Explaining heterogeneity in medial entorhinal cortex with task-driven neural networks

Aran Nayebi

neuromatch conference

NMC4
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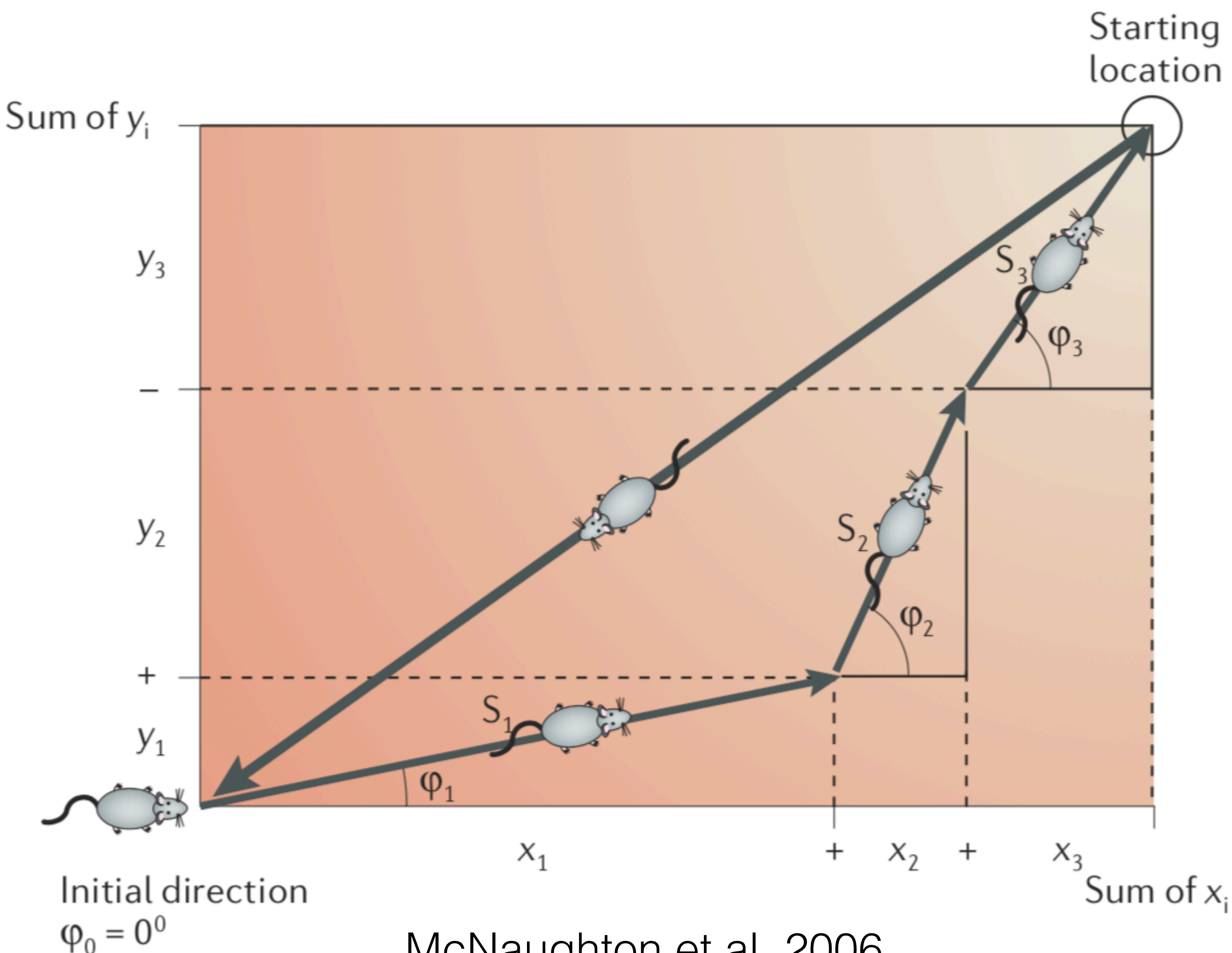
NeurIPS 2021 Paper: https://www.biorxiv.org/content/10.1101/2021.10.30.466617
Code: https://github.com/neuroailab/mec

Hippocampal-Entorhinal Spatial Map



McNaughton et al. 2006

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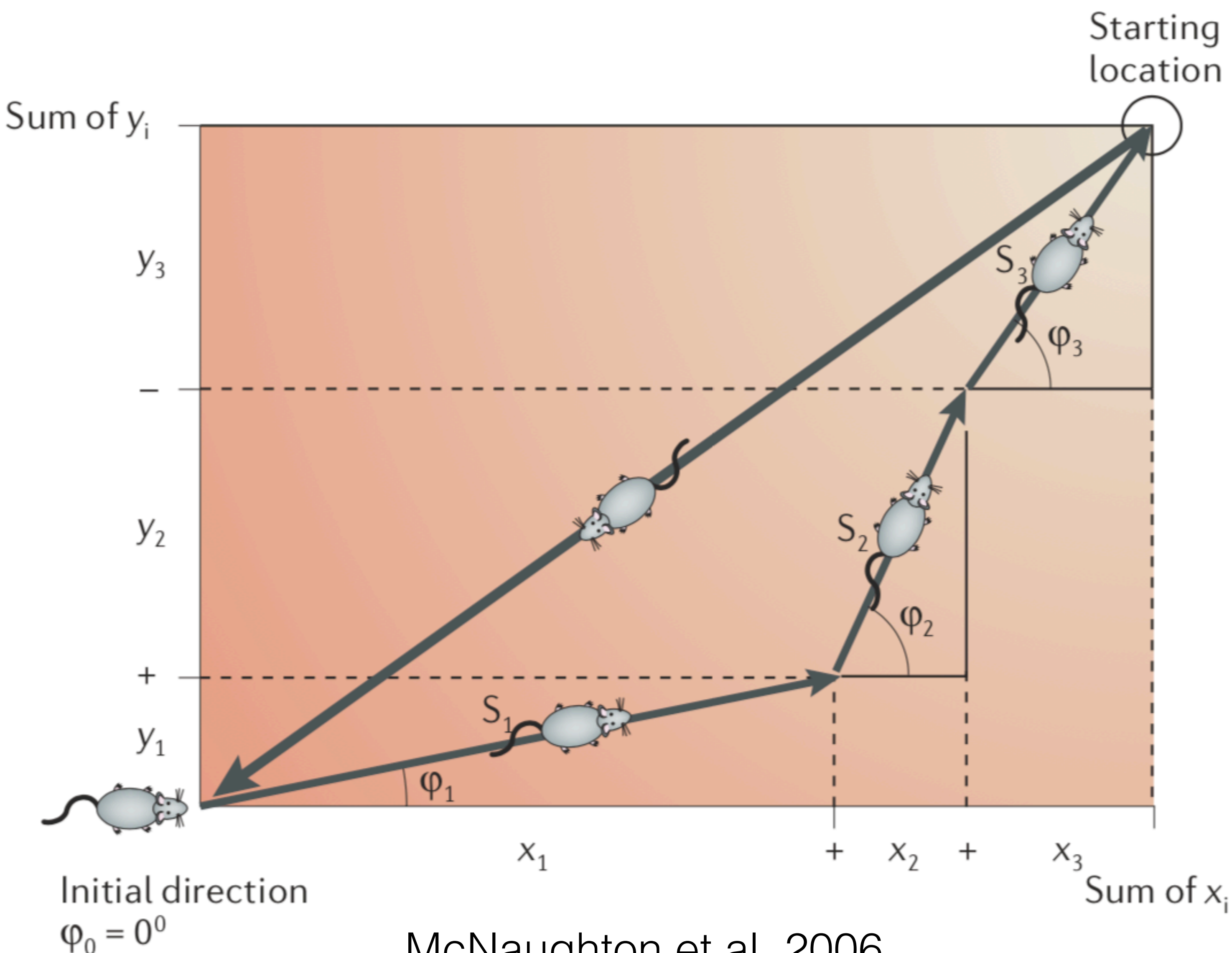

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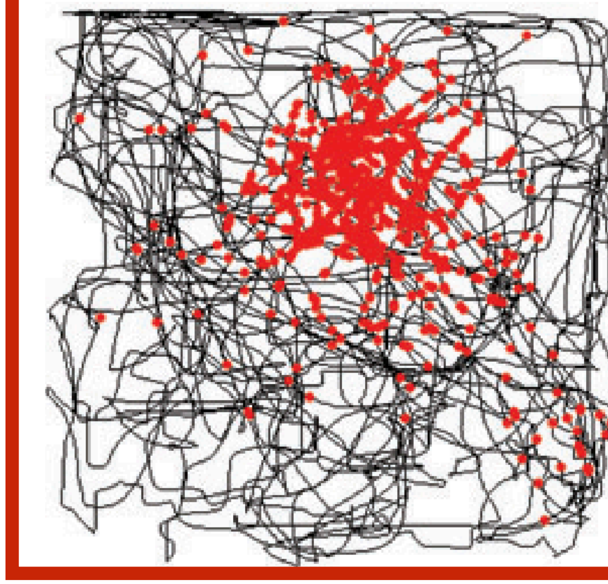
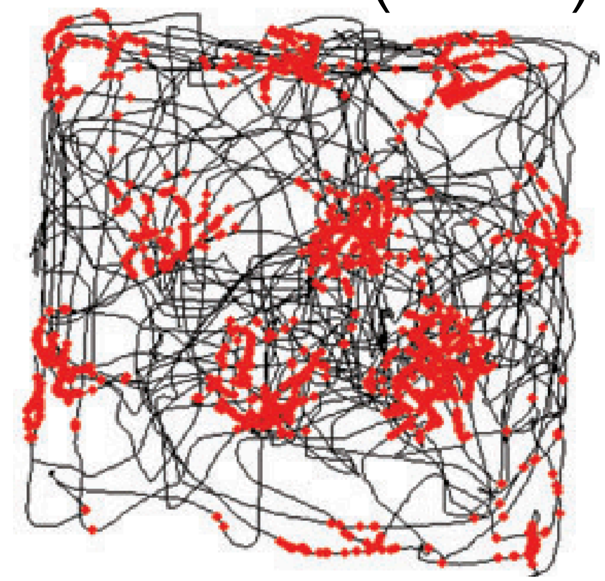
Place Cell (HPC)



Grid Cell (MEC)



Moser et al. 2008

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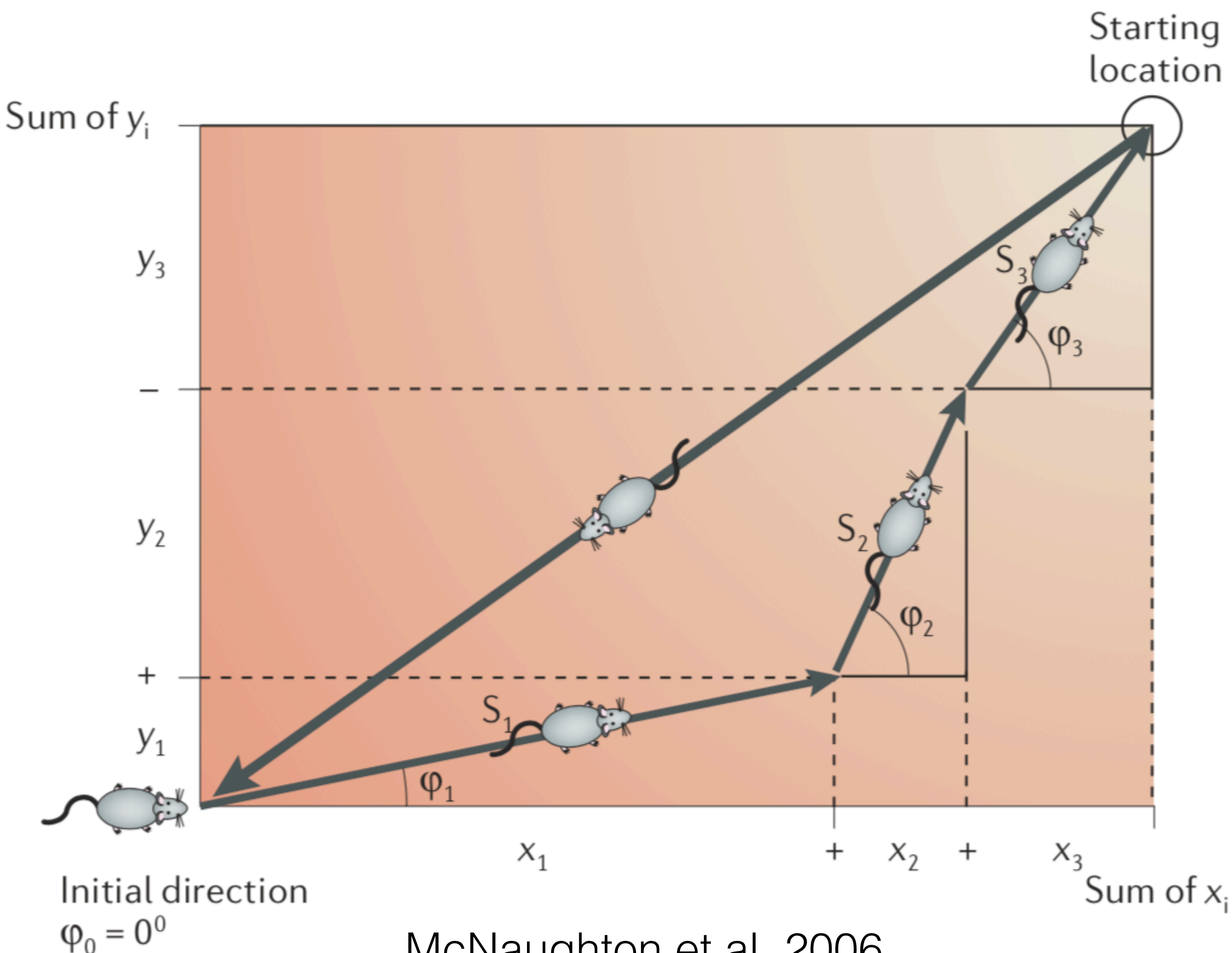

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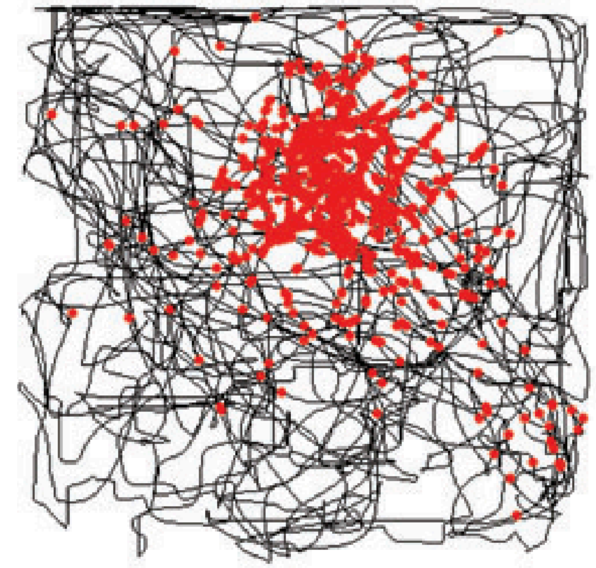

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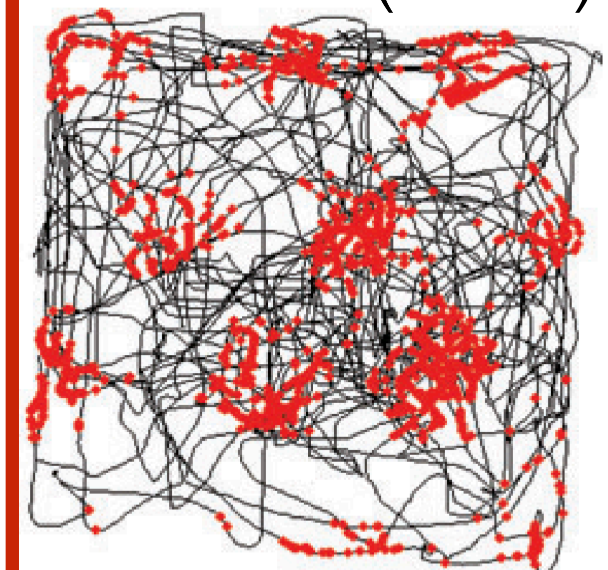

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Accounting for heterogeneous code?

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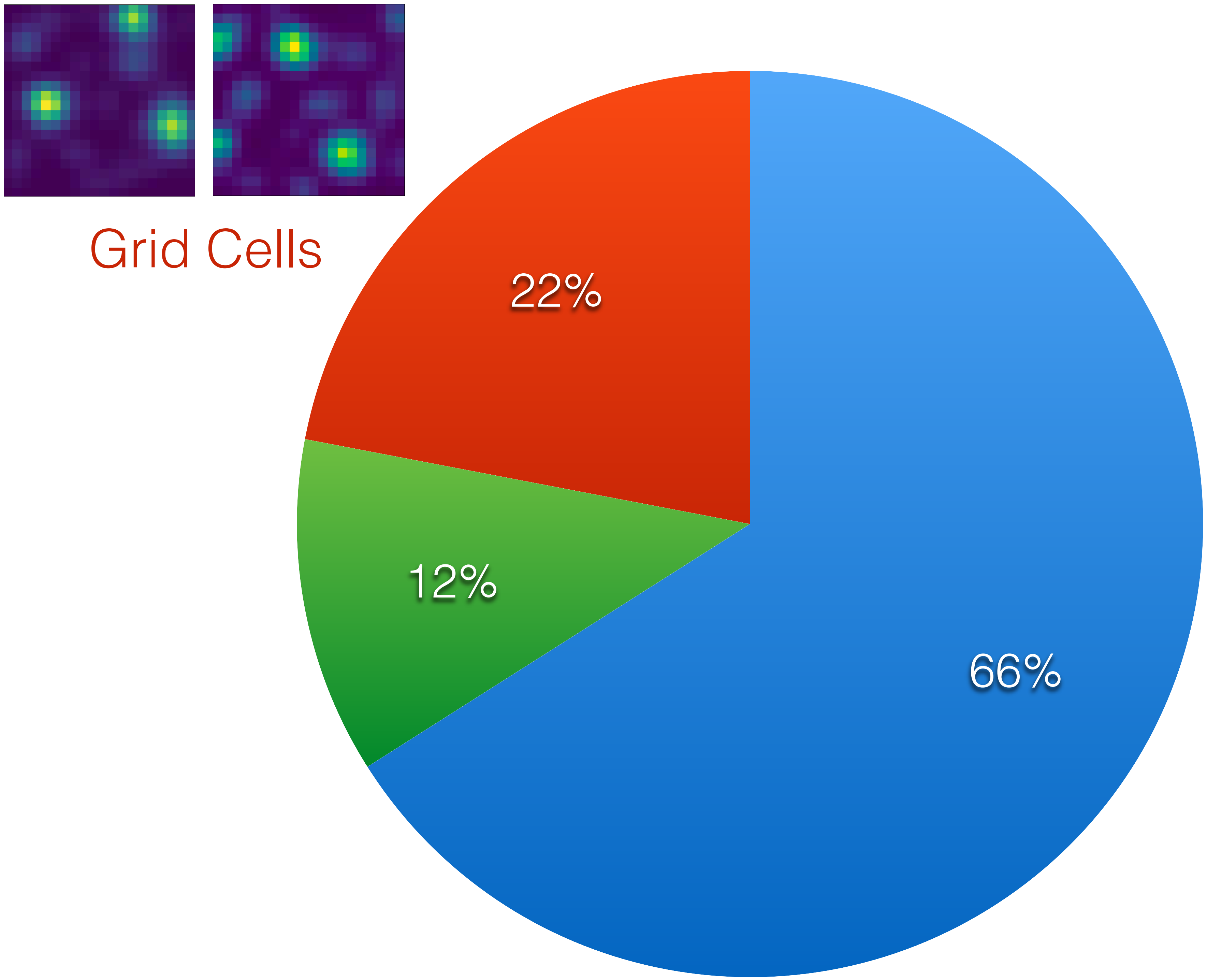

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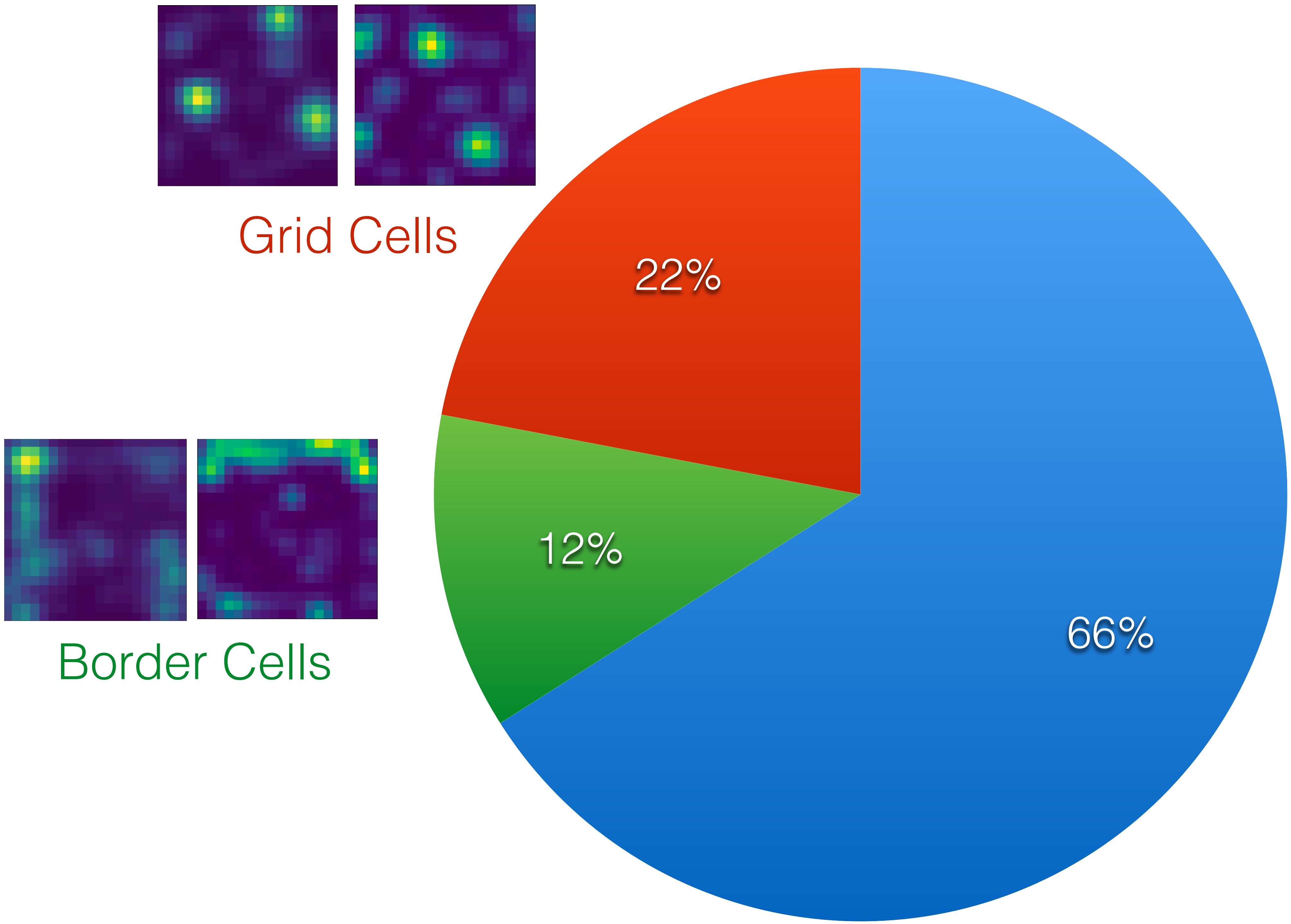

