Path Integration using the Fourier Transform

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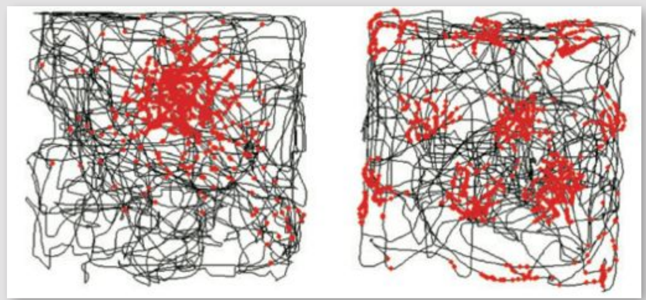
Introduction

How do animals perform path integration, or dead reckoning?

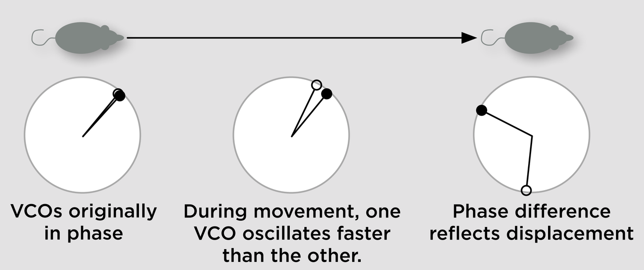
In 2005, Hafting et al. reported that some neurons in the entorhinal cortex (EC) fire bursts when the animal occupies locations organized in a hexagonal grid pattern in their spatial environment. Previous to that, place cells had been observed, firing bursts only when the animal occupied a particular region of the environment. Both of these types of cells exhibit theta-cycle modulation, firing bursts in the 4-12Hz range.

Activation Maps

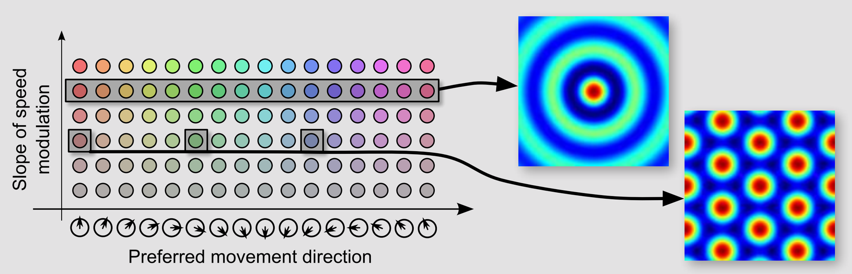


Velocity-Controlled Oscillators

Some neural oscillators alter their frequency according to the animal's velocity, so-called Velocity-Controlled Oscillators (VCOs). As a result, the animal's position is encoded in the phase differences between VCOs.



In 2D, Welday et al. showed that different combinations of VCOs could yield different spatial activation maps, like place cells and grid cells.

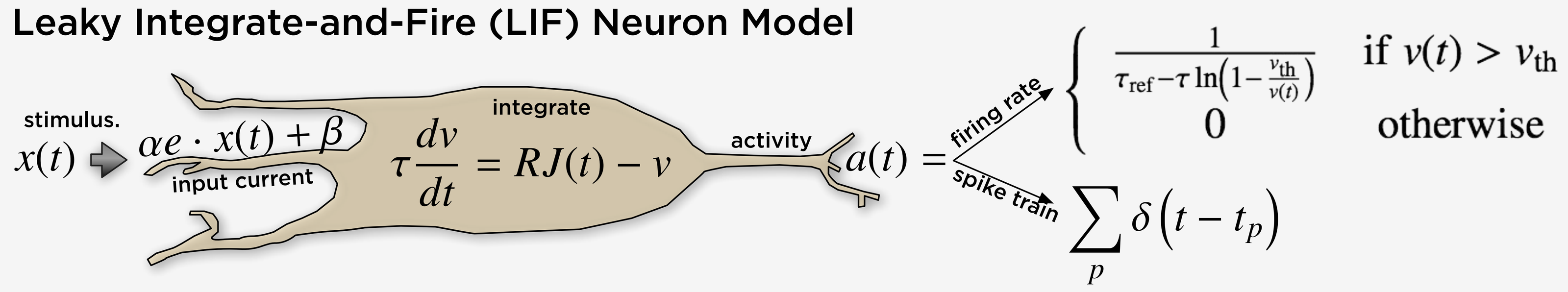


Our Theory

We propose that the EC is implementing its spatial coding using the Fourier Transform. We show how the Fourier Shift Theorem relates to the phases of velocity-controlled oscillators (VCOs), and propose a model for how various other spatial maps might be implemented.

