HIPPOCAMPAL PLACE CELL FIRING DURING HEAD-SCANNING MOVEMENTS IS ASSOCIATED WITH THE FORMATION OF NEW PLACE FIELDS

97.13

Joe Monaco, Geeta Rao, and James J. Knierim

Zanvyl Krieger Mind/Brain institute, Johns Hopkins Univ.

JOHNS HOPKINS UNIVERSITY

INTRODUCTION

The firing rate of a place cell as the animal runs through its place field is variable from one entry to the next (Fenton and Muller, 1998). It has been hypothesized that the firing may be dynamically modulated by attention (Kentros et al., 2004; Muzzio et al., 2009; Fenton et al., 2010). During locomotion on a circular track, the animal often pauses to examine the environment, even a familiar one, with lateral movements of the head away from the track. This behavior is likely to coincide with heightened attention to environmental features (Drai et al., 2001), particularly to distal cues. We examined whether the execution of a head-scanning event (HSE) in a particular location modulates subsequent place cell firing on the track at that location. Twenty rats were trained to run clockwise 15-17 laps on a circular track inside a curtained enclosure for randomly placed food reward. The circular track contained local cues, consisting of 4 quadrants with unique textures. Distal cues were located at the periphery, either on the floor or on the curtains. In this protocol, all of the animals paused to execute HSEs at various times, and these scans were associated with the onset of firing of new place cells. Head scans may underlie one avenue of information about external environmental features that becomes incorporated into the hippocampal spatial code.

DOUBLE ROTATION

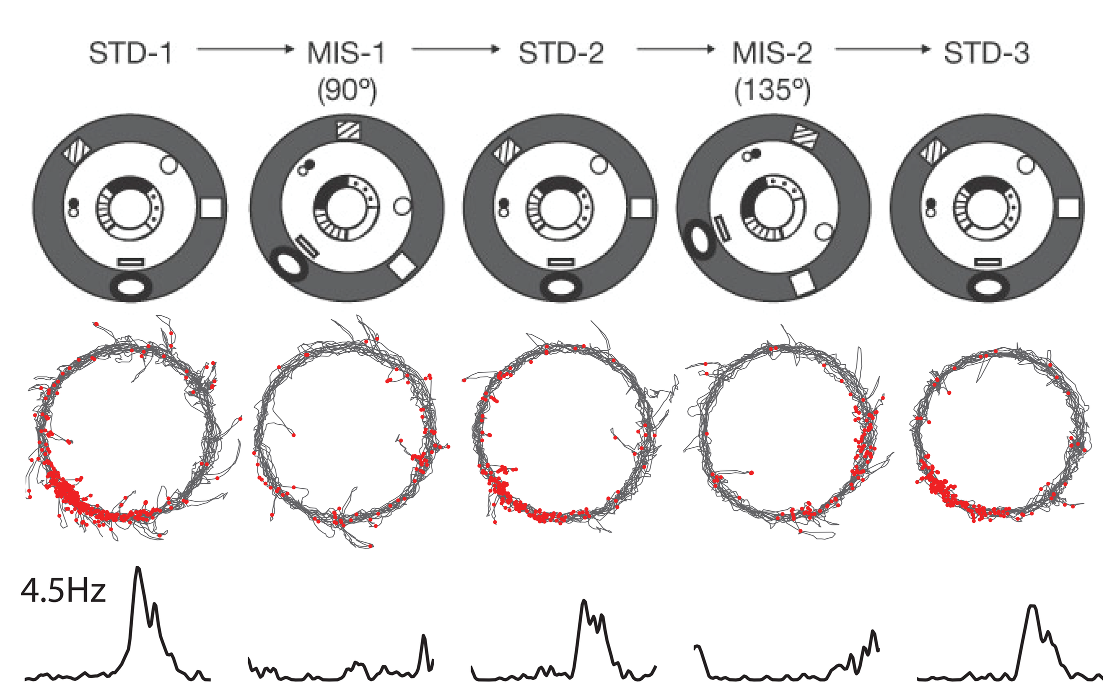
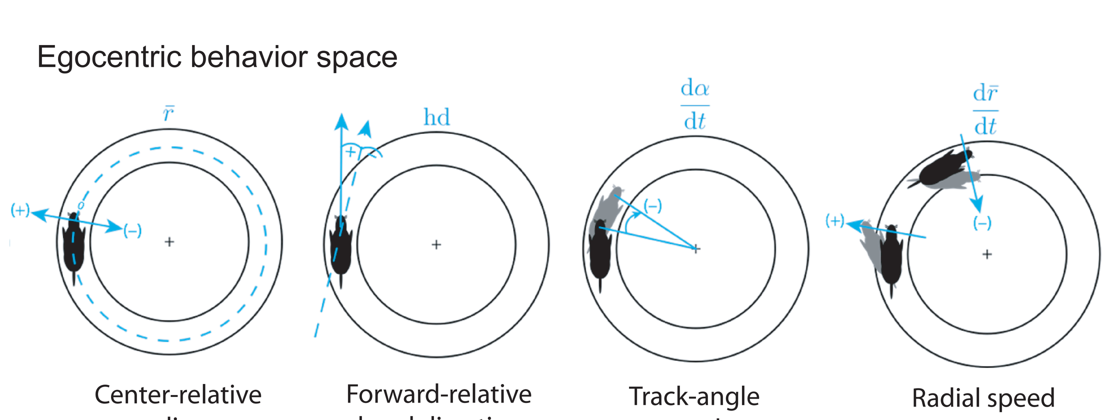