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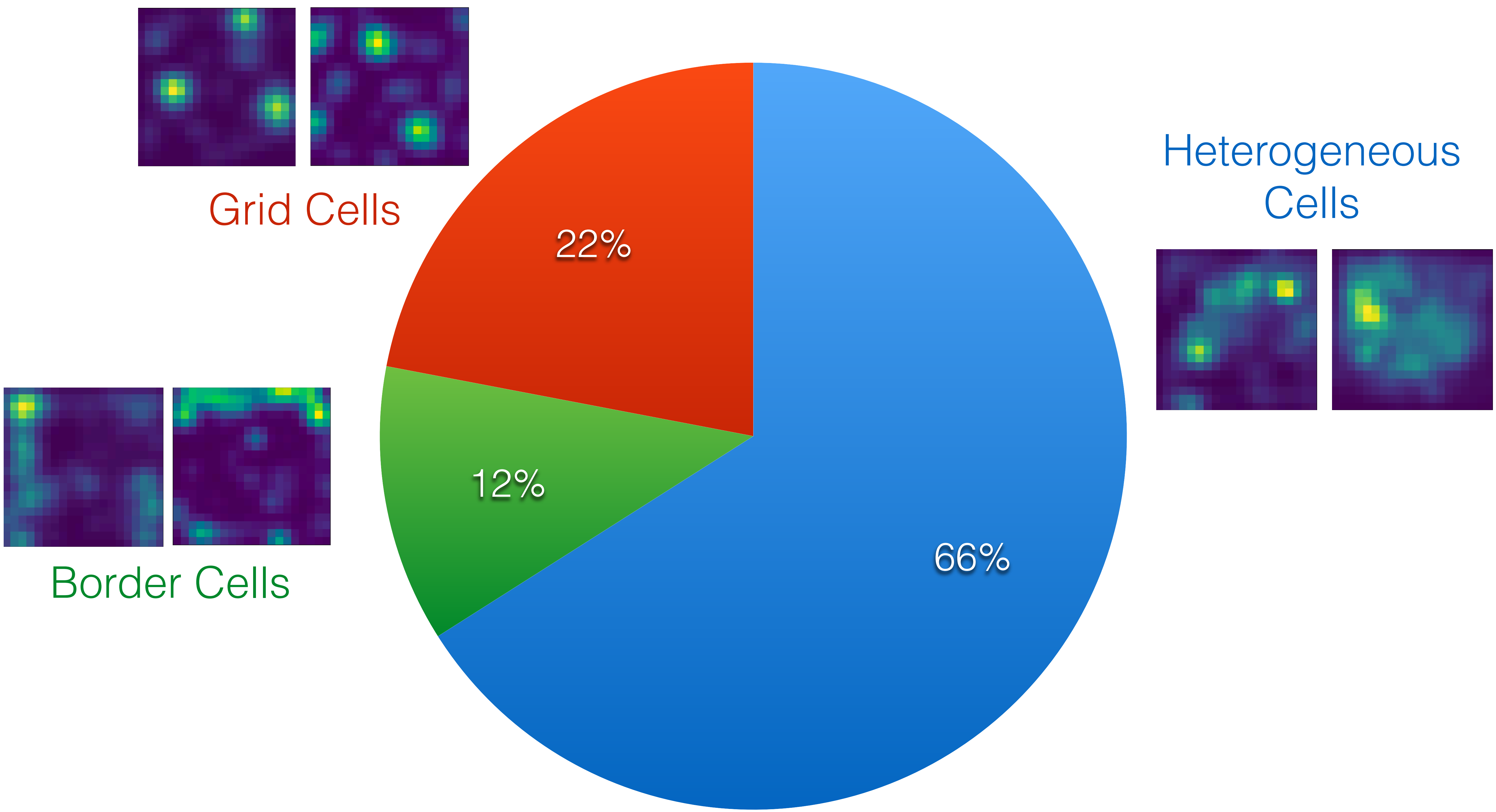

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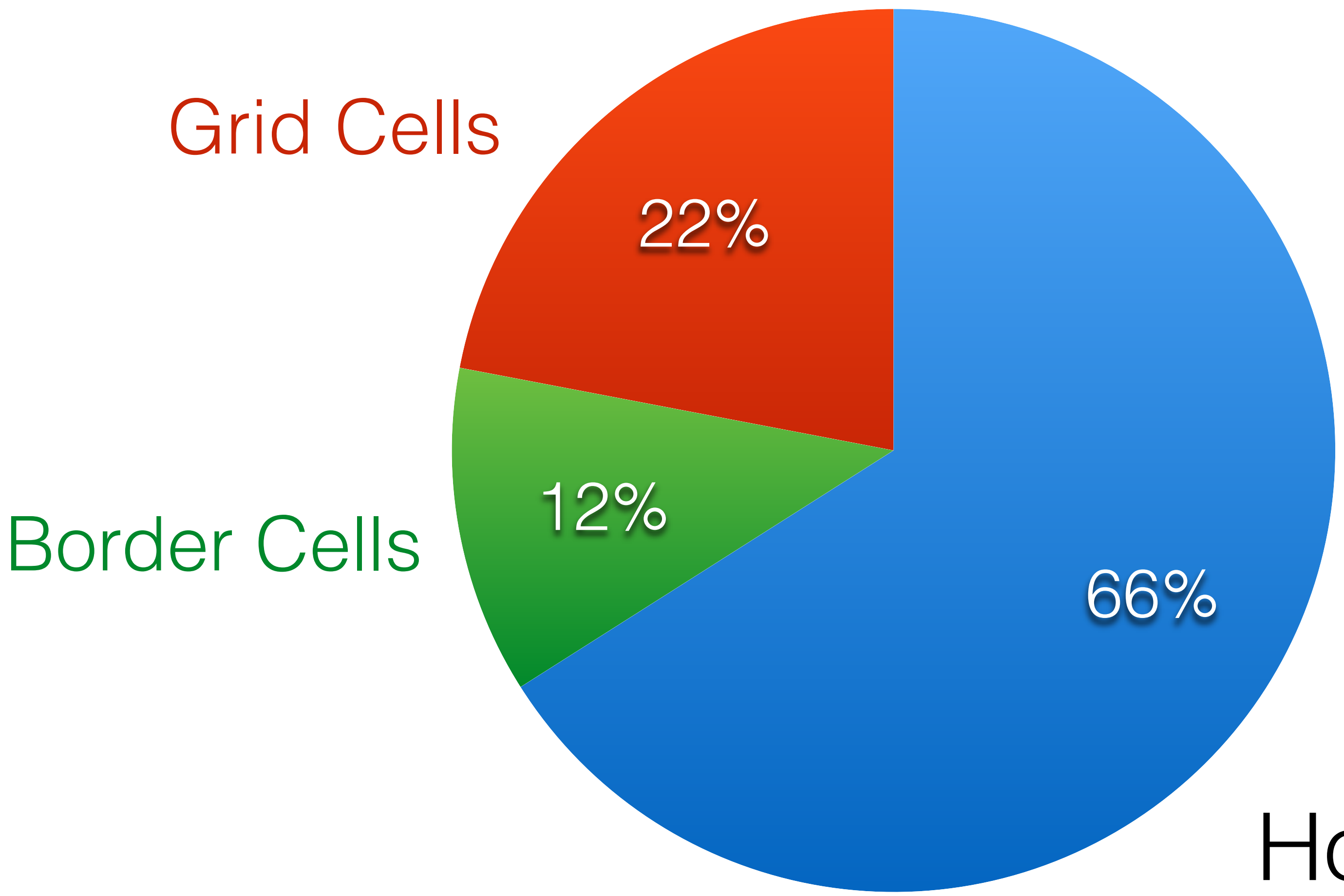
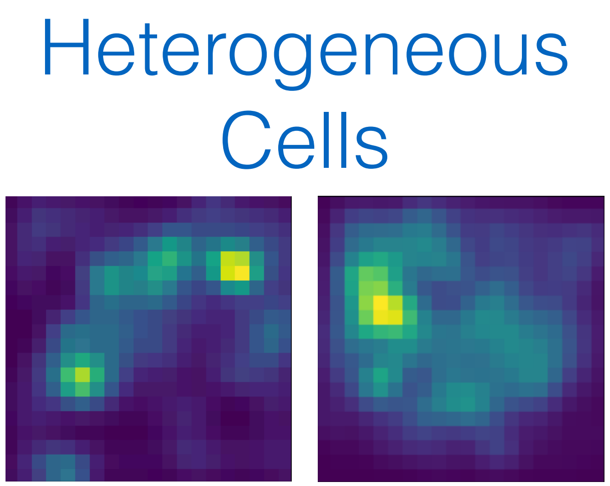
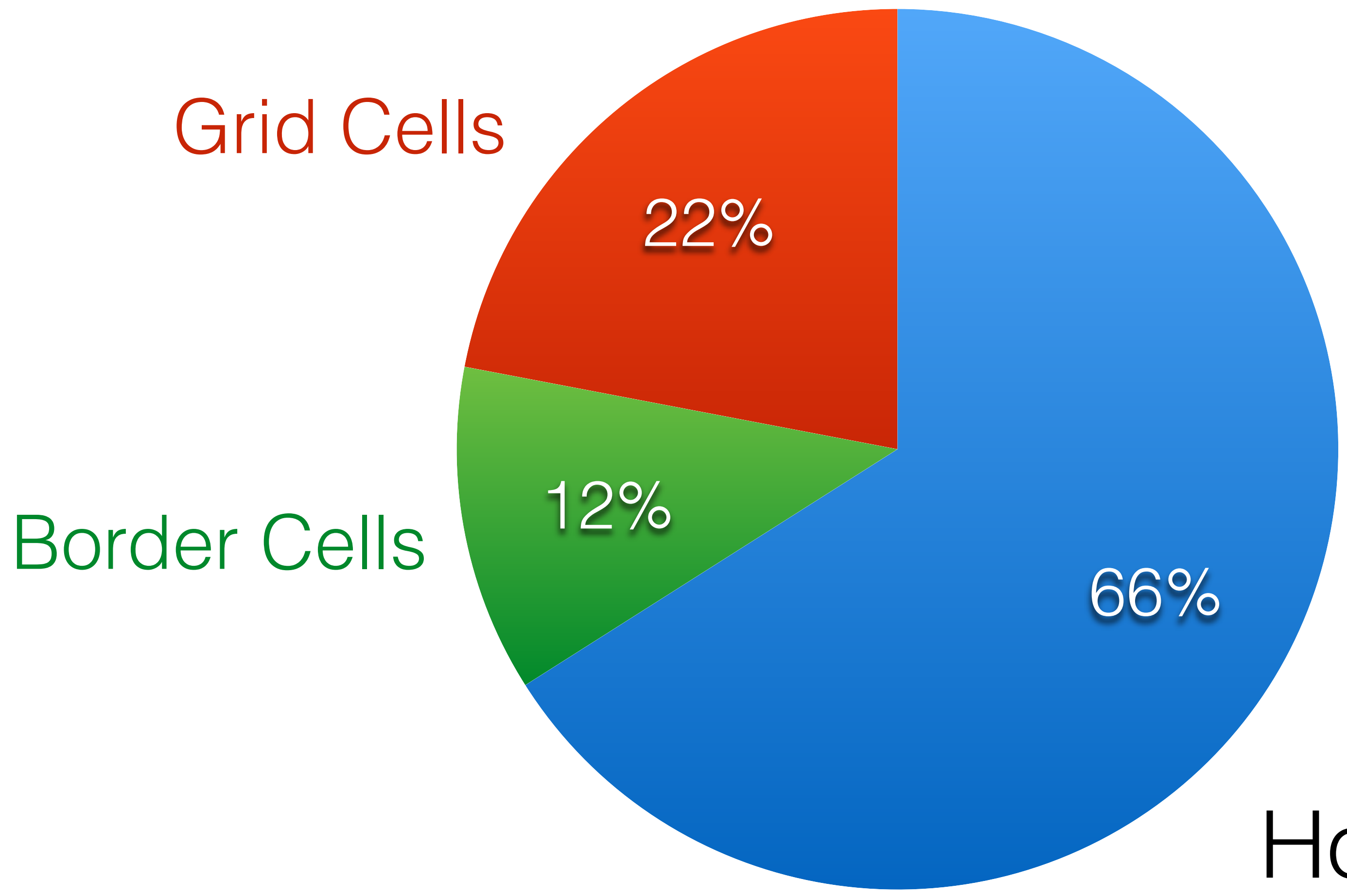
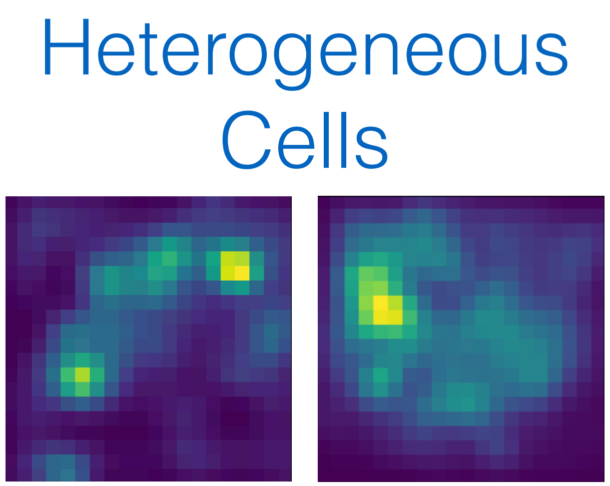




How might we characterize the response patterns of these heterogeneous cells?

Accounting for heterogeneous code?

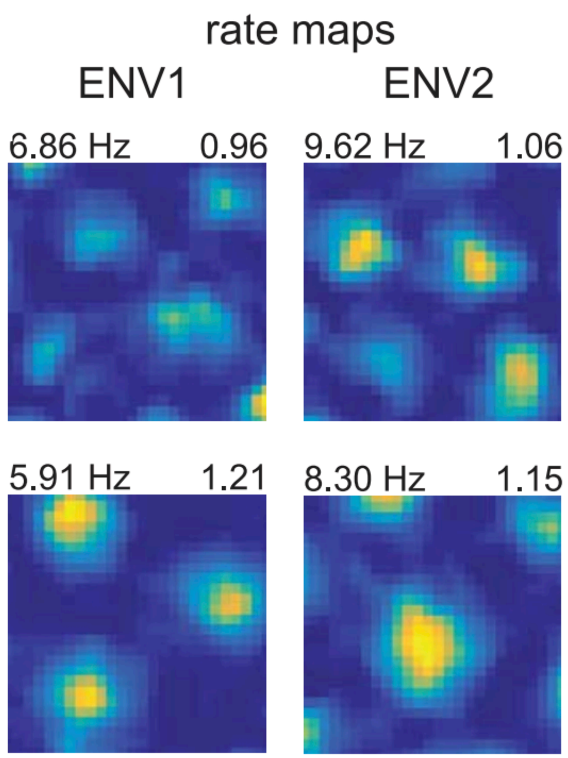




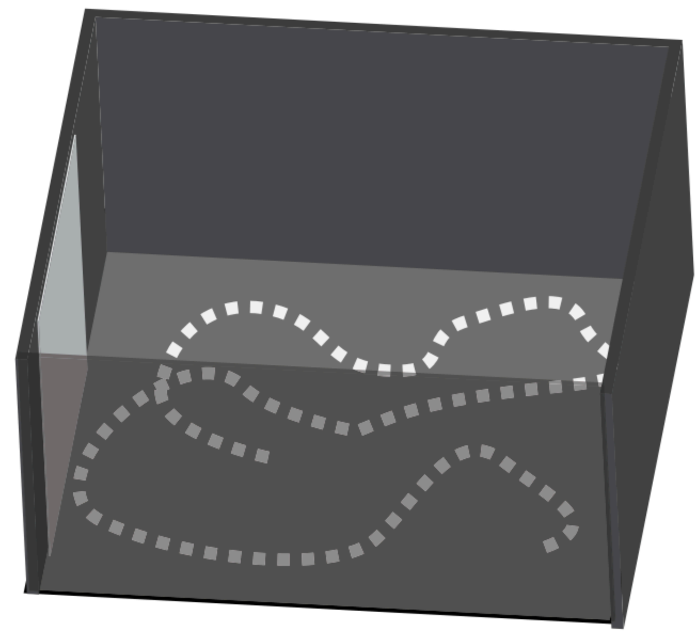
How might we characterize the response patterns of these heterogeneous cells?

What functional role do these cells serve in the circuit, if any?

Accounting for heterogeneous code in the presence of rewards?



Butler*, Hardcastle*, Giocomo 2019



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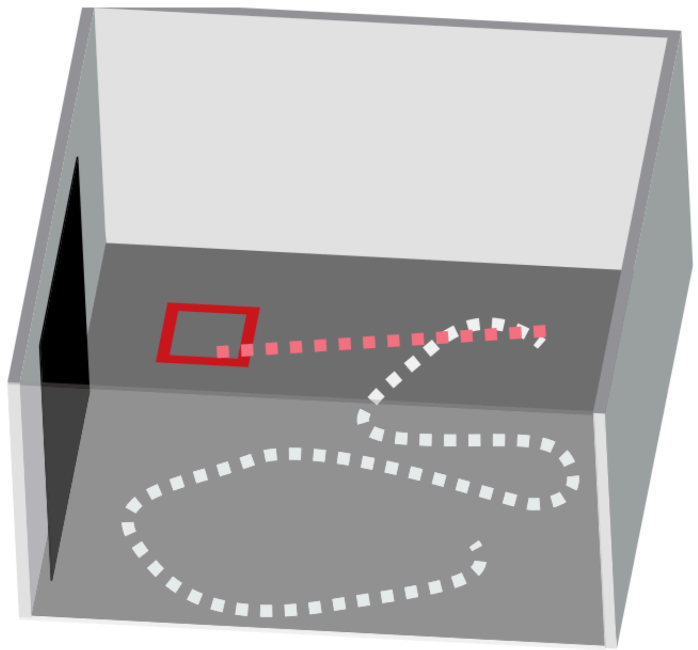
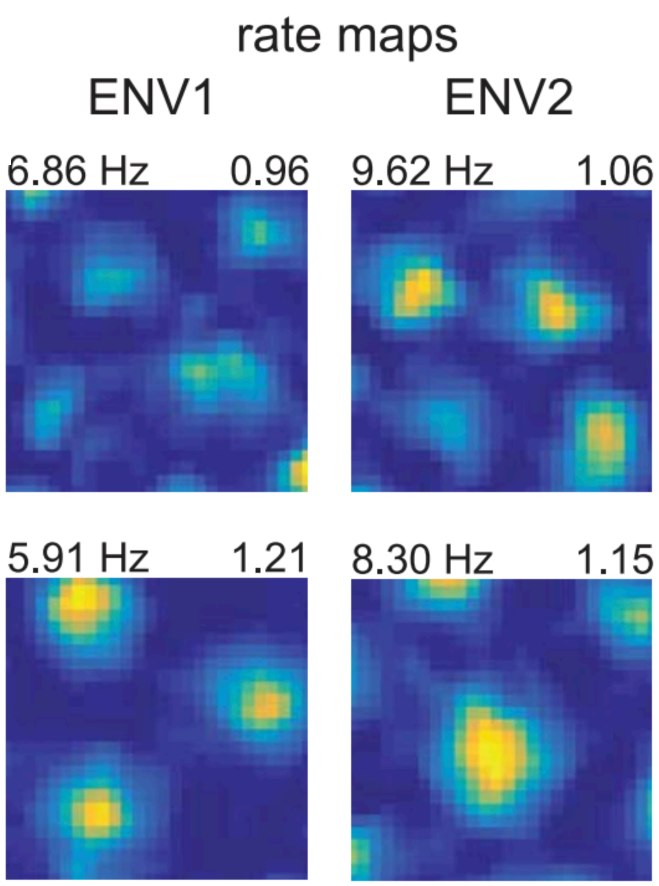


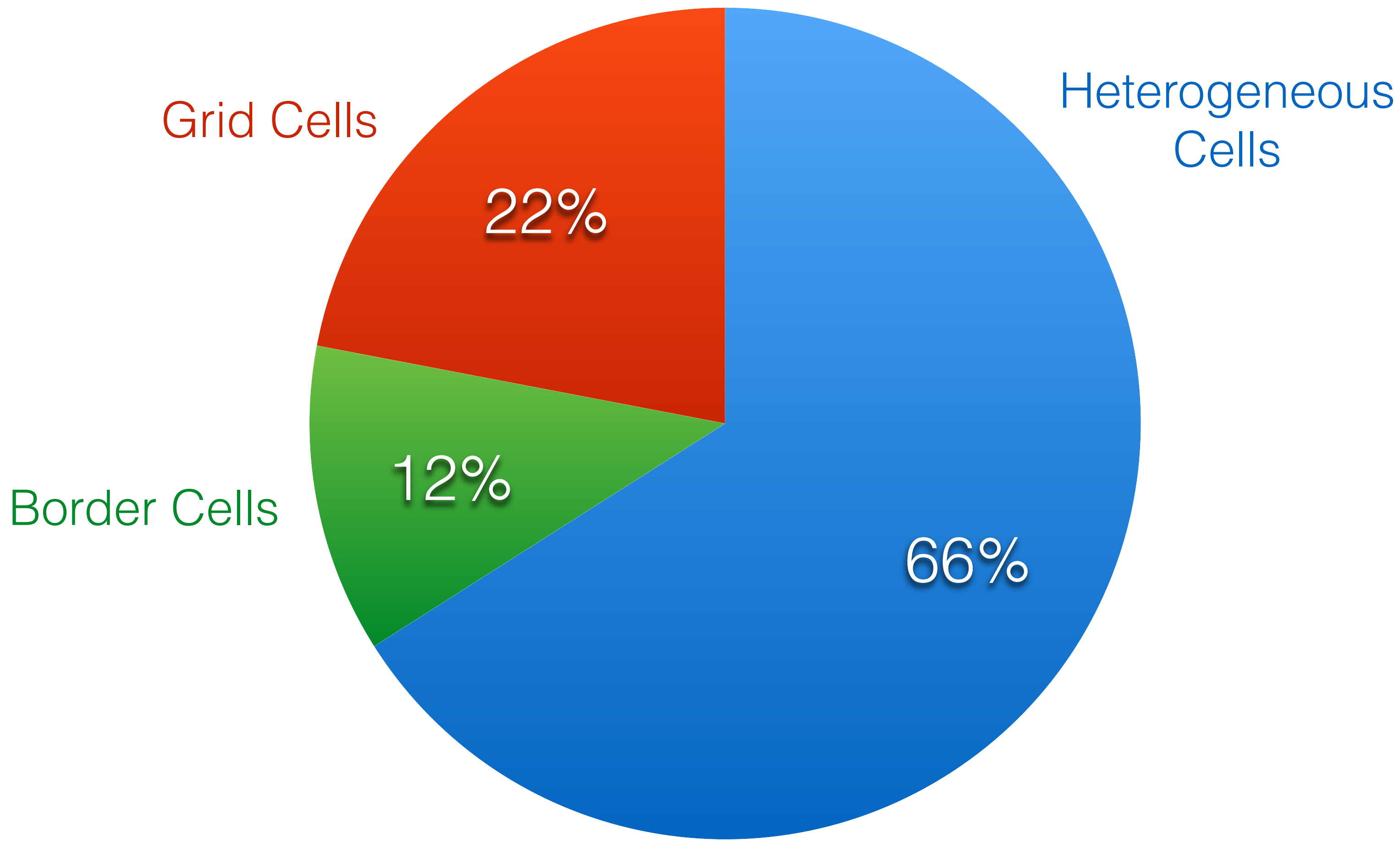
spatial task (ENV2)

In fact, MEC remaps in the presence of rewards… so what describes the joint interaction between these heterogeneous cells and reward?

