

Modeling the Insect Mushroom Bodies: application to sequence learning

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Abstract

Learning and reproducing temporal sequences is a fundamental ability used by living beings to adapt behavior repertoire to environmental constraints. This paper is focused on the description of a model based on spiking neurons, able to learn and autonomously generate a sequence of events. The neural architecture is inspired by the insect Mushroom Bodies (MBs) that are a crucial center for multimodal sensory integration and behaviour modulation. The sequence learning capability coexists, within the insect brain computational model, with all the other features already addressed like attention, expectation, learning classification and others. This is a clear example that a unique neural structure is able to cope concurrently with a plethora of behaviours. Simulation results and robotic experiments are reported and discussed.

Key words: neuroscience, insect brain, insect mushroom bodies, spiking neurons, learning, neural model, context

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1. Introduction

Learning is a fundamental feature used by living beings for adaptation. We can identify two well-defined forms of learning: *Classical conditioning* when correlations between *unconditioned* and *conditioned* stimuli are learned, leading the animal to provide conditioned responses, and *Operant learning* when animals are requested to acquire knowledge from the consequences of their own actions. However, the complexity of the environmental conditions sometimes requires more sophisticated learning mechanisms. Sequence learning is one of the most powerful kinds of behavioural improvement in living beings. For example, learning a sequence of sensory/motor actions is a key aspect of motor learning; recognizing a sequence of objects can be useful for orientation behaviors. The capabilities to learn time-constrained associations are fundamental elements for sequence learning.

The problem of sequence learning has been faced in literature using different approaches based on artificial models (Sun and Giles, 2001), most of them derived from Jordan and Elman's recurrent networks (Elman, 1990; Jordan, 1986). Hebbian learning schemes were proposed in Wang and Arbib (1990) where neural networks eliciting short term memory (STM) were able to learn and recognize temporal sequences. Later on Billard and Hayes (1999) proposed a connectionist architecture, DRAMA (Dynamical Recurrent Associative Memory Architecture), for dynamic control and learning of autonomous robots. This is a time-delay recurrent neural network, using Hebbian update rules able to learn spatio-temporal regularities in discrete sequences of noisy inputs.

Nowadays the study of animal brains and the modeling of relevant neural structures on the basis of behavioral experiments continuously improve the knowl-

edge about learning mechanisms. Several attempts can be found in literature related to the development of algorithms or bio-inspired networks able to model the functionalities expressed by specific brain centers of mammals, molluscs and insects (Webb and Consi, 2001). Looking in details inside the insect world, there are very interesting species where, in spite of the relative small number of neurons, the complexity of their behavior repertoire is impressive.

Discovering where and how sequence learning is formed, retained and extracted, is a hard task, however insects can represent a good starting point. In fact in insects there are neurobiological evidences of processes related to spatio-temporal pattern formation and time-dependent learning mechanisms that can be used to solve tasks that include sequence learning. The most plausible brain structures involved in these processes are the *Mushroom Bodies* (MBs) that, together with the *Lateral Horns* (LHs), are principally devoted to olfactory learning (Liu and Davis, 2006). The spatio-temporal olfactory information coming out from the Antennal Lobes (ALs) are processed and stored in spatial patterns that can evolve in time and can be associated to specific behavioral responses (Huerta, 2009). The spatio-temporal coding in such neural structures has been investigated in Nowotny *et al.* (2003), where a model for codifying spatio-temporal patterns into spatial patterns has been implemented. Taking into consideration this spatio-temporal pattern formation process that has been unravelled from a different perspective in other works (Arena *et al.*, 2008), we investigated the possibility to extend the processing capabilities of the MBs system to model an artificial bio-inspired structure for sequence learning.

The olfactory model of locusts illustrated in Nowotny *et al.* (2003) clearly underlines the inhibitory effect of the LH circuit on the MB cells. Each Kenyon

cell is strongly connected with the cells of its neighborhood, and connections between this layer and the Antennal Lobes-like layer are randomly generated. A coincidence detection approach allows the model to codify sequences of events in a spatial pattern of firing neurons. However no learning is implemented in the model even if successive works started to introduce classification mechanisms to the network with the support of reinforcement learning mechanisms used to associate the MBs sparse activity to predefined classes (Huerta, 2009).

