A model of hippocampal circuitry mediating goal-driven navigation in a familiar environment

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Abstract

Considerable data demonstrates a role for the hippocampus in spatial navigation. Here we present a detailed model of how the components of hippocampal circuitry might guide movement toward flexible goal locations in a familiar environment. The model contains the following features: (1) Route planning is based on the spread of activation; (2) The spread of activation is gated by environmental constraints; (3) Multiple goals are visited sequentially; (4) Spatial representation is goal-independent; (5) Place cells predict the future position by about one θ-cycle; (6) The model selects the shorter path among alternatives. This model can be further extended to address complex navigational functions.

Key words: Goal-driven navigation; Hippocampus; Computational modeling

Many models have focused on the role of the hippocampus in spatial navigation toward particular goal locations [2–4,7]. However, most previous models utilize the same long-term memory representations for both the spatial environment and the goal location. For example, the strength of CA3 recurrent connections might depend upon the direction to the goal [2,7] or output connections from hippocampal place cells are directly modified to store the direction to the goal [3,4]. These representations would be very difficult to utilize in navigation tasks where goal location changes on a regular basis – as in the 8-arm radial maze [12], or the Morris water maze [11] with day to day changes in platform location.

Recordings show that at least in rodents many of hippocampal neurons have spatial receptive fields. These place cells were identified in all regions of the hippocampus and dentate gyrus [10], as well as in the entorhinal cortex [13], the subiculum [14], and parasubiculum [15]. Evidence suggests that the hippocampal place code preserves the topology of adjacent locations at the cost of absolute distance, and, therefore, the hippocampal formation itself is responsible for route following navigation [16].

Our model utilizes pathway based representations of the environment, which can be flexibly used to navigate toward any arbitrary goal or multiple goals that change on a trial by trial basis. This is obtained through the use of a set of learned pathways through the environment, with spread of activation along these pathways initiated within the network dependent upon goal locations and current location.

In addition, experiments have demonstrated that a number of physiological variables in these areas show phasic changes relative to hippocampal θ rhythm. Here, a combined model of the hippocampus and entorhinal cortex describes the θ-linked rhythmic interaction of these regions for guiding goal-directed spatial navigation in behavioral tasks.

1 Method

The general theoretical foundations for the model were discussed in the greater detail elsewhere [9]. Here we attempt to lay the ground work for the full scale implementation of that model, as well as to test the simplest performance-related functionality. The model is focusing on the activity in entorhinal cortex (EC) and hippocampal regions CA3 and CA1, and contains five major and four supplementary neural fields depicted in Figure 1. Corticohippocampal connectivity employed by the model was more extensively studied in monkeys [1], but we assume that functionally similar connections exist across species.

The model makes one step through the environment per θ cycle. Each cycle the activity of the goal cells in prefrontal cortex drives the activity spreading in EC-III. This spread is gated by the environmental constraints (adjacency of the locations on the path in the simplest case discussed here, but it can be expanded to accommodate additional information in future) provided by postrhinal cortex. As soon as the cell in EC-III that corresponds to the current location gets activated, its activity allows the current location representation from posterior parietal cortex to activate the corresponding EC-II cell. EC-II activation propagates to CA3, and also provides the feedback to EC-III, which prevents the further spreading of activation in the neighborhood of current location, so that only the adjacent locations that belong to the first
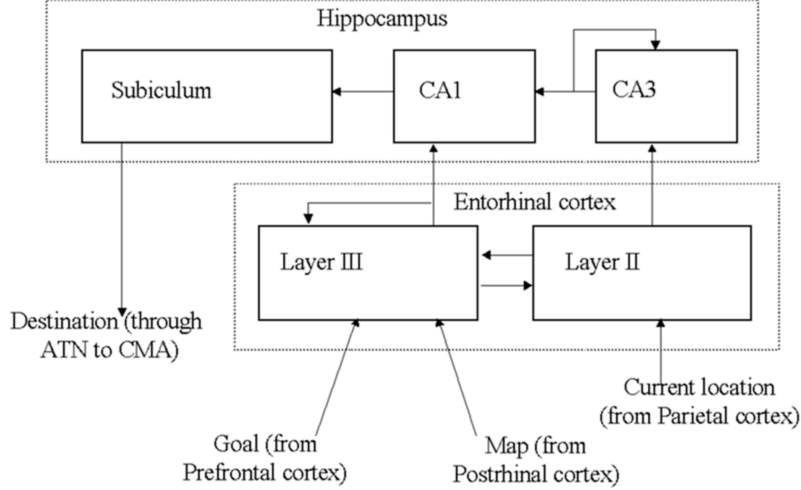
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Fig. 1. Five major neural fields of the model are shown with the employed connectivity. Three supplementary fields: prefrontal, parietal, and perirhinal cortices provide goal locations, map of the environment, and current location, respectively. The fourth supplementary field, medial septum, is omitted from the figure and is used for system self-regulation. Anterior thalamic nucleus (ATN) and cingulate motor area (CMA) are assumed to be the targets for the output of the model, but are not explicitly implemented.

found (and most likely the shortest) path to the goal are activated.

CA3 receives the current location from EC-II and starts the forward signal propagation to activate the possible paths from the current position. This activity reaches CA1 where it is compared with the EC-III activity reaching CA1 directly. The match between forward spread in CA3 and backward spread from goal in EC-III indicates the preferred path to the nearest goal. CA1 activation then reaches the subiculum, where it serves as a drive for the competition between adjacent locations to select the next step. When the next location is selected, it signals the model to move there. This cycle repeats itself as long as there are active goal cells in the representation of prefrontal cortex.