Taking a modeling approach

It would be useful to have a **unified** model that can simultaneously explain different types of neural responses in MEC.





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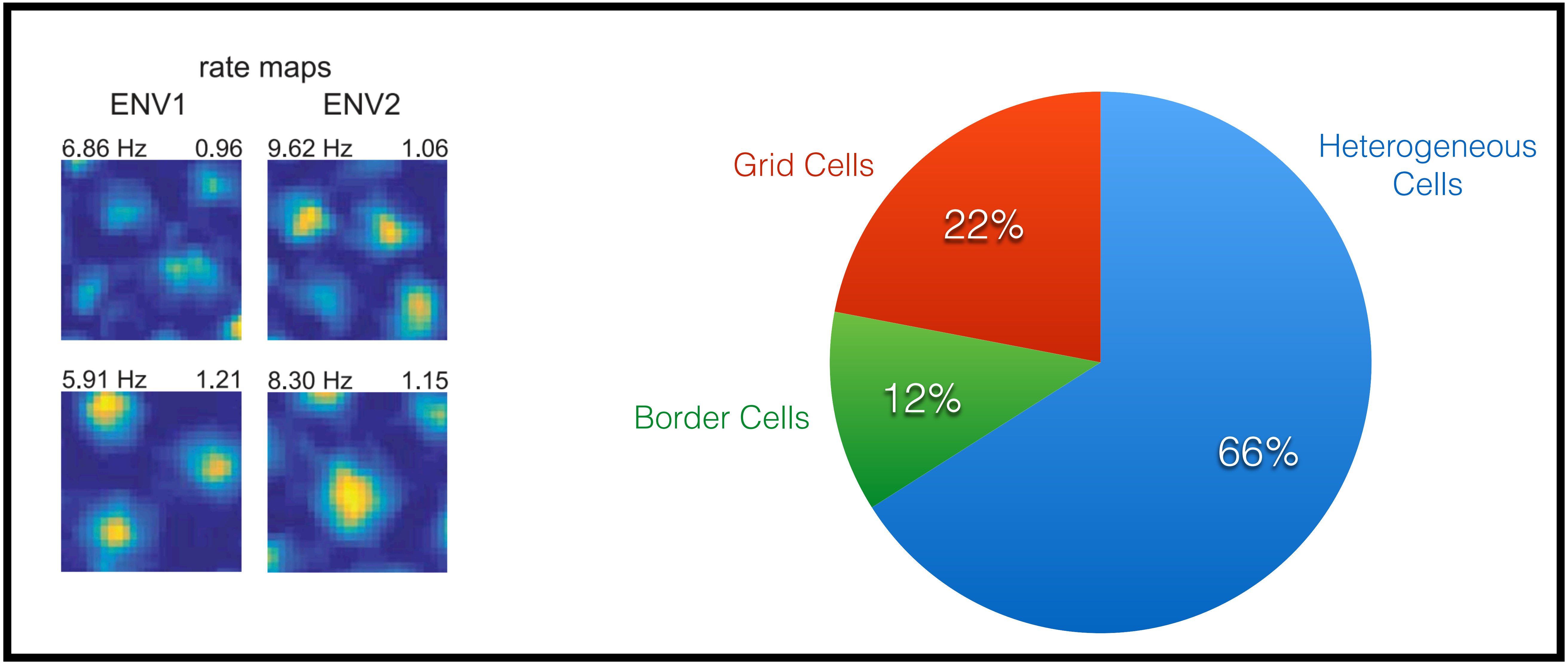
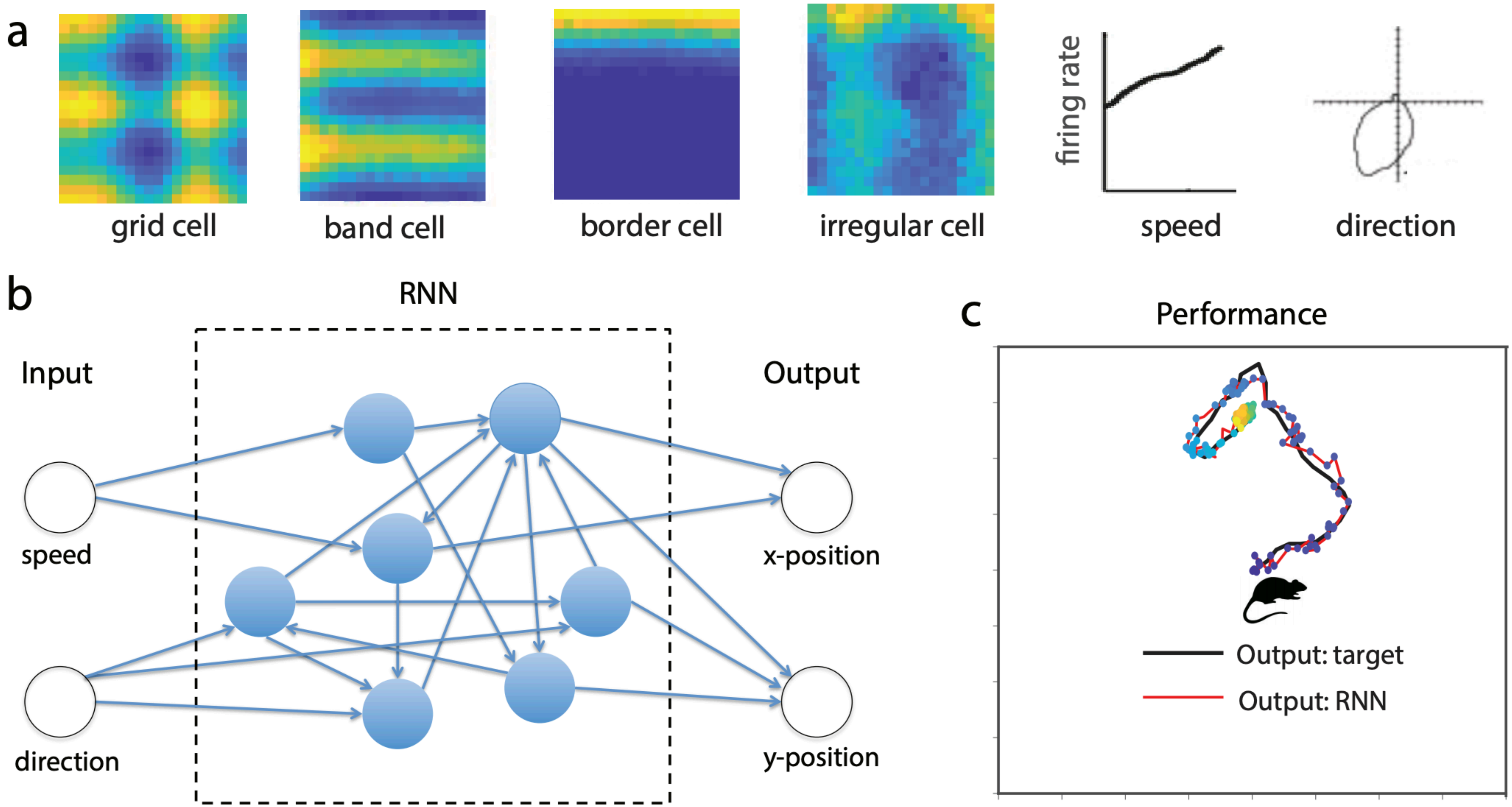


Where do we begin?

Task-driven neural network models can “develop” these cells…



Cueva* & Wei* 2018

Main Questions

But are they a good ***quantitative*** model of these responses?

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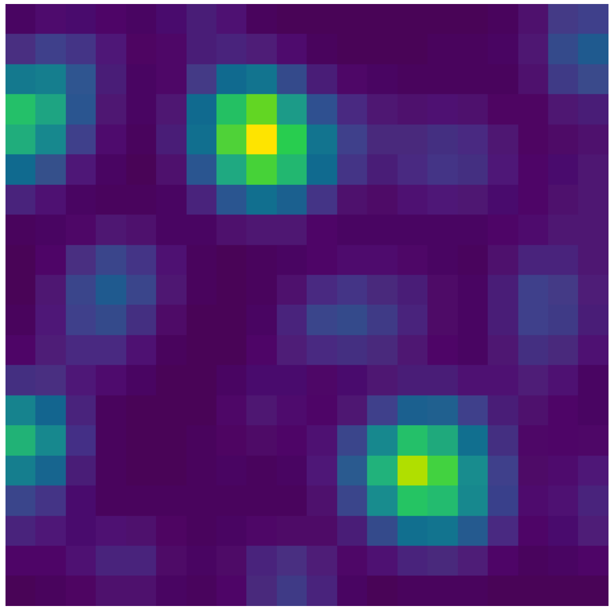
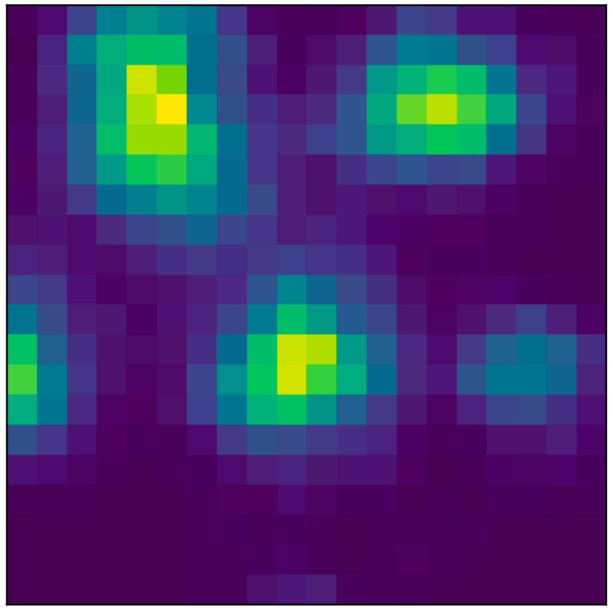
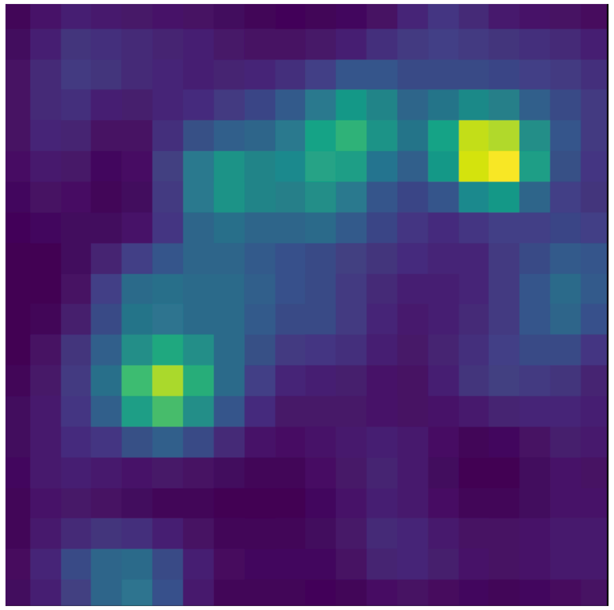
MEC Grid Cell



Model Grid Cell

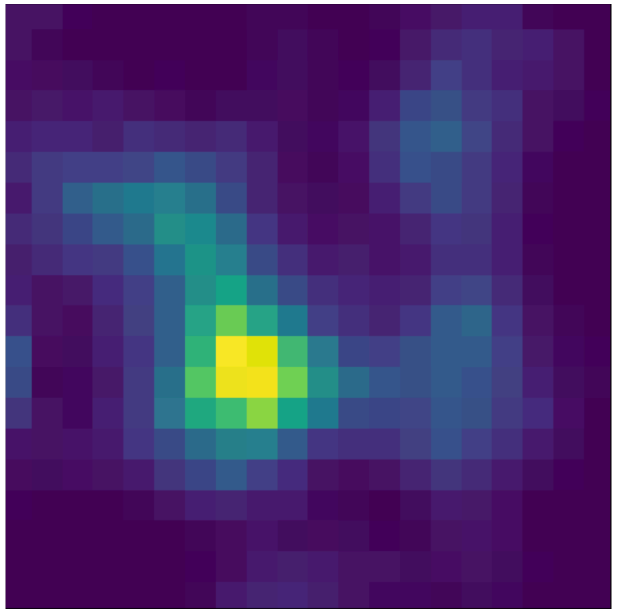


MEC Heterogeneous Cell



?

Model Heterogeneous Cell



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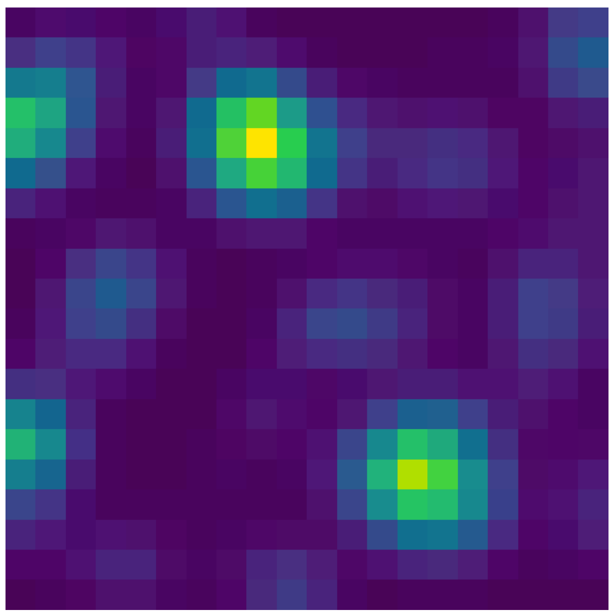
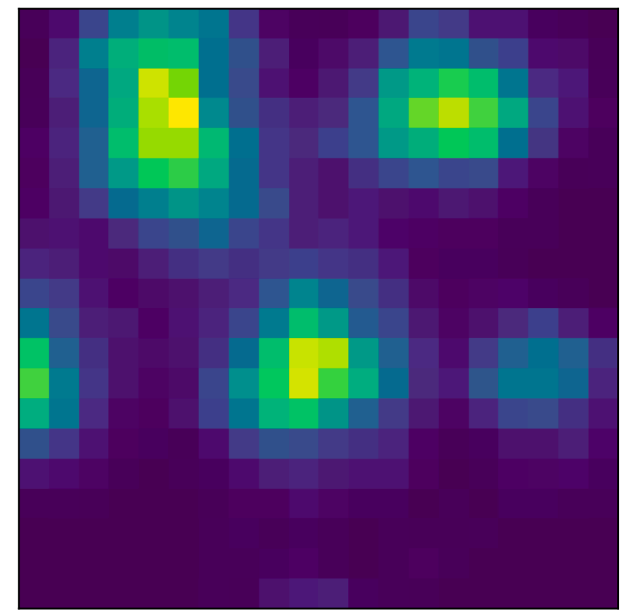


Model Grid Cell



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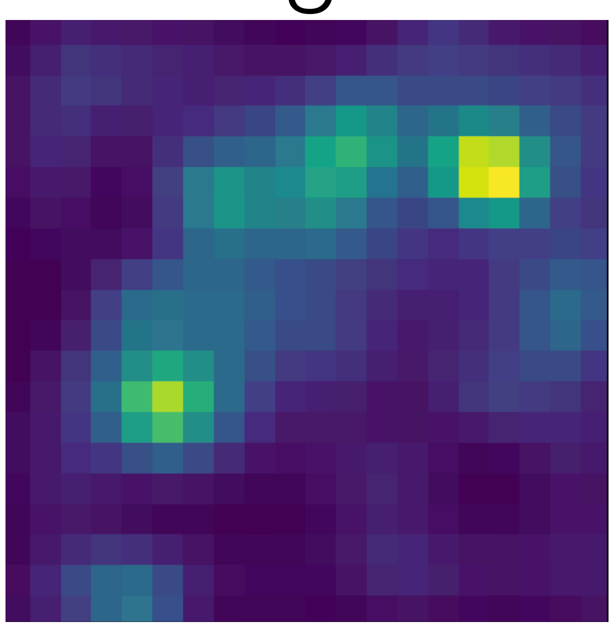

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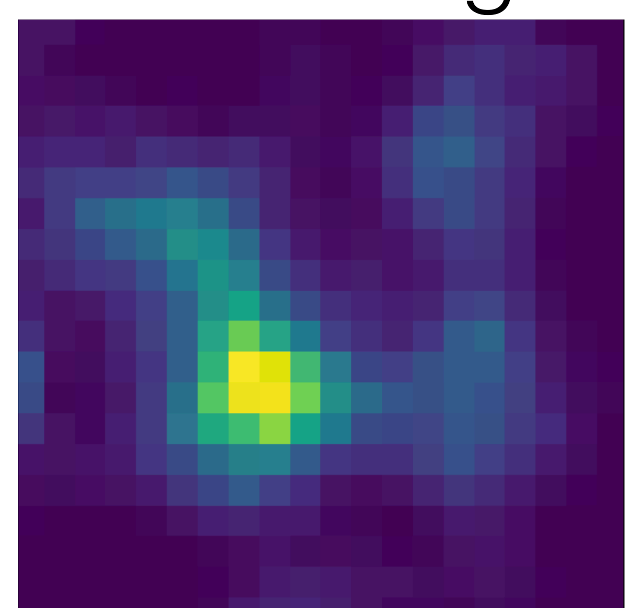
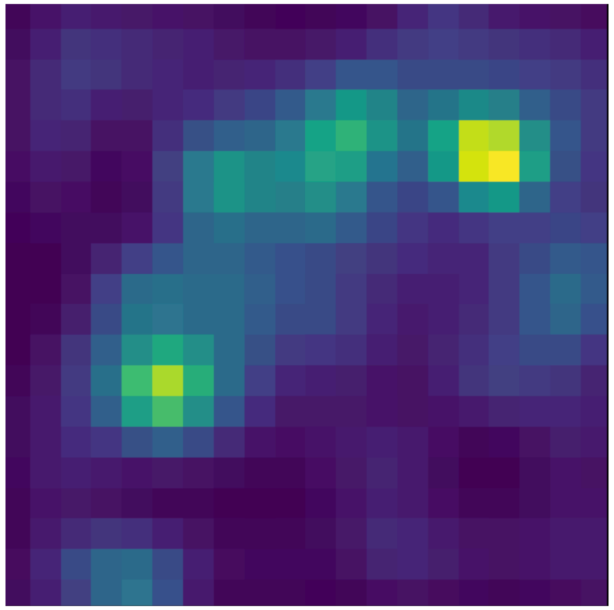


Not all models are equal!

Main Questions

How do we define similarity between sets of heterogeneous responses we can't adequately describe in words?

MEC Heterogeneous Cell



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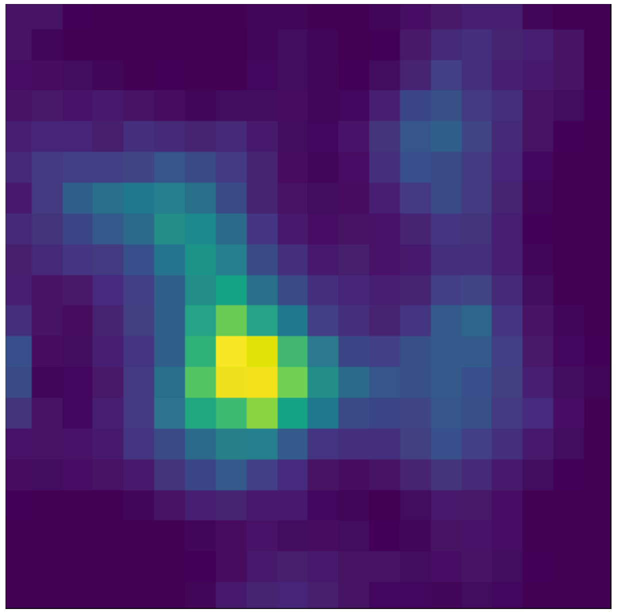


Goal-Driven Approach

"behavior"

1.

