Abstract— Neurophysiological experiments in the hippocampal formation of echolocating bats have found grid cells (thought to be used for odometry) as in other mammals, but without continuous theta frequency oscillations (~8 Hz) prominent in other mammals. We describe a ‘theta-free’ model of grid cell property creation for echolocating bats that is amenable to VLSI implementation of hippocampal models of spatial navigation. We demonstrate a hybrid implementation of a 2-D model (microcontroller and neuromorphic VLSI) using recorded input from a sonar system.

In the oscillatory-interference models, translational motions of the animal result in persistent phase changes of oscillators (i.e., memory of position), resulting in position-dependent phase-synchronization at downstream grid cells. Notably, with this model, it is possible to build a single isolated grid cell at a given frequency using minimal synaptic connectivity. A requirement for good performance, however, is that the oscillators have very good phase stability.

In the attractor network models, translational motions of the animal result in an asymmetrical pattern of recurrent activity, resulting in a global shift in the phase of the grid activity pattern on the sheet (i.e., memory of position). In this model, it is not possible to create a single grid cell at a given frequency because the grid pattern emerges from the network. Due to the high neuron count, extensive synaptic interconnectivity, and complex pattern-movement wiring, this model is challenging for neuromorphic VLSI implementation unless some simplifications are made [7]. Fabrication mismatch readily creates drift and trapping in local minima.

Fig. 1. Left: A two-dimensional movement vector (thick red arrow) is projected onto each of the three ring integrator orientations. The resulting vectors are then translated into a ring activity-bump rotational phase rate. Projection vectors with ‘+’ signs produce positive phase rotations and vectors with ‘−’ signs produce negative phase rotations. Note that these vectors are defined in the world frame of reference (allocentric). While not simulated here, this could be accomplished using a speed-modulated, head-direction (HD) cell [2] that has trigonometrically-appropriate, synaptic projection strengths onto cells that control each ring-integrator’s rotation rate. Right: Neurons from each integrator representing a particular phase, project activity to a single grid cell configured to detect a three-way coincidence using saturating synapses.

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Recent neurophysiological experiments have discovered place cells in the big brown bat [8] and both place cells and grid cells in the Egyptian fruit bat [9]. While these place and grid fields are similar to those in the rat, continuous theta oscillations are not present, suggesting that theta oscillations are not fundamental to the creation of grid cell or place cell formation in bats. In contrast, transient theta oscillations occur in 1-2 sec bouts mostly during short periods during active echolocation behavior [8].

In the attractor-network model of grid cells, the memory of the animal’s position is stored in the combination of phases of the activity patterns found on the grid cells of different spatial frequencies. In our model, like the phase interference model, the memory of the animal’s position is stored in the combination of phases of the different ring O/I networks of different spatial frequencies (upstream of the grid cells), which likely represents a much smaller number of neurons than would be necessary for the attractor network model. Like the phase interference model, the grid cells only need to be driven by the inputs of the ring-integrator networks, allowing the properties of a given grid cell to be independent of neighboring grid cells. This arrangement avoids boundary condition effects that arise in the attractor networks.

II. SOFTWARE MODELING

A. Ring Integrators

The ring-integrator networks were simulated in MATLAB® to be 36 non-spiking neurons per ring with analog activation values. The activity bump was Gaussian with a sigma of 1.9 radians. A specific movement neural network was not implemented; the phase (i.e., position of the Gaussian) was simply advanced with time according to the direction and speed of travel. Using a simulated bat following a specified trajectory, the velocity vector was projected onto each of the three ring-integrator orientation vectors (see Fig 1.) and the magnitude of the projections were scaled into the rotation rate for each ring-integrator network. An example of the evolution of ring activity is shown in Fig. 2 where a simulated bat flies in a circle. Note that the starting and ending phase for all three integrators is the same. Changing the scaling factor produces different spatial frequency grid fields.

B. Simulated Grid Cells

Although earlier models from Burgess and colleagues used a summation of the three orientation inputs to drive the grid cell, multiplication of the three inputs that target different dendritic branches [4] appears to fit the data better [11]. In fact, logarithmic compression (i.e., saturation of the dendritic contributions) of the individual inputs prior to summation at the soma can produce this multiplicative effect and is very
close to a logical AND of the inputs. Fig. 3 shows two examples of spatial grid patterns resulting from two ring integrator speed scaling factors.