Looking to mammals we can also find interesting works on the olfactory bulb for instance in rabbits where the presence of chaotic dynamics in the formation of perceptual states is discussed (Freeman, 1987, 2004). Freeman and coworkers developed a model of the chaotic dynamics observed in the cortical olfactory system called K-sets that has been used for classification and pattern recognition and further extended for action selection in an autonomous robot (Harter and Kozma, 2005).

Winnerless competition networks were also implemented to model sequences of firing activities in olfactory networks (Rabinovich *et al.*, 2001) and later used in Arena *et al.* (2009b) for perceptual purposes.

Another model for sequence learning was proposed in Berthouze (2006) where a neural network was developed to implement context-dependent learning of complex sequences. The model utilizes leaky integrate-and-fire neurons to extract timing information from its input and modifies its weights using a learning rule with synaptic noise. The context layer is used to solve ambiguities where identical inputs should be associated to different outputs in the sequence depending on the previous provided elements. Similarly we started from unravelling the functionalities of the insect MBs trying to extend the neural model basic capabilities, mainly

devoted to olfactory learning, to perform more complex tasks related to sequence learning. The idea is to create a unique neural structure able to show multiple functionalities as demonstrated in several experiments in which the MBs are involved (Glenn *et al.*, 2007; Gronenberg and Lopez-Riquelme, 2004). This is very next to the concept of Neural Reuse, another additional characteristics of biological neural networks (Anderson, 2010). The architecture here proposed is a multilayer spiking network based on *Izhikevich's* neuron model (Izhikevich, 2004), in which the interaction among the different layers, similarly to its biological counterpart, allows the generation of different capabilities that range from the classical odor learning to other more complex behaviors like attention, expectation and sequence learning.

The MB-inspired architecture proposed in this work can be used to retrieve information from a sequence of elements to generate the proper actions. Learning and retrieving of simple sequences can be performed using the MB model as discussed in Arena *et al.* (2012) where the sequence is generated by the temporal activation of a chain of neurons linked through learnable plastic synapses.

However to deal with complex sequences (e.g. containing stimuli that cannot unambiguously predicted from the previous one) it is necessary to know the context of each element, this is faced with the introduction of the Context layer which is fundamental to retrieve this information. The activity of the Context layer is guided by an integration process where previous information diffuses spatially and temporally to create the context for the next presentation. Another important element used in the architecture is the *End sequence neuron* that is activated when no other elements are presented and the sequence is considered concluded. The End sequence neuron performs a reset in the Context layer allowing the presenta-

tion of a new sequence.

2. Sequence learning in Nature

Beside their small brain, insects show a very interesting complexity in their behavior repertoire. Among the different insect species, bees, locusts and flies are certainly the most investigated. When looking for food, bees often have to visit several sites during one foraging trip. They are able to learn how to reach each new site encountered during the travel. From the details about the complexity of the learned sequence we can retrieve information about the neural structures involved in the process. Bees have shown to follow fixed routes between two known locations (Janzen, 1971; Heinrich, 1976; Manning, 1956). To understand how honeybees might acquire such routes, Collet and coworkers examined the capabilities of bees to learn motor sequences, to correlate motor instructions to visual stimuli and if their visual memories are triggered by contextual cues related to their position in a sequence (Collett *et al.*, 1993). A route may thus be composed of individual path segments which are separated items linked together through external learned signals.

Sequence learning is a difficult task also for ants and preliminary studies indicate that ants perform conditional discriminations reliably when stimuli are simultaneous, but they usually fail when stimuli are sequential (de Ibarra *et al.*, 2011). However other studies showed that ants can learn stereotyped foraging routes guided in part by the visual features that they encounter along the route (Macquart *et al.*, 2008). Ants could then sequence together the successive basic motor programs into a site-specific serial program as a kind of signature route. Such a procedure would facilitate animals reducing cognitive needs imposed by

learning and remembering numerous visually identified landmarks when directing towards a target. Therefore ants can learn to negotiate a maze using the shapes for guidance rather than a fixed motor strategy. Trained ants could not only discriminate positive from negative shapes, but also learn the correct sequence of choices. Experiments described in Chameron *et al.* (1998) show that the contextual signal must come from previous events in the sequence and be stored internally. However, the experiments cannot clarify whether ants store the whole sequence, or internal linkages extend only one step back in the chain.