Neural Engineering Framework

Leaky Integrate-and-Fire (LIF) Neuron Model

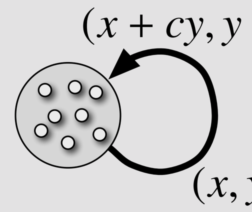


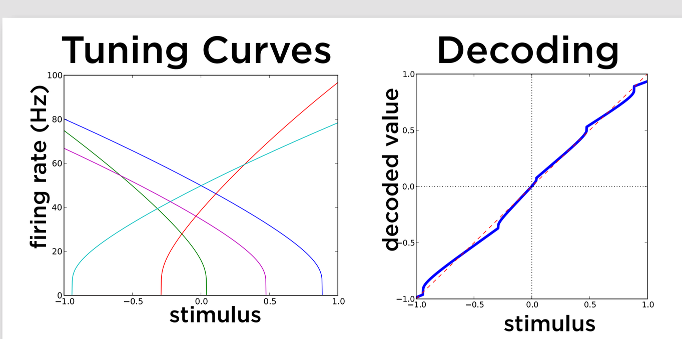
$$x(t) \Rightarrow \alpha e \cdot x(t) + \beta \quad \tau \frac{dv}{dt} = RJ(t) - v \quad a(t) = \begin{cases} \frac{1}{\tau_{ref} - \tau \ln\left(1 - \frac{v_{th}}{v(t)}\right)} & \text{if } v(t) > v_{th} \\ 0 & \text{otherwise} \end{cases} \quad \sum_p \delta(t - t_p)$$

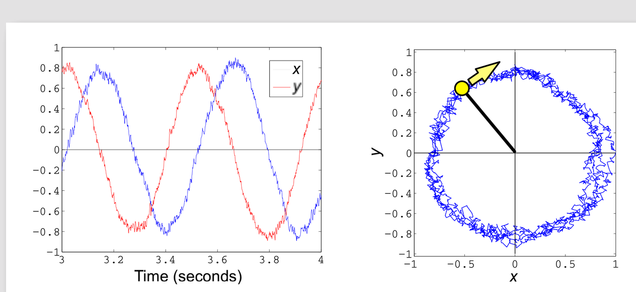
If we know the tuning curves, then we can use lease-squares to infer the input from the pattern of neural firing rates. This is called decoding. Vectors can also be encoded/decoded, as well as functions of those values.

We can also implement dynamic processes, like a simple harmonic oscillator.

$$\begin{cases} \frac{dx}{dt} = cy \\ \frac{dy}{dt} = -cx \end{cases}$$







Fourier Theory

Discrete Fourier Transform

$$F_k = \sum_{n=-\frac{N}{2}}^{\frac{N}{2}-1} f_n \exp\left(-2\pi i \frac{nk}{N}\right)$$

Inverse Discrete Fourier Transform

$$f_n = \frac{1}{N} \sum_{k=-\frac{N}{2}}^{\frac{N}{2}-1} F_k \exp\left(2\pi i \frac{nk}{N}\right)$$

Fourier Shift Theorem

$$G_k = \sum_{n=-\frac{N}{2}}^{\frac{N}{2}-1} f_{n-x} \exp\left(-2\pi i \frac{nk}{N}\right)$$

