The Hippocampus and spatial representation

Aims

• Introduce the hippocampus and place cells

• Explore an unsupervised, competitive learning model of place cells (Sharp, 1991)

• Discuss subsequent experiments emphasising importance of boundaries to place cells, and a fixed feed-forward model sufficient to explain place cell firing (Hartley et al., 2000)

• Revise the model to accommodate results suggesting place cell stability and robustness requires synaptic plasticity (Barry and Burgess 2007)
The Hippocampal Formation

Hippocampus with its subfields (DG, CA1,2,3)
Entorhinal cortex
(Parahippocampal cortex)

Importance of the Hippocampus: Oliver Sacks and Jimmie G

"isolated in a single moment of being.... he is a man without a past
(or future), stuck in a constantly changing, meaningless moment”
(Sacks, 1985)
In-vivo electrophysiology

Recording single neurons in behaving animals

Single neuron responses in the hippocampal formation

Head-direction cells
allocentric orientation
Papez' circuit

Place cells
allocentric location, Hippocampus

Grid cells
path integration, Entorhinal cortex

Boundary/Object Vector cells
allocentric direction and distance of objects/boundaries

In humans too!
Robertson et al. 1999; Ekstrom et al. 2003; Jacobs et al. 2010; Doeller et al. 2010; Horner et al. 2016; Shine et al. 2019
Place fields are receptive fields (for location)

Compare to well known receptive fields in sensory space

Place cells
Some properties of place cell firing

1. Firing is independent of the rat’s orientation in open but not narrow-armed mazes

2. Firing is robust to the removal of sensory cues

Recap: Unsupervised, competitive learning

- ‘Winner-takes-all’: For each input pattern $x^n$, output $o_k$ (i.e. $h_k > h_i$ for all $i \neq k$). Set $o_k = 1$, $o_i = 0$ for all $i \neq k$
- Random initial connection weights. All-to-all connectivity
- Hebbian learning: $W_{ij} \rightarrow W_{ij} + \varepsilon o_i x_j^n$
  i.e. $W_{ij} \rightarrow W_{ij} + \varepsilon x_j^n$, other weights don’t change where $o_i = 0$
- Normalisation: reduce total size of connection weights to each output (so $|W_j| = 1$) by dividing each by $|W_j|
- Process repeats with presentation of each input pattern

The output whose weights are most similar to $x^n$ wins and its weights then become more similar. Different outputs find their own clusters in input data

Rumelhart and Zipser 1986.

PDP book freely available on J. McClelland’s website
Sharp’s (1991) place cell firing model

The hippocampus and spatial representation

Simulated place cell firing is resistant to cue-removal

The hippocampus and spatial representation
Sharp’s (1991) model continued

Simulated place cells are omni-directional only after random exploration and not following directed exploration

Summary

• Sharp’s competitive learning model explains robustness and directionality of place fields
What are the inputs to place cells?

Other place fields appear to respond at fixed distances from walls, with nearer walls more important than further ones.

O’Keefe and Burgess, 1996
The hippocampus and spatial representation

BVCs as hypothesised inputs to place cells

• Each BVC tuned to respond when a barrier lies at a specific distance from the rat in a particular *allocentric* direction

**Boundary Vector Cell (BVC)**

Hartley et al. 2000

BVCs as hypothesised inputs to place cells

• BVC firing determined by product of two gaussians, defining distance and angle tuning to boundary:

\[
g_i(r, \theta) \propto \exp\left[-\frac{(r - d_i)^2}{2\sigma_{rad}^2(d_i)}\right] \times \exp\left[-\frac{(\theta - \phi_i)^2}{2\sigma_{ang}^2}\right] \times \frac{1}{\sqrt{2\pi \sigma_{rad}^2(d_i)}} \times \frac{1}{\sqrt{2\pi \sigma_{ang}^2}}
\]

• Sharper tuning for shorter distances, reflecting uncertainty in inputs to BVCs

Hartley et al. 2000
A fixed, feed-forward model of place cells from BVCs

Place fields are modelled as the thresholded sum of 2 or more BVC firing fields.

Modelling O’Keefe and Burgess 1996 with BVCs

2-4 BVCs orientated at right angles to one another and thresholded are sufficient to fit most fields.
BVCs predict boundary-referenced firing of PCs across environments

1. Record some place cells
2. Find BVCs that best fit those place cells
3. Use those model BVCs to predict firing in other environments
4. Record same cells in predicted environments

Data (Lever et al)
Model
BVCs

Discovery of BVCs

Importance of synaptic plasticity to place field stability

- Synaptic plasticity the putative biological instantiation of weight-updating.
- ‘Vanilla’ plasticity requires NMDA receptors.
- Place field stability falls when NMDA receptors are blocked:

```
Saline

CPP (NMDAR antagonist)
```

*Kentros et al. 1998*

Importance of synaptic plasticity to place field stability

- Robustness of place fields to cue removal also depends on NMDA receptors.

```
Saline

CPP (NMDAR antagonist)
```

*Nakazawa et al. 2002*
Slow, experience-dependent changes to place fields

Lever et al. 2002

Likely reflect synaptic plasticity. Can’t be explained by a ‘fixed’ model.

Summary

• Sharp’s competitive learning model explains robustness and directionality of place fields

• Subsequent results showing place cell firing is determined by geometry of environmental borders can be explained by a simple feed-forward model, given that boundary vector cells are the inputs to place cells

• But, such models cannot account for long-term dynamics of place fields in similar environments, nor the importance of synaptic plasticity in place field stability
Extended BVC model: added learning

• **Update weights using BCM rule**

  requires pre & post-synaptic activity ($x_j$ and $y_i$)
  reduction if post-synaptic activity low
  increase if activity high

  $y_i = f(\sum_j w_{ij} x_j)$
  $\Delta w_{ij} = x_j \phi(y_i, \theta)$
  $\theta \sim <y_i^2>$

  $\phi(y_i, \theta)$

  Post synaptic activity $y_i$

  Barry & Burgess (2007)

Extended BVC model: added learning

BVC firing  →  Calculate place cell firing  →  Update weights with BCM

Iterations 20 40 60 80 100

4.7 3.3 3.8 4.0 4.3

The hippocampus and spatial representation
The hippocampus and spatial representation

Extended BVC model: added learning

<table>
<thead>
<tr>
<th></th>
<th>Iterations</th>
<th></th>
<th>Iterations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>5.7</td>
<td>3.7</td>
<td>3.9</td>
</tr>
<tr>
<td></td>
<td>4.9</td>
<td>2.8</td>
<td>3.6</td>
</tr>
<tr>
<td></td>
<td>6.5</td>
<td>2.8</td>
<td>2.8</td>
</tr>
</tbody>
</table>

Extended BVC model: added learning

<p>| | | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>day2</td>
<td>21.1</td>
<td>17.2</td>
<td>14.2</td>
<td>18.4</td>
</tr>
<tr>
<td>day9</td>
<td>21.2</td>
<td>9.3</td>
<td>20.0</td>
<td>21.1</td>
</tr>
</tbody>
</table>

Barry (2006)
Summary

• Sharp’s competitive learning model explains robustness and directionality of place fields

• Subsequent results showing place cell firing is determined by geometry of environmental borders can be explained by a simple feed-forward model, given that boundary vector cells are the inputs to place cells

• But, such models cannot account for long-term dynamics of place fields in similar environments, nor the importance of synaptic plasticity in place field stability

• Combining the feed-forward BVC model and BCM learning accounts for long-term remapping