For the simulation we used the W-maze environment replicating the experimental settings of Frank et al [6]. Cells in EC-III and CA3 were implemented as membrane shunting equations, and subiculum cells as a recurrent competitive field equation. Due to lack of space we omit the discussion of the equations here. All cells were continuous firing rate neurons with the signal representing the current firing rate as a fraction of a maximal firing rate and ranging from 0 to 1. These signals were recorded by the means of KInNeSS [1] (custom package developed in our lab) and plotted using kpl.

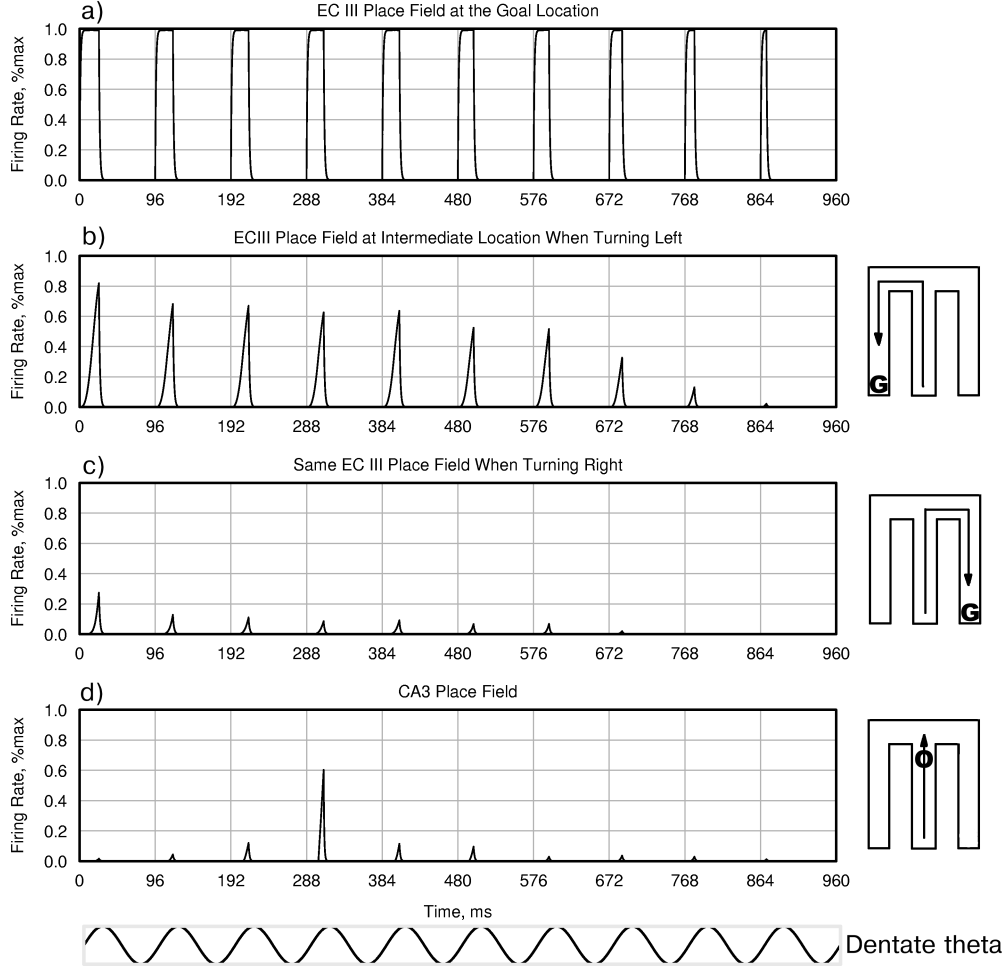[1] KDE Integrated NeuroSimulation System

Fig. 2. Several examples of cell activations in the model. All panels show 10 consecutive θ cycles (each cycle was 96 ms) of the animat moving along the path from central arm. At $t \approx 400$ ms it makes the decision whether to turn left or right. Panel a shows the entorhinal pyramidal cell driven by the prefrontal (goal) input. Panels b and c both show another entorhinal place cell responding to the movement from the central arm to the left and to the right arms, respectively. Panel d shows the CA3 place cell activity with the place field one step before the intersection (marked with O on the map).

2   Results

The model performed two simple tasks: selecting the arm with the reward versus non-rewarded arm while moving from the central arm, and selecting the arm with the reward positioned closer to the intersection first and visiting the remaining reward afterwards. In both cases the model performed as expected. Examples of the cellular activations recorded along the path are presented at Figure 2.

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3 Discussion

The prefrontal drive influences the firing of the place cell in EC-III that corresponds to goal location and makes it stronger, but as the topmost panel of the Figure 2 shows, the activity of this cell remains current position-dependent, decreasing along the path, which makes this prefrontal drive harder to verify experimentally.

As the comparison of the panel d with other panels in Figure 2 shows, the model is consistent with the evidence for highly localized place cell representations in region CA3 and CA1 and more distributed place cell representations in the entorhinal cortex [6]. Moreover, the two middle panels demonstrate the phenomenon of "predictive coding" described by Frank et al [6].

In addition, the model uses activity timing dependent upon the relative timing of θ frequency oscillations in the hippocampus, which appear during exploration [5] and are phase locked to stimulus acquisition in working memory [8]. Due to simplicity of the current implementation, phase precession is weak, but noticeable in the bottom panel of Figure 2.

4 Conclusion

The success of the current simple implementation of our model encourages us to continue its development and incorporate the learning procedures to make the model able to explore novel environments and memorize the goal locations there. These modifications will make this model a full scale implementation of the theoretical background provided by Hasselmo et al [9].

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