The Hippocampus as a Cognitive Map II

modern models

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Computational Models of Neural Systems

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Outline

Data

Unifying ideas

The Burgess/Recce/O'Keefe model

The Redish/Touretzky model (CRAWL)

Comparing the two models

Data

Place cells

Phase coding

Head direction cells

Path Integration

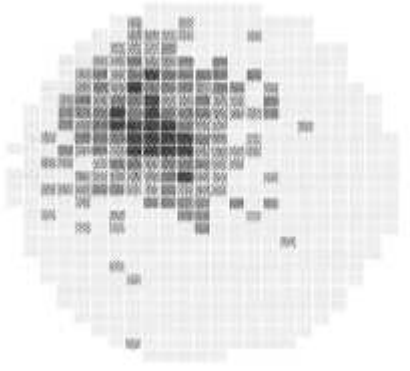
Behavior

learning a goal location

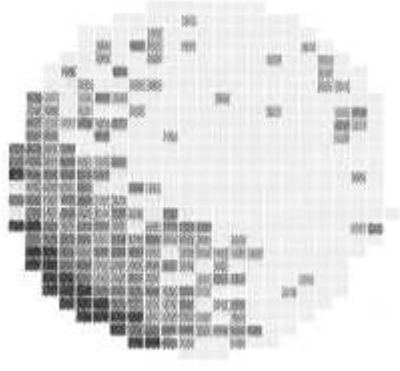
- using distal cues
- using local cues

Place cells

CA3/CA1 pyramidal cells



A sample place field.



A typical *crescentic* place field

Place cells - data

- compact, continuous place fields
- one field/cell/environment
- responsive to sensory cues
- continue to show place fields in the dark
- set of all place cells cover the environment

Place cells - phase coding

Terms

EEG

Measure of extracellular current flow of large ensembles of neurons

θ-rhythm

5-12 Hz. oscillation occurring during walking, running, swimming

LIA

Less coherent oscillation occurring during grooming, eating, staying stationary.

Place cells - phase coding

[Burgess fig 3]

When a rat on a linear track runs through a place field, the cell fires groups of spikes, with each successive group occurring at an earlier phase of the θ cycle.

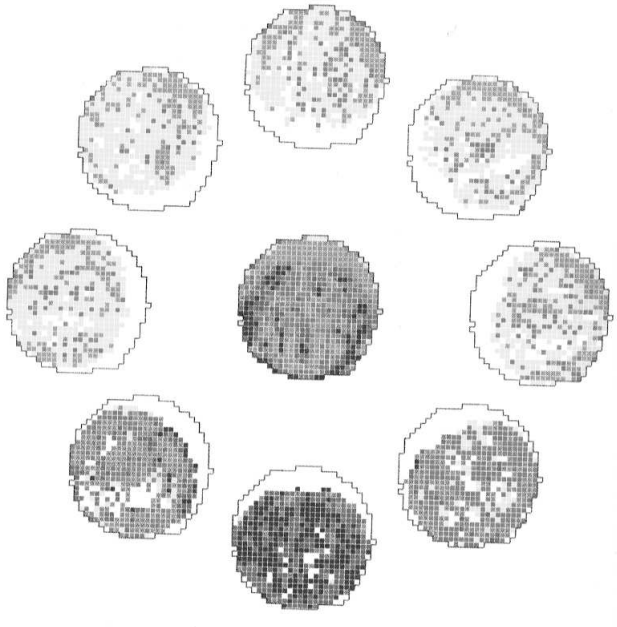
[Burgess fig 4]

This means that place fields firing **early** in the θ cycle are behind the rat, and **late** in the θ cycle are ahead of the rat.

Head direction cells

Found in

- subiculum
- pre- and post-subiculum
- lateral dorsal nucleus of the thalamus (LDN)
- anterior thalamic nuclei (ATN)
- (also striatum and parietal cortex)



A sample head direction cell.

Head direction cells -- data

- Constant preferred direction in an environment.
- Constant relation to other HD cells across environments.

Path Integration

Rodents maintain a vector from *current* position to a *home* position.