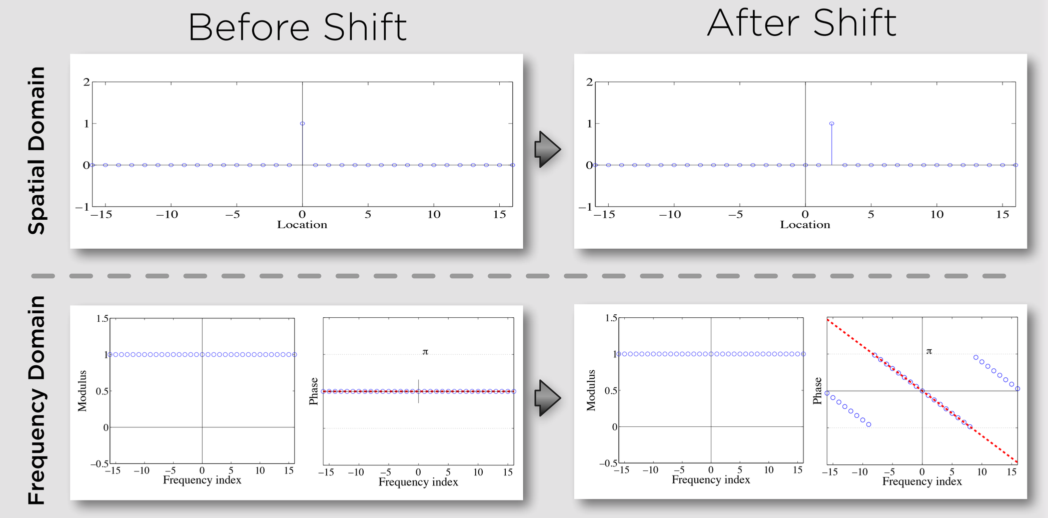
shifted by x

slope of ramp

$$G_k = \exp\left(-2\pi i \frac{xk}{N}\right) F_k$$

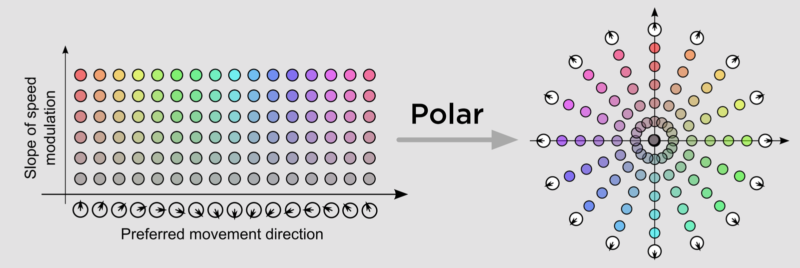
phase ramp

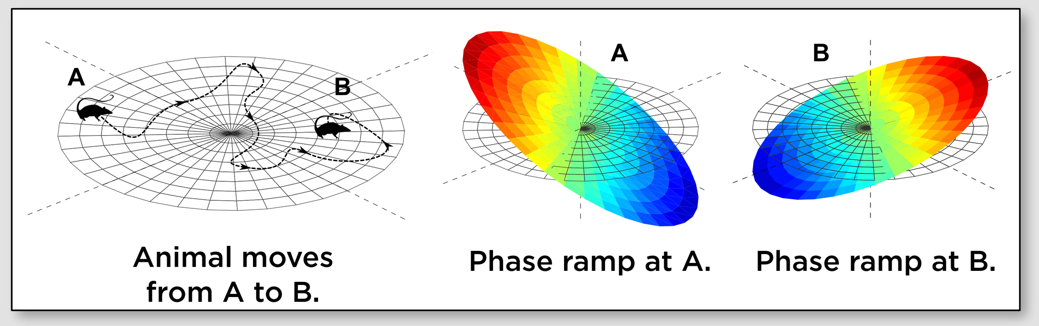
Example: Shifting a delta function



Fourier Model

When viewed in a polar arrangement (rather than rectangular), the phases of the VCOs create a 2D ramp.

