

A spiking network for spatial memory formation: towards a fly-inspired Ellipsoid Body model

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Abstract—Neural centers devoted to spatial memory and path integration were largely studied in rats and in different insect species like ants and bees. In this paper a neural-based model for the formation of a spatial working memory is proposed mirroring some peculiarities of the *Drosophila* central brain and in particular the ellipsoid body. Simulation results are reported opening the way to applications on roving platforms.

I. INTRODUCTION

Bioinspired solutions for visual place learning and path integration are widely investigated in view of their application to robotic systems. Within the animal world, different insect species navigate in cluttered environments using orientation mechanisms that allow both to track temporarily obscured objects and to find a place of relevant interest like a food source or the nest (e.g. landmark navigation and path integration). Homing mechanisms were deeply studied in the desert ant *Cataglyphis* [1]. This insect is able to return to its nest after long and tortuous foraging excursions. This behavior can be explained by path integration, a mechanism particularly important in unfamiliar terrain. However, path integration systems that depend exclusively on self-generated motion signals have accuracy problems due to rapid accumulation of errors [2]. In familiar environments, navigation by using landmarks can either integrate or substitute path integration. Landmark navigation can increase the accuracy of navigation compensating the cumulative errors when a familiar landmark is found. Path integration can be used to reach the successive landmark giving also a degree of reliability to landmarks solving ambiguity problems [3].

Neural architectures, able to model the navigation behavior of *Cataglyphis* ants, were proposed considering neural structures based on chains of excitatory and inhibitory populations mutually coupled [4]. The formation of a hill of activity within the excitatory population is the key element used to store the neural information related to the agent orientation. Other models proposed mathematical formulations using sinusoidal arrays, which allow an efficient representation of vector information [5]. Moreover, interesting approaches for landmark navigation using recurrent neural networks were also proposed to explain the ant's behavior [6]. Applications on robots were realized in [7] where the home vector is encoded in a population of circular array of cells that integrate the heading input.

Interesting studies were also performed on rats where head direction cells were identified in the limbic system [8], [9].

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During spatial navigation, the head orientation of the animal is encoded internally by a neural persistent activity in the head-direction system. A self-sustained hill of activity can be created in a population of excitatory neurons while other two rings of inhibitory neurons are used to shift the position of the peak of spiking activity when the animal turns its head to a new direction, depending on the angular head velocity [8].

Migrating from mammals to insects, *Drosophila melanogaster* is particularly interesting, since it allows, through the application of genetic manipulation tools, to unravel the brain areas and the neural processes involved in the generation of a specific behavior. As already mentioned, it has been demonstrated that insects are capable of visual place learning, that is the ability to use spatial information to recall specific locations identifying and remembering visual features such as size, color and contour orientation; insects are also able to solve the Morris water maze problem [10]. However, it is less known about the neural circuits that mediate these behaviors and what kind of structures are necessary for visual place learning.

In nature, flies do not create a nest like other insects and the acquisition of homing strategies could be considered not relevant for this species. However, targeting behaviors are commonly used: flexible goal-driven orientation requires the storing of the position of a target, especially when target moves out of sight. The capability to retain, recall and integrate such positional information into guiding behaviour needs the formation of a spatial working memory.

The detour paradigm is just an example used to demonstrate the capability of *Drosophila melanogaster* to store the position of a target when it moves out of sight also after the presentation of a distracter [11], [12].

Thanks to genetic manipulation tools available on this insect, by targeted manipulations of neural centers in the *Drosophila* brain, the fundamental role of the central complex and in particular of the ellipsoid body (EB) has been identified in the spatial memory formation process.

One prominent type of neuronal cells of the ellipsoid body is the group of GABAergic ring neurons. The fibres of these neurons run in a prominent tract, the RF tract (ring-neuron and tangential fan-shaped-body neuron tract), and form bushy thin endings in the ipsilateral lateral triangle (ltr) and bleb-like endings in the ellipsoid body (i.e. near the ltr, the neurites of the R neurons split to send dendrites into the ltr, and axons into the EB [13]). Four different kinds of ring neuron (R1 to R4) can be distinguished by their arborization pattern around the ellipsoid body canal. R1 and R3 neurons project outwards from the ellipsoid body canal, whereas the arborization of

R1 is restricted to the inner zone, that of R2 to the outer zone, and that of R3 to both zones. R4 neurons project from the periphery inwards and arborize in the outermost zone. The GABAergic ring neurons of the ellipsoid body in the central brain are necessary and their plasticity is sufficient for a functional spatial orientation memory in flies [11].