Fig. 1. Schematic of the double-rotation experimental paradigm in which sets of local and distal cues are put into conflict. Mismatch (MIS) sessions presenting cue conflict are interleaved with standard (STD) sessions presenting the familiar cue configuration. The spiking activity (middle) and linearized firing rate maps (bottom) of a CA3 place cell (rat 72,day 1, tetrode 11, cluster 8 from [3]) are shown across the five sessions of an experiment.

HEAD SCANNING EVENTS (HSEs)



Linear scan index:

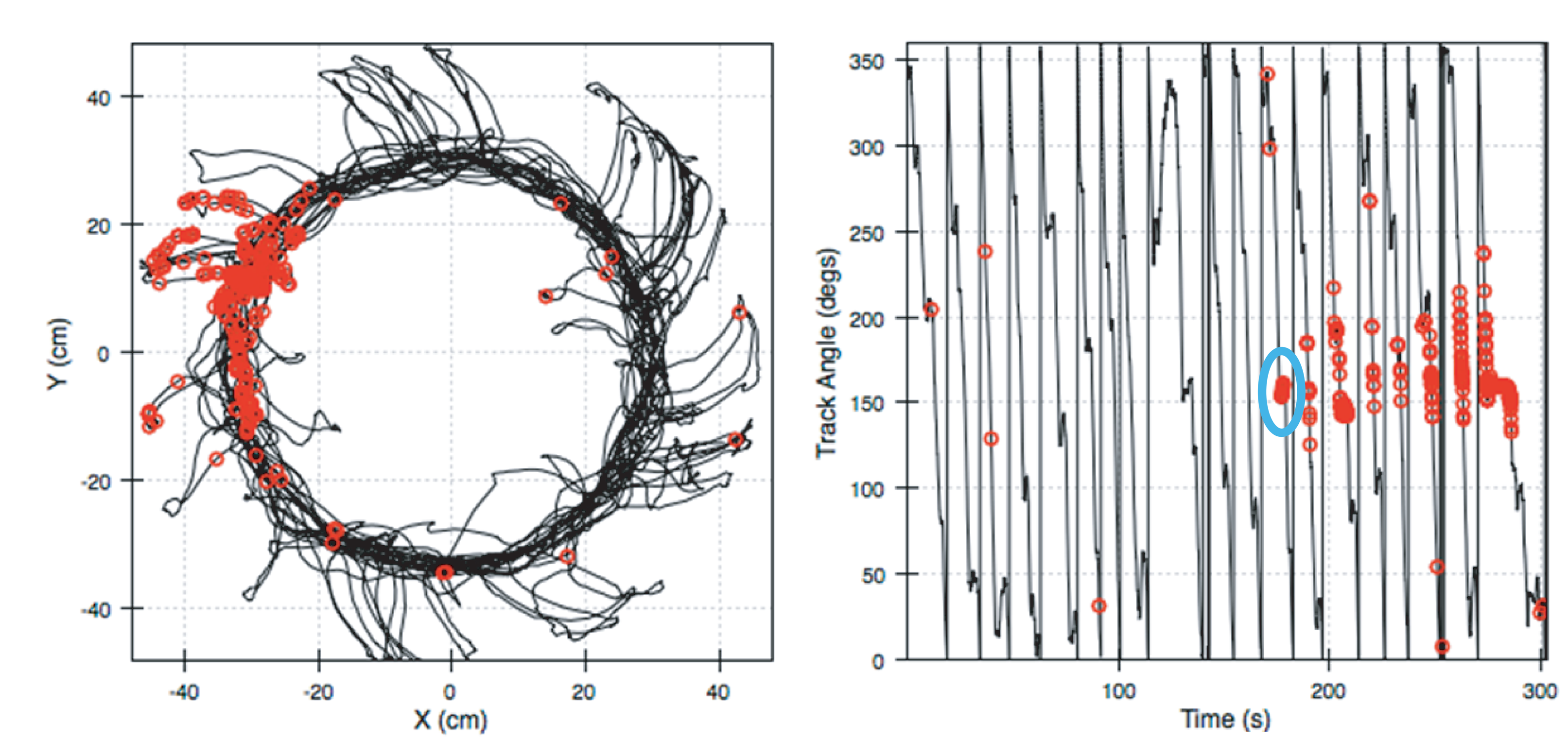
$$L_{\text{scan}} = \beta_0 \frac{d\alpha}{dt} + \beta_1 |\bar{r}| + \beta_2 \left|\frac{d\bar{r}}{dt}\right| + \beta_3 |\text{hd}|$$

This is thresholded, like a simple perceptron

$$\text{HSE}_i = \Phi\left[L^i_{\text{scan}} - \xi\right]$$

Fig. 2. Methodology for algorithmic detection of head-scanning events is based on finding suprathreshold episodes of a head-scanning index. The index is a perceptron output classifier based on the first equation.

WITHIN SESSION FIELD FORMATION



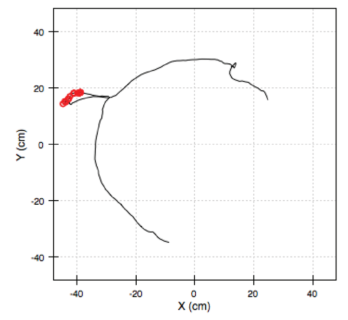


Fig. 3. Above left: An example trajectory with spiking activity showing a robust place field that appeared suddenly more than halfway through a recording session on the circular track. Above right:The first spikes fired by this cell in that location are indicated by the blue oval and correspond to robust firing during an HSE on the previous lap, shown at left.

