specific frequency “landmarks” during the auditory sequence (Aronov et al., 2017). The CA1 were, thus, argued to be capable of tuning to abstract variables and were designed to map out sequences of events/stimuli in their own spatiotemporal patterns of activity.

The ubiquity of neural sequences in a wide variety of systems has been discussed previously (Bhalla, 2019; Conen & Desrochers, 2022; S. Zhou et al., 2020) and over a century of research has discovered remarkable physiological features that may be used to identify neurons that participate in these sequences. However, research is still required to carefully dissect out the contribution that each participant neuron has to behaviour, an important goal in neuroscience (Ranck, 1973, 1975).

The use of user-configurable, categorically labeled synthetic calcium activity profiles allowed us to probe and compare a range of different time cell detection algorithms, identifying strategies to best classify time cells. We were able to identify Temporal Information as a strong contender for the choice of algorithm for such classification (Ananthamurthy & Bhalla, 2023). The algorithms developed along the way were tested within the time scales of ~100 ms, that correspond to Replay Sequences or other behaviour timescale sequences. We expect the analysis routines to be useful in a variety of different experiments that could potentially help describe the neural code in more detail.

Better temporal resolution requires new techniques

There are many other techniques that experimenters in the field have employed to record activity. Many of these techniques do, in fact, achieve much better temporal resolution. Here are some examples:

1) Resonant Scanning based 2p calcium imaging can achieve even up to 30 Hz for 4x larger fields of view, or more frame rates for smaller fields of view (Bonin et al., 2011; Leybaert et al., 2005; Nguyen et al., 2001; Rochefort et al., 2009). At the time when we started the experiments for the thesis, Resonant scanning microscopes required a lot of additional, expensive components to be purchased. Towards this, we co-wrote a sanctioned DBT grant application (BT/PR12255/MED/122/8/2016) and began setting up the new microscope. However, we did not have this technology available for experiments before 2020.

2) High-density tetrodes can be used to perform electrical recordings at >=20 kHz, as compared to ~14.5 Hz for our galvo-scanning 2p calcium imaging experiments. This technique typically achieves yields of ~40 cells for hippocampal recordings, and we argued that we could achieve a higher yield (>100 cells) with galvo-scanning 2p calcium imaging. The relative sparsity of the hippocampal neural code in terms of cells participating in any engram, mandates high-yield recordings to identify the full temporal sequence of CA1 activations (Foster, 2017).

3) Neuropixels (Jun et al., 2017) can be used to perform electrical recordings at >=20 kHz. At the time when we started the experiments for the thesis, these sorts of electrical probes had yet to be successfully deployed in published literature.

We discuss all of these techniques while comparing electrical vs imaging based recording strategies in Chapter 1 – “Introduction”. Fundamentally, given the technological constraints at the time, we had devised combined behaviour with galvo-scaning 2p calcium imaging as the principle for the experiments described in this thesis.

Does the brain create or predict?

An important directive to neuroscience research is to understand the brain and nervous system, in how these structures allow animals to interact meaningfully with their environment. More humbly, however, the ultimate goal of this thesis was to help provide a multi-disciplinary toolkit to study time cells in the hippocampus. Predictive coding has been considered as a way for the brain to ultimately use external sensory information to minimize prediction errors during tasks (Doya et al., 2007; Rao & Ballard, 1999). One of the core ideas of Bayesian approaches to neurophysiology and behaviour is that the brain could be modeled as a prediction machine that is constantly modeling the change of variables. These variables may be external or internal yet salient concepts to any experimental animal, arguably expressed in neurophysiology as the dynamics of engrams. The ability of the mammalian hippocampus to bind both information streams to create new, more elaborate engrams, is likely crucial to the learning of new concepts behaviourally (N. J. Cohen & Eichenbaum, 1993; Eichenbaum, 2017).

Attentional states have been shown to have a bidirectional relationship with the expression of memory and learning (Chun & Johnson, 2011;

Hutchinson & Turk-Browne, 2012; Uncapher et al., 2011). Specifically, Trace Eye-Blink Conditioning (TEC) performance has been suggested to be positively correlated with attention (Manns et al., 2000). The question of the effect of attentional states on the dynamics of the associated engram motivated an important milestone for the Thesis, *viz.*, to combine stable, adaptable behaviour studies with large-scale neurophysiology.

We were able to train head-fixed mice to TEC and confirm adaptable conditioned responses to task variables. We were also able to simultaneous record from ~100 hippocampal CA1 cell bodies as the animals acquired top behavioural performance. We observed in our preliminary results that many identified time cells showcased the ability to tune to different time points across sessions or days, as has been previously reported (Mau et al., 2018). This standardization of simultaneous behaviour and imaging ensured that colleagues from our lab were able to generate production quality data, quickly.

Several more high quality recordings and behaviour modulations would be required to conclusively describe time cells physiology and engram dynamics, at least at the level of a sub-population of hippocampal CA1. However, progress has been made to suggest the best time cell detection algorithm(s) based on their sensitivity to different recording parameters (Ananthamurthy & Bhalla, 2023). We hope that the Thesis is of aid to future research on the neural mechanisms of Learning and Memory by the nervous system.

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