To unravel the problem, understanding which neural centers and neural paths are responsible for these behaviors we considered as reference animal the *Drosophila melanogaster* where, using genetic tools, it is possible to create mutants showing deficit in learning caused by modifications in the relevant neural centers involved.

The experiments reported in Murphey (1965) and May and Wellman (1968) represent a first attempt to test the fruit fly behaviour in a multiple T-maze scenario where a sequence of choices have to be performed. The results showed that in some configurations the fruit fly statistically prefers to persist in the selected chosen action (e.g. left turn) repeating it multiple times (sequential repetition) whereas in a different set-up it preferred switching the decision in time (sequential alternation). From these results, a clear behavior is not evident and recent publications on this topic are missing. From preliminary behavioral experiments the possibility for flies to learn complex sequences seems a difficult task to be accomplished even if the *Drosophila melanogaster* brain contains the neural circuits and learning functions needed.

In previous works a *Drosophila*-inspired insect brain computational model was developed (Arena and Patané, 2009a, 2014). The proposed architecture, ap-

plied to simulated and real roving and walking robots, allowed to reproduce a series of behaviors shown by fruit fly and other insects in focused experiments. Besides basic navigation skills like visual targeting, visual learning, detour and spatial memory (Arena *et al.*, 2011; Mronz and Strauss, 2008) the role of MBs in scenarios that include attention, expectation and delayed match-to-sample tasks was discussed (Arena *et al.*, 2013). Here, following those previous works, we extended the MB-inspired architecture to show more complex behaviors like sequence learning. The idea is to demonstrate that the neural structures available in *Drosophila* are sufficient to show this kind of behavior, even if such capability has not yet been discovered in behavioural experiments. The proposed model and the obtained results could be the starting point for new biological experiments to answer to this open question. To name similar situations, only recently the capability of *Drosophila melanogaster* to face a Morris water maze-like experiment was demonstrated and this capability seemed to be out of its behaviour repertoire until this recent evidence (Foucaud *et al.*, 2010).

3. The Mushroom Bodies in *Drosophila* as a reference system for sequence learning

Taking inspiration from insects and in particular from *Drosophila melanogaster*, we considered the Mushroom Bodies as a multimodal neural center fundamental to develop a neural structure able to deal with sequence learning.

The Mushroom Bodies are a paired structure of the protocerebral hemispheres spreading out in three dimensions. They are next to the *Central Complex* without known direct connections. In the fruit fly, the most important constituents of the MBs are the 2500 Kenyon cells per side, which run in parallel from the *ca-*

lyx through the *peduncle* and to the *lobes* (see Fig. 1). The lobes are the output regions of the MBs, involved in different aspects of the learning process (Junko *et al.*, 2009). Christiansen and coauthors observed that neurons in γ -lobe can form presynaptic areas that support short and long term memory similarly to α and β -lobes where the memory is generated, whereas α' and β' -lobes are responsible for consolidation of memory (i.e. post-synaptic areas) (Christiansen *et al.*, 2011). There is a prominent olfactory input from the antennal lobes into the calices. Inputs from other sensory modalities are not evident in *Drosophila*, however the role of MBs in visually related tasks has been already demonstrated (Tang and Guo, 2001).. Instead in honeybees, MBs receive prominent visual (Gronenberg and Lopez-Riquelme, 2004), gustatory and mechanosensory input (Schroter, 2003). Furthermore, in flies and bees, the MBs lobe region receives information on sugar reward (via octopaminergic neurons) or electric shock (via dopaminergic neurons).