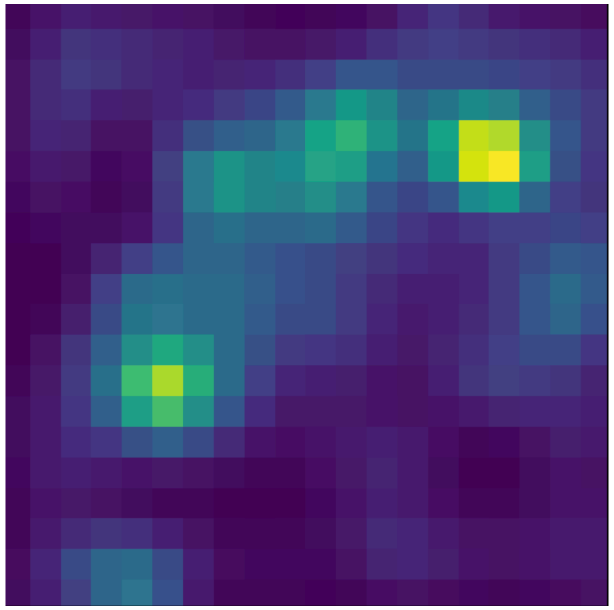
L = *loss function* ***D*** = *dataset*

"circuit"

2.

A = *architecture class*

MEC Heterogeneous Cell



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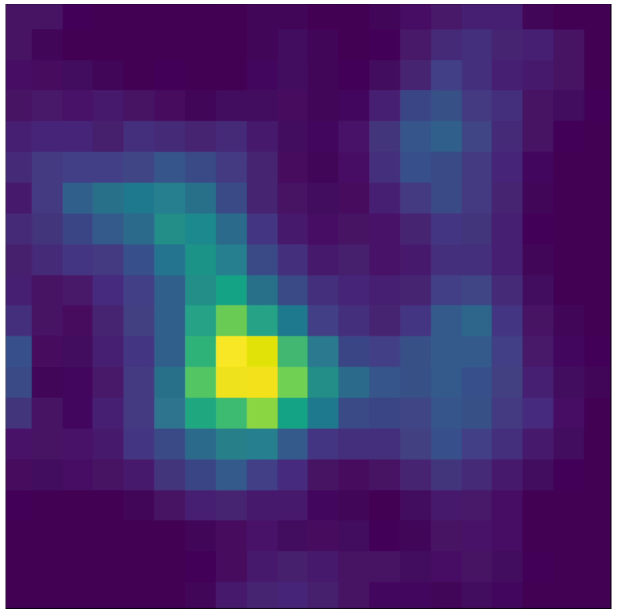


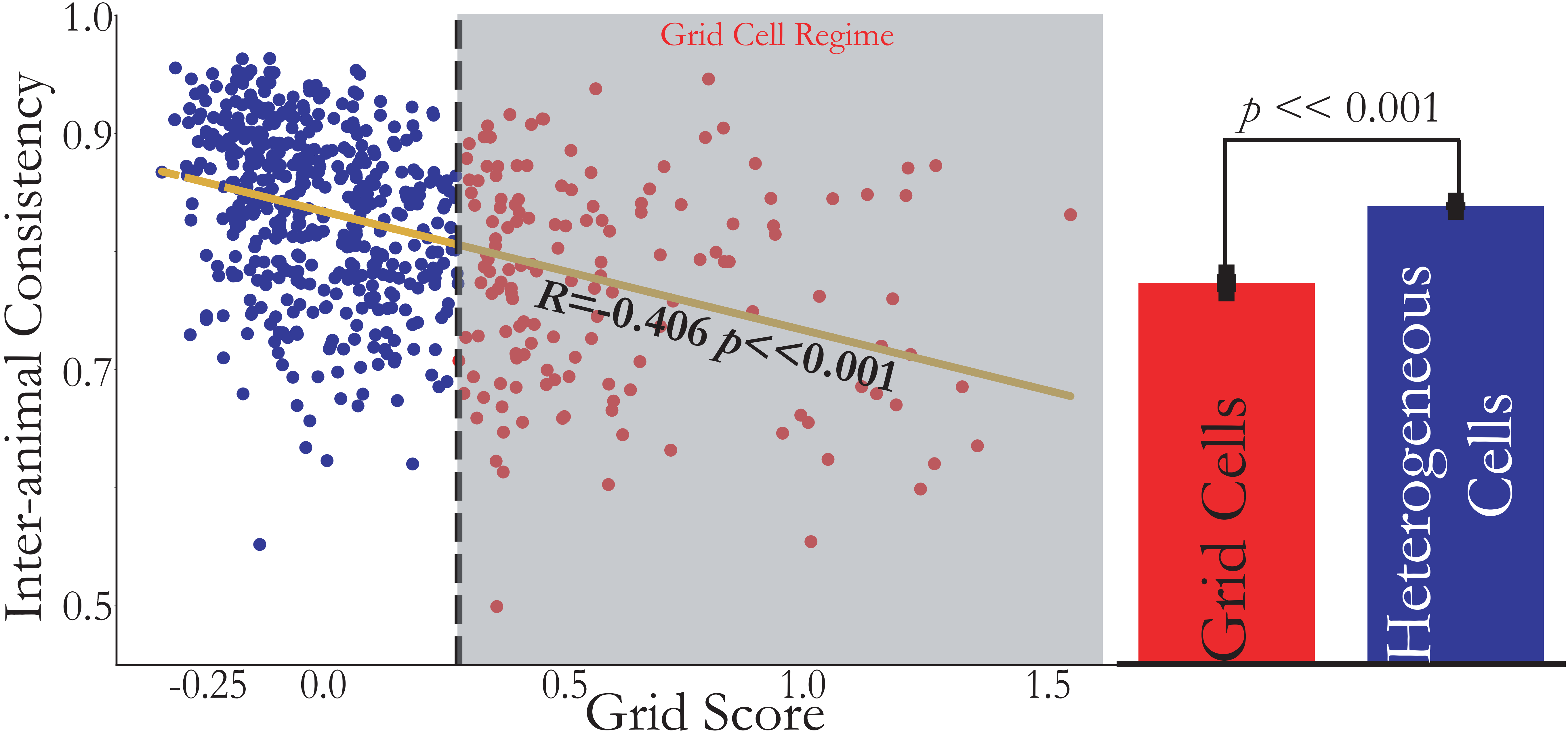
Main Questions

Before we do the goal driven approach, how do we even measure if a model is correct?

Our approach is that a model should be like the system is unto itself.

Heterogeneous cells are reliable targets of explanation

Consistent reliability *across* all cells

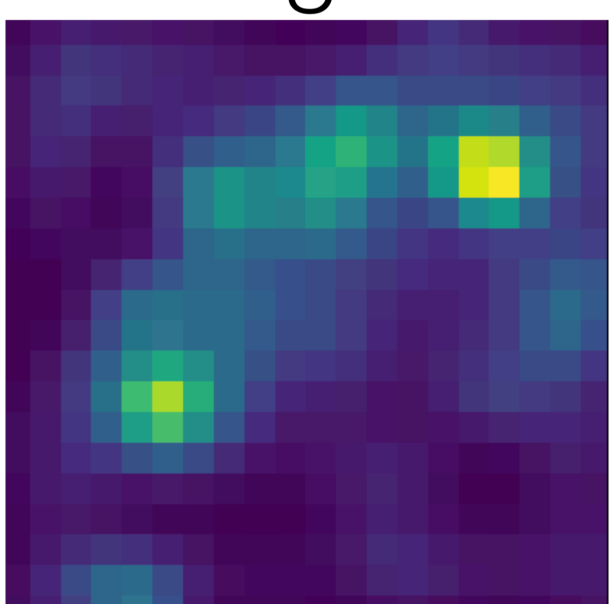


Heterogeneous cells are reliable targets of explanation

So far, we have shown how to measure similarity of the responses of the heterogeneous cells, and that these responses are reliable

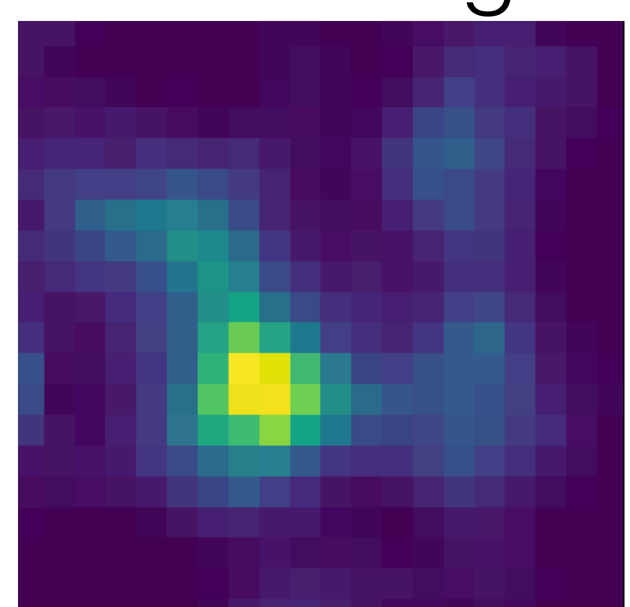
Now, we are going to describe what the constraints are that give rise to these reliable responses

MEC Heterogeneous Cell

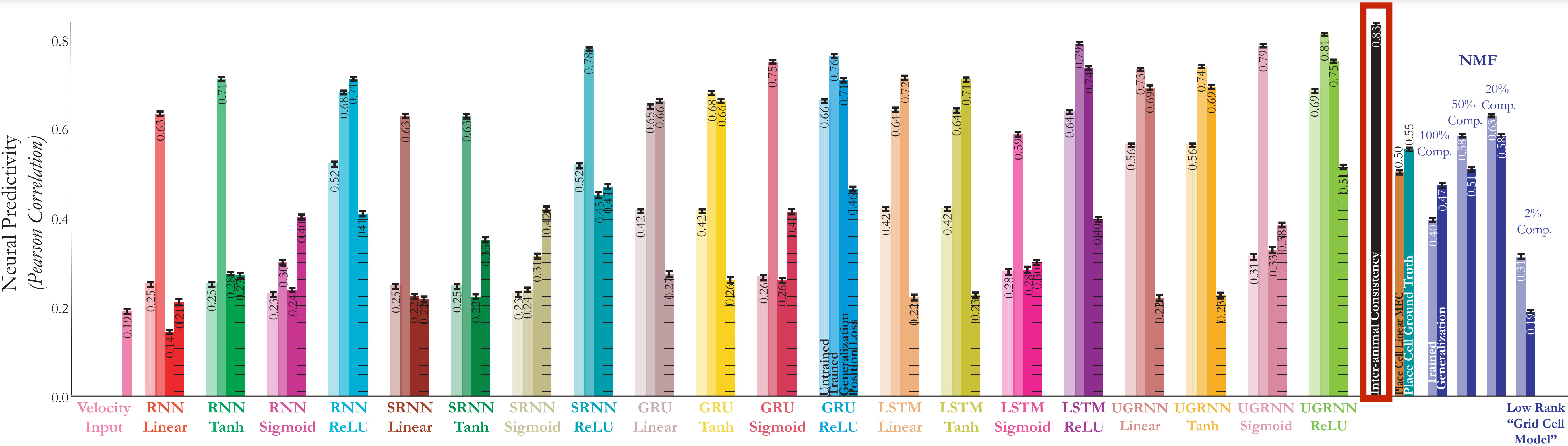


?

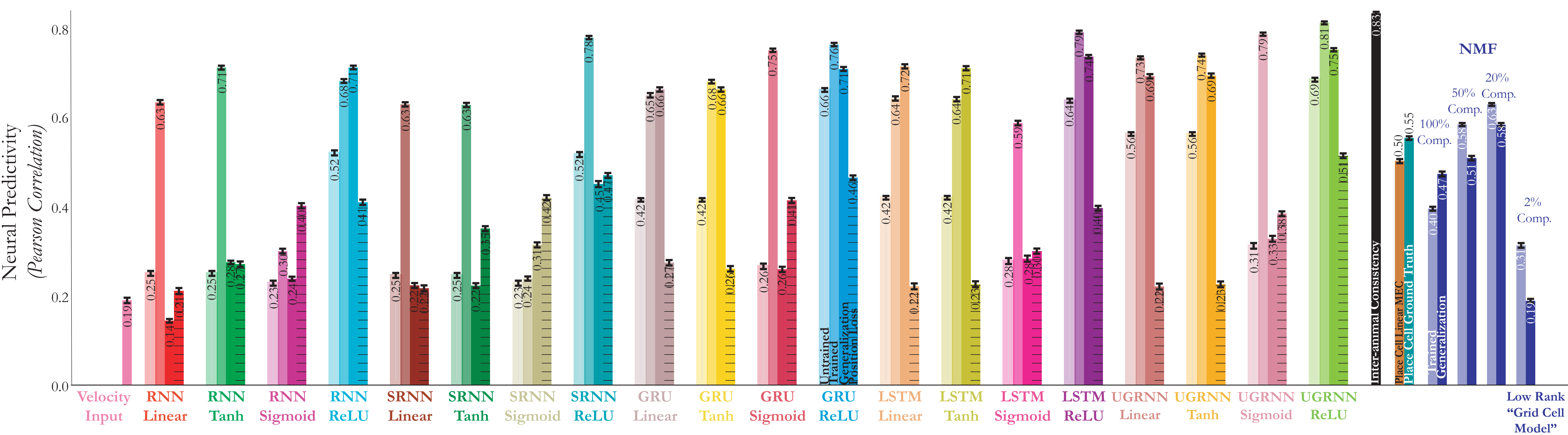
Model Heterogeneous Cell



Benchmarking models with the same transform as between animals



Task-optimized navigational models best predict the entire MEC population



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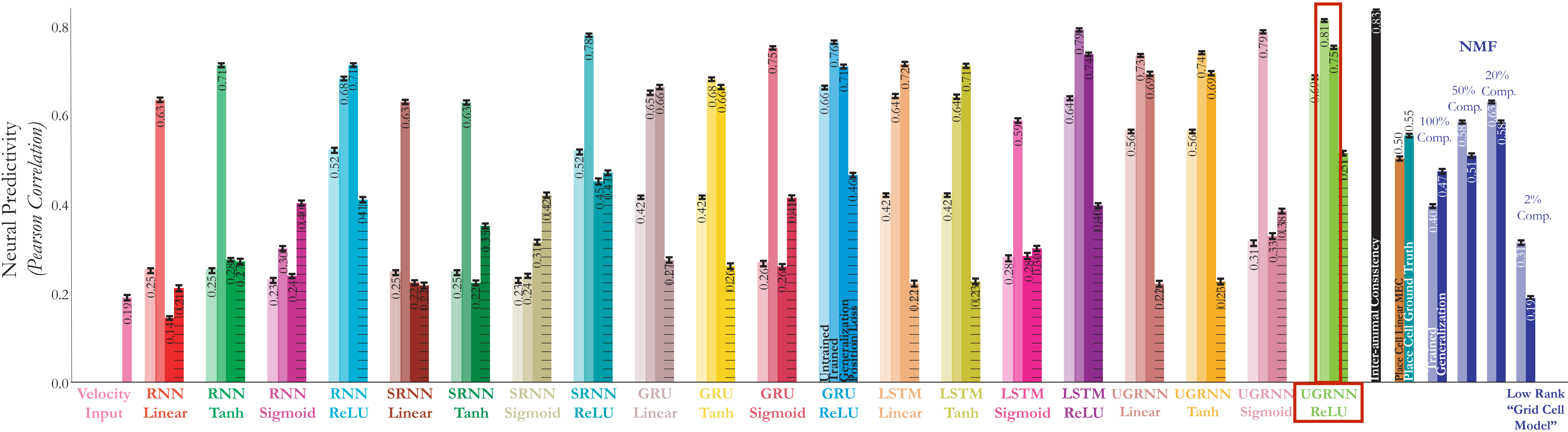
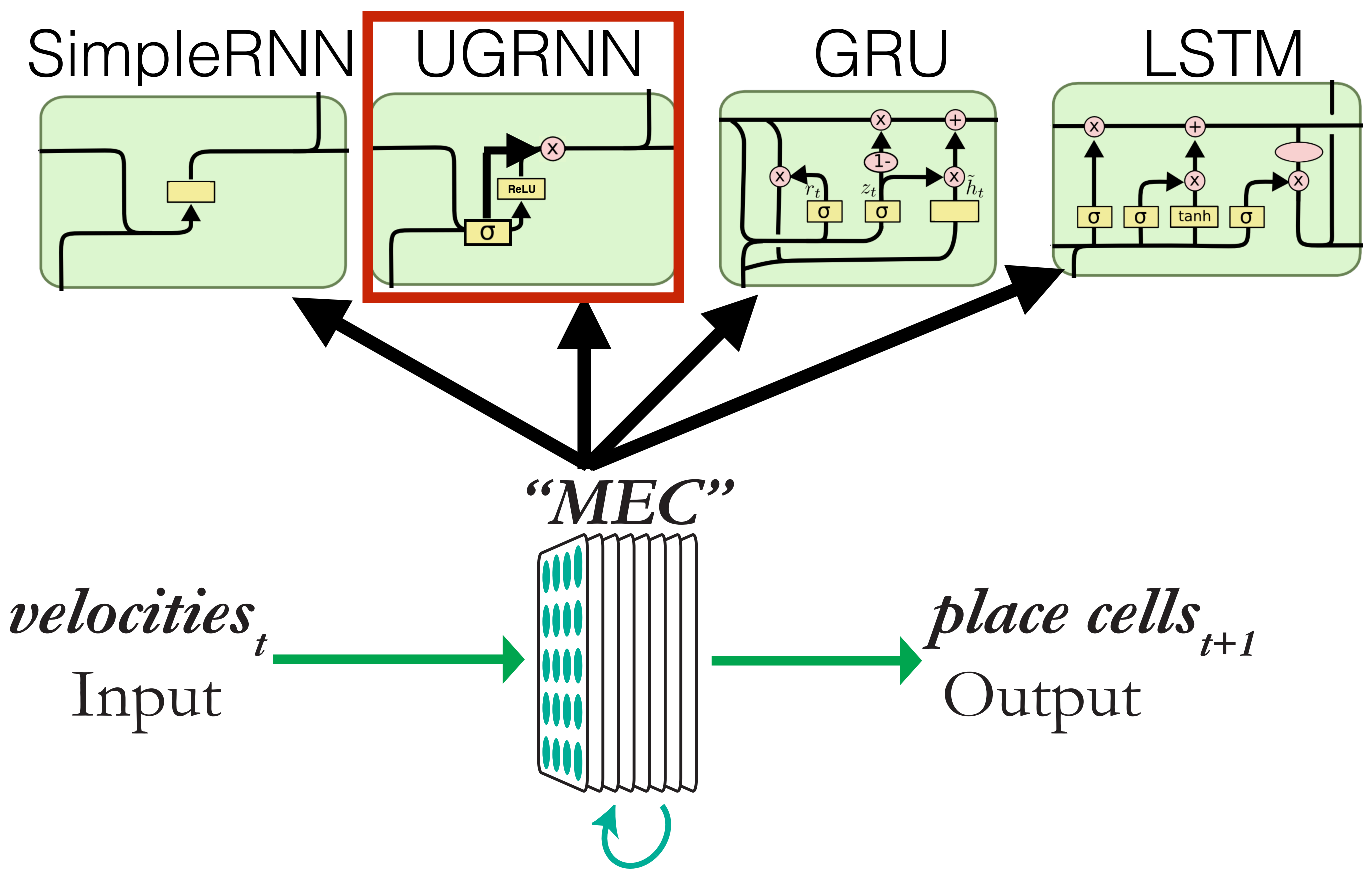
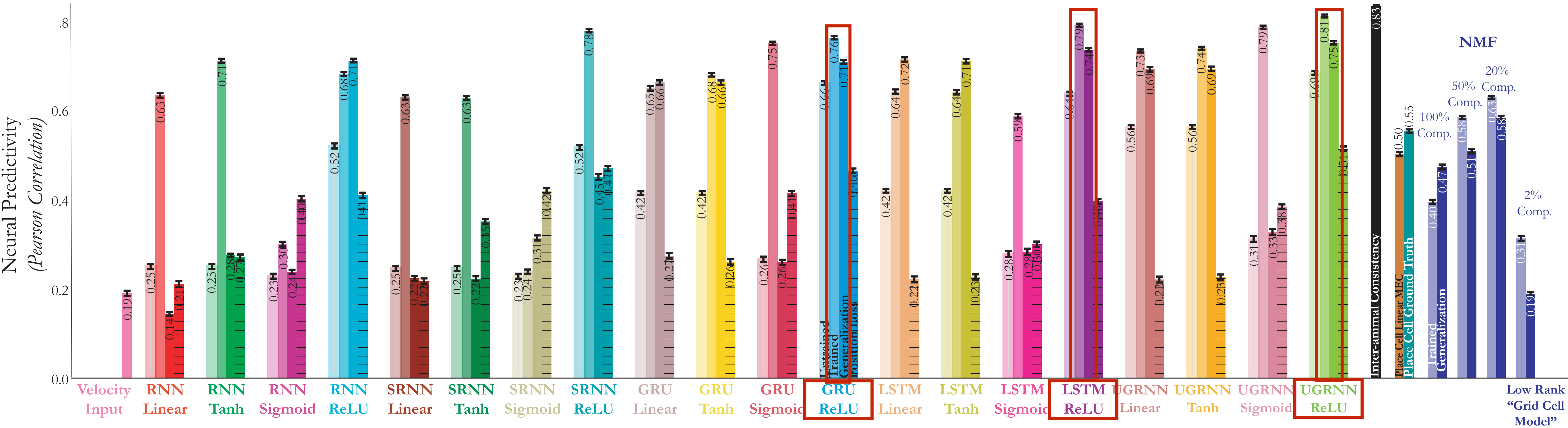