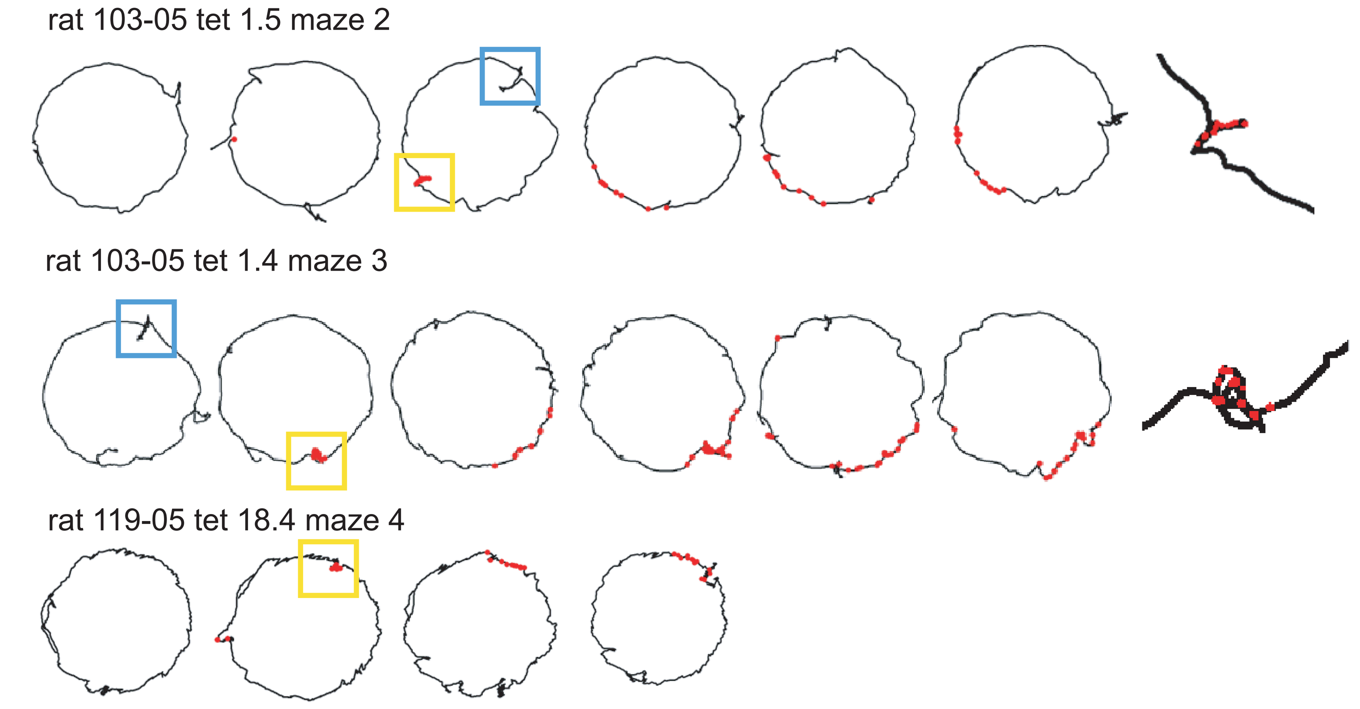


Fig. 4. Examples of place fields developing only in the location where the cell actually fired during the HSE (yellow boxes). A larger amplitude head scan unaccompanied by cell firing (blue boxes) did not appear to be sufficient for genesis of a place field.

