

Space and brain: a *tabula rasa* for the sense of direction

Paul A. Dudchenko

University of Stirling

Psychology, School of Natural Sciences

Stirling, FK9 4LA

United Kingdom

Phone: +44 131 650 3531

[p.a.dudchenko@stir.ac.uk](mailto:p.a.dudchenko@stir.ac.uk) <mailto:p.a.dudchenko@stir.ac.uk>

**Two recent studies have shown that neurons which fire in a compass-like way – head direction cells – are present before rat pups open their eyes. Upon eye opening, the firing direction of these cells is anchored rapidly to visual landmarks.**

*Let us then suppose the mind to be, as we say, white paper, void of all characters, without any ideas:—How comes it to be furnished? Locke (1690) [1]*

A central question in philosophy has recently become a question for neuroscience: what do neural circuits look like before experience with the world? For Locke, the mind before experience was a *tabula rasa* – a blank slate. For Bjerknes et al. [2] and Tan et al. [3], the mammalian brain possesses a representation of direction even before the animal sees the outside world.

Rats are functionally blind until about two weeks after birth, at which point their eyes open. Bjerknes et al. and Tan et al. exploited this transition to record from a neural representation of direction in the rat pup brain both immediately before and after the animal opened its eyes. The representation they recorded from, the head direction cell system, is comprised of neurons whose firing is tuned to specific directions in the environment. An individual head direction (HD) cell typically fires in one direction in the animal's environment, with a range of approximately 90 degrees, and does not fire when the animal faces other directions [4]. However, different HD cells fire in different "preferred directions", and these cells appear to form a ring attractor that is anchored to landmarks in the environment [5-7].

Previous work has shown that spatially tuned neuronal activity appears early in the rat's development [8, 9]. Specifically, HD cells show stable directionality at post-natal day 16 of development. Place cells – neurons in the hippocampus that fire in specific locations in the

environment – are also present from day 16 of development. Grid cells – neurons in the entorhinal cortex and adjacent brain regions that show grid-like tuning fields in the environment – appear at around the same time, but their spatial tuning becomes much sharper by days 24-30 of development. The observation that stable place cell firing precedes stable grid cell fields implies that the former do not necessarily require the latter [9, 10].

Do head direction cells require experience to exhibit their compass-like firing? These neurons show a remarkable signal-to-noise ratio, and are found in an interconnected series of brain regions extending from the dorsal tegmental nuclei to the medial entorhinal cortex (MEC) [11, 12]. Changes in their firing direction correlate with changes in spatial behaviour [13, 14], and damage to the brain regions in which head direction cells are found produce impairments in spatial cognition [15, 16].

The results Bjerkenes et al. and Tan et al. show that direction firing precedes visual experience. Bjerkenes et al. recorded from the presubiculum, parasubiculum, and medial entorhinal cortex of different rat pups between post-natal days 11-15, prior to the opening of their eyes. They found head direction cells in each of these brain areas. The head direction cells, however, showed significant drift in firing directions across the first and second half of a 10 minute recording session, and between adjacent recording sessions. Thus, directionally tuned firing was evident, but was not tied strongly to the environment. Simultaneous recordings of more than one HD cell showed that the drift in the preferred direction of one cells was similar to that of any other cell. Thus, the cells behaved in the same way, consistent with the idea that head direction cells form an attractor network [17].

Next Bjerkenes et al. recorded from the HD cells just after the rat pups opened their eyes. A basic property of HD cells is that their “preferred directions” are anchored to visual landmarks in the environment. The author found that this was also the case with the rat pups, indicating that the head direction cell system can be anchored to visual landmarks as soon as they are visible.

Tan and colleagues found similar results. They recorded from the dorsal presubiculum and the anterodorsal thalamus in rat pups aged post-natal day 12-20. Before the pups’ eyes opened, head direction cells were observed in both brain areas. The cells showed some stability in firing directions within sessions, but this stability was much better once the eyes opened. Interestingly, the percentage of cells showing directional firing increased dramatically once the eyes opened, particularly in the anterodorsal thalamus. Finally, Tan and colleagues also observed that the firing direction of head direction cells was anchored to a visual landmark in a reliable way about a day after the eyes opened. These results suggest that the head direction circuit may rely on some type of non-visual information prior to visual experience, but that visual experience stabilises the representation, and may be critical for the development of a subset of the head direction cells found in the anterodorsal thalamus.

Together, these two studies make several contributions. First, they show that the head direction cell system does not require visual input to form. HD cells develop prior to the animal’s ability to see the world, and this is consistent with the view that vestibular or other non-visual inputs contribute to the basic directional tuning of these cells [18]. Second, it’s clear the link between HD cells is evident from the start, thus suggesting that the cells function as a coherent network. Third, before visual access to the world the stability of the

directional firing, while not entirely absent, is poor. Fourth, when vision does come online, the stability of the cells is much improved, and some HD cells – particularly those in the anterodorsal thalamus – appear to develop directional firing. Finally, the capacity for HD cells to form an associational anchor to visual landmarks appears within a day of access to these landmarks.

Thus, a blank slate or compass *is* present in the mammalian brain prior to experience with the visual world. With vision, this directional slate is rapidly honed and an associational process allows this internal representation to become linked to the contents of the outside world.