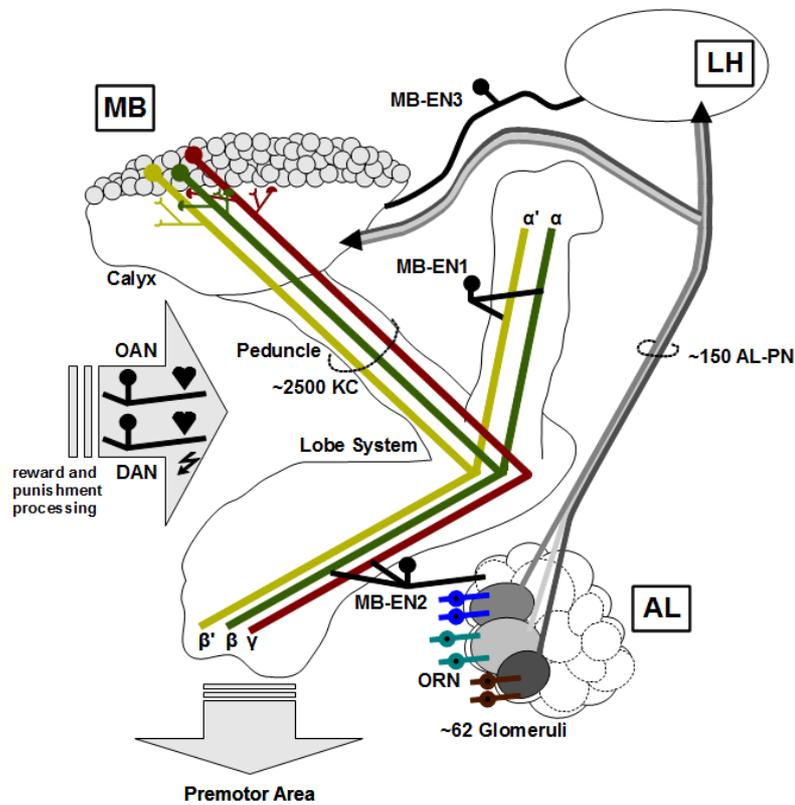


Figure 1: Block scheme of the structures devoted to odor processing in insects. Olfactory receptor neurons (ORN) transfer information to the Antennal Lobes (AL). The ALs' activity is transferred through the Projection Neurons (AL-PN) to the Kenyon Cells (KC) in the Mushroom Body (MB) and to the Lateral Horn (LH) region. The calyx of the MB is the KC input region for PN odor information, but KCs have also internal connections. The peduncle of the MB is composed of KC axons which project into five different lobes: α and β -lobe, α' and β' -lobe and γ -lobe. The KCs, through axo-axonal connections lead to the formation of spatio-temporal patterns at the level of the lobes (MB-EN1). Projections from the lobes to the AL would be well suited for controlling filtering of sensory information there (e.g. expectation driven selective gain control). MB extrinsic neurons (MB-EN3) coming from the LH are resetting the MB activity with inhibitory input to the calyx. Octopaminergic Neurons (OAN) mediate the unconditioned stimulus in the reward processing, whereas dopaminergic Neurons (DAN) play important roles in the acquisition of aversive and appetitive olfactory memory. The Premotor Areas of the insect brain are modulated by the MBs, but direct neuronal connections are still unknown Arena *et al.* (2013).

The mostly studied function handled by MBs is related to olfactory learning. Analyzing the flow of information between the different neural centers, it is possible to investigate the learning mechanisms involved in this process. In vertebrates the olfactory bulb is a layer in between the sensory neurons and the olfactory cortex. In insects the Antennal lobes interconnect the sensory layer with the MBs, the structure responsible for the memory formation and retrieval (Glenn *et al.*, 2007).

In *Drosophila melanogaster*, there are different types of olfactory sensing neurons that can be combined to define the features (e.g. odorant components) of the source that provides the stimuli.