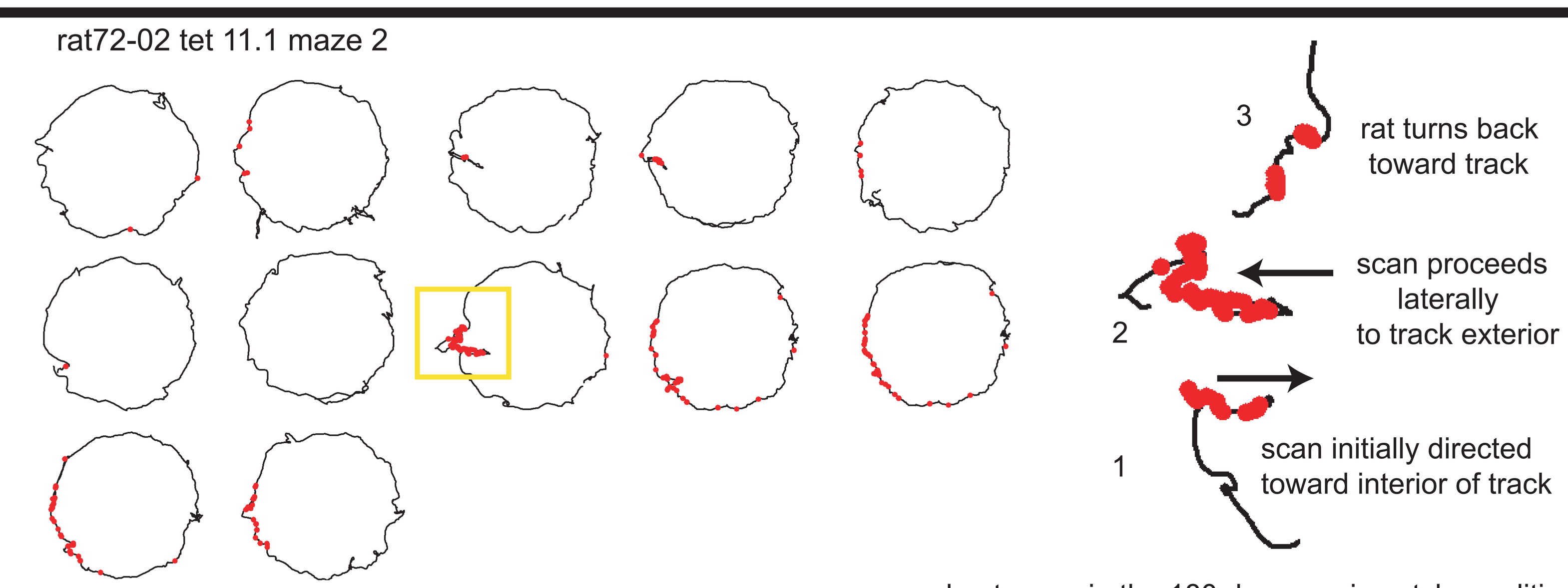


Fig. 5. An example of a robust scan in a session in which the rat first encountered the maximum mismatch of 180 degrees between the local and distal cues. The animal made a complex head movement in which it initially scanned the interior of the track (1), then made a further lateral head movement toward the exterior of the track (2) during which the cell fired robustly.The firing of the cell diminished as the rat turned back toward the track (3). The field appeared stronger in the remaining 4 laps of the session (only 12 laps were acquired in this session).