## References

1. Locke, J. (1690). An essay concerning human understanding. (Adelaide: eBooks@Adelaide).
2. Bjerknes, T.L., Langston, R.F., Krugé, I.U., Moser, E.I., Moser, M-B (2015). Coherence among head direction cells before eye opening in rat pups. *Current Biology* 25, 1-6.
3. Tan, H.M., Bassett, J.P., O'Keefe, J., Cacucci, F., Wills, T.J. (2015). The development of the head direction system before eye-opening in the rat. *Current Biology* (in press).
4. Taube, J.S., Muller, R.U., Ranck, J.B. (1990). Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *Journal of Neuroscience* 10, 420-435.
5. Skaggs, W.E., Knierim, J.J., Kudrimoti, H.S., McNaughton, B.L. (1995). A model of the neural basis of the rat's sense of direction. In: *Advances in Neural Information Processing Systems Vol 7*.
6. Redish, A.D., Elga, A.N., Touretzky, D.S. (1996). A coupled attractor model of the rodent head direction system. *Network. Comput. Neural Syst.* 7, 671-685.
7. Zhang, K. (1996). Representation of spatial orientation by the intrinsic dynamics of the head-direction ensemble: a theory. *Journal of Neuroscience* 16, 2112-2126.
8. Langston, R.F., Ainge, J.A., Couey, J.J., Canto, C.B., Bjerknes, T.L., Witter, M.P., Moser, E.I., Moser, M-B. (2010). Development of the spatial representation system in the rat. *Science*, 238, 1576-1580.

9. Wills, T.J., Cacucci, F., Burgess, N., O'Keefe, J. (2010). Development of the hippocampal cognitive map in preweanling rats. *Science* 328, 1573-1576.
10. Bush, D., Barry, C., Burgess, N. (2014). What do grid cells contribute to place cell firing? *Trends in Neuroscience* 37, 136-145.
11. Taube, J.S. (2007). The head direction signal: origins and sensory-motor integration. *Annual Review of Neuroscience* 30, 181-207.
12. Boccara, C.N., Sargolini, F., Thoresen, V.H., Solstad, T., Witter, M.P., Moser, E.I., Moser, M-B. (2010). Grid cells in the pre- and parasubiculum. *Nature Neuroscience* 13, 987-994.
13. Dudchenko, P.A., Taube, J.S. (1997). Correlation between head direction cell activity and spatial behavior on a radial arm maze. *Behavioral Neuroscience* 111, 3-19.
14. van der Meer, M., Richmond, Z., Braga, R.M., Wood, E.R., Dudchenko, P.A. (2010). Evidence for the use of an internal sense of direction in homing. *Behavioral Neuroscience* 124, 164-169.
15. Vann, S.D. (2010). Re-evaluating the role of the mammillary bodies in memory. *Neuropsychologia* 48, 2316-2327.
16. Vann, S.D., Aggleton, J.P. (2004). The mammillary bodies: two memory systems in one? *Nature Reviews Neuroscience* 5, 35-44.
17. Yoganarasimha, D., Yu, X., Knierim, J.J. (2006). Head direction cell representations maintain internal coherence during conflicting proximal and distal cue rotations: comparison with hippocampal place cells. *Journal of Neuroscience* 26, 622-631.

18. Stackman, R.W., Taube, J.S. (1997). Firing properties of head direction cells in the rat anterior thalamic nucleus: dependence on vestibular input. *Journal of Neuroscience* 17, 4349-4358.



## Figure legend

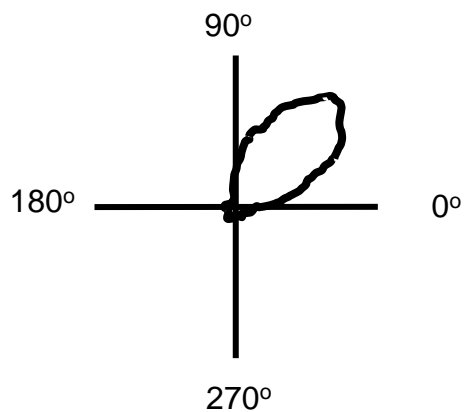
### Figure 1. Development of the head direction cell system.

The results of Bjerknes et al. [2] and Tan et al. [3] show that rat pups have head direction cells before the eyes are opened. Though directional, these cells appear to show within-recording session drift in firing directions. Once the eyes are opened, these cells are much more stable, and are anchored to visual landmarks in the environment.

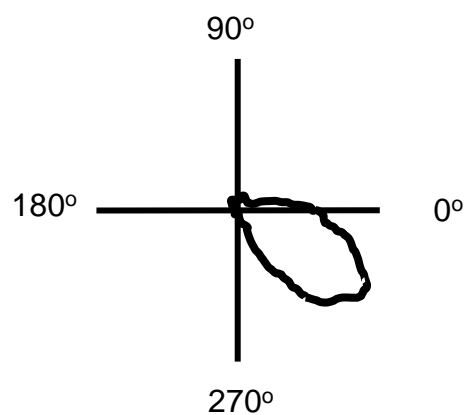


eyes closed

beginning of session



end of session



eyes open

