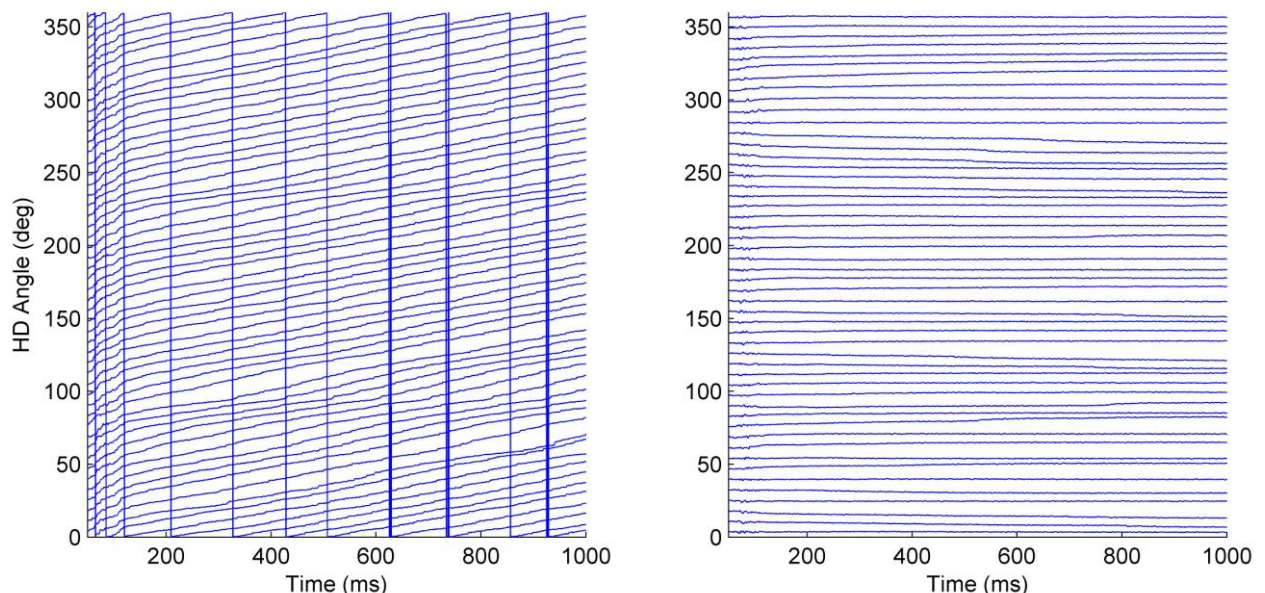


Head direction (HD) neurons are so-called because they fire preferentially when an animal is facing in specific directions relative to invariant cues in the animal's environment. Head angular velocity (HAV) neurons fire to indicate head turning speed in either both turning directions equally (*symmetric* HAV neuron) or just one direction (*asymmetric* HAV neuron). More than half the HAV cells in the rat dorsal tegmental nucleus (DTN) are symmetric; the computational function of these cells is unknown (Taube and Bassett 2003).

The aim of this study was to investigate a potential mechanism of HD attractor tuning for the integration of head position over time; specifically, to shed light on the role that symmetric HAV neurons may play in such a mechanism, and on the synaptic learning rules that are hypothesised to be involved in this process. The tuning mechanism introduced in this report utilises the activity of the symmetric HAV neurons to control the update of the attractor synapses in order to solve HD tuning requirements. There are two components to the mechanism; Part 1 solves the first requirement of keeping the attractor still when there is no vestibular input, and Part 2 solves the second requirement of moving the attractor at the same speed in both directions given turns of the same speed. Both components work in a similar way. HD cells maintain a representation of the instantaneous change in their firing rates, which corresponds to how fast the activity packet is moving through the HD network. The HD cells also receive input from the symmetric HAV cells which convey how fast the head is currently physically turning. If the movement of the HD packet does not correspond to the head movement indicated by the symmetric HAV cells, the recurrent HD connection strengths are adjusted so that the packet more closely follows the indicated movement. Note that the connections from the HAV cells are not modified; these connections only carry the physical head movement information. Rather it is the connections that maintain the packet dynamics – the recurrent excitatory HD connections – that are adjusted. The implication for synaptic learning is that the efficacy of one synapse onto a postsynaptic neuron (the HD cell) can be controlled in part by the activity received by that cell on a different synapse.

Training an HD network with noisy, off-centre connections and with poor stability in the HD activity packet position, resulted in the network being able to maintain a stable representation of head direction over time (see Figure 1).



**Figure 1: HD network pre- and post-training.** For both graphs, 50 activity packets were initiated in turn, spaced evenly around the attractor; each curve tracks the position of one of those HD activity packets over the next 1000 ms. **Left:** HD attractor connections were initially noisy and off-centre, which induced a continuous drift in the packet position. **Right:** After training, the packet was stable at each position it was initiated. The packet was also able to successfully integrate changing head position over time (data not shown).

There are three major requirements for this learning mechanism to function.

- 1) Neurons must have a representation of their current firing rate.
- 2) Neurons must have a representation of the *change* in their firing rate.
- 3) For Part 2 of the adaptation algorithm, weight change in one type of connection must be modulated by presynaptic activity impinging on the postsynaptic cell from a different synapse to the one where the weight change is effected. Specifically, the HD weight updates must take into account the vestibular input from the symmetric HAV cells.

Synapses which are close together are known to be able to influence each other. Potentiation in one synapse can lead to potentiation of adjacent synapses (Engert and Bonhoeffer 1997). Also, the locations of synapses between different brain regions are known in some cases to be very specific (for example the high laminar specificity of most hippocampal connections). Therefore modulation of synaptic connection strength by signals received on another, perhaps spatially proximal, synapse cannot be ruled out. Implications of this latter requirement are far-reaching. If the existence of such a synaptic update mechanism is confirmed, then it is a concrete demonstration that learning rules in nervous systems are not limited to purely local connection updates (i.e. to just the connection between the pre- and postsynaptic neurons). It is conjectured that the synapses involved in this rule all have a common postsynaptic cell and hence are able to influence each other through either their spatial proximity or through signalling mechanisms in the cell.

Because connection updates are calculated and applied on a local, HD cell-by-cell basis, every HD cell must have at least one connection from a symmetric HAV cell in order to receive the information required to update its excitatory recurrent connections. This helps explain why so many HAV cells must be of the symmetric type – there must be enough of them that every HD cell is very likely to receive symmetric HAV input. Thus the theory would predict that there should be more connections from symmetric than asymmetric HAV cells to the HD network. This could be accomplished with a greater number of connections *per se*, or else with a greater number of symmetric cells, as is known to be the case in the DTN of the rat (Taube and Bassett 2003).

Due to its line attractor dynamics and susceptibility to drift, the HD system requires precise tuning in order to adequately serve its function of stably representing head direction over time. This paper presents a learning algorithm which is able to fulfil this precise tuning requirement, and makes specific predictions for the supporting biological mechanisms:

- 1) Neurons are able to detect change in their firing rates.
- 2) Connections from symmetric HAV cells in the DTN modulate efficacy of the self-sustaining HD activity packet, which helps explain the existence and indeed the abundance of these symmetric HAV cells, for which no prior theories existed (Taube and Bassett 2003). The mechanism of action of this learning rule generalises the concept of changes in synaptic efficacy spreading to closely adjoining synapses (Engert and Bonhoeffer 1997).

Clearly, if its existence in biological networks is confirmed, the above mechanism has the potential to add significantly to our understanding of synaptic plasticity, and additionally hints at a powerful new set of learning strategies that may be employed by nervous systems.

#### References

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