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**Title:** Learning accurate path-integration in ring attractor models of the head direction system

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**Abstract:** Head direction (HD) cells track an animal's head direction in darkness by integrating angular velocity signals, a phenomenon called path integration (PI). Ring attractor models for angular PI have received strong experimental support. To function as integrators, HD circuits require precisely tuned connectivity, which is costly to pass down genetically. Furthermore, HD circuits have been shown to adapt to changes in gain between idiothetic and allothetic inputs. These facts suggest that synaptic plasticity is crucial in setting up and fine-tuning these circuits.

We propose a network model in which a local, biologically plausible learning rule adjusts synaptic efficacies during development, guided by supervisory allothetic cues. The learning rule is inspired by layer-5 pyramidal neurons assumed to be the fundamental associative unit in the cortex, where backpropagating APs implement coincidence detection. The learning rule contains an anti-Hebbian component which implements predictive coding, whereby inputs arriving in distinct compartments get associated so that inputs in one compartment can predict inputs to another. Applied to the Drosophila HD system, the model learns to PI accurately for the full range of angular velocities that the fly displays, and develops a connectivity strikingly similar to the one reported in experiments. The mature network is a quasi-continuous attractor (CAN), and reproduces key experiments in which optogenetic stimulation controls the internal representation of heading, and where the network remaps to integrate with different gains akin to experiments conducted in augmented reality.

Our model predicts that PI requires supervised learning during development, and proposes a general framework to learn gain-1 PI, even in architectures that lack the physical topography of a ring. Finally, we develop an analytically tractable reduced model that exploits symmetries present in CANs, follows learning in "bump-centric" coordinates, and offers a rigorous mathematical framework to study self-organization of CANs for PI in general.