (as in reversals, [8]). Thus, if paths and contingency change, but strategy remains the same, as in reversals, strategy-selective neurons should fire with similar rates after the change in contingency. This is indeed so in our model, since the response-strategy cell fired with similar rates during the 'before' and 'after' phases in response reversal (Fig. 4E); similarly, the place-strategy cell fired with similar rates before and after spatial reversal (Fig. 4F). This is in contrast to the case when contingency, paths *and* strategy change, where neurons change significantly their rates as shown in Fig. 4A (the figure is similar in the case of switch from place to response strategy, not shown).

3.3 Prediction about DA activity in the PFC during strategy switches

The results above suggest that different strategies are indeed encoded in the activities of the strategy-selective cells in our model, in a manner resembling

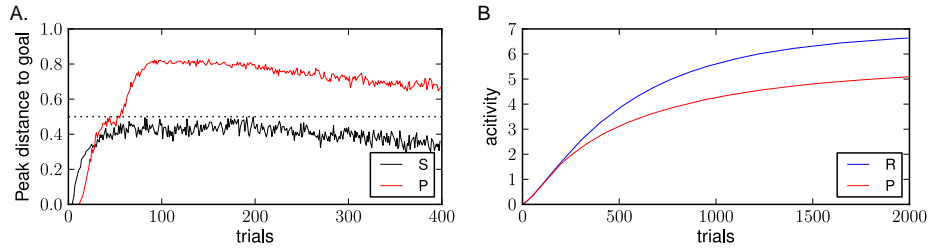


Fig. 5. A. Evolution of the distance between peak δ location and the goal across trials for place-strategy network (red) and strategy-selection network (black). The distance is measured by fractions of total distance L of the maze: 0 corresponds to reward site, while 1 corresponds to start position. The starting positions were either N or S in pseudo-random order, the goal location was fixed (E). B. Evolution of Q-values of the response strategy (blue) and place strategy (red) across trials. For this simulation, we decreased the learning rate to $\eta = 0.001$ in order to minimize the influence of noise. The starting position (south) and goal location (north) were constant for all trials.

the strategy encoding by the rat PFC neurons [8]. It is interesting to see what predictions can be derived from this simple model. The principal feature of the TD learning algorithm that is used in our model to learn strategies and strategy selection is the reliance on the reward-prediction error δ (Eq. 3). It has been hypothesized that activities of dopaminergic neurons in the VTA encode the reward-prediction error [11]. This hypothesis is supported by experimental data from conditioning experiments showing that DA activity is increased immediately after reward delivery in the beginning of learning, while after learning the increase in DA activity occurs upon the presentation of a reward predicting stimulus, i.e. before the reward is received [14]. If this hypothesis is true, then reward propagation dynamics in our model may suggest how DA activity should change during goal learning in our plus-maze navigation task

In order to describe the reward propagation dynamics, we measured the evolution across trials of the mean distance between the location where δ was maximal and the goal location for the place-strategy network and strategy selection network during a stable performance session (i.e., 400 trials with pseudo-random starting positions and a fixed goal arm). Similarly to what has been observed in the conditioning experiments [14], the peak of δ propagated from the reward site to locations closer to the starting position (Fig. 5A). In terms of DA signaling, this corresponds to the shift of a peak in DA activity away from the reward site with training. Moreover, in our simulation the peak of δ shifted further from the goal in the place strategy network than in the strategy selection network (as shown by the difference between the red and black lines in Fig. 5A). Thus, the general testable prediction derived from our model is that propagation of the peak DA signal in the prefrontal cortex will be limited by the choice point of the maze.

4 Discussion

We presented a simple model of strategy switching in the plus maze in which place and response strategies, as well as selection between those strategies, were learned using a standard Q-learning TD algorithm. The architecture of the model can be directly mapped to the architecture of neuronal networks implicated in navigation. In spite of its simplicity, the model has been able to learn successfully spatial reversals, response reversals and strategy switches in the simulated plus maze task. The learning time was comparable to the learning time of real rats in behavioral experiments [8]. Moreover, activities of strategy-selective cells in the selection model were similar to those of strategy-selective biological neurons recorded from the PFC of behaving rats. In addition, a testable prediction concerning DA signaling in the PFC has been derived from our modeling results.

There are several limitations of the presented model in relation to available experimental data concerning the role of prefrontal cortex in behavior. First, it is known that strategy switches and reversals in the plus maze are mediated by different subareas of the prefrontal cortex, medial PFC (mPFC) and orbito-frontal (OFC) cortex, respectively [6, 7]. Moreover, there is experimental evidence suggesting hierarchical organization of these two subareas [15]. In our model, both switches and reversals are learned within a single network which can be considered as a combined model of mPFC/OFC. We will address the differential roles of mPFC and OFC in future versions of the model. Second, it has been shown that when rats were trained to perform multiple strategy switches, lesions to mPFC did not impair switching performance after the third switch. These data suggest that by the third switch rats acquired a mPFC-independent strategy (possibly depending on reactive or habitual mechanisms) which allowed them to immediately switch strategy when reward was not obtained in the predicted location. Our model can not explain these data, since from the point of view of the selection network all switches are identical. Finally, our model is only partially consistent with the data suggesting that place strategy is preferred early in training, while this preference shifts towards response strategy with prolonged training [4]. In Fig. 5B, we plot the evolution of the Q-values for the response and place strategies (which are equal to the activities of strategy-selective cells in the selection network) across trials. The Q-value for the response strategy at the asymptote of training is higher than that for the place strategy, consistent with the preference for the response strategy after overtraining. However, this result is the consequence of the particular model of the sensory input that we chosen for the response-strategy network and hence is not general enough to provide a valid explanation for the experimental data. A more detailed model of sensory input (see, e.g. [13]) may be required to make a stronger claim.

The architecture of the model presented here is similar to a model proposed previously [16, 17]. However, the learning algorithm is substantially simplified and is identical in the strategy learning networks and in strategy selection network, greatly simplifying the analysis of the model. In addition, we provide a comparison between strategy selective neurons in our model with new data from experimentally recorded mPFC neurons. Finally, we note that the number of

input cells in the model can be increased without decreasing the model's performance. We used a small number of cells to speed up simulations, but any number of input cells can be used.

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