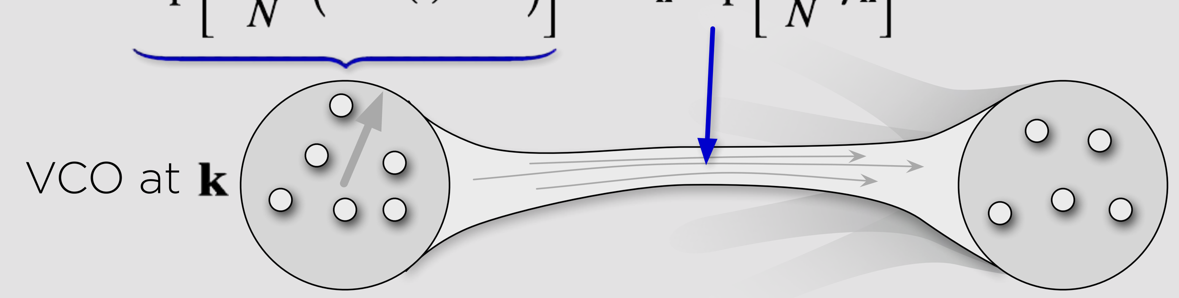




Fourier Shift Theorem... in Neurons

$$\exp\left[\frac{-2\pi i}{N}\left(\mathbf{k} \cdot \mathbf{x}(t) + \theta t\right)\right] \times r_{\mathbf{k}} \exp\left[\frac{2\pi i}{N} \gamma_{\mathbf{k}}\right]$$

Phase ramp, encoding position; Theta rhythm; Fourier coef. of spatial activation map

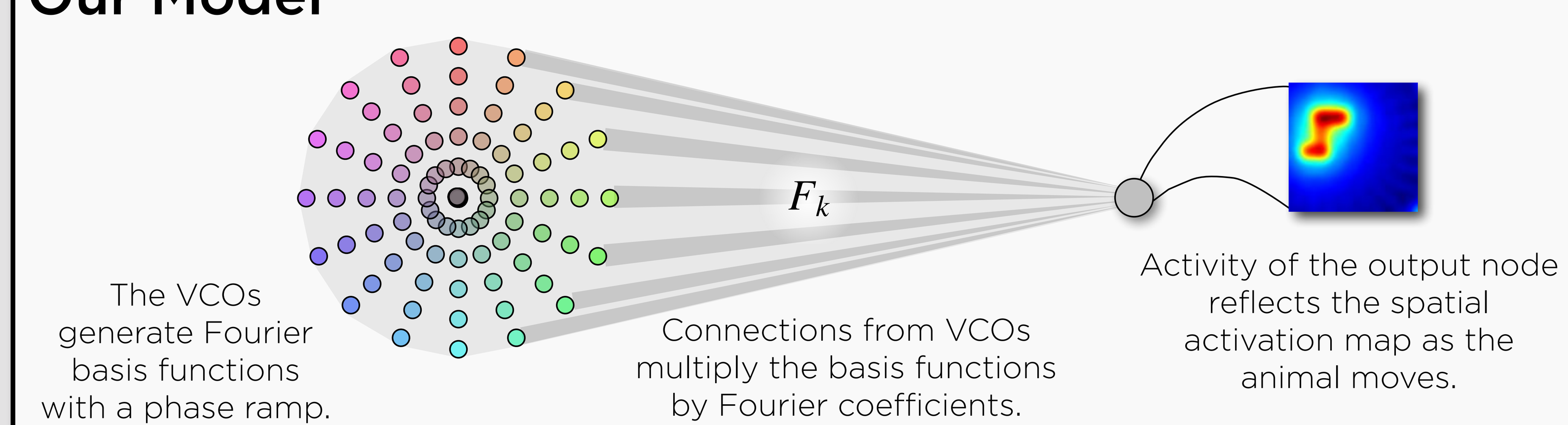


Readout node combines the output from all VCOs

In Cartesian... $(x + iy) \times (\alpha + i\beta) = (x\alpha - y\beta) + i(x\beta + y\alpha)$

VCO phase; Fourier coef.

Our Model



The VCOs generate Fourier basis functions with a phase ramp.