The antennal lobes (ALs) are the first neuropile encountered in the olfactory path. ALs consist of glomeruli linked to olfactory receptors that transfer information, through projection neurons (PNs), to the protocerebral areas (Stocker *et al.*, 1990). The connection with the MB cells is sparse, allowing an explosion in dimensionality needed to improve the representation space (Glenn *et al.*, 2007). At the same time PNs are connected to the Lateral Horn (LH) that inhibits, after a delay, the activity of the MBs neuron. This inhibitory effect has been experimentally found in locusts where the time constant is around 50 ms (Nowotny *et al.*, 2003); similar detailed information on *Drosophila* are still under studies. Therefore the Kenyon Cells (KCs) in the MBs receive a sequence of excitatory and inhibitory waves from the PNs and LH respectively. The distance between two consecutive waves defines the time window used for information processing through the maintained spiking activity in the KCs (Gupta and Stopfer, 2012). This evidence guided the choice to define an event driven mechanism to trigger the sequential stimuli provided to the system during the learning process.

Axo-axonal connections among the KCs have been identified (i.e. MB-EN1

in Fig. 1); hypotheses on the role of these connections in the formation of spatio-temporal patterns were formulated to modelling complex phenomena like the *delayed match-to-sample* present in bees. These are able to elaborate concept like sameness and difference between objects whereas this capability is still under investigation in *Drosophila* (Arena *et al.*, 2013).

Each neuron within the lattice in the ALs codifies an odorant component considered here as a feature of an abstract object. The learning mechanism is based on Spike-Timing-Dependent Plasticity (STDP) both inside the AL lattice and for the outer connections.

The basic neural elements needed to show complex sequence learning abilities identified in the fruit fly brain are here summarized:

1. the presence of a basic but efficient neural circuit (the MBs) responsible for multiple learning processes (e.g. olfactory learning; attention, adaptive termination and others);
2. the presence of different lobes, within the MBs, with feedforward and feedback loops able to encode time dependent signals;
3. the presence of axo-axonal connections in the KCs, which can be modelled as generating reaction diffusion phenomena, useful to create space-time relations between events;
4. the presence of dopaminergic/octopaminergic extrinsic neurons involved in reward based learning;
5. the presence of feedback loops: feedback in general implies memory which is the basis of any complex behavior.

Therefore *Drosophila melanogaster* can be considered as a model organism, that can offer a simple but efficient way to discover the neural basis of the complex ca-

pabilities encountered in bigger brains. In *Drosophila melanogaster*, much more is known about structure and function than in other insects like bees. These show sequence learning with a brain one order of magnitude larger than the fly one. Starting from this basic structure it can be possible to address interesting behaviors that could finally be discovered also in the fly.

The MBs neuropile contains a larger number of neurons and connections than the developed functional computational model. It is in many cases still beyond the actual neurobiological knowledge to identify which neuron in the MBs is responsible for what. We decided to extract the known information about topological connections among the different areas involved in the considered processes (e.g. the Antennal lobes, the Lateral Horn, etc.) to develop a basic model. The network contains a minimal number of neurons able to show the learning skills and behavioural responses as in the biological case of the insect model organism. Basically we are trying to identify the core of the structure that can be enlarged in terms of number of neurons and connections if we need to boost the network capabilities in terms of number of classes or sequence depth. This scaled-down model is also needed to reduce the computational time for the implementation on robotic platforms.

Time encoding is an important element in learning temporal events and has been investigated both in mammals and in insects. There are studies that try to perform a parallelism between the Hippocampus/Cerebellum and the Mushroom bodies from several sides, both anatomical and functional (Farris, 2011). It is also well known that cerebellum has a role in motor sequence learning (Buonomano and Mauk, 1994) together with other brain structures like the supplementary motor area in the cerebral cortex as experimentally found in primates (Tanji and

Shima, 1994). Furthermore, for example, the studies of Laurent and co-authors on the olfactory processing in Locusts (Wehr and Laurent, 1996) emphasise the role of time. One of the key elements underlined there, was that the encoding of complex natural stimuli such as odors may involve a temporal element, i.e. the precise timing of neuron activity. All these results were exploited in our model, where the olfactory system and neural circuits are used as a basic structure to produce a series of behaviours, and in addition, to map time into a space-distributed structure to face with sequence learning. The proposed model is therefore the results of known facts in insect neurodynamics and of some hypotheses on their role in the processing of time related events. *Drosophila melanogaster* brain has all the ingredients to solve the problem, even if, either for the lack of suitable experiments, or for the missing development of suitable readout maps in its brain, such capabilities have not yet been discovered or shown. In one or the other case, owing to structural and functional facts, we can state that MBs are a perfect candidate to be involved in this spatio-temporal learning process.