Best task-optimized models "solve" the neurons

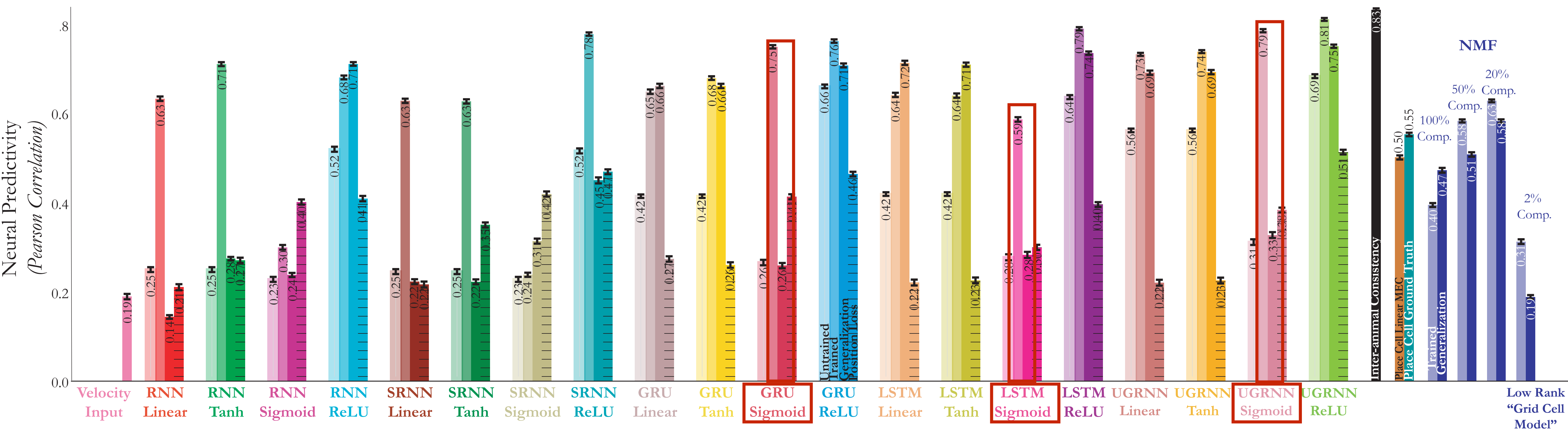


Nonlinearity affects generalization



Nonnegativity constraint + gating aids in generalization across environments

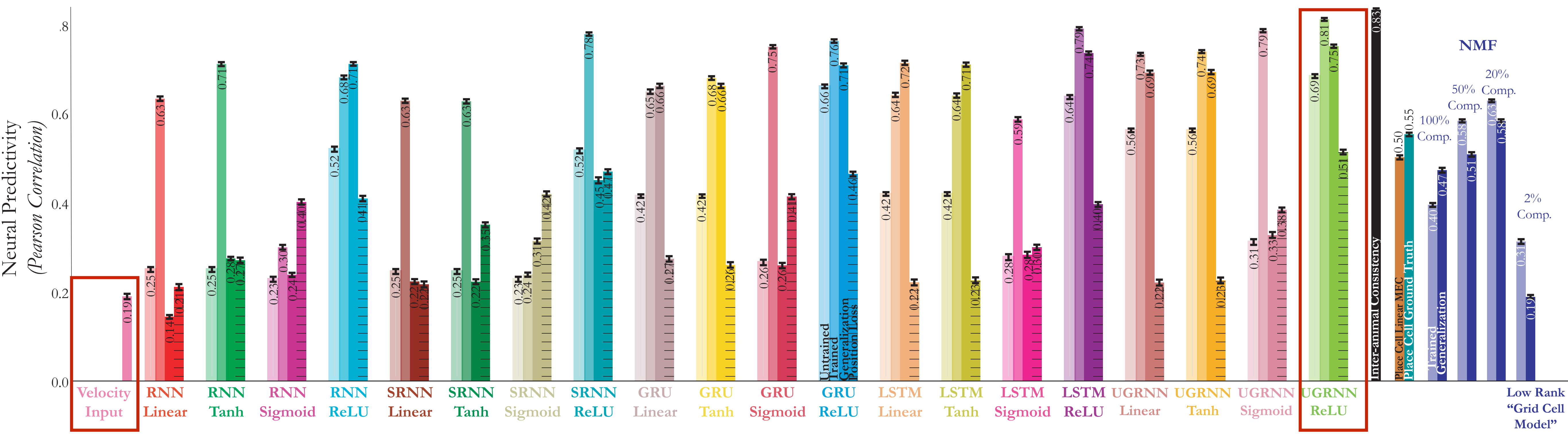
Nonlinearity affects generalization



Nonnegativity constraint + gating aids in generalization across environments

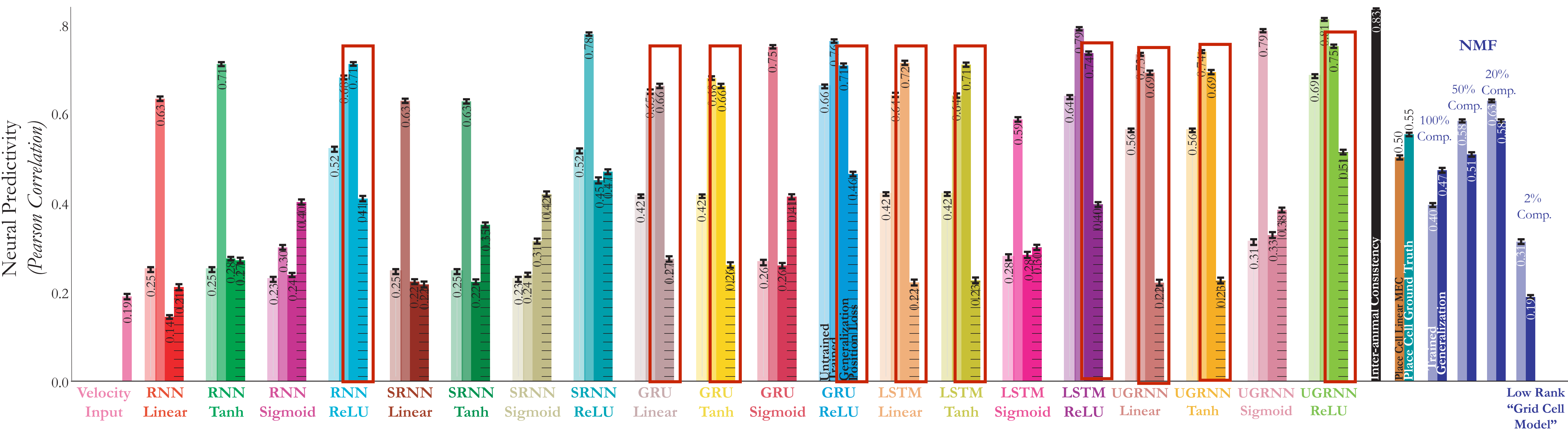
But this nonnegativity constraint must *not* saturate either!

Model input is a poor predictor of population



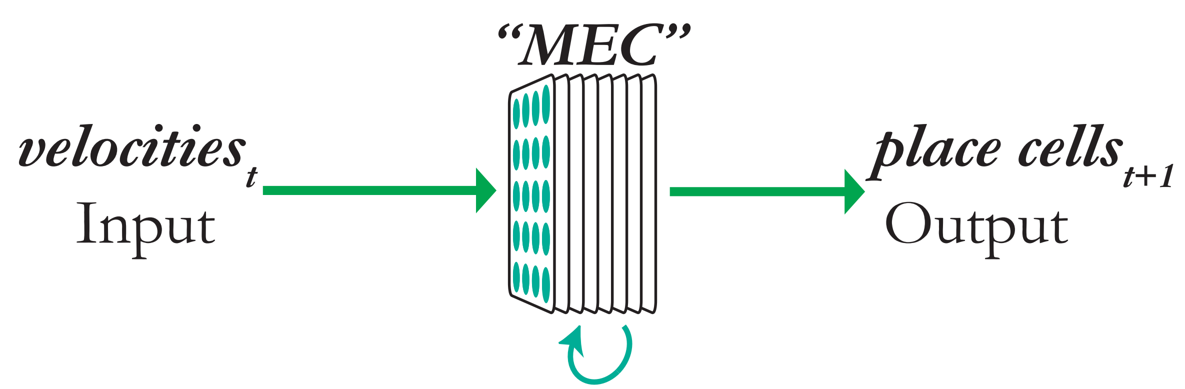
Models add a lot of predictive power to their inputs

Directly supervising on Cartesian coordinates fails to generalize

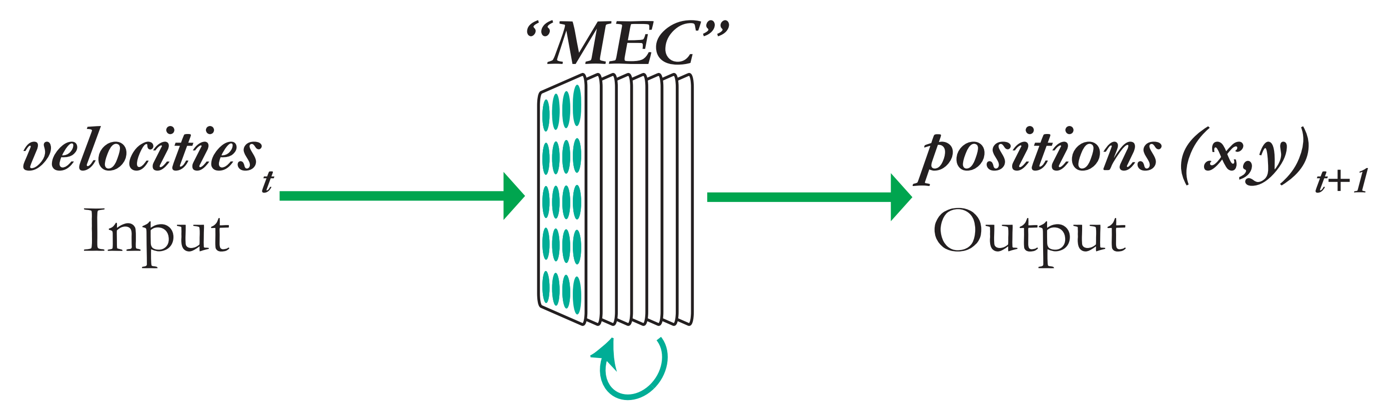


Output place cell supervision provides better generalization over direct supervision of position

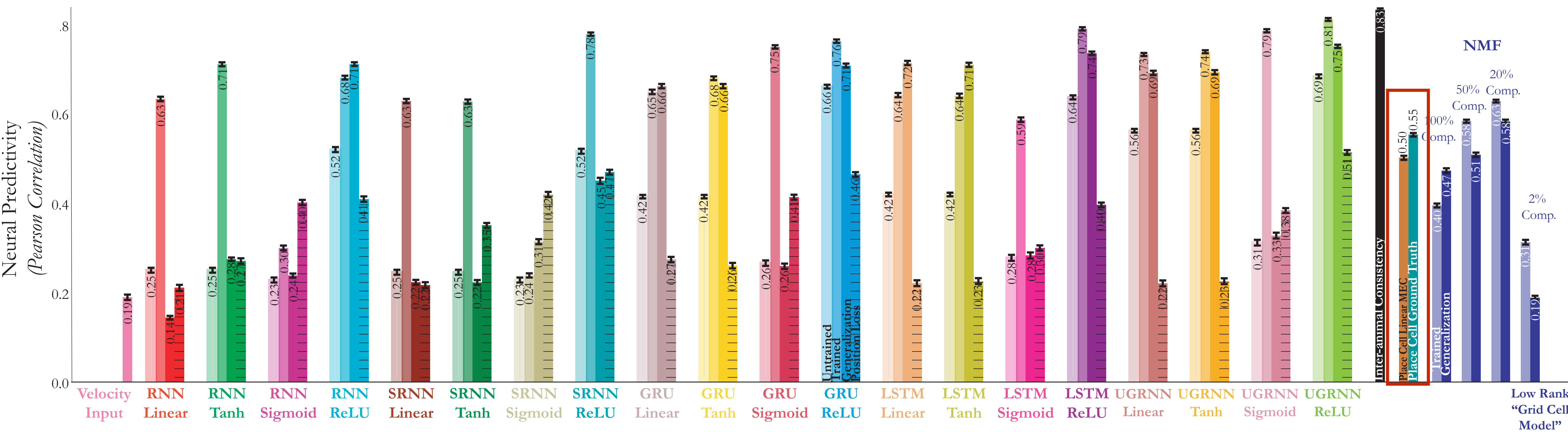
$$\mathcal{L}(\hat{p}, p) := -\frac{1}{T}\sum_{t=1}^{T}\sum_{i=1}^{N_p} p_i^t \log \hat{p}_i^t$$



$$\mathcal{L}(\hat{p}, p) := \frac{1}{2}\frac{1}{T}\sum_{t=1}^{T}\left(\left(p_x^t - \hat{p}_x^t\right)^2 + \left(p_y^t - \hat{p}_y^t\right)^2\right)$$

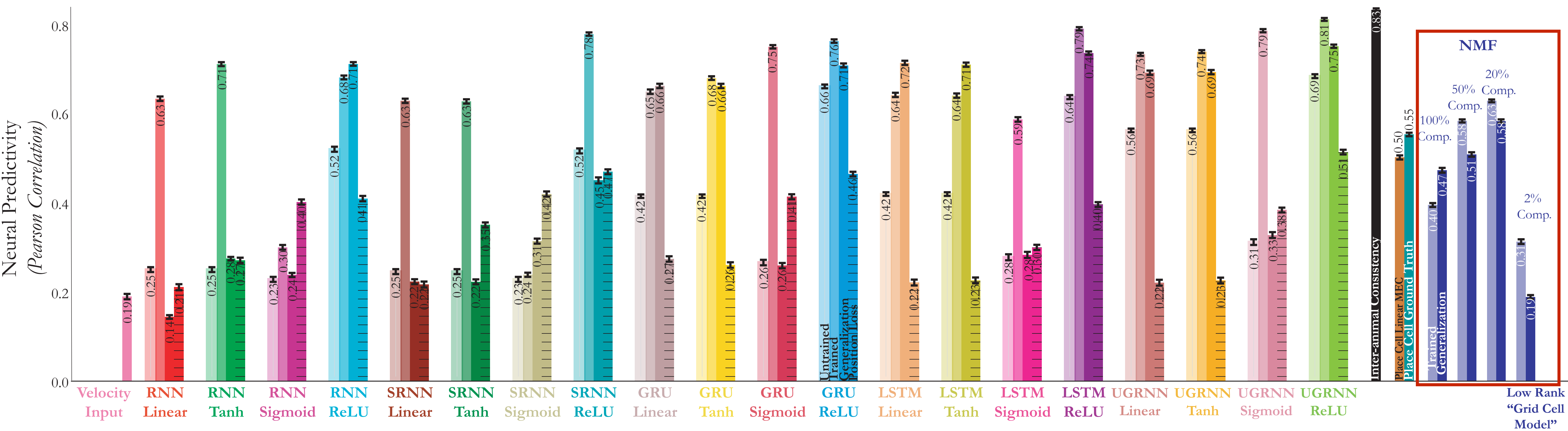


Place cells alone are a poor predictor



But place cells alone are not a good predictor of MEC (good!)

…as is NMF

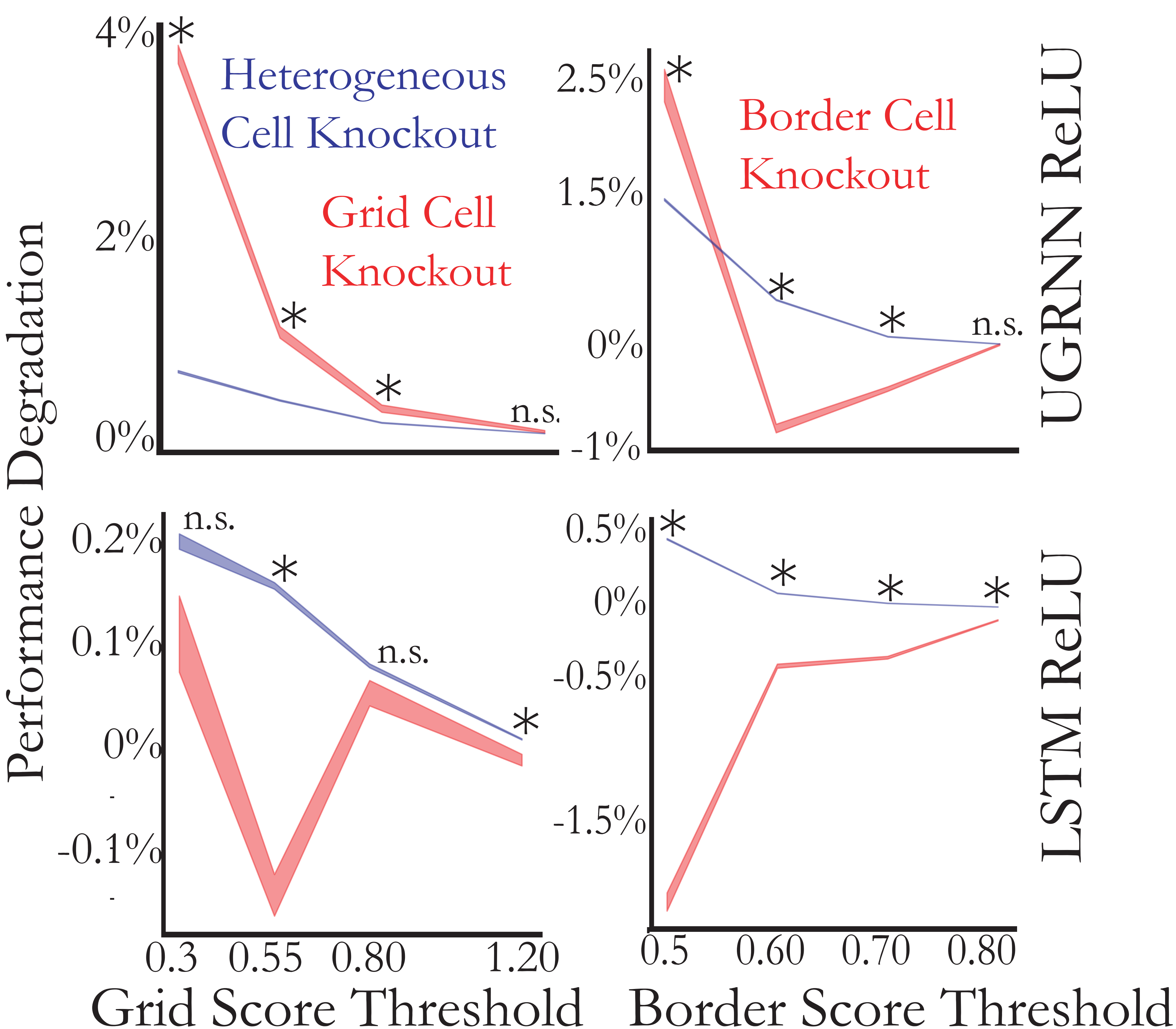


Dimensionality reduction on place cells is not a good predictor of MEC either

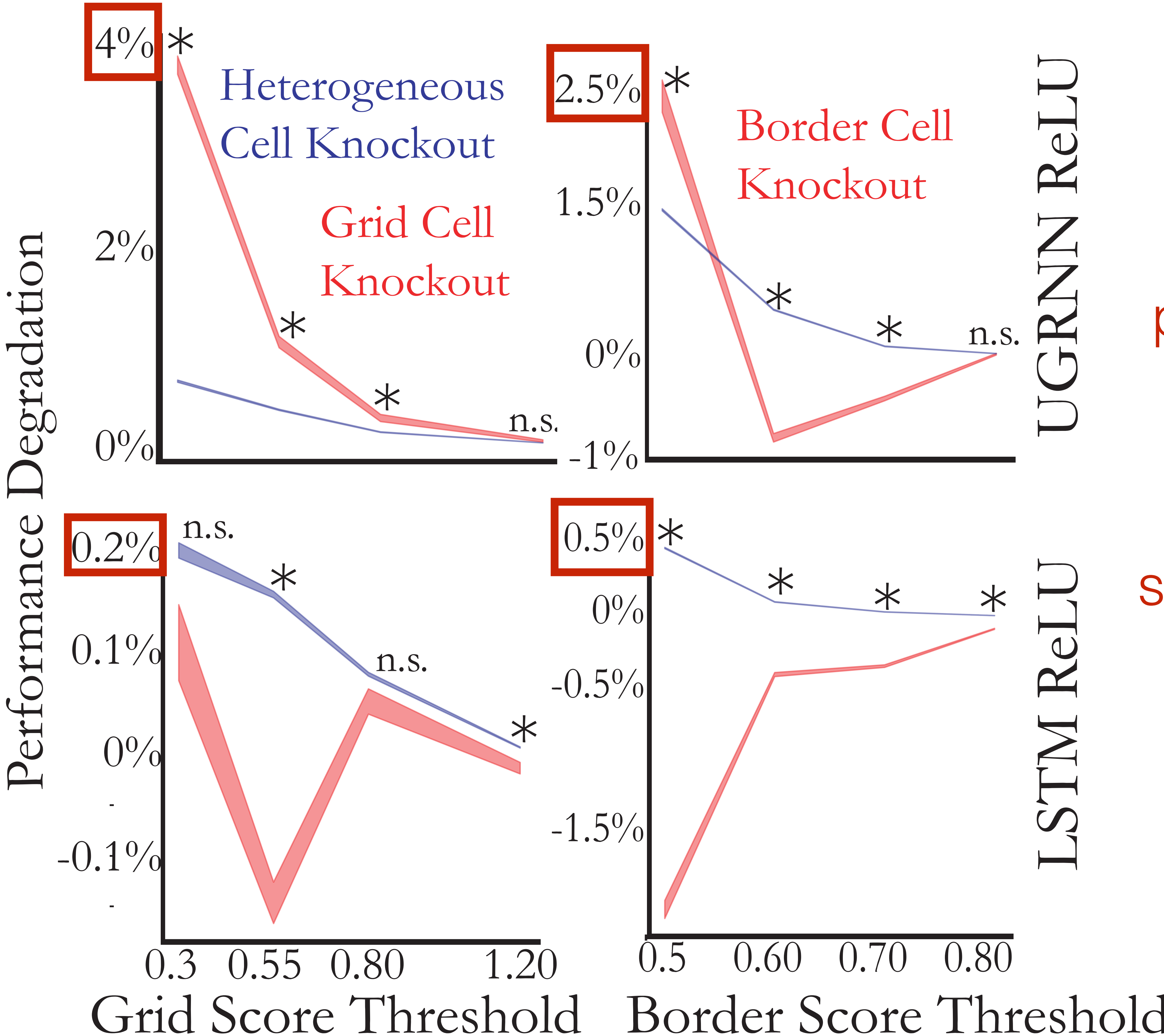
Knockout experiments

Given that we have a model that exhibits close similarity to MEC, we can use it to generate predictions for experiments that are very difficult to do