III. A NEUROMORPHIC VLSI GRID CELL

A. A Hybrid Implementation Using VLSI Hardware

In the previous section, the model was simulated in MATLAB® to provide the cleanest definition of the model. In this section, we demonstrate the implementation of the grid cell calculation on a neuromorphic VLSI circuit using saturating synapses in a single compartment neuron model to mimic the multiplicative model (using the concept of dendritic branch saturation). The ring integrator portion of the model was implemented on an 18F series PIC® microcontroller with motion signals coming from a computer. The microcontroller provided neuron outputs for the three ring-integrator networks (corresponding to one spatial frequency) as spike trains that were transmitted to a microcontroller. The microcontroller provided neuron outputs for the three ring-integrator networks (corresponding to one spatial frequency) as spike trains that were transmitted to a microcontroller. The microcontroller provided neuron outputs for the three ring-integrator networks (corresponding to one spatial frequency) as spike trains that were transmitted to a

![Fig. 5. The neuron circuit used to convert excitatory and inhibitory input currents into conductances.](image)

The neuron circuit (Fig. 5) is a subthreshold-regime, current-mode, conductance-based neuron design (similar to [12]). In this design, the membrane potential is represented as a current ($I_{\text{mem ss}}$, drain current of M10) with a current threshold for firing a spike (drain current of M11). The excitatory input current acts as a conductance, pulling the membrane "potential" up above the threshold level. The inhibitory current also acts as a conductance, pulling the membrane below the firing potential. This competition determines the steady-state value of the membrane "potential" and thus determines if the neuron will fire a spike or not. The current representing the membrane "potential" reaches a steady-state value given by:

$$I_{\text{mem ss}} = I_0 \cdot e^{\frac{\kappa(V-\text{mem})}{V_T}} \left( \frac{I_{\text{exc}}}{I_{\text{exc}} + I_{\text{inh}}} \right)$$

(1)

Where $I_0$ represents the subthreshold scaling current and $\kappa$ represents the gate capacitive coupling factor. Because the

![Fig. 6. Spatial grid patterns generated by a neuromorphic VLSI neuron driven by three saturating synapses (VLSI) to detect a three-way coincidence of particular phases from three ring-integrator networks (microcontroller). Three spatial frequencies are demonstrated by changing the scaling factor between movement speed (e.g., m/sec) and the phase rate (e.g., rad/sec).](image)

three synapses saturate, we can select a threshold current
(controlled by $V_{\text{threshold}}$) and inhibitory current to only produce a spike if all three inputs are active. In this circuit, the capacitor $C_1$ only acts as a lowpass filter.

C. Grid Cells

In our implementation of the model, using a single compartment VLSI neuron, saturating synapses are used to mimic the effect of separate dendritic compartments. The result is close to a logical AND (to approximate the multiplicative solution). To demonstrate the use of this neuromorphic VLSI implementation and to visualize the firing field of the grid cell, we moved the position of simulated bat to all locations in a square grid to produce the grid field pattern seen in rat experiments (Fig. 6).

D. Sonar-Driven Grid Cells

To demonstrate the system with a natural spatial movement signal closer to our intended application, we used a single sonar transducer observing a moving pole to simulate an aerial vehicle (e.g., a robot bat) using a fixed pole as a position reference. The sonar samples were at 10 Hz and the range rate was fed into the ring integrator network assuming a fixed angle (zero radians).

The initial integrator phases were selected such that the line of travel aligned with the nodes of the grid field.

IV. DISCUSSION

The use of the ring-integrator networks to replace pairs of interfering theta oscillators provides a much simpler model for the bat grid cell system, retaining many of the desirable properties of the original phase-interference model, without resorting to a full 2-D attractor circuit as in [7]. Two-dimensional movements of the animal are implemented as one-dimensional movements on multiple rings, arguably simplifying the required network. While this paper only explored the grid cell portion of the model in silicon, implementing a spiking neuron-based ring-integrator network with good rotational control has already been demonstrated for a neuromorphic VLSI head-direction cell system [14].

Recent work [15] has shown that large numbers of grid cells at each frequency are not necessary to generate compact place fields. This model allows for targeted construction of grid field properties for efficient neuromorphic VLSI-based implementations of place cells in the hippocampus that may require a diversity of grid cell inputs. Perhaps most interesting for both VLSI and biological implementation, expansion of the model to 3-D only requires one additional ring-integrator.

ACKNOWLEDGMENT

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