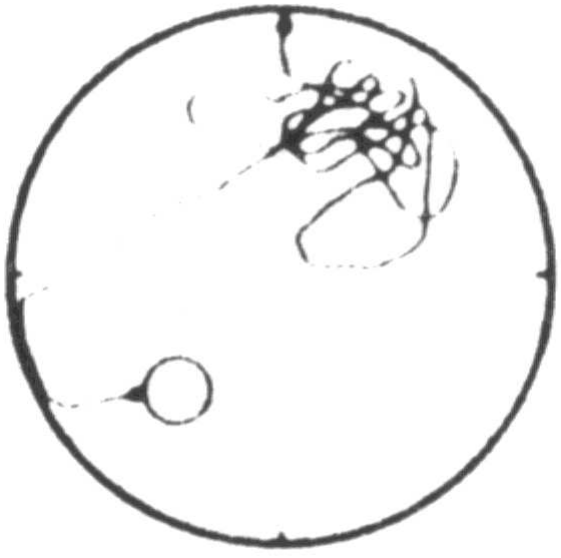
- Gerbils searching for pups take a circuitous route, but when they find them, they return directly home.
- If the nest is moved, they search where the nest was, ignoring the strong sensory cues of the displaced nest.

The neural basis of path integration is unknown at present, but any such representation must enable vector arithmetic.

Path integration presupposes a reliable directional sense.

Behavior: locating a goal

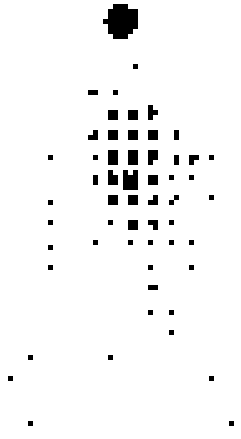
Distal cues



An animal trained to find a platform in a milky water-filled arena.

Behavior: locating a goal

Local cues



Histogram of search time of a gerbil trained to find food at a constant distance and bearing to a single landmark. (Collett et al. 1986)

Unifying ideas

- Place fields formed by multi-dimensional radial basis functions.
- The collection of all place cells in an environment produce a *Place code*.
- Place code used in navigation.

  Compare to Hippocampus in memory models (mostly primate literature).

- The collection of HD cells produces a *Head direction code*,

- Multiple spatial representations
- Interacting spatial representations

Burgess/Recce/O'Keefe

[Burgess fig 5]

The model

Key points

- Phase coding in entorhinal cells drives phase coding throughout model.
- Phase coding produces a "sweep" through space of activity in the place code.

θ *cycle*	**Early**	**Middle**	**Late**
Active place cells	Behind the rat	Centered at the rat	Ahead of the rat

- Very broad place fields adjacent to the goal drive navigation.

Burgess: cell types

Sensory input cells

Tuned to distance from a single landmark.

Entorhinal cells (ECs)

Activity: broad place fields at centroids of pairs of widely separated cues

Phase coding:

[Burgess figure 9]

Phase coding in ErC

Analogous to sensory sweep?

Evidence relating θ to whisker sweeping?

Burgess: cell types

Place cells (PCs)

Activity:

5 blocks of 50 PCs each

4 max. of each block are active

performing an *and* operation

(k of n conjunction)

Phase coding: Driven by ECs

Learning:

Seeded by random connections,

hebbian learning.

Subicular cells (SCs)

Activity: 10 blocks of 25 SCs each, same as PCs

performing an *or* operation

Phase coding: Driven by PCs

Learning: same as PCs

Burgess: cell types

Head direction cells (HDCs)

Goal cells (GCs)

Activity: Very broad position of animal, incorporating all of environment in one direction from goal.

Phase coding: None.

Burgess: Learning at the goal

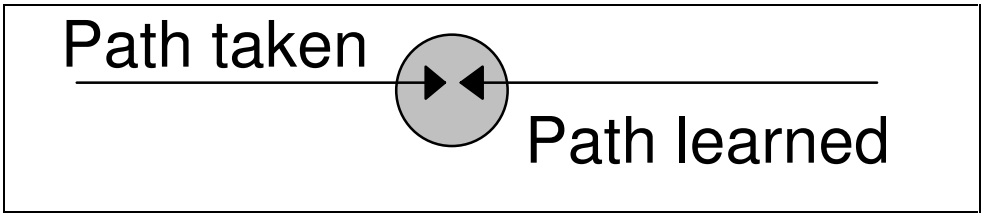
Head direction cells gate enhancement of subicular cell → goal cell synapses.

