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The Sinusoidal Array: A Theory of Representation for Spatial Vectors

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Abstract

We describe a theoretical model of spatial representation in cortex, including computer simulations, that is compatible with data from single neuron recordings. Our proposed architecture, called a sinusoidal array, *encodes a polar vector $\vec{v} = (r, \phi)$ as distributed activity across a neuronal population. We demonstrate how sinusoidal arrays might be used for vector computations such as addition, subtraction, and rotation in tasks such as primate reaching and rodent navigation.*

1 The Sinusoidal Array

Spatial representation in the mammalian brain has been widely studied in hippocampus, parietal cortex, and throughout the motor system. But most of the modeling work to date has focused on place cells in hippocampus and on the transformation of retinal to head centered coordinates in parietal cortex. Our work models spatial representations in the motor system, but it is also applicable to certain navigational tasks.

We offer a general computation mechanism, the *sinusoidal array*, which is capable of representing n-dimensional vectors. (We will be primarily concerned with 2 and 3 dimensional spatial vectors.) The sinusoidal array is an encoding of a vector as a distributed pattern of activity over N neurons. The firing rate of each neuron i encodes the value $F(r, \phi, i) = b_i + k_i \cdot r \cos(\phi - \phi_i)$ where b_i is a baseline value that attempts to keep $F(r, \phi, i)$ positive, k_i is a scale factor, and ϕ_i is a preferred direction. We assume that preferred directions are uniformly distributed. Thus, for each cell we associate a *preferred vector* (in polar coordinates) $\vec{r}_i = (k_i, \phi_i)$. With $\vec{v} = (r, \phi)$ the vector being represented, and $SA_{\vec{v}}$ the sinusoidal array represention of $\vec{v}$, the firing rate of neuron i is $F(SA_{\vec{v}}, i) = b_i + \vec{v}.\vec{r}_i$ where the dot denotes inner product. The sinusoidal array is an extension of the *population vector* [6]. Because the sinusoidal array includes magnitude information, it is capable of supporting vector arithmetic.

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Figure 1: A sinusoidal array representation of the vector $\vec{v} = (r, \phi)$ using 50 neurons. The orientation of each line indicates prefered direction ϕ_i; line length is proportional to firing rate. For clarity, the b_i and k_i values were made the same for all neurons.

2 Computing With Sinusoidal Arrays

Let $\vec{v}_3$ (represented by SA_3) be the vector sum $\vec{v}_1 + \vec{v}_2$ (SA_1 and SA_2 respectively). Because vector addition distributes over dot product, this sum can be accomplished by allowing SA_3 neurons to sum spikes from a subpopulation of cells in SA_1 and SA_2. The probability of making a synapse between a cell in SA_1 or SA_2 and a cell in SA_3 is proportional to a Gaussian function of the difference between their preferred directions. In order to keep the average baseline of cells in SA_3 equal to B (the average baseline for SA_1 and SA_2), SA_3 neurons must have a bias term of $-B$.

Vector subtraction is equivalent to the addition of the negation of a vector. Thus subtraction is analogous to addition, but the probability of a synapse from SA_2 to SA_3 must be inversely related to the difference between their preferred directions, that is, a difference of 180° has a maximal probability of synapse and 0° a minimal probability.

Vector rotation in phasor notation is equivalent to a phase shift. In an earlier formulation of the sinusoidal array [12], we proposed a special-purpose circuit for rotation by shifting. However, this proposal is incompatible with the more general formulation described here. Instead, vector rotation in our new formulation could be performed by the repeated addition of tangent vectors with magnitudes that are a constant fraction of the rotating vector. Such tangent vectors are obtainable from the rotating vector using a maximal probability of synapse at 90°. This would predict a linear relation between rotation time and angle of rotation, which is compatible with results in both humans [11] and monkeys [8].

3 Computer Simulations

Our simulations are based on an abstract pyramidal cell, modeled at a simpler level than compartmental models, but retaining many important neuronal properties such as spiking behavior. Each cell integrates synaptic input linearly over time, and when the internal sum passes threshold, it fires a spike. A spike lasts for one clock tick, after which the cell enters a refractory state, modeled by a higher threshold which decays exponentially over time until the threshold returns to normal. During the refractory period, cells continue to integrate inputs. If the internal sum surpasses the high threshold, the cell spikes and starts a new refractory cycle. We add noise to a cell by adding or subtracting a percentage of the average baseline at each time step.

Sinusoidal arrays in our simulations are of two types: *input arrays* and *summation arrays*. Neurons in input arrays are constrained to spike at a desired frequency $F(SA, i)$. To accomplish this, the internal sum is increased by $F(SA, i) \cdot \Delta t$ at each time step. Summation arrays take synaptic input from two sinusoidal arrays (which may themselves be either input or summation arrays) as described above. In order to implement the necessary bias factor $-B$, at every clock tick the net activation of each cell in the summation array is decreased by $B \cdot \Delta t$. We have not modeled synaptic or axonal delays.

It is important to note that input arrays are purely an artifact of our simulations. All sinusoidal arrays in real neural tissue would be summation arrays, their non-array inputs being generated in some manner beyond the scope of the current model. In the simulations reported here, each array contains 1500 neurons.