PREDICTIVE VALUE OF HEAD SCANS AND NEW FIELDS

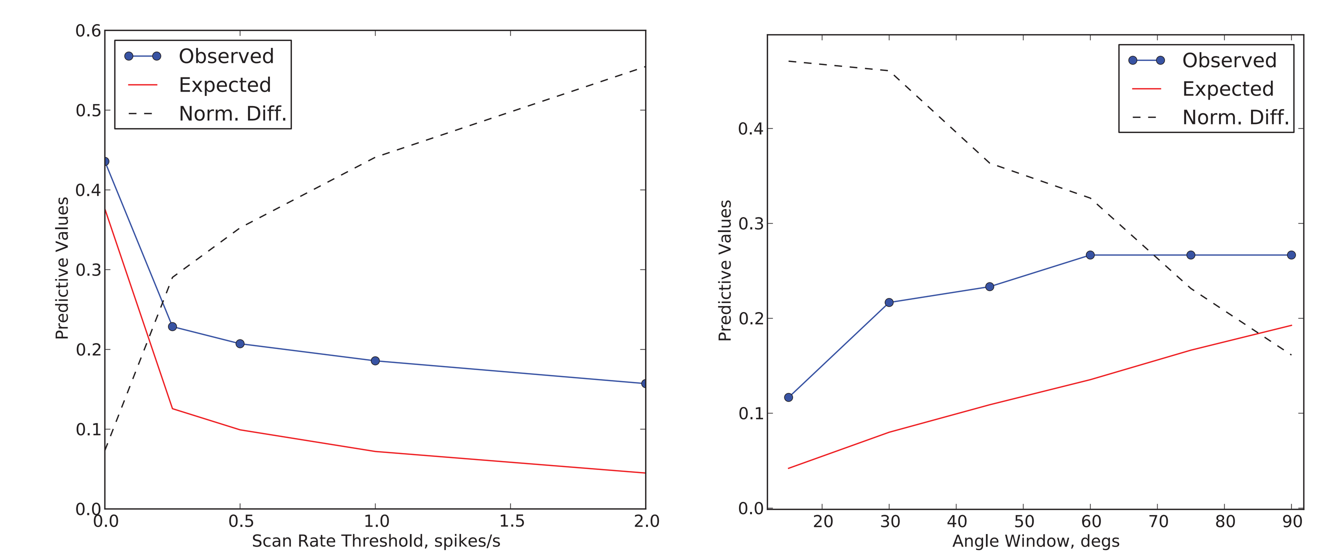


Fig. 6. Using algorithmic detection of place fields that first develop sometime in the middle of the experimental session, we computed the positive predictive value of an HSE on the lap previous to the emergence of the field. The predictive value is computed as the ratio of new place fields that are preceded by an HSE to the total number of new place fields. For every positive detection of a new field, we ran N=1000 bootstrap shuffles of the timing of scans within the session. The predictive value computed based on the bootstrap (red lines above) forms the expected baseline for the observation predicted value. Prior scan detection is based on a threshold for the firing rate of the scan and on a track-angle-based spatial window centered on the center-of-mass of the newly formed place field. For a 60-degree track window, the observed and expected predicted values are shown for series of scan firing-rate thresholds (Left). For a rate threshold of 1 spike/s, values are shown for a series of track-angle windows (Right).