Knockout experiments

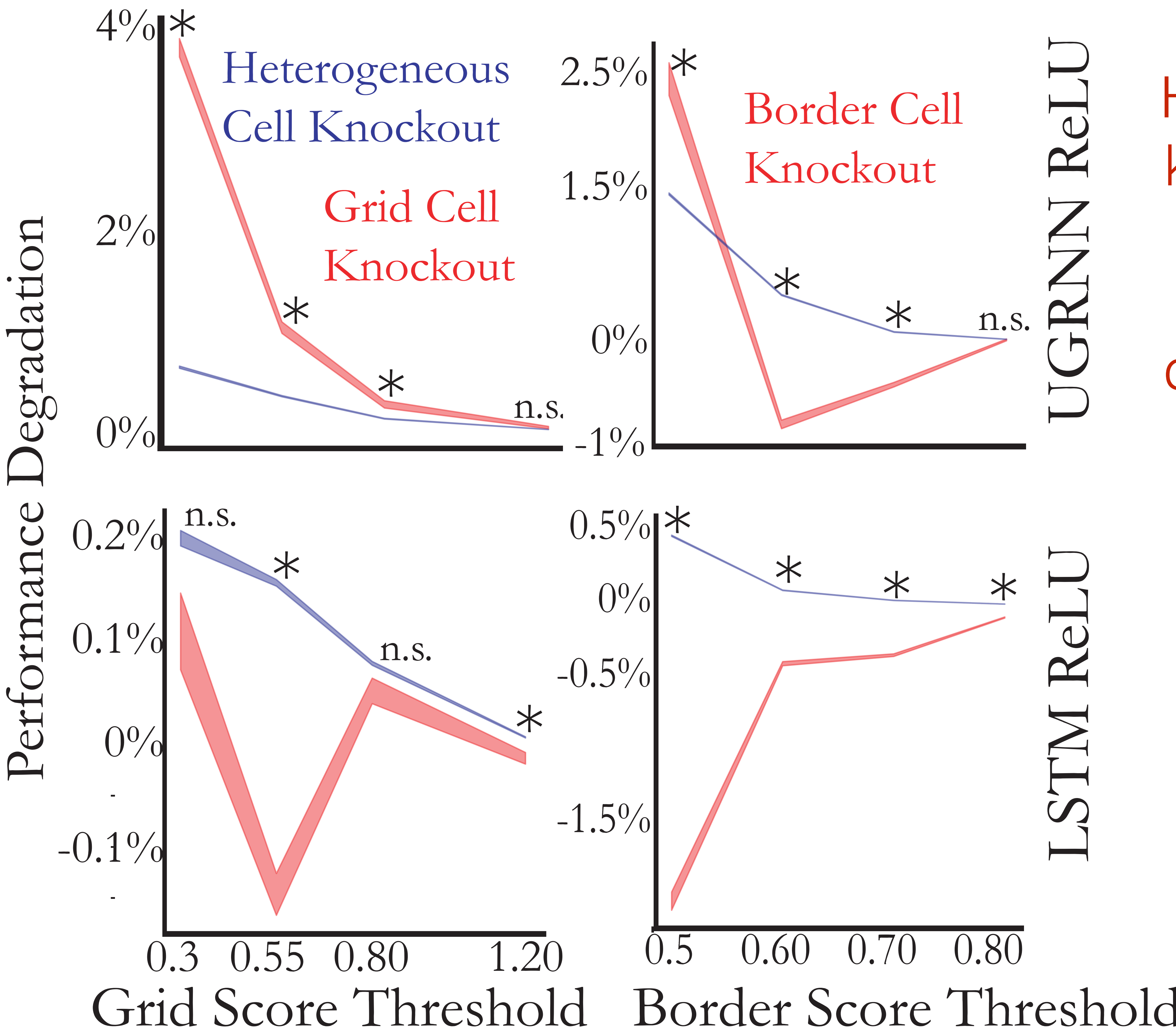


Networks are robust to knockouts



Network performance is robust to knockouts on the order of several hundred units

Heterogeneous cells are relevant to navigation



Heterogeneous knockout gives similar performance degradation as cell type specific knockout, especially as threshold increases

Accounting for rewards

Why do we want the same model to account for rewards?

Accounting for rewards

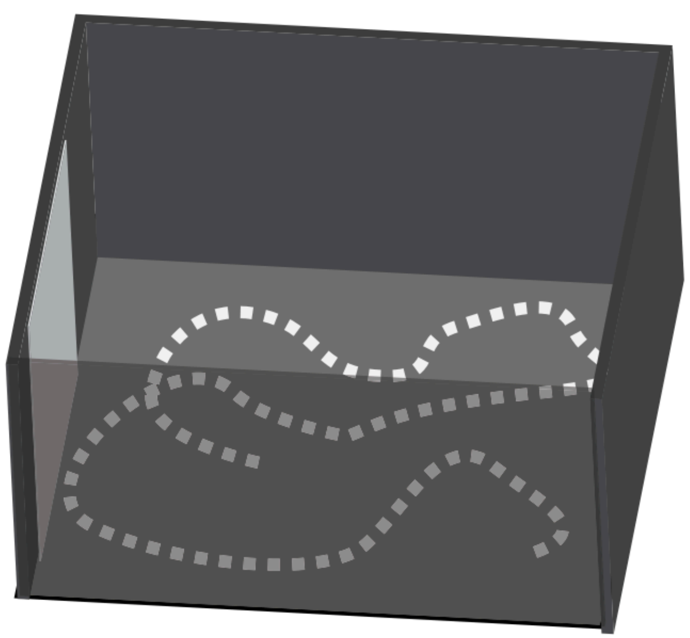
Why do we want the same model to account for rewards?

Because we think that non-spatial rewards are nonetheless part of the same underlying framework.

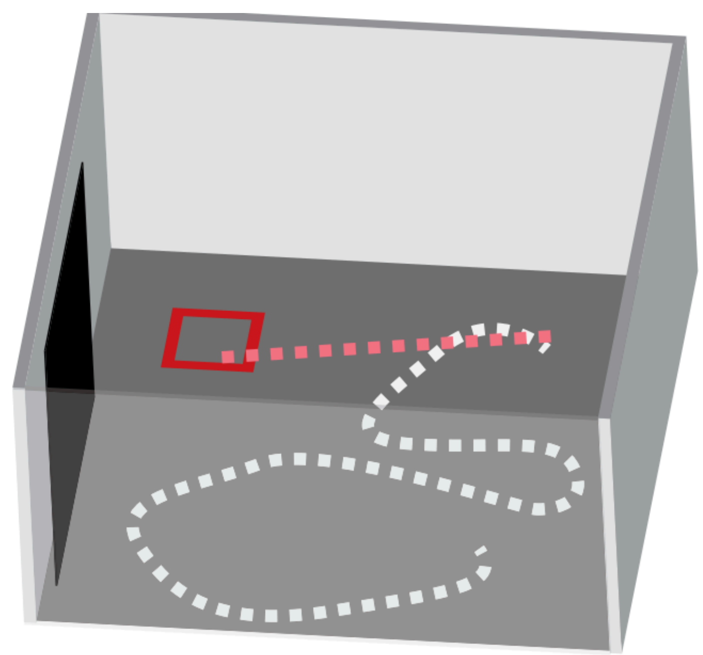
Remapping in the presence of reward

Remembered reward locations restructure entorhinal spatial maps

William N. Butler*, Kiah Hardcastle*, Lisa M. Giocomo†



free foraging (ENV1)



spatial task (ENV2)

Remapping in the presence of reward

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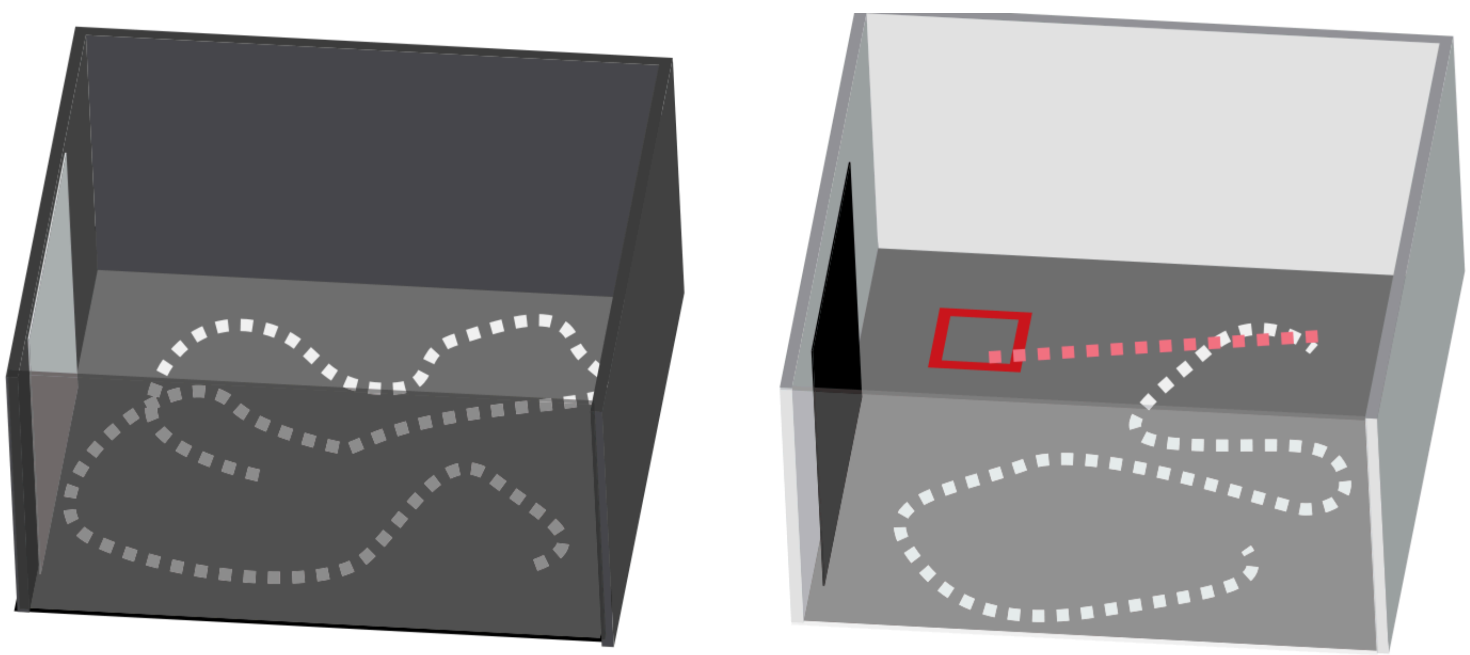
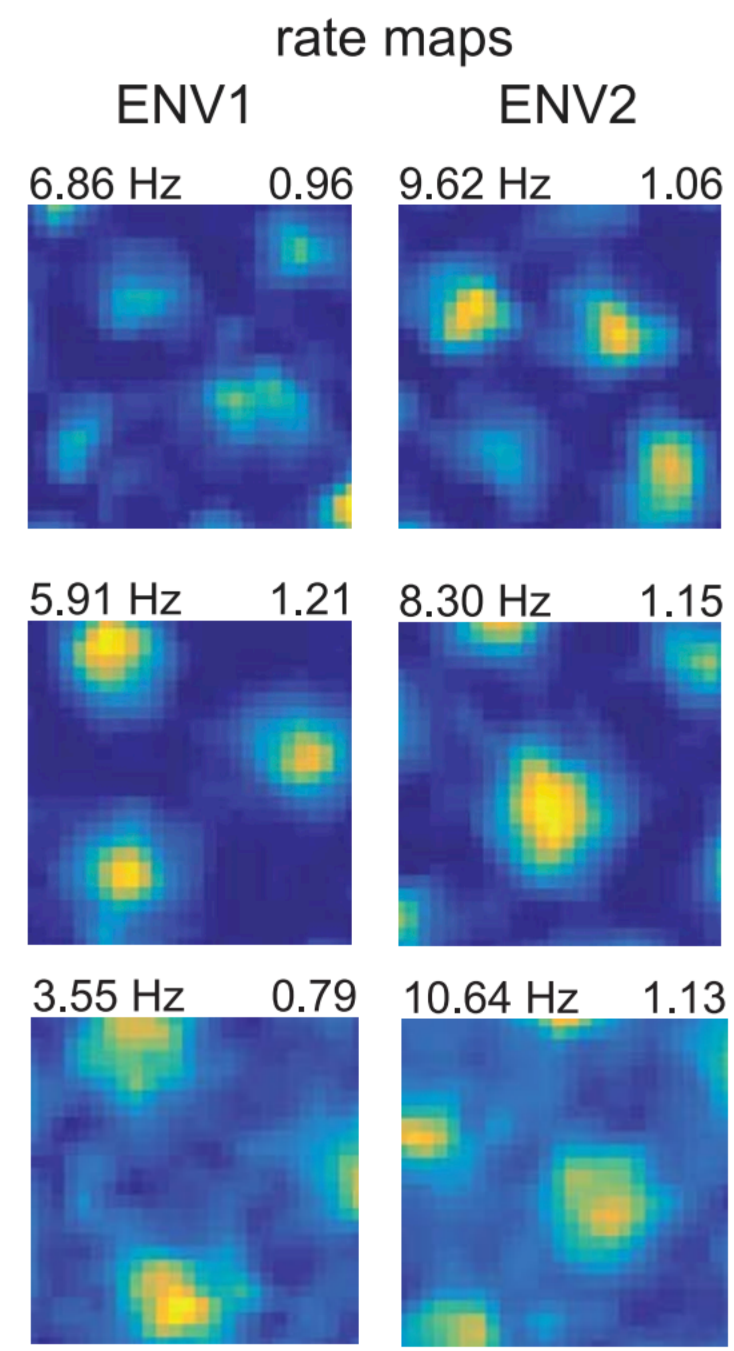
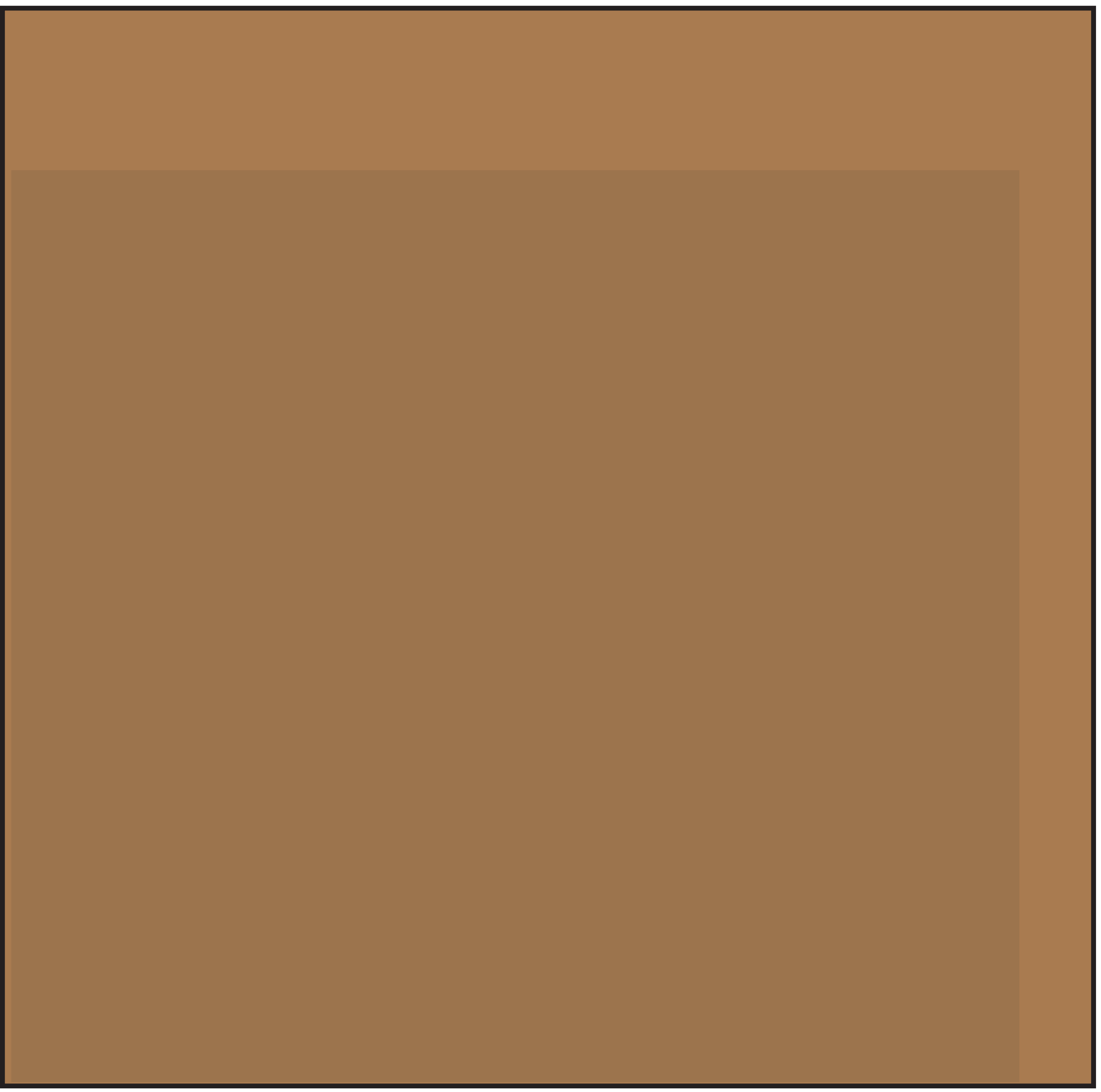


free foraging (ENV1) spatial task (ENV2)