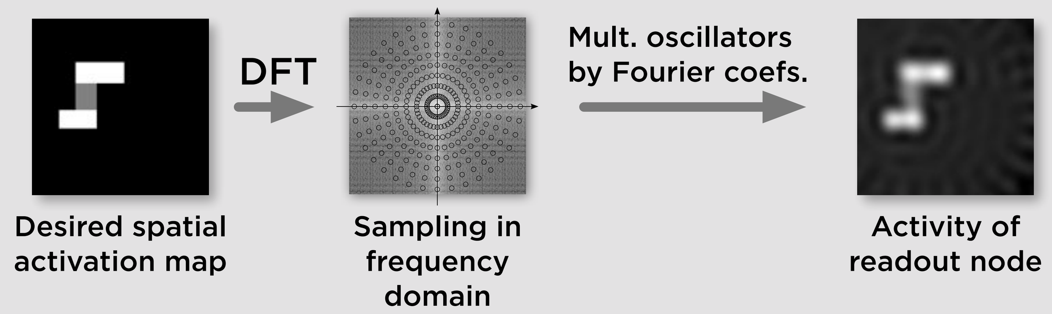
Connections from VCOs multiply the basis functions by Fourier coefficients.

Activity of the output node reflects the spatial activation map as the animal moves.

Implementation

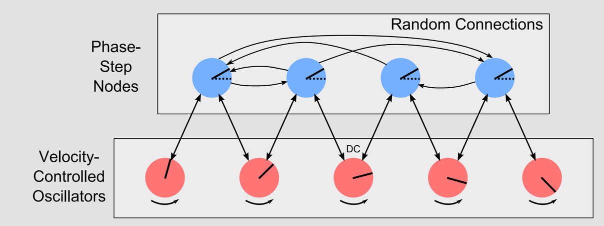
Theoretical

We constructed an idealized model using trigonometric functions (instead of neural oscillators) to test the Fourier model.