Only synapses ←subicular cells firing **late** in the θ cycle are enhanced.

Only synapses → the goal cell corresponding to the current head direction are enhanced.

Implies

- what is learned is not the path followed but the path ahead.



- in order to learn to approach goal from all directions, must look in all directions from goal. **Not** must approach goal from all directions.

Burgess: navigation

ECs have broad sensory dependent place fields.

PCs have small localized place fields.

PCs localize the animal.

SCs have broad place fields.

GCs have very broad place fields to one side of goal.

Each GC suggests a direction to the goal.

By taking the weighted directional mean of the GC directions, can decide **direction** to goal.

Burgess: strengths

- ECs have broad sensory dependent place fields.
- PCs have small, less sensory dependent place fields.
- Direct model of behavior (navigation).

Burgess: weaknesses

- PCs will not fire in the dark.
- Very limited model of navigation.
- Distances to distal cues are used.
- No evidence for GCs.
- Evidence for SCs weak.
- Requires goal cells to cover entire environment to one side of the goal.
- What does the place cell-subicular cell sequence contribute to the model?

Burgess: predictions

- Phase relationship of Entorhinal Cells and sensory cues.
- Very broad place fields in subicular cells.
- "Goal" cells one synapse beyond SC.
- If the rat cannot look around from the goal location, its navigation to the goal will be less accurate.
- If the rat has place cells for the whole environment but is only allowed to look from the goal in a single direction, it will only learn to approach the goal from that direction.

Redish/Touretzky (CRAWL)

The model

Key points

Four spatial representations:

- Head direction
- Local View
- Path Integration
- Place code

Place code associates path integrator coordinates and local view.

CRAWL: Representations

Head direction (HD)

Representation of head direction, Φ_h

Local view (LV)

Non-neural representation of local landmarks.

$$\langle T_i, r_i, \phi_i \rangle$$

T_i = type of landmark i

r_i = distance to landmark i

ϕ_i = allocentric bearing to landmark i

Path integrator (PI)

Representation of position in coordinate system that enables vector addition.

$$\mathbf{C} = \langle x_p, y_p \rangle$$

CRAWL: Place code

Place code (PC)

Conjoint representation of LV and PI.

$$A(u) = C(u) \lozenge F_1(u) \lozenge F_2(u) \lozenge \ldots \lozenge F_n(u)$$

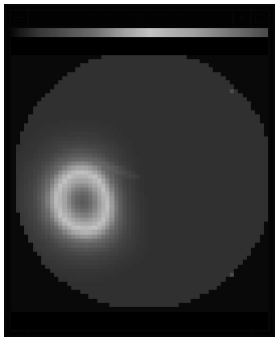
$\lozenge$ = multiplication with the ability to drop out terms

C(u) = gaussian tuning (radial basis function) to path integrator coordinates

$F_i(u)$ = gaussian tuning (radial basis function) to feature:

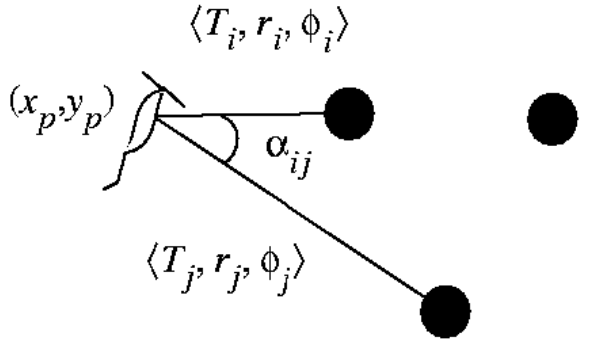
- distance to landmark
- allocentric bearing of landmark
- angle between landmarks

A sample place field



CRAWL: Training the model

Requires that an environment be *familiar*, that is that there exist a place code that suitably covers the space.



Recruiting a place cell.