NEW PLACE FIELDS PREDICTED BY HSE FIRING

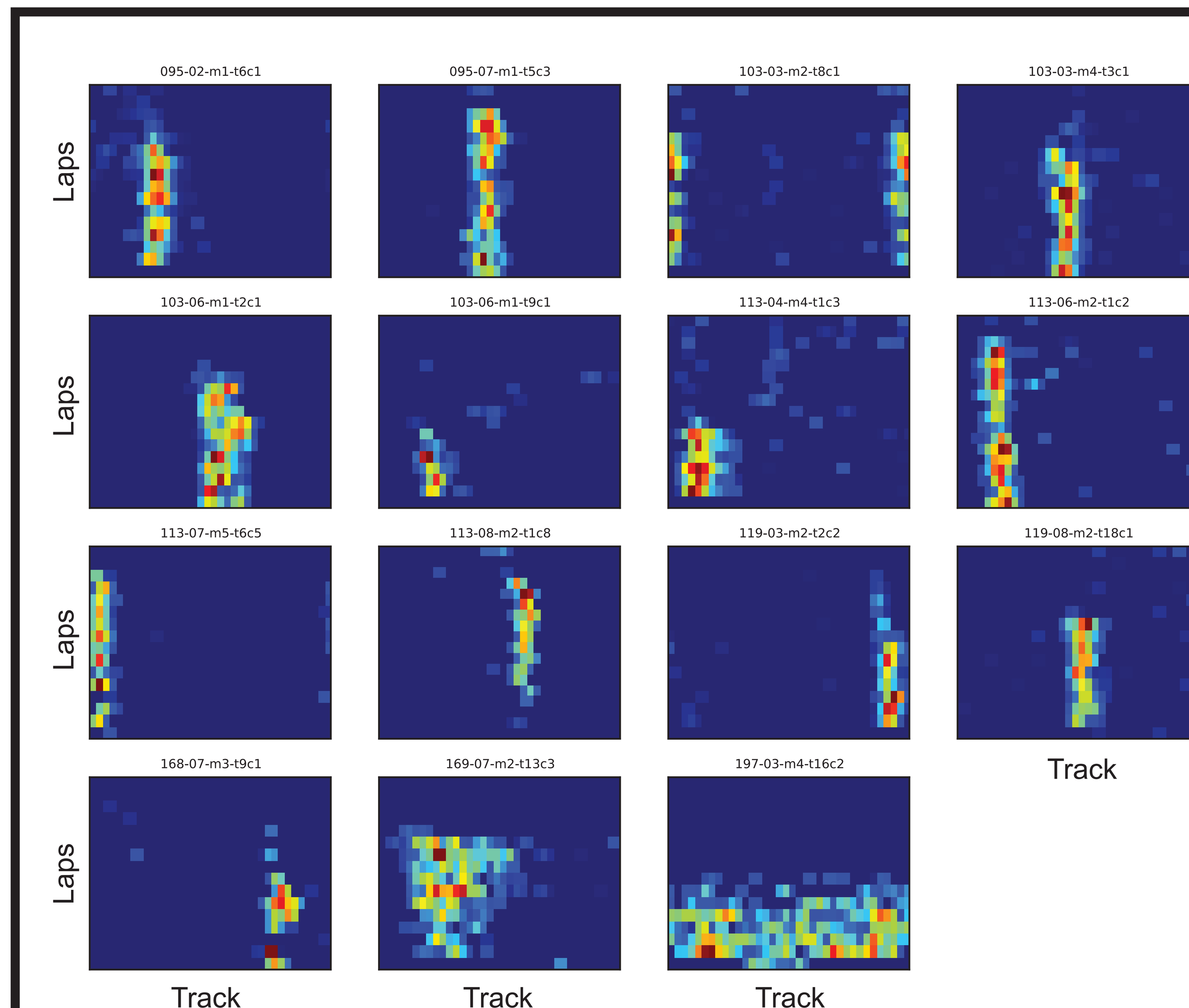


Fig. 7. Example ratemaps of place cells that developed a new place field in the middle of an experimental recording session that were predicted by an HSE with firing activity on the lap previous to field formation. These new fields are typically strong enough that they last from the first lap with spatially-modulated activity until the end of the session. Laps (ordinate) are ordered from top to bottom, with the track angle (abscissa) going counter-clockwise from 0 to 360 degrees.