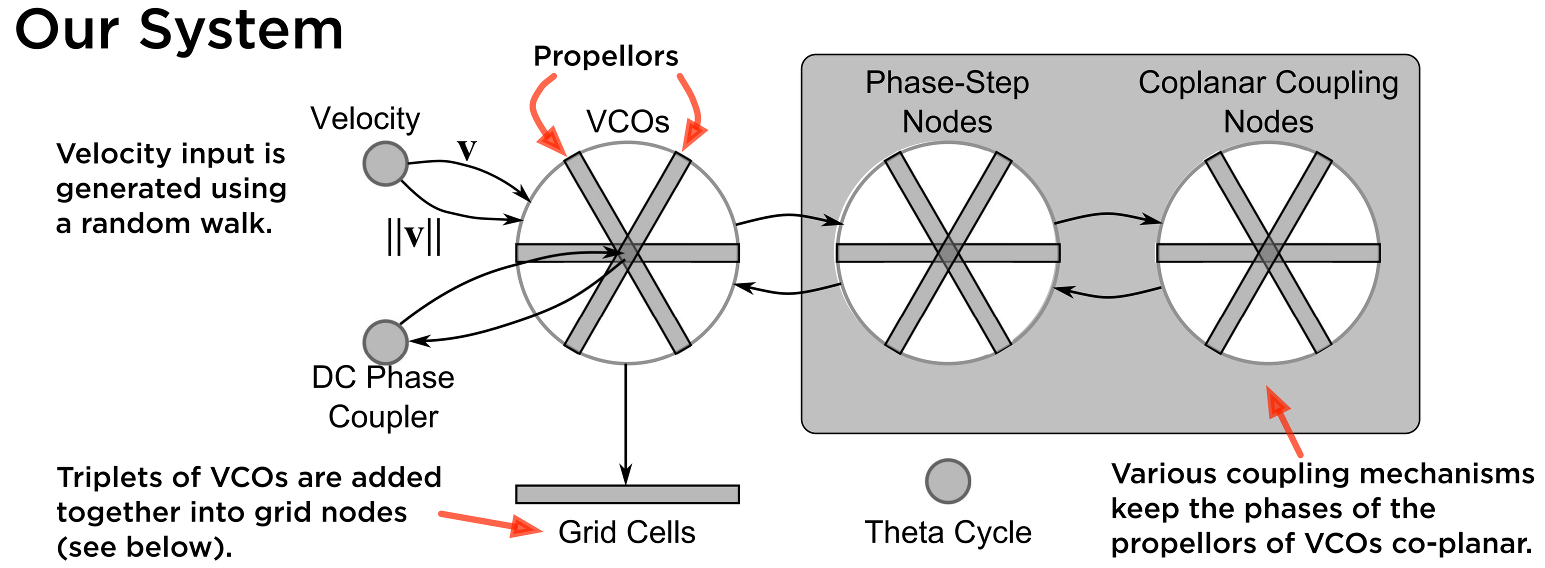
Nengo Model

We used the nengo neural simulation language (nengo.ca) to simulate a bank of 51 VCOs arranged in three "propellors" of 17 VCOs each. The model involves 68,700 spiking LIF neurons.



Sample propellor with phase coupling

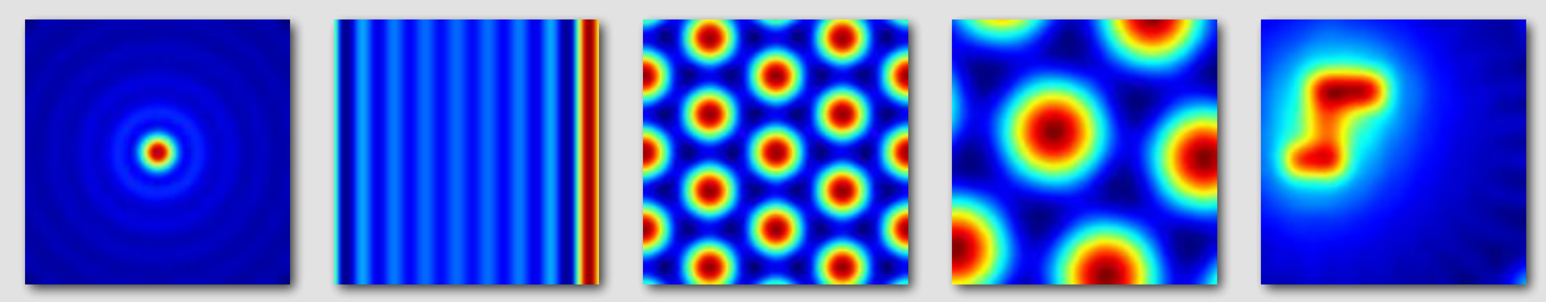
Our System



Results

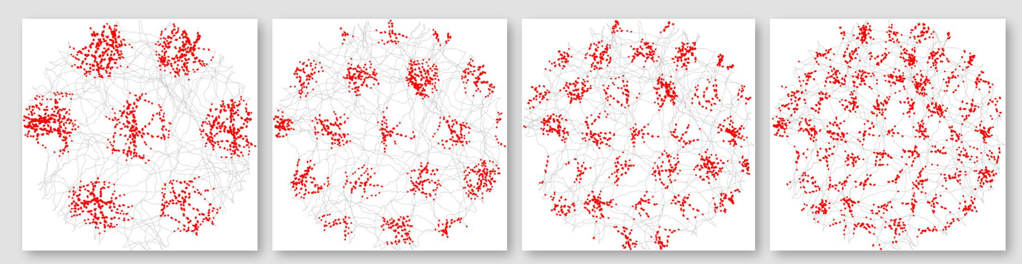
Theoretical

A sampling of spatial activation maps generated using the theoretical framework.



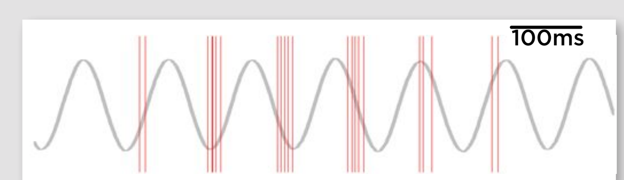
Spiking Neurons

Grid Cells: A sampling of grid cells taken from different grid nodes.



Phase Precession

Our model also exhibits phase precession.



Drift

Even though we included measures to correct for VCO phase drift, the encoded location tends to drift away from the true location. Incorporating sensory input to correct these errors is addressed in an accompanying paper.