Modeling rewards



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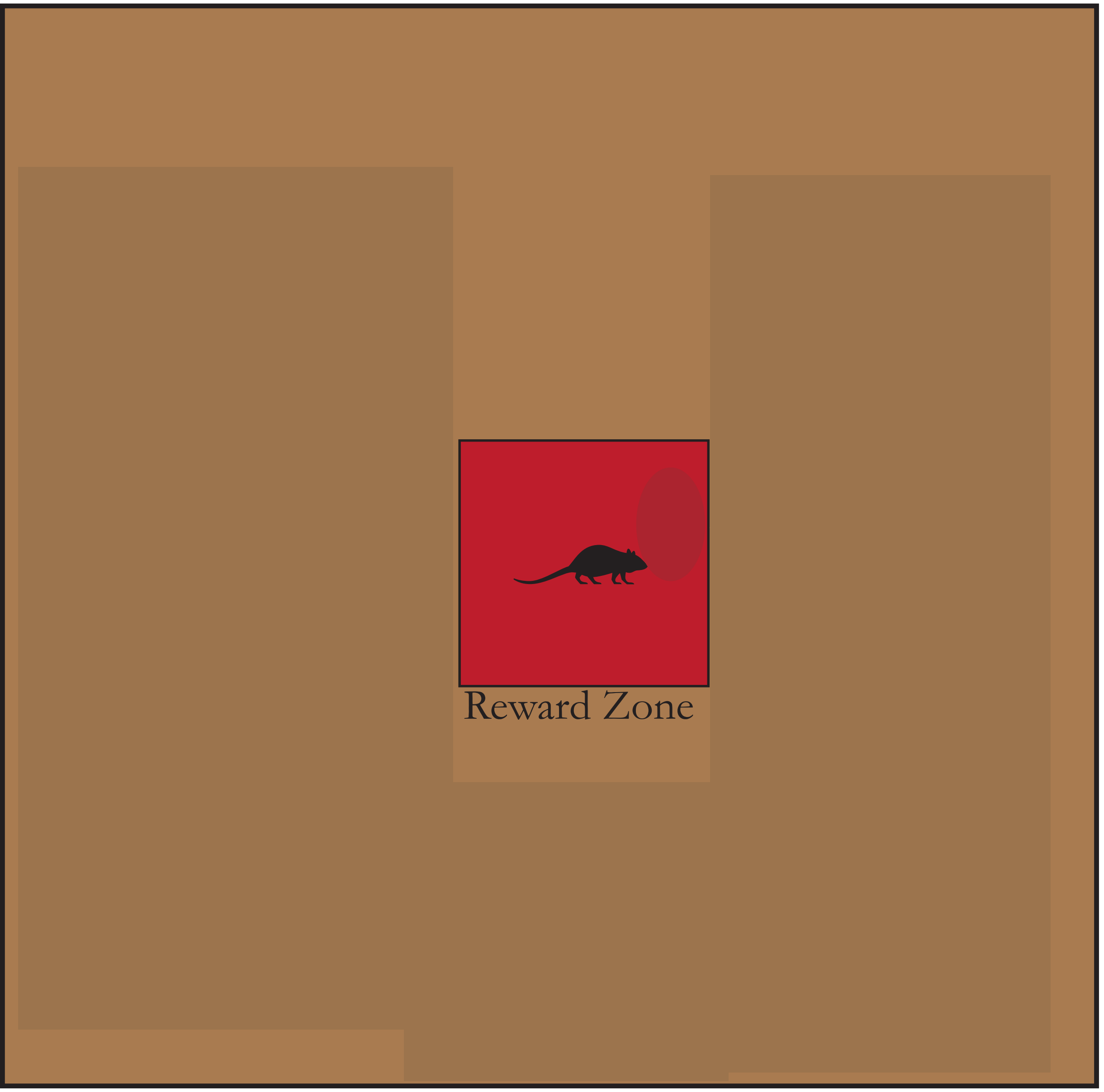
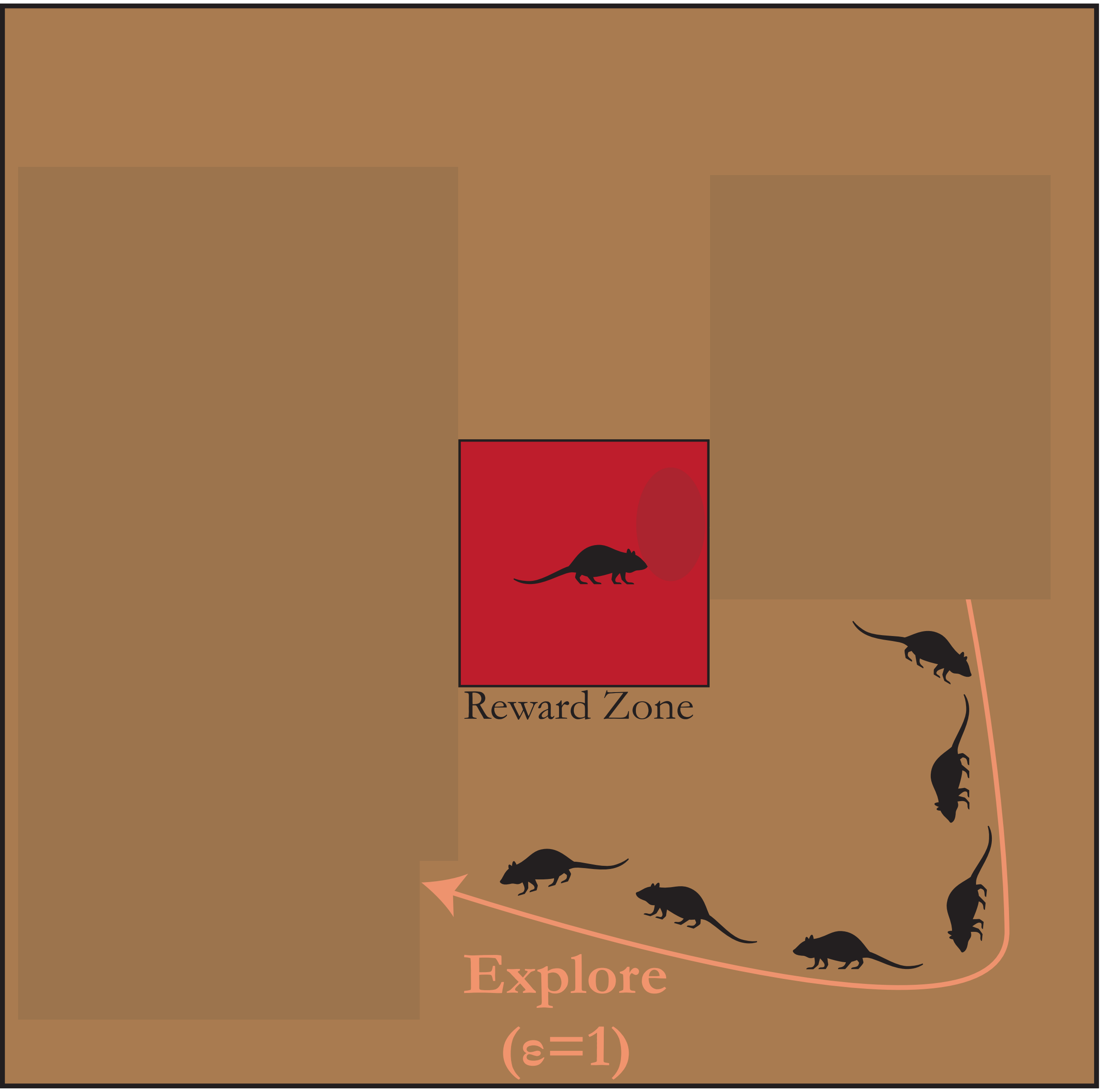
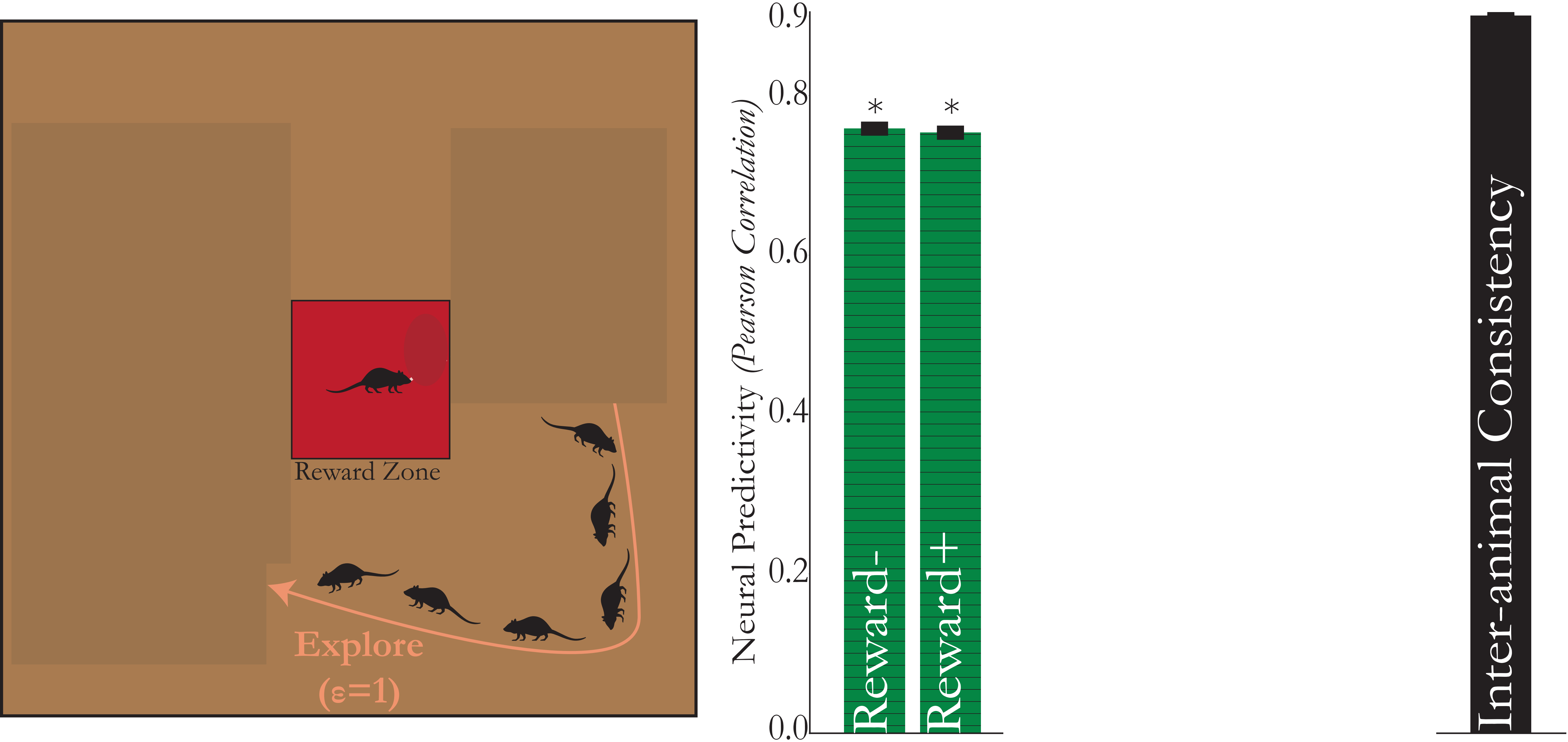


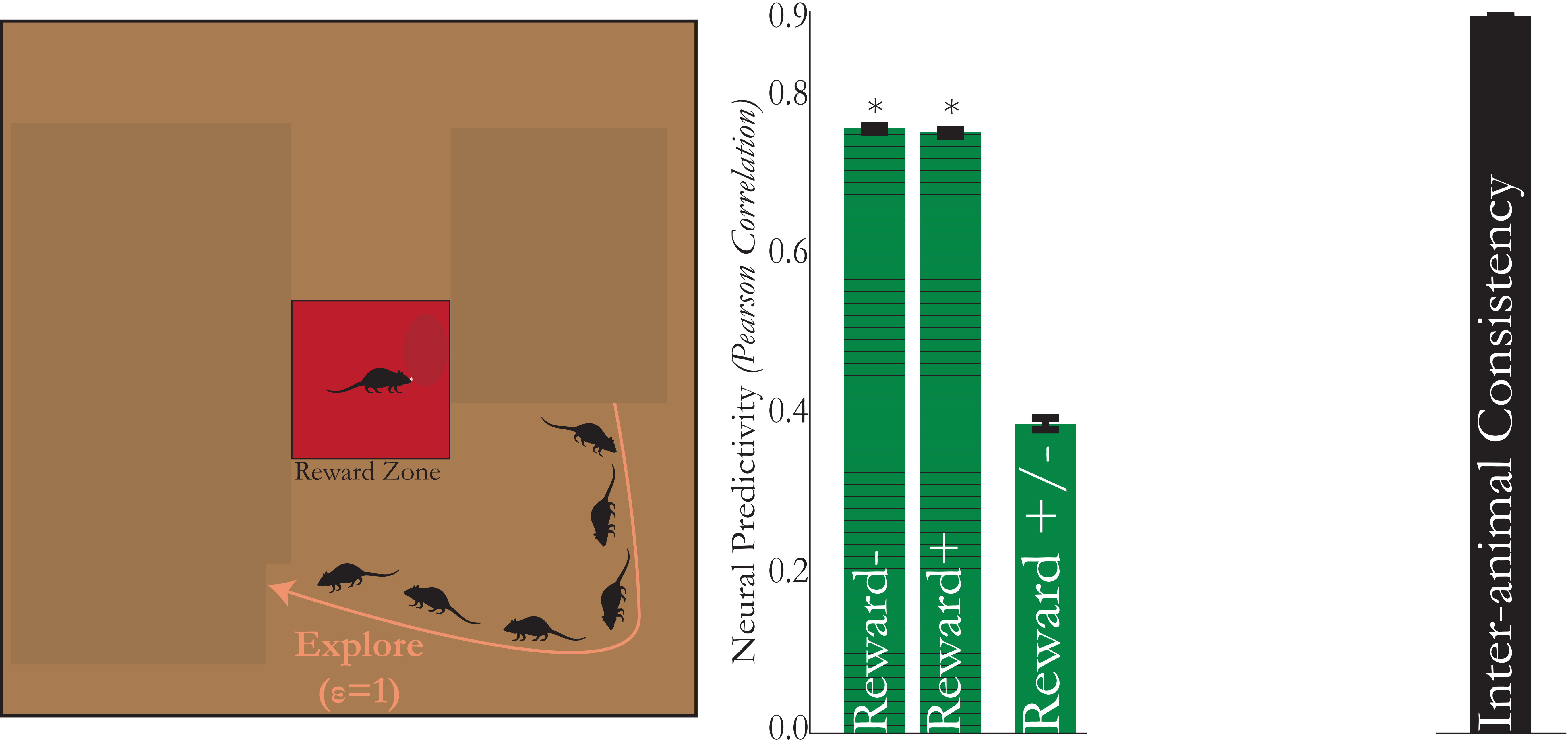
Modeling rewards - What we have done previously



Exploration only model captures each condition *separately*

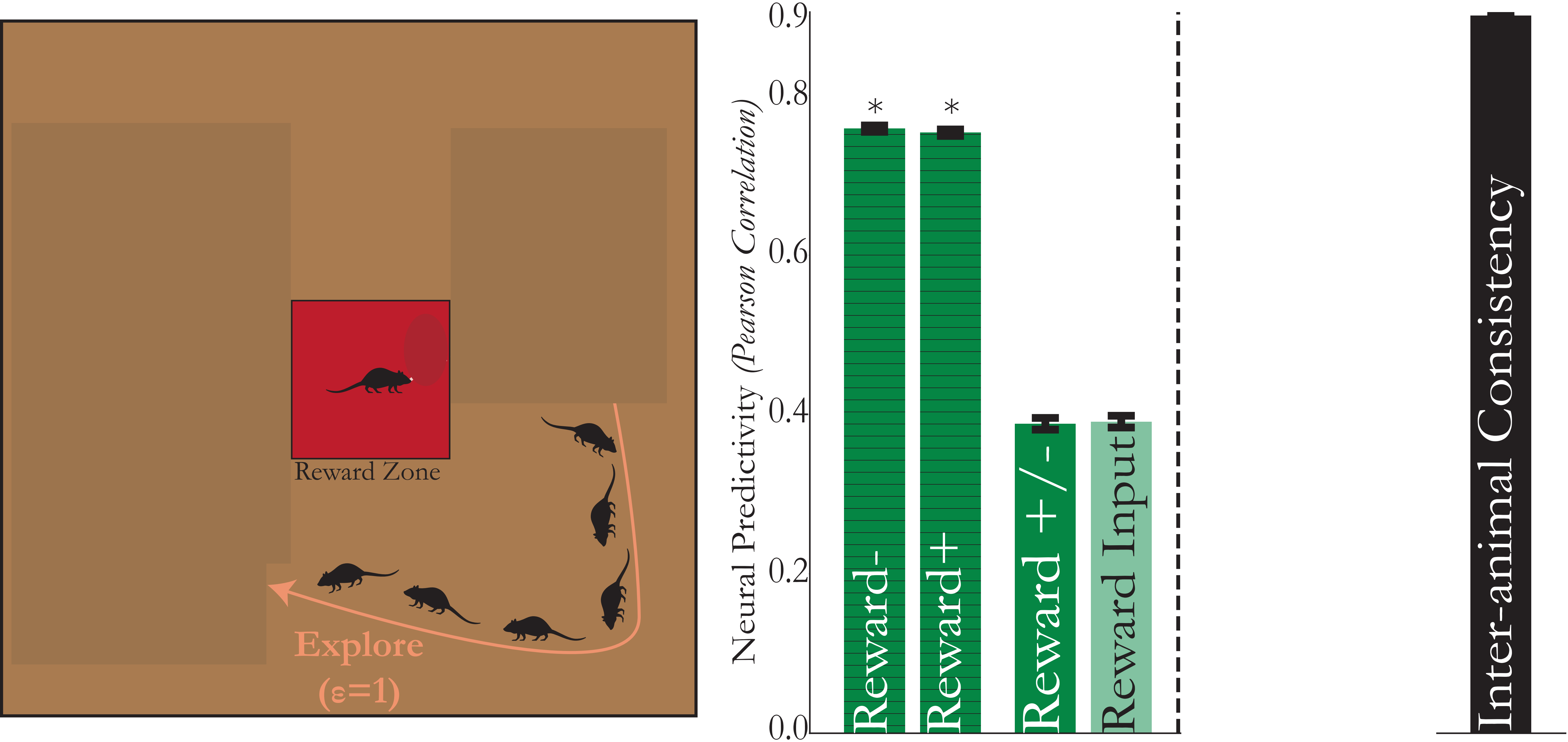


Exploration only model fails to capture remapping



Failure of pure exploration!

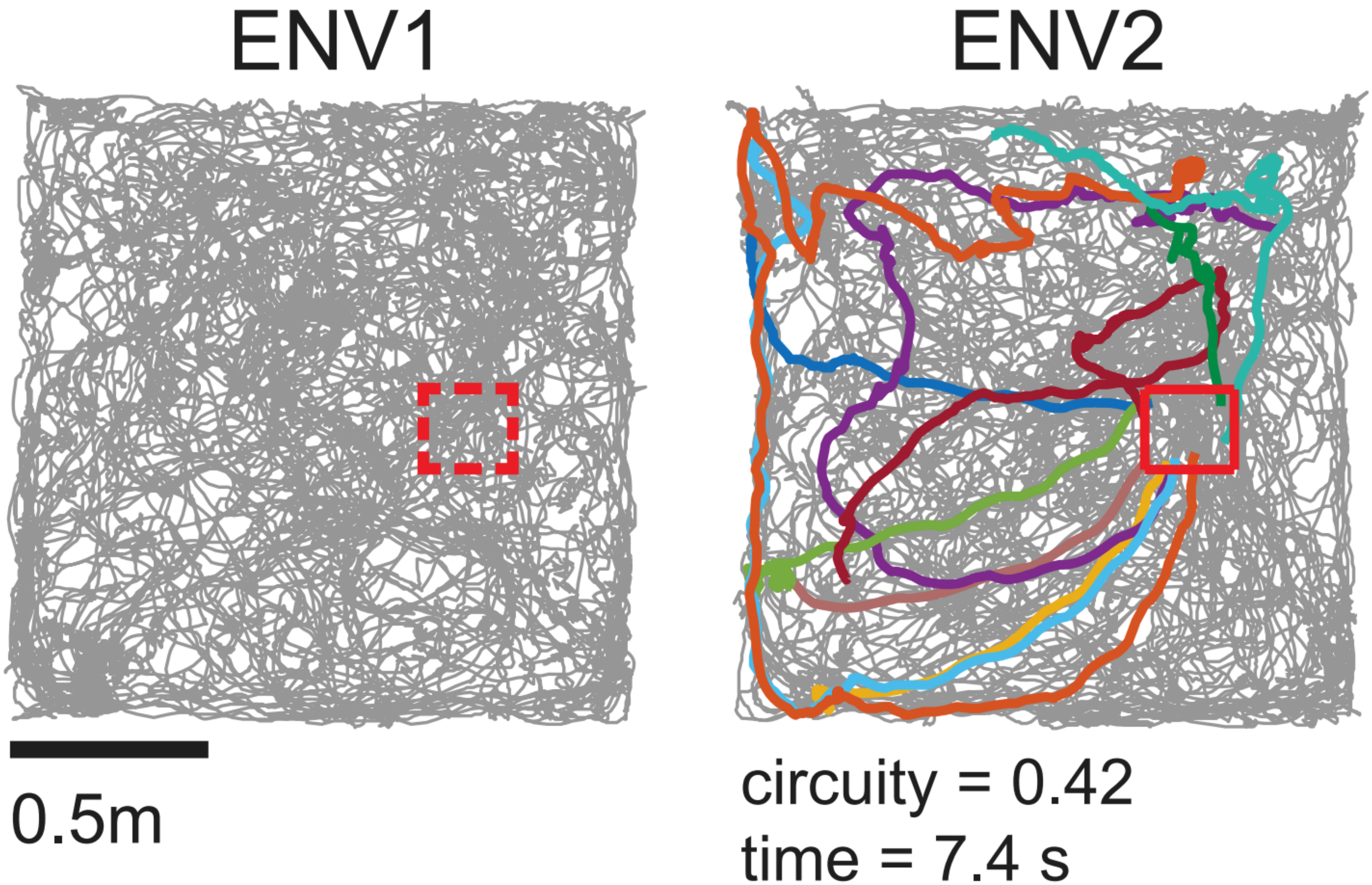
Reward must be extrinsically modeled



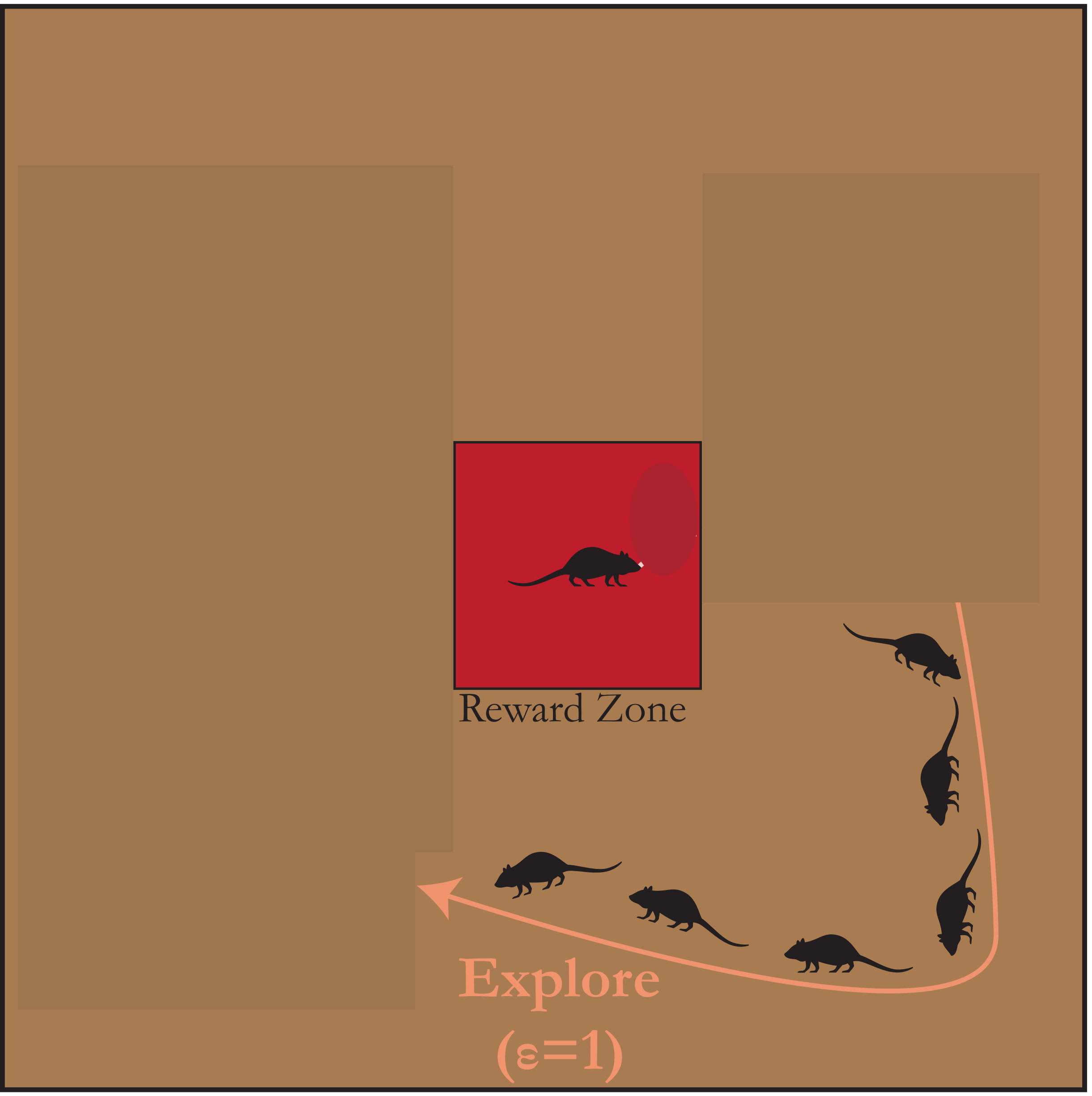
Simply augmenting inputs does not help either