CRAWL: Self-localization

Path integrator coordinates unknown.

Place units driven by local view.

Set path integrator to weighted average of place unit "coordinates".

Set tuning to C(u) to very large number.

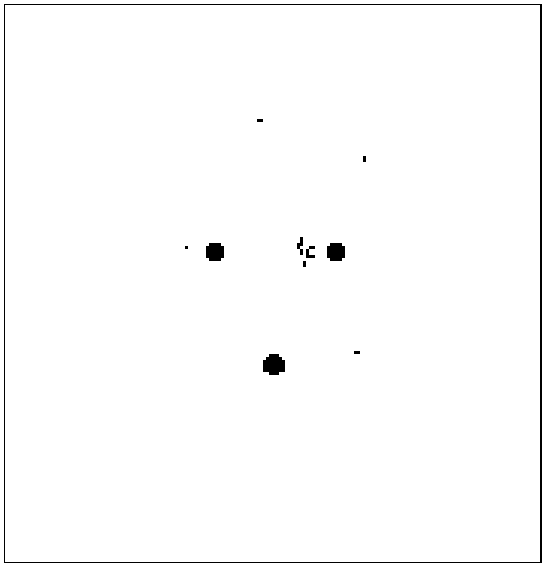
Activate place units.

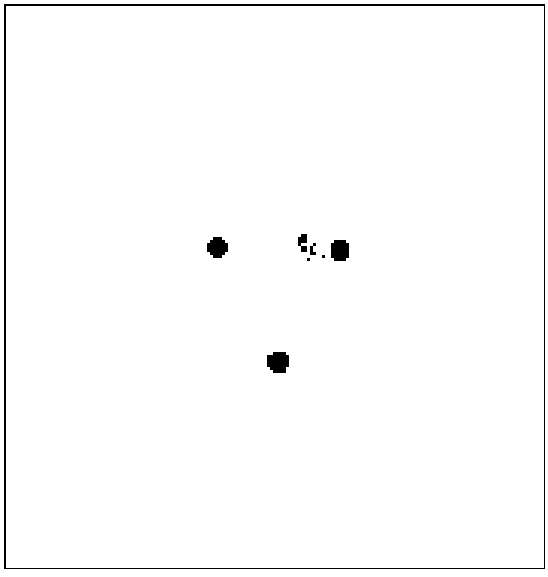
Calculate PI coordinate value.

Shrink tuning to C(u).

If tuning to C(u) above normal continue...

CRAWL: Parallel relaxation for self-localization





CRAWL: Results

No explicit behavior.

Enter at a random position

Localize self

Predicts goal location

Repeat 100 times.

Histogram goal predictions.

Sample results slides.

CRAWL: Strengths

Replicates both neurophysiological and behavioral results.

Explicit about interactions of multiple spatial representations.

General navigation applicability.

Explains place cells firing in the dark.

CRAWL: Weaknesses

Does not model learning of place code.

Non-neural representations in path integrator, local view, and head direction.

No explicit model of behavior.

CRAWL: Predictions

- Viewing the self-localization procedure

  On re-introduction into a familiar environment, the place code should be initially inconsistent. After some (short) time, the place code will return to being consistent. In ambiguous environments, place cells should show a multi-modal distribution of activity during the transitory initial period.

- Shifting goal locations

  The place code should shift **before** the animal changes goal locations.

Comparison: Similarities

- Hippocampus used for navigation.
- Place cells form place code.
- Head direction cells form head direction code.
- Incorporates both neurophysiological and behavioral results.

Comparison: Differences

Burgess et al.	CRAWL
Place cells driven by direct sensory stimulation of Entorhinal cells	Place cells driven by non-neural *Local view* and *Path integrator*
Phase coding	No phase coding
Explicit navigation	No explicit navigation
Uses distal cues. (Note: This theory breaks down when applied to local cues.)	Uses local cues (Note: This theory has been applied to other exps that use distal cues.)
Matched to general behavioral ideas	Matched to actual behavioral experiments
Matched to general neurophysiological ideas	Matched to specific neurophysiological results
No separate learning and recall stages	Separate learning and recall stages
Explicit learning mechanisms	No explicit learning mechanism