NEW PLACE FIELDS AND NOVELTY

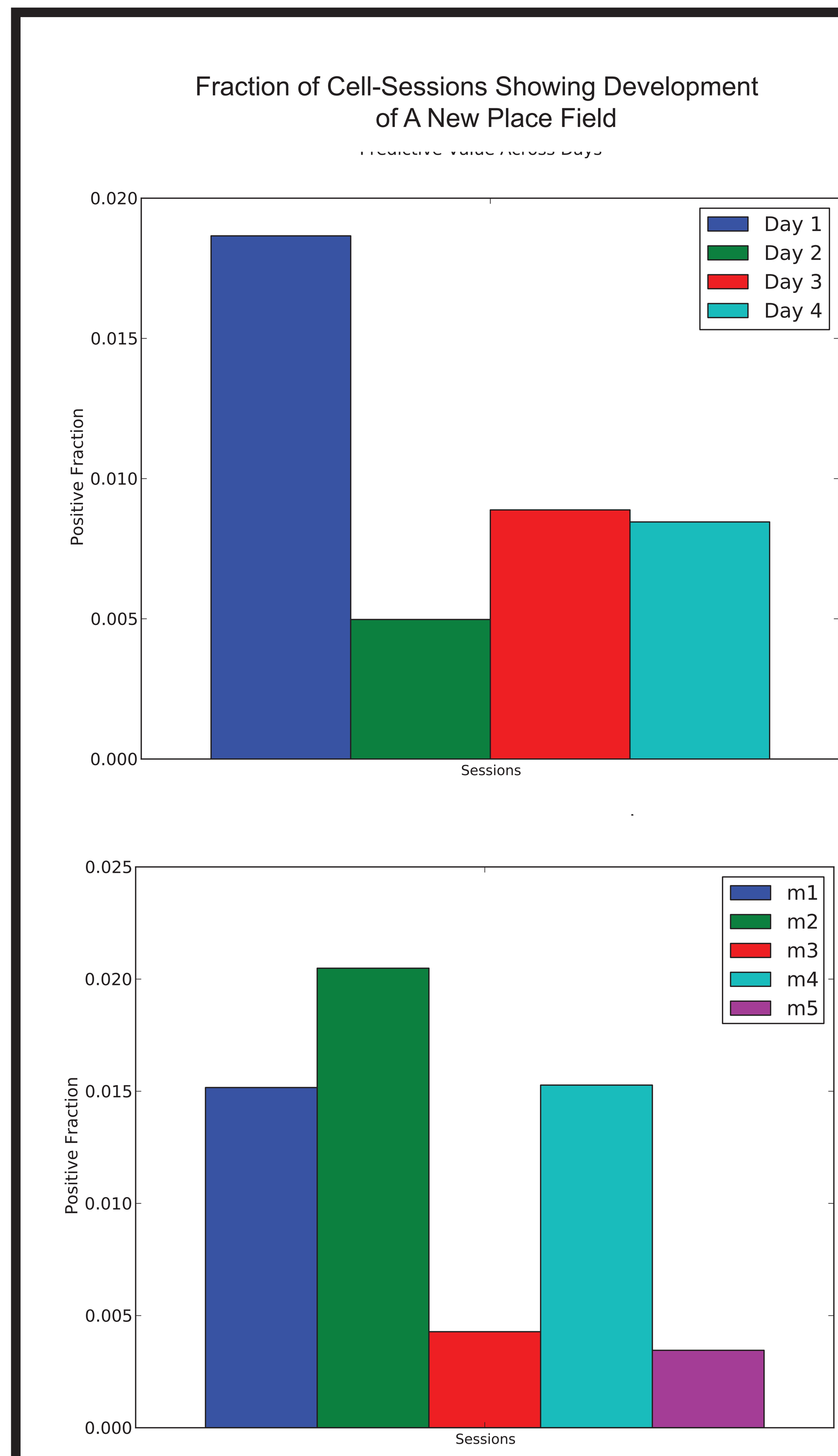


Fig. 8: Across all CA1 and CA3 place cells in our double rotation data set, we computed the proportion which developed a new place field mid-session according to the algorithm used to determine the predictive value of HSE activity (Fig. 6). The fraction of cells developing new fields across recording days (Top) and across maze sessions within a recording day (Bottom) demonstrate that new fields are strongly associated with novelty. Both Day 1 (Top) and Maze 1 (Bottom) show increased mid-session field formation, and cue mismatch experimental sessions (m2 and m4, Bottom) show much higher prevalence of new field formation than the recurring standard configuration of cues (m3 and m5).

CONCLUSIONS

When new place fields appear in the middle of a behavioral recording session, this onset of firing is associated with the firing of that cell during a head-scanning event at that location on the previous lap.

Head scanning events appear to be associated with the animal's investigation of its remote environment. The sudden formation of a place field may reflect the incorporation of information about the external environment into the spatial framework encoded by hippocampal place cells