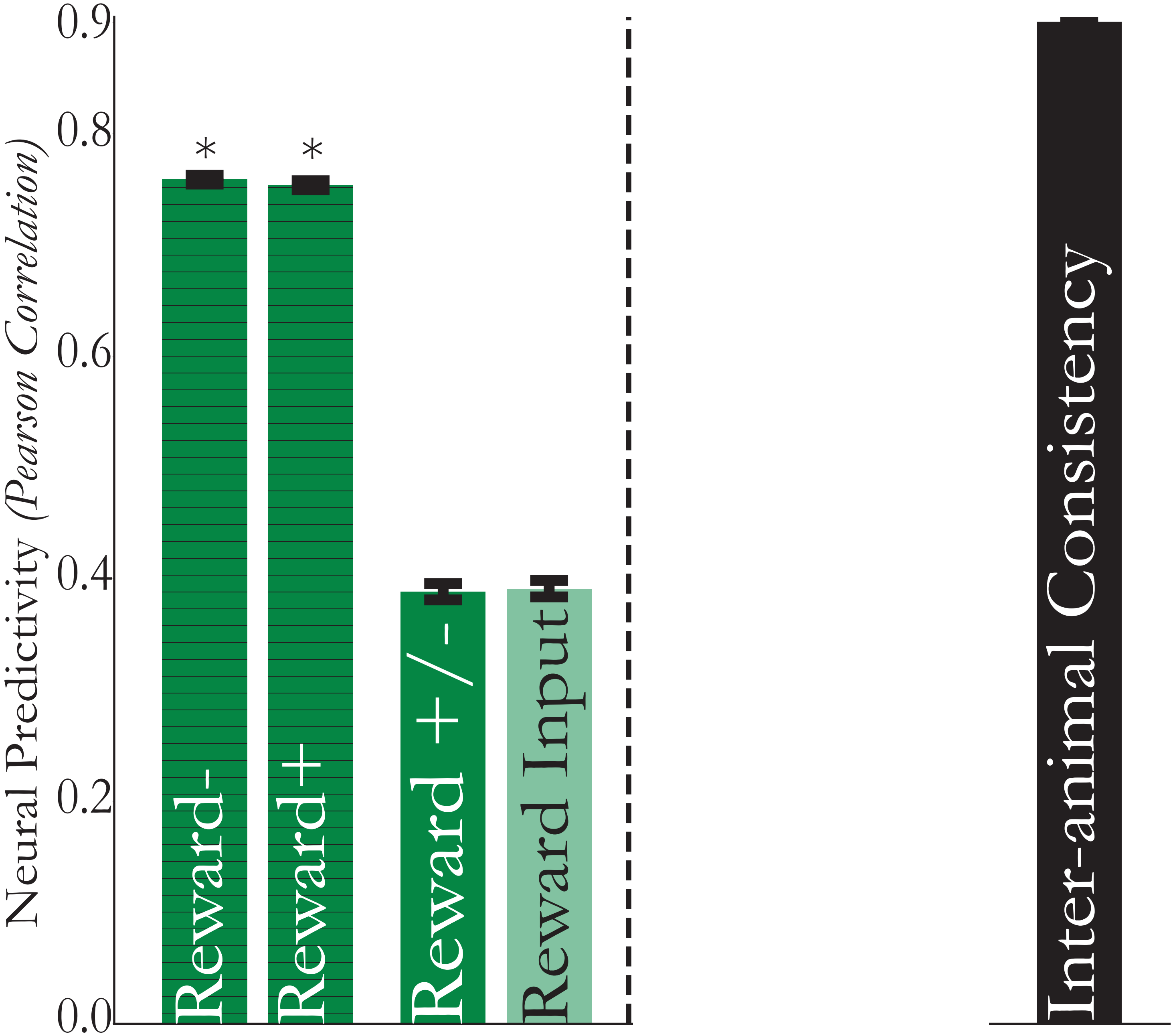
Inspiration from animal behavior — rapid, direct paths

Animals tend to take rapid, direct paths to reward zone

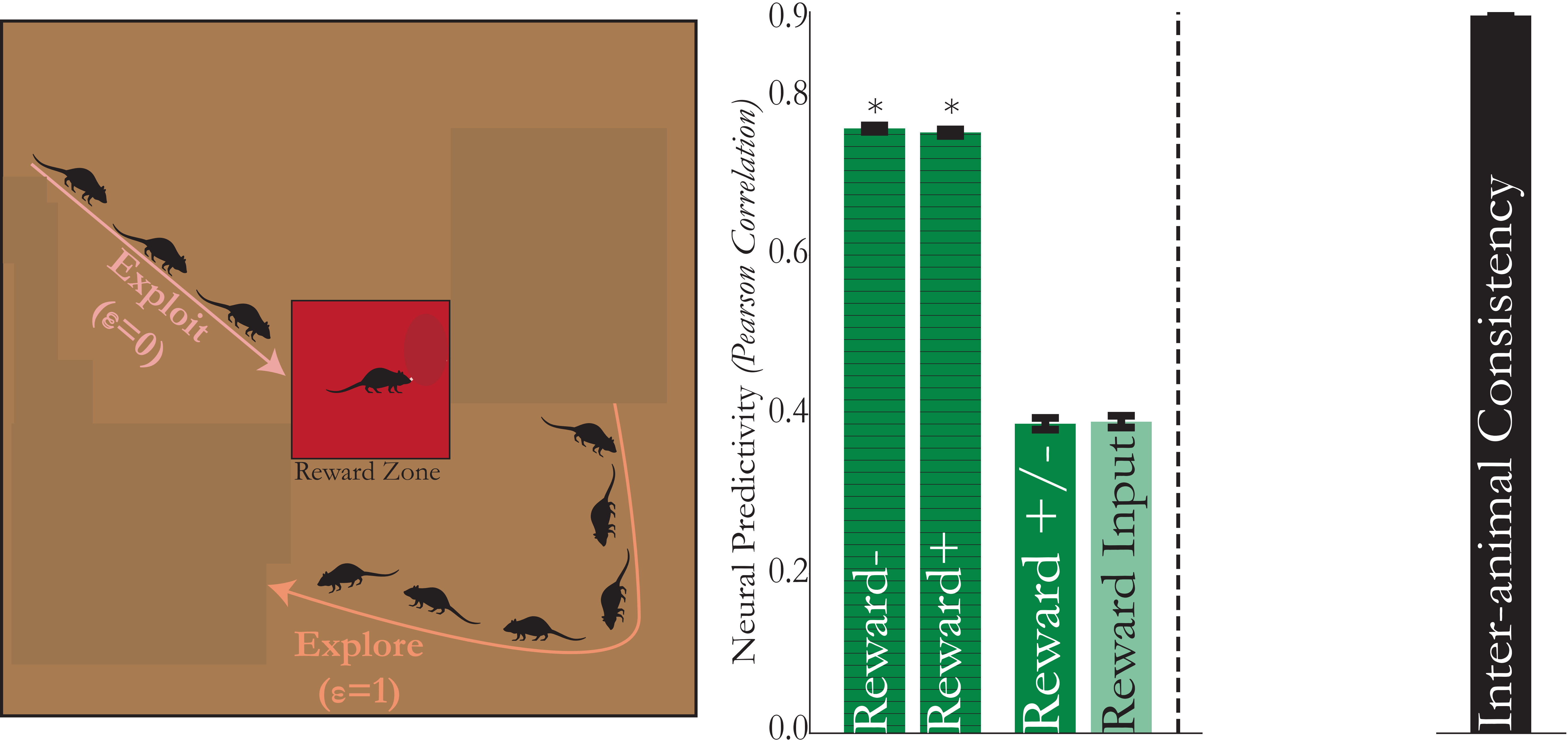


Reward must be extrinsically modeled





Modeling rewards as biased path integration



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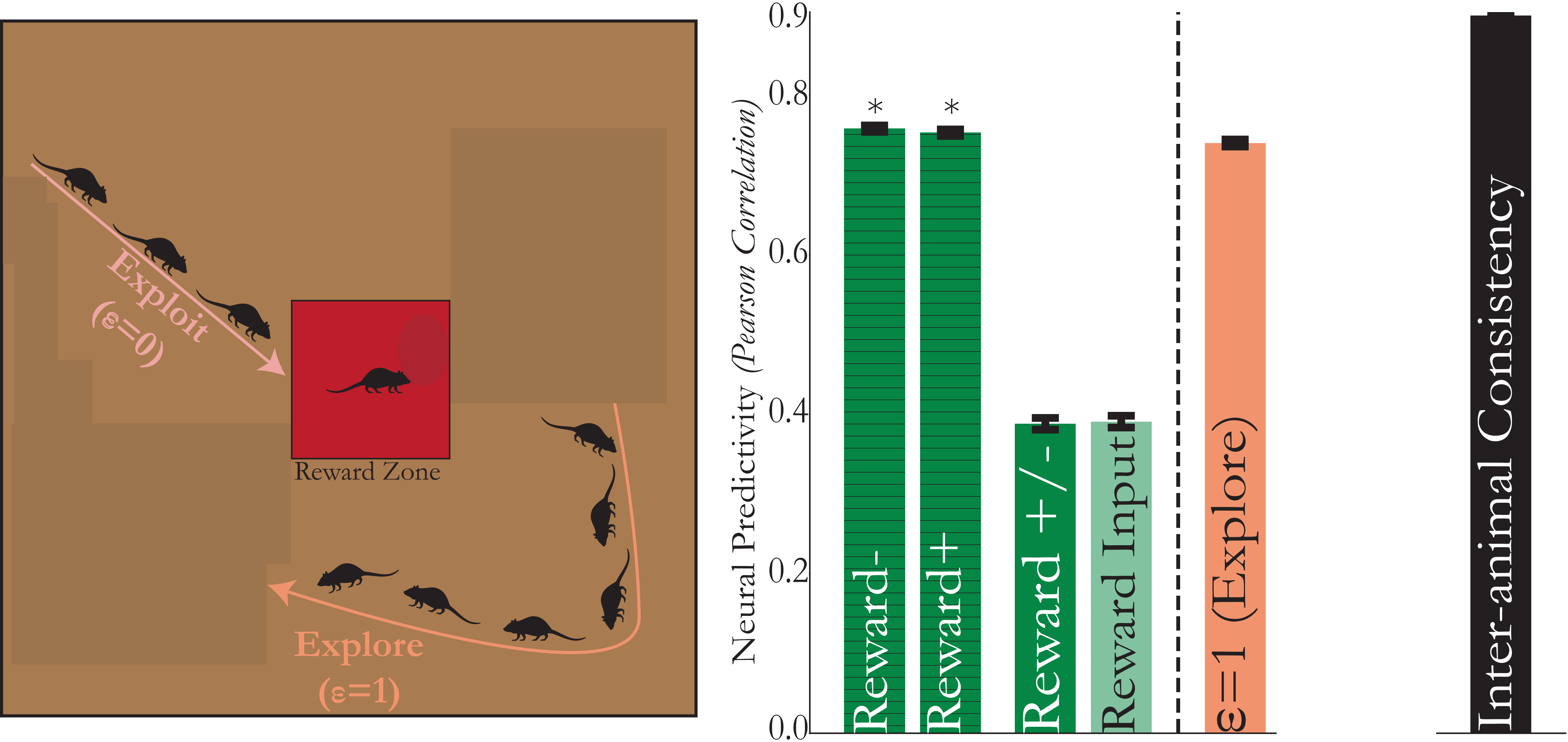

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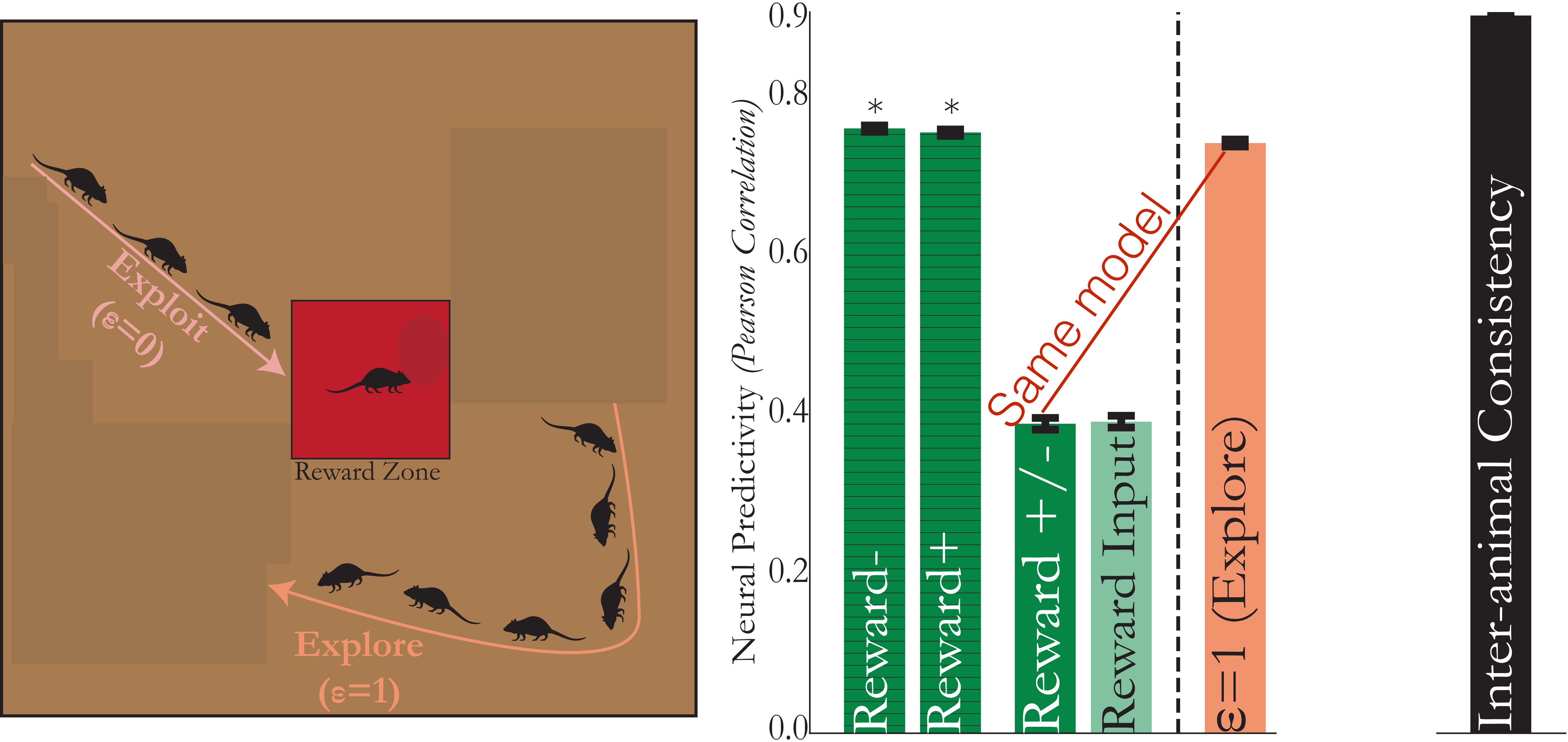
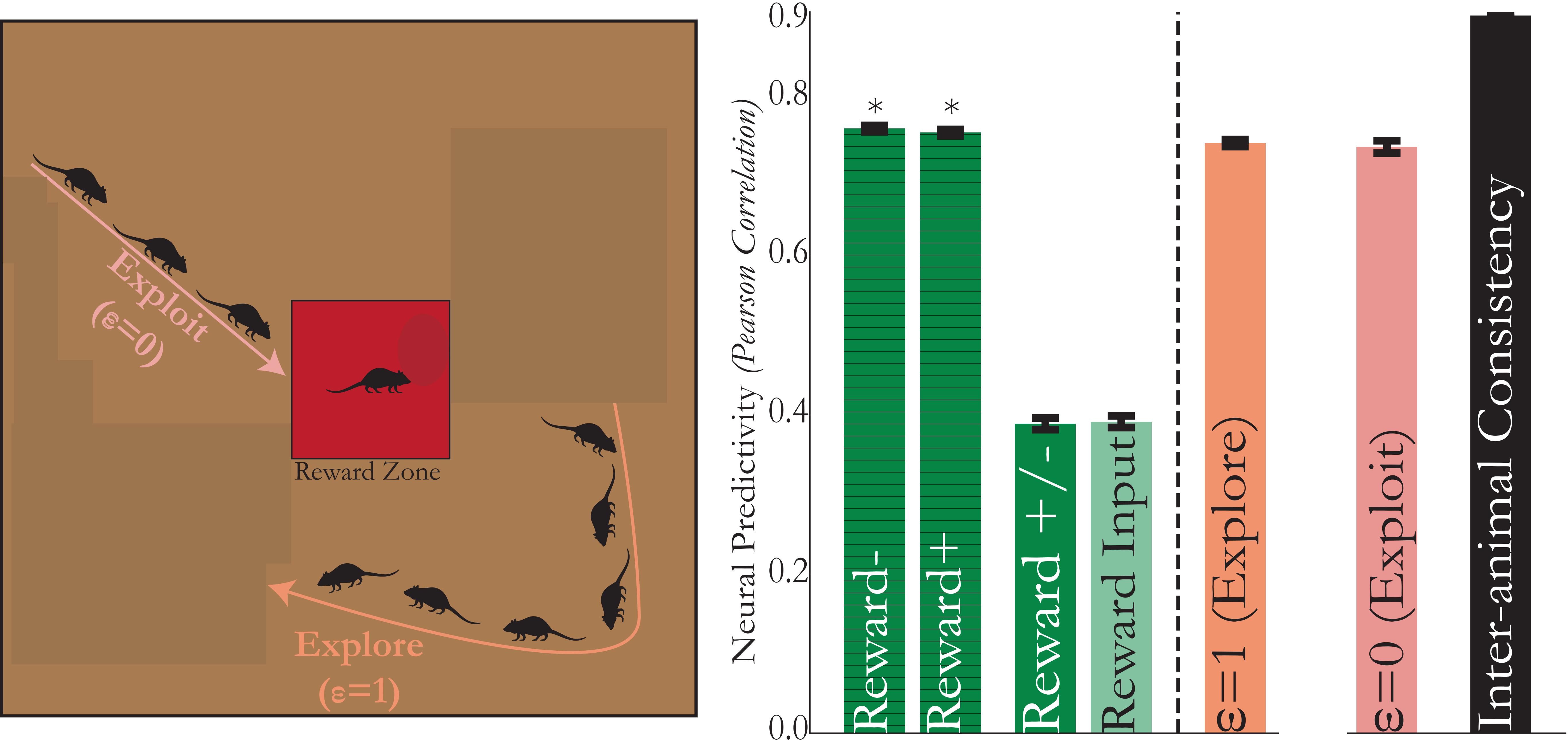
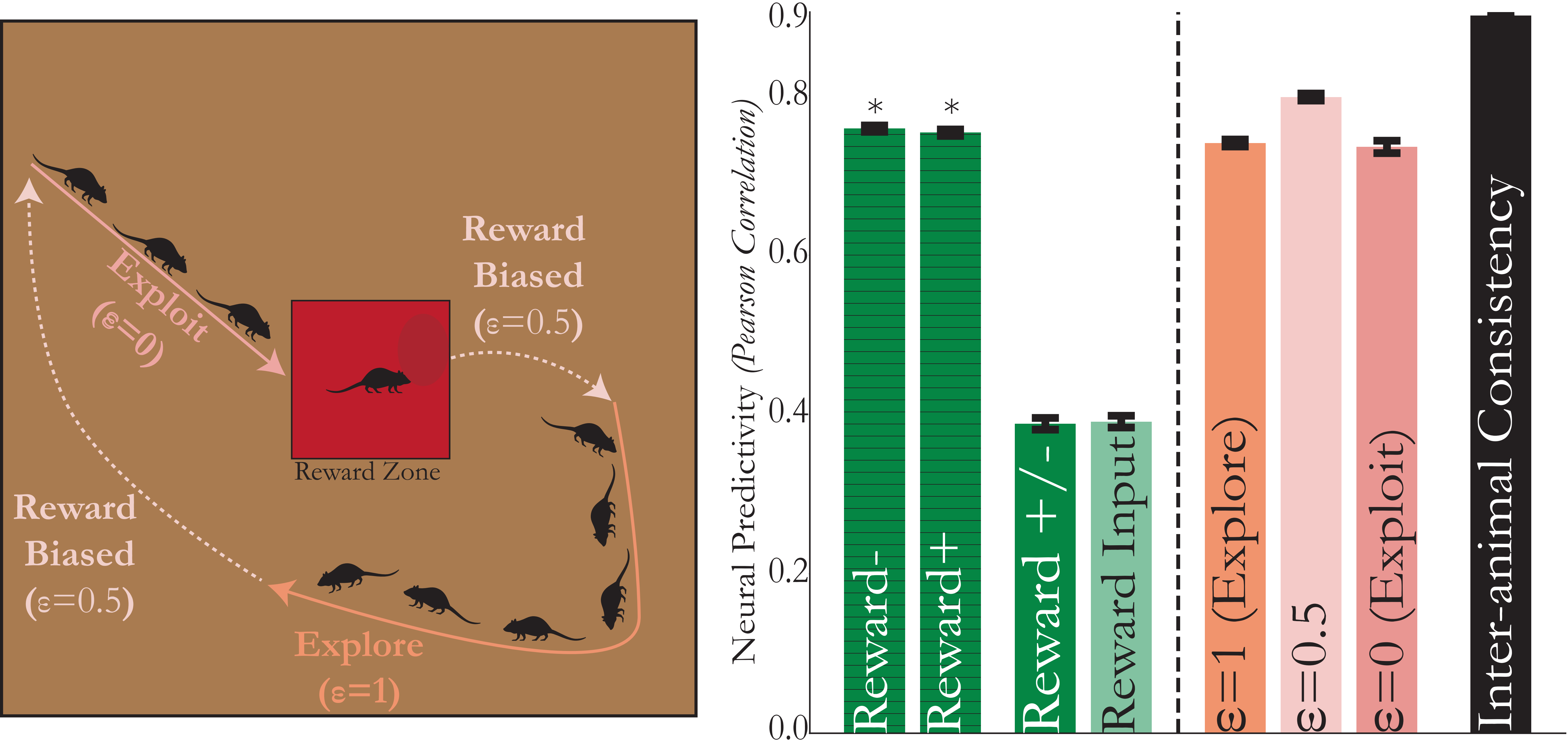


Reward remapping strongly input driven!

Pure exploitation isn't any better



Reward-biased path integration captures remapping of responses in the presence of reward



Reward-biased path integrator best captures remapping

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Overall Conclusion: A process of biological performance optimization directly shaped the neural mechanisms in MEC as a whole *(normative explanation for grid & non-grid cells alike)*.

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Pretrained Models & Neural Fitting Pipeline: https://github.com/neuroailab/mec

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