4. MB-inspired computational model

In this section the computational model of the MB-inspired architecture is described in details, starting from the neuron level and growing up presenting the different layers, communication paths and learning mechanisms involved in the whole structure.

4.1. Neural model

The spiking network used to model the neuropiles of the insect brain previously introduced is based on Izhikevich spiking neurons proposed in Izhikevich (2004). This neural model is well known in literature and offers many advantages

from the computational point of view. It is represented by the following differential equations:

$$\begin{aligned} \dot{v} &= 0.04v^2 + 5v + 140 - u + I \\ \dot{u} &= a(bv - u) \end{aligned} \quad (1)$$

with the spike-resetting

$$\text{if } v \geq 0.03, \text{ then } \begin{cases} v \leftarrow c \\ u \leftarrow u + d \end{cases} \quad (2)$$

where v is the membrane potential of the neuron, u is a recovery variable and I is the synaptic current. The values used for the parameters are different between the ALs and MBs. In the first case a Tonic Spiking model has been used whereas to model the KCs the parameters have been optimized to guarantee an efficient and robust clustering formation capability. Moreover for the End neuron used to detect the end of the sequence in absence of inputs in the AL, the inhibition induced spiking model has been considered. Neurons are connected through synapses. The synaptic model transforms the spiking dynamics of the pre-synaptic neuron into a current that excites the post-synaptic one. The mathematical response of the synapses to a pre-synaptic spike is ruled by the following equation:

$$\varepsilon(t) = \begin{cases} GWt/\tau_{syn} \exp(-t/\tau_{syn}), & \text{if } t > 0 \\ 0, & \text{if } t < 0 \end{cases} \quad (3)$$

where t is the time lasted from the emitted spike, τ is the time constant, G is a gain factor and W is the efficiency of the synapse. This last parameter can be modulated through experience. The Spike-Timing Dependent Plasticity (STDP)

can reproduce Hebbian learning in biological neural networks (Song *et al.*, 2000; Song and Abbott, 2001). The algorithm works on the synaptic weights, modifying them according to the temporal sequence of occurring spikes. The updating rule can be expressed by the following formula:

$$\Delta W = \begin{cases} A^+ \exp(\Delta t / \tau^+), & \text{if } \Delta t < 0 \\ -A^- \exp(-\Delta t / \tau^-), & \text{if } \Delta t > 0 \end{cases} \quad (4)$$

where Δt is the time delay between pre and post synaptic spikes. In this way the synapse is reinforced if the pre-synaptic spike happens before the post-synaptic one, it is weakened in the opposite situation. Parameters τ_+ and τ_- represent the slope of exponential functions, while positive constants A^+ and A^- represent the maximum variation of the synaptic weight. Interesting applications of this learning paradigm to biorobotics, together with details on the parameters, are reported in Arena *et al.* (2009a); Arena and Patané (2009b).

Another characteristic of any type of memory, including sequence learning, is the presence of a decay, i.e. a gradual forgetting of information (Rubin and Wenzel, 1996) that is an essential attribute when dealing with changing environments. A decay rate is used, in our model, reducing the synaptic weight about 10% each epoch. Further details and the parameters chosen in the reported experiments are given in Table 1.

4.2. Architecture description

Taking into account the biological key elements that characterize the MB structure, we developed a computational model designed as a multi-layer network based on spiking neurons. The proposed model, taking into account the morphology of the MBs, includes the presence of two distinct layers that take the role of

Table 1: Network parameters

Neuron Current		
Parameter	Value (pA)	Description
I_{in}	40	Input current for the Antennal Lobes
I_{rew}	100	RN input current
I_{sam}	100	SN input current
Time constant		
Parameter	Value (ms)	Description
dt	0.08	Time step
τ_{syn}	4	Synaptic time constant
$\tau_+ = \tau_-$	0.2	STDP time constant
$A^+ = A^-$	0.025	STDP maximum synaptic variation
Synaptic weights		
Parameter	Value	Description
W_{exc}	10	fixed excitatory weight in the α -