In this paper, on the basis of the neural model proposed in [8] an adaptation to the insect EB structure has been considered. Moreover an additional processing level needed for the integration and exploitation of the spatial information contained in the spiking neural structure was included.

II. NEURAL MODEL

The neural model proposed to describe the processing mechanisms of the ellipsoid body for the creation of a spatial working memory consists of three populations of interconnected neurons. This kind of structure is similar to other existing models where a hill of spiking activity is created to store the heading position of the system integrating the heading velocity acquired by proprioceptive sensors [4] [8]. The model contains one population of excitatory cells ($N_E = 20$) and two populations of inhibitory cells ($N_{I1} = 20$ and $N_{I2} = 20$ neurons). The number of neurons used in the network is related to the known neurobiological information on the central complex in *Drosophila* [14]. Neurons in each population are labeled by their heading directions and distributed uniformly along a ring which runs along the EB circular shape. The connection weights between any two neurons depend only on the difference between their angular positions. A scheme of the system is reported in Fig. 1 where the three populations of neurons, the connection topology and the external inputs are reported. Each inhibitory population contains all-to-all connections between its neurons, with synaptic weights that follow the distribution reported in Fig. 2. The same connectivity is present between the two inhibitory populations (not reported in Fig. 1 for the sake of simplicity). The excitatory neurons have all-to-all connections with the inhibitory populations with a weight profile reported in Fig. 2, whereas each neuron of the inhibitory population is connected with only one neuron of the excitatory population: the neuron that corresponds to the angle $\theta + \theta_0$ in population I_1 , inhibits the excitatory neuron that corresponds to the angle θ ; this receives also a current contribution from the neuron labeled with $\theta - \theta_0$ in population I_2 ($\theta_0 = 110^\circ$ in the following simulations). In the original model the connection scheme included all-to-all connections also for the interaction between these layers [8]; the simplification presents minimum drawbacks in terms of level of noise in the network as will be discussed in the simulations.

Both excitatory and inhibitory neurons are modeled by a leaky integrate-and-fire (LIF) model [15][16]. The time evolution of the membrane potential $V_m(t)$ of each neuron is described by the following equation:

$$C_m \dot{V}_m(t) = -g_L(V_m(t) - V_L) - I_{syn}(t) \quad (1)$$

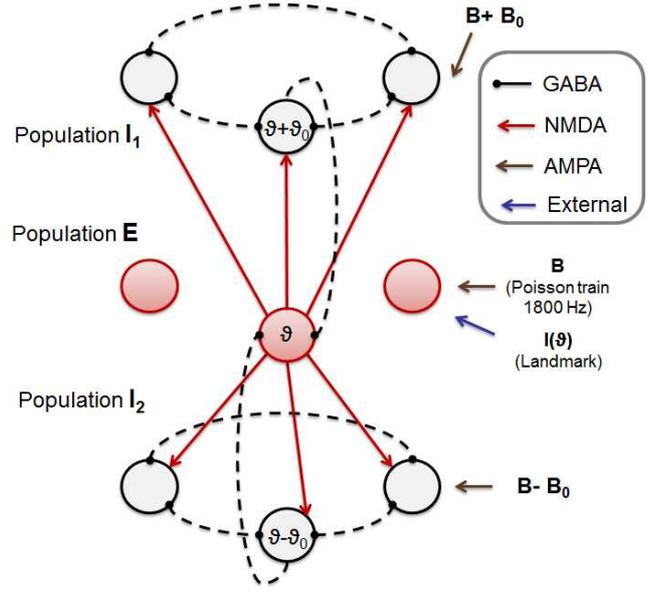


Fig. 1. Scheme of the ellipsoid body model constituted by three populations of excitatory (E) and inhibitory (I_1 and I_2) neurons. Synaptic currents are mediated by AMPA and NMDA for excitatory and GABA for inhibitory connections. Two external inputs are also provided, in the corresponding neuron depending on the angular position: a poisson train at 1800 Hz for all the network neurons and a constant input that acts only in presence of a landmark. All-to-all connections between the inhibitory layers and within them (not shown in figure) are present in the model.