4 Evidence from Single Neuron Recordings

The sinusoidal array representation of a vector $\vec{v} = (r, \phi)$ requires that the constituent neurons have a cosine relation to angle (ϕ) and a linear relation to magnitude (r). Cells with a cosine response to head direction have been found in parietal cortex of rats navigating on an 8-arm maze [2]. As yet there is no evidence for a linear relation between firing time and vector magnitude, but experiments are under way to investigate this. In primates performing a reaching task, cells have been found throughout the motor system with a cosine response to hand motion direction [1, 5, 6, 7] and a weak linear correlation with reaching distance [10].

In the primate reaching task, eight light emitting diodes (LEDs) are arranged at equidistant points on a circle in front of the animal, with a ninth LED in the center. The monkey points to the center LED until a peripheral LED is lit, at which time the monkey points to the peripheral LED.

In the context of this task, cosine tuning functions have been observed in single neuron recordings throughout the monkey motor system, including motor cortex (area 4) [6], premotor area (area 6) [1], superior parietal cortex (area 5) [7], and cerebellum [5]. Although the linear response to distance is weak [10], the response to torque is sigmoidal with a large linear range [3].

Even if individual neurons only respond with a cosine function of angle and not linearly to r, it is still possible to obtain an ensemble linear response by assigning cells with the same preferred direction a variety of magnitude thresholds. Cells with similar preferred directions would then be recruited in proportion to magnitude.

5 Rodent Navigation

Rodents can find a hidden food reward by judging distance and angle to visual landmarks [4]. In one experiment, gerbils learned to find food at a constant distance and compass bearing from a cylindrical landmark which was moved to a different location on each trial.

If the animal remembers the vector $\vec{M}$ from the food to the landmark and can determine the vector $\vec{P}$ from itself to the landmark, the vector from the animal to the goal can be found by vector subtraction: $\vec{G} = \vec{P} - \vec{M}$. We propose the sinusoidal array as a mechanism for representing these quantities and computing the vector difference.

6 The Primate Reaching Task

In one variant of the reaching task [7], which we believe provides evidence for a vector subtraction operation in the motor system [9], a load is attached to the manipulandum in such a way that the load vector can be applied in any of eight directions. This allows the dissociation across trials of the target or "goal" direction from the direction in which the monkey actually has to exert force in order to reach the goal.

In [9], we postulate that the animal constructs a goal vector $\vec{G} = \overline{CT}$ which points from the center hold location C to the indicated target location T. Given a load vector $\vec{L}$ applied to the manipulandum, the motor command is equal to the vector subtraction $\vec{M} = \vec{G} - \vec{L}$. See figure 2.

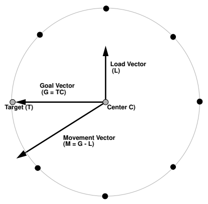

Figure 2: Vector arithmetic interpretation of the variant of the reaching task described in [7]. The monkey must move the manipulandum from the center point C to the target point T while counter-acting the load vector $\vec{L}$. $\vec{G}$ is the goal vector $\overline{CT}$ and $\vec{M}$ is the actual motor vector required.

Cells in the summation array representing $\vec{M}$ show a sinusoidal response to $-\vec{L}$ and to $\vec{G}$. We define the peak of the response to $-\vec{L}$ to be the *load axis* and the peak to $\vec{G}$ to be the *goal axis*. We expect the phase difference between the load and goal axes to cluster around $180°$. Plots from our simulations bear a striking resemblance to recordings done by Kalaska et al. [7]. See figure 3.

Figure 3: Comparison of load axes with respect to goal axes for area 4, showing distribution of angular difference between goal and load axes. Left, data from [7], used by permission of the author. Right, output of our simulations. The goal and load axes of each cell have been rotated so that the goal axis of each cell points to the left. We then plotted a unit vector in the direction of the load axis.

7 Discussion and Predictions

We have described the sinusoidal array, a computational mechanism for vector arithmetic. We cite recordings of neurons that could be components of sinusoidal arrays, but await system-level studies that will confirm or falsify our theories. Specifically, we predict that representations of the vectors forming the input to the summation arrays will be located somewhere previous to the activity of the summation array.

In the case of rodent navigation, we predict one should be able to find neurons with a cosine response to angle and a linear function of distance for each of the vectors $\vec{M}$, $\vec{P}$, and $\vec{G}$ in either egocentric or allocentric coordinates. We also predict that the areas in which the vectors $\vec{M}$ and $\vec{P}$ are represented will synapse on the area in which $\vec{G}$ is represented.

In the case of primate reaching, neurons with the required properties to represent the goal vector $\vec{G}$ (notably, cosine response to angle, no neuronal response to load) have already been found in premotor cortex (area 6), and neurons with the required properties to represent the motor activation vector $\vec{M}$ (cosine response to angle for both goal and load, preferred load axis approximately 180° off preferred goal axis) have been found in primary motor cortex (area 4). We predict that a representation of load can be found in some area that synapses on area 4, such as, perhaps, thalamus.

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