ACKNOWLEDGEMENTS

We thank Inah Lee, D. Yoganarasimha, Joshua Neunuebel, Eric Roth and Xintian Yu for assistance in data collection. Supported by NIH grants MH094146 and NS039456.

REFERENCES

Drai,D., Kafkafi, N., Benjamini, Y., Elmer, G., and Golani,I. 2001. Rats and mice share common ethologically relevant parameters of exploratory behavior. Behav Brain Res 125:133-140.

Fenton, A.A. and Muller, R.U. 1998. Place cell discharge is extremely variable during individual passes of the rat through the firing field. Proc Natl Acad Sci 95(6):3182-7.

Fenton, A.A., Lytton, W.W., Barry, J. M., Lenck-Santini, P.P., Zinyuk, L.E., Kubik, S., Bures, J., Poucet, B., Muller, R.U., and Olypher, A.V. 2010. Attention-like modulation of hippocampus place cell discharge. J Neurosci 30(13):4613-25.

Kentros, C.G., Agnihotri, N. T.,Streater, S., Hawkins, R.D., and Kandel, E. R. 2004. Increased attention to spatial context increases both place field stability and spatial memory. Neuron 42(2):283-95.

Muzzio, I.A., Levita, L.,Kulkarni, J., Monaco,J., Kentros, C., Stead, M., Abbott, L.F.,Kandel, E.R. 2009. PLoS Biol. 7(6): e1000140.