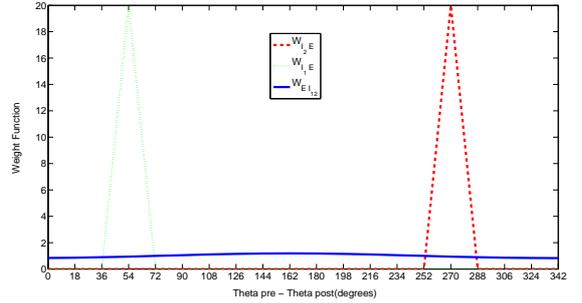


Fig. 2. Weight distribution between the neurons of population E, I_1 and I_2 .

where C_m is the membrane capacitance, 0.5 nF for excitatory cells and 0.2 nF for inhibitory cells; g_L is the leak conductance, 0.025 μS for excitatory cells and 0.02 μS for inhibitory cells; and V_L is the resting potential, -70 mV for both excitatory and inhibitory cells. When the membrane potential of a neuron reaches a threshold (i.e. -50 mV) a spike occurs and the membrane potential returns to a reset potential (i.e. -60 mV). The last term $I_{syn}(t)$ represents the total synaptic input current for the cell. Every neuron receives inputs from the other neurons as described above, and also an external excitatory synaptic input mediated by AMPA receptors. Synaptic currents exchanged between neurons include both excitatory (glutamatergic) mediated by AMPA and NMDA receptors and inhibitory (GABAergic) contribution. Details

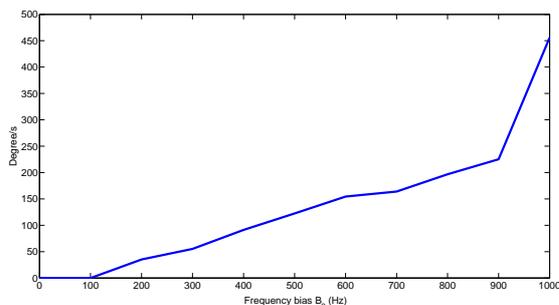


Fig. 3. Relation between the parameter B_0 used to modify the frequency of the Poisson train and the corresponding angular velocity obtained in the network.

about the synaptic connections are reported in [8] where the parameter values related to rats were considered. However, recent studies on the central complex in flies identified the presence of several receptors [17] and in particular the role of NMDA for long-term memory consolidation in the ellipsoid body [18].

The network receives external inputs used to provide information on the angular head velocity that is integrated in the system to provide the head orientation. The angular head velocity signal is modeled as uncorrelated Poisson spike trains B with frequency $f=1800$ Hz. Experiments with regular train of spikes were also performed obtaining similar results. When a rotation is performed, the corresponding angular velocity is provided to the network unbalancing the input on the two inhibitory populations.

We first consider the behavior of our model in absence of sensory and/or self-motion signals. This corresponds to the case in which animals head direction is held fixed. In our model, this is implemented by setting to zero ($B_0 = 0Hz$) the head velocity bias of the external afferent inputs to the two inhibitory populations. In this case, the network quickly reaches a stationary state with a bell-shaped activity profile. Because of the symmetries of the network, the peak of the activity hill can arise anywhere in the network (depending on the initial condition). Due to the absence of synaptic connections between cells in the excitatory population, the hill of activity is generated and maintained by a combination of uniform external excitatory input and distributed inhibitory inputs from the two inhibitory populations. When the frequency bias B_0 is positive (negative) a clockwise (anti-clockwise) rotation of the hill of spiking activity is obtained. The mapping between B_0 and the head velocity was obtained characterizing the response of the network as shown in Fig. 3. As previously underlined, the presence of visual landmarks can be helpful to improve the system performance.

Visual landmarks are modeled as an input current to neurons in the excitatory population that corresponds to the landmark position. The landmark can be used as a calibration mechanism: in fact the hill of activity can arise in any position of the ring due to the symmetry of the neural structure; the landmark can shift the hill to a specific neuron

used as reference point. During movements the accumulated error can be compensated using specific landmarks placed in known positions.

The architecture until now depicted, is able to provide continuously the animal's instantaneous head direction that is internally represented by the peak location of the bell-shaped activity profile of the excitatory population. To solve more complex tasks like the detour paradigm [11], a spatial integration of the distance traveled by the agent is needed. For sake of simplicity we consider two distinct motion behaviors: forward movement and turning on the spot.

To store in the network the path traveled in time, an additional outer ring of neurons has been added to the excitatory population (i.e. compass neurons). These neurons (i.e. population P) have a match one-to-one with the population E and can be modeled with a simple linear transfer function. A scheme of the complete network is reported in Fig. 4 where four distinct rings of neurons are considered. The synaptic connections used to connect population E and population P neurons, are supposed to be characterized by a facilitating dynamics [19], and can be modeled with the following dynamical system:

$$\dot{u}_n = U - u/F + k\delta_n(t - t_s)\delta(B_0) \quad (2)$$

where $n=1..N$, $U=0$, F is related to the fading memory and k is a gain related to the system speed, $\delta_n(t - t_s)$ represents the spikes emitted at time t_s by neurons of population E and $\delta(B_0)$ is a gating function that allows the contribution of a spike at time t_s only if the system is in forward motion and then $B_0 = 0Hz$. When the system is turning, the population P is not activated because the action is performed without spatial translation. The parameter F represents the rate of discharge of the state variable and has been fixed to a value that allows to retain the information in the time window used for the simulations that is about 5s similarly to the biological case [11].

III. SIMULATION RESULTS

To evaluate the capabilities of the proposed neural structure, a series of tests have been performed. The first analyzed problem consists in the positioning of the hill of activity on a reference angle to reset the processing. Due to the symmetry of the structure, depending on the initial conditions, the starting position of the hill is unpredictable. To force the formation in a specific area of the ring a landmark is applied. In Fig. 5 the average firing rate within populations E and I_1 is shown. The behavior of population I_2 is similar to I_1 but slightly shifted in order to create two barriers on the two sides of the population E containing the hill in a narrow band. During the first 0.5s a landmark is applied to the neurons next to 180° through an input current formulated as a gaussian function:

$$I = Ae^{-\frac{(\vartheta - \vartheta_0)^2}{2\sigma^2}} \quad (3)$$

where $A = 9.4nA$, $\sigma = 24^\circ$ and $\vartheta_0 = 180^\circ$.

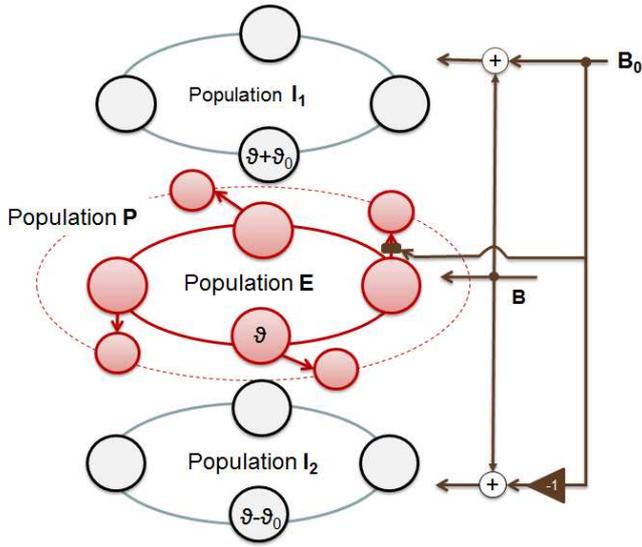


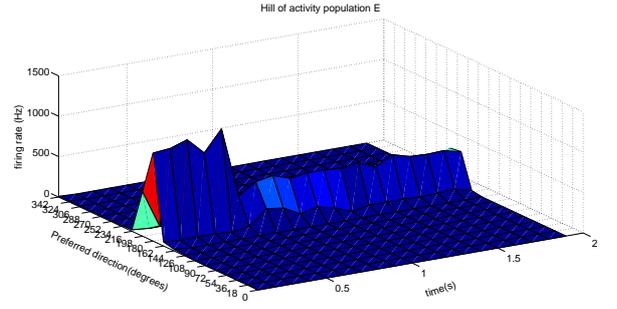
Fig. 4. Four ring network used to model the EB behavior and to reproduce the detour experiments. The external input B acts as a gate for the population P avoiding an integration during the turning on the spot manoeuvres.

The reduction of the synaptic connections between layers that, in our actual model, are more local than global, and the reduced number of neurons with respect to the original model in [8], can produce a limited activity also in some neurons out of the hill. However extensive simulations showed that the dynamics of the network remains stable. The spikes emitted by population E after transient, when the landmark is applied, are cumulated by the population P that integrates the activity depending on the robot speed that is used as a gain (k in eq. 2). Through a calibration it is possible to find the gain value that converts the neural activity into a distance traveled expressed in a generic measurement unit.

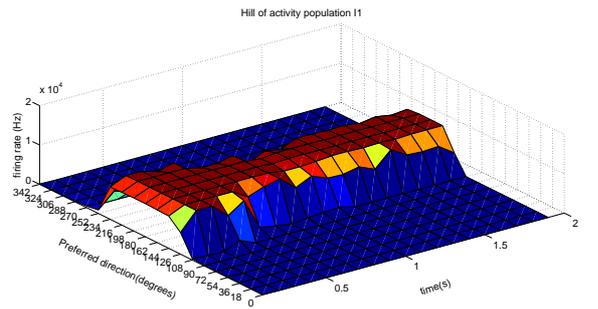
Another experiment was performed moving the agent forward for 1s: making a rotation of 130° and proceeding forward for another 1s, a constant speed of 1m/s was adopted. The angular velocity was provided to the network through a $B_0 = 920Hz$ for 0.5s. Initially a landmark was used to facilitate the formation of the hill around 0° . The final outcome of the network that works as a short term spatial memory, is the estimated position and orientation of the agent.

During the rotation the population P is disconnected from population E using the gating parameter $k = 0$ in eq. 2 and the rotation is considered on the spot (see eq. 2). The network integrates in time the speed movement of the agent making an estimation of its spatial position. The heading angle stored by the system during the 3s simulation is reported in Fig. 6. The normalized activity of population P that integrates in time the state of population E, is shown in Fig. 7. To obtain, step by step, the internally estimated current position of the agent, a vectorial summation is performed considering neurons in population P as polar representation of spatial vectors.

Finally the comparison between the real trajectory and the internally memorized one is reported in Fig. 8. The



(a)



(b)

Fig. 5. Average firing rate within the population of neurons E , I_1 . The behavior of population I_2 is similar to I_1 but slightly shifted. A landmark is applied from the beginning for 0.5s to guide the hill formation in a given region of the ring.

accumulated error is a consequence of the processing structure and in particular it is due to the relative low number of neurons distributed in the rings that determines the spatial resolution (i.e. about 18° each neuron).

For robotic applications the spatial resolution could be improved to obtain performance compatible with the assigned tasks. The behavior of the system can be appreciated also in standard tests used in robotics like navigation on a square path [20]. In this simulation each rotation of 90° corresponds to a $B_0 = 800Hz$ applied for 0.5s, and each segment to a forward movement at 1 unit/s for 0.5s. In Fig. 9 the real trajectory is compared with the step-by-step estimated position provided by the network.

The proposed network can also replicate the detour experiment reproducing behaviors shown by real flies. When the fly is attracted by a visual target, the CX is mainly involved in determining the insect behavior. When the target disappears and a distractor appears, the insect stores in the EB neural structure the current estimated position of the obscured target. This estimation can be obtained using parallax information and the distance is coded using, as measurement unit, the number of steps estimated to reach the

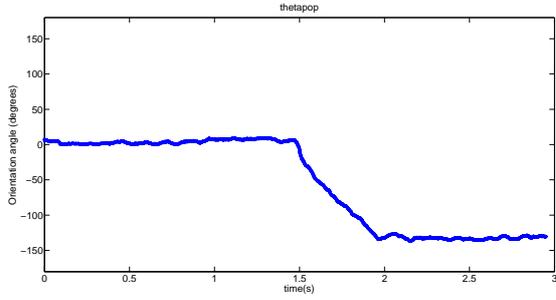


Fig. 6. Heading angle of the agent during a 3s simulation where after a forward movement, a on-the-spot rotation of 130° is performed.

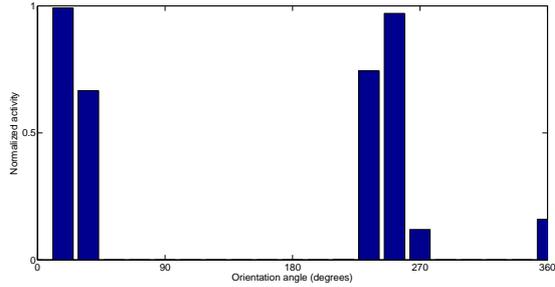


Fig. 7. Normalized activity of Population P. The estimated position is obtained performing the vector sum of the contribution of each neuron that codifies the information in a polar coordinate system.

object. This spatial vector is coded in the neural population P. The trajectory followed while the insect is attracted by the distractor is integrated in the network to allow the recovery of the original target position within a limited time due to the fading memory. The simulation is divided into three parts: first when the target disappears, the EB stores the target estimated position in polar coordinates charging the corresponding neuron of population P with a current proportional to the distance (coded in number of steps). Then the hill of activity of population E is forced to arise in a position rotated by 180° . Subsequently the path followed during the presence of a distractor placed at 90° is memorized. When the distractor disappears, the

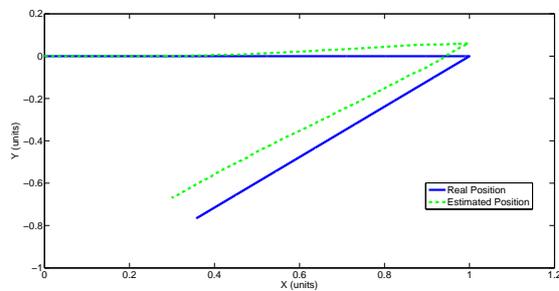


Fig. 8. Comparison between the real trajectory followed by the agent and the internal estimated position stored in the EB.

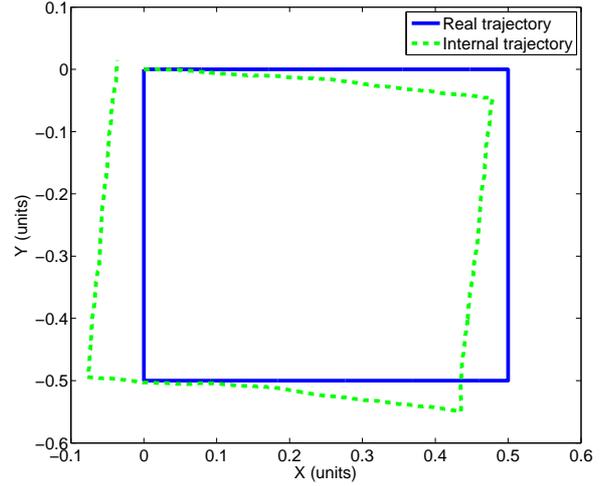


Fig. 9. Comparison between the real trajectory followed by the agent and the estimated position stored in the EB.

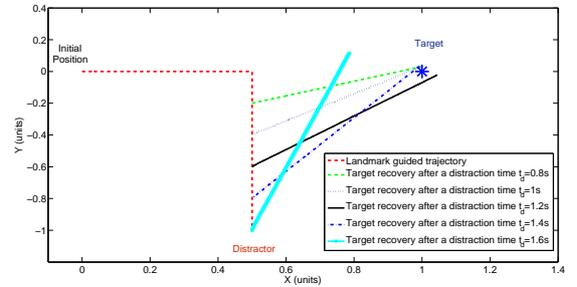


Fig. 10. Detour experiment: trajectory stored by the system attracted by the distractor and estimated trajectory to reach the position of the disappeared target whose position is marked with an asterisk. The distractor was applied for different time windows from 0.8s to 1.6s and the correctness of the information stored in the EB model about the target position decreases for longer distraction events.

information accumulated in population P is used to estimate the spatial position of the first target. The trajectory stored by the architecture during the effect of the distractor and the estimated trajectory followed to reach the disappeared target are reported in Fig. 10. For further analysis the model will be included in a dynamic simulation environment with a simulated fly.

IV. CONCLUSIONS

Bio-inspired solutions for spatial memory are widely investigated and different models were provided on the basis of ants, bees and rats behaviors. In this paper a computational model of the *Drosophila* ellipsoid body based on a four-ring spiking network is proposed. The neural structure is able to create a hill of spiking activity that moves in a ring coding the heading angle of the insect. Several experiments illustrate the capability of the system to store the spatial position of the insect on a polar coordinate system. The proposed

model is able to replicate experimental results obtained with *Drosophila* in the detour paradigm. The architecture could be easily improved modifying the spatial resolution for reliable robotic applications.

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