Hippocampus

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By Fax
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Dear Dr. Touretzky:

I have received the reviews of your paper H-668-03, Deforming the Hippocampal Map. The reviewers have raised a number of substantive concerns about the paper which necessitate substantial revision. The kinds of revisions requested are clearly set out in the reviewers' comments.

When you return the revised manuscript, please include a cover letter indicating the modifications that you have made to the paper and how these have addressed the concerns raised by the reviewers. Please submit one original and four copies of the paper and I shall arrange for it to be re-reviewed as promptly as possible.

Thank you for submitting your work to **Hippocampus**. I look forward to receiving the revised manuscript.

Best regards,

Howard Eichenbaum, Ph.D.
Editor-in-Chief

Deforming the hippocampal map

Touretzky et al

This paper presents different models that account for the experimentally observed deformations of the hippocampal spatial map by rotations of landmarks in an open field: a maximum-likelihood formulation, and an attractor network implementation. The results represents an important improvement compared to the purely descriptive model of Fenton et al (2000). However, there are several problems that should be addressed before the paper can be published. These problems are all related to the attractor network model. The basic problem is that it would be impossible for a reader to reproduce the results, given the absence of relevant details:

- Feedforward inhibition term discussed p.17 not defined. It does not seem to appear in Eq.(14). Furthermore, it is hard to see what would be the biological equivalent of such a term (and the authors certainly do not provide any). It is not clear why such a term is more effective that the recurrent shunting inhibition.
- The authors should provide an equation for w_{ik}^{EF} (similar to Eq.20), and $FD_k(t)$.
- They should provide the values of the parameters, like w^{EI}, w^{IE}, w^{II}, τ_I.
- It seems the model mixes parallel synchronous updating in discrete time (the $t+1$ in equation 14) with a continuous time description (equations 15 and 18). Please clarify. Why this mixed scheme? How do τ_E, τ_I compare with the '1' appearing in equation (14)? Why not obtain $V_i(t)$ as an instantaneous function of F_j, FI, and FD, by removing the $+1$ in Equation (14)?

Other comments.

It looks the paper has not been properly checked before submission. E.g. address of one of the authors missing, question marks appearing p.9 instead of a reference, etc.

p.3. The paper has no introduction. It would be good to present a brief introduction about place cells and their control by external cues.

p.9 l-6: The justification for using σ proportional to the perceived distance should appear earlier, when equation (6) is introduced.

p.10, eq.(11) 'which bears a strong resemblance to Equation 3', please explain better what the resemblance is.

p.12, eq.(12): there is a problem with the normalization, because of the limited available space. Better use a normalization constant as in Eq.(6). Also, σ_a should be defined.

p.14, l-9: the model of Zhang (1996) is a model for head direction cells not hippocampal place cells.

p.16: l12: 'This approximation...', what approximation are you talking about?

p.22, the link with the approach of Pouget and collaborators should be made more clear. These authors actually demonstrated (not suggested) that a suitably wired attractor network can implement maximum likelihood in some cases (see Pouget et al Neural Computation, 10:373-401 1998, Deneve et al Nature Neurosci 2(8):740-745. 1999). The authors should discuss in more detail this point since it is very much related to their central claim.

Reviewer 2

This paper describes two models of the way in which hippocampal place fields are transformed in two specific experiments of Fenton et al. (2000a). The emphasis is on how objects in the environment control the location (and shape) of place fields in a familiar environment. This was probed in the experiments by relatively subtle cue manipulations which lead to smooth and moderate changes in place field characteristics. These data can, albeit indirectly, provide information about the mechanisms within (and outside) the hippocampus which turn sensory information about individual cues into the hippocampal place cell representation. Models of these data are useful insofar as they provide additional insight into the possible underlying mechanisms.

In this respect, both of the models presented in this paper represent a significant improvement over the purely descriptive model of the same data proposed by Fenton et al. (2000b). The first model offers a rationale for the observed changes by proposing that they represent maximum likelihood probabilistic inference about the animal's location given the observations about available cues. The second model complements the first by offering a mechanistic account in terms of the dynamics of a recurrent network. The two types of model, taken together, have the potential to provide a more or less complete account of the experimental findings. Both models employ relatively well-established techniques, which are handled convincingly by the authors.

One important and, especially in view of the list of authors, somewhat surprising shortcoming of the paper is that it fails to compare the results from the models with the original experimental data. Comparisons are made solely with the vector field model of Fenton et al. (2000b). This seems unsatisfactory especially since Fenton et al. (2000b) acknowledge that their model does not capture some aspects of their data (in particular, the radial displacement of the fields) particularly well. Therefore, it would have been very informative to see whether either of the new models can achieve a better fit to the data than the vector field model. Provided that the original data are available, even a quantitative test of the models' goodness of fit, similar to the one applied by Fenton et al. (2000b), should have been feasible.

In addition, it should be noted that although both models could potentially be used to explain the consequences of a large number of experimental manipulations, here their predictions are tested only in the situations investigated by Fenton et al (2000a).

One slight problem that I had with the interpretation of the maximum likelihood results was the following. The main strength of the ML approach

is that it is based on some sense of optimality. However, optimality really applies at the behavioral/ecological level, and therefore what matters is the inference that the animal makes about its position based on the activities of place cells. On the other hand, ML is used in the paper to determine the movement of place field centers. Does this also lead to a ML estimation of the rat's position? Presumably, this will depend on assumptions about how the place cell code is utilized to come up with an estimate of the rat's position.

Finally, I believe that one of the conclusions in the Discussion section is erroneous. In particular, on page 24, the authors claim that if the recurrent connections dominated over the external input, "map distortions caused by relative motion would not be possible." The authors are right that in this case, at any given place in the environment, the possible shapes of the activity bump in the abstract space of unit activities are determined by the recurrent connections, and that the external input can only select among these attractors. However, the shape of place fields and the relative positions of place field centers in real space are determined by which attractor is selected at any particular location in the environment, and this in turn depends on how the input to the place cell population shifts as the animal's position changes. In fact, Kali and Dayan (2000), whose model, I believe, operates in this attractor--dominated regime, report a stretching of the place cell map as the shape of the environment is manipulated.

In summary, this is a fairly interesting and solid piece of modeling. Although it introduces few radically new ideas or techniques, the simultaneous application and comparison of maximum likelihood estimation and attractor network computation in relation to hippocampal place cell data is worthy of attention. On the other hand, I believe that the paper could benefit substantially from including the results of a direct comparison between the models and the original experimental data of Fenton et al. (2000a).

Minor points:

- setting a convenient reference direction by fiat is a crucial part of the final solution in practically all the models discussed; ideally, the mechanism responsible for finding a reference direction should be implemented at the same level as the rest of the model; at the least, the importance of this step should be emphasized further

- page 12: why are 4 pairs of landmarks used? Only 3 angles are independent (even for a naive observer).

- page 12: it would be more appropriate to use a probability distribution

designed for angular variables, such as the circular Gaussian, in Equation 12.

- pages 18-19: the weights between the feature detectors and the place cells, and feedforward inhibition, which seem to have a crucial bearing on the results, should be described in detail

- page 23: The argument about changing place field shape is incorrect in its current form -- a location closer to the place field center does not mean a higher firing rate if the shape of the field in the two cases is different (also see related comment above). However, this can be rectified, at least in the strong attractor limit, by flipping the argument around: due to the same attractor being activated, cell j should actually fire at the same rate at location c_i' in the new environment as it did at c_i in the old environment; since c_i' is closer to c_j' than c_i was to c_j, and the rate change is the same, the shape of the field must be different.

Typos, etc.:

- front page: one author's address is missing
- page 3, etc.: the name of the second author in the Fenton et al. (2000a,b) papers is consistently misspelled
- page 5: I do not think the notation "atan2" is often used outside programming environments
- page 9: there is a missing reference near the bottom of the page
- page 10: an obvious typo in Equ. 9
- page 14: it is not the likelihoods, but rather the log likelihoods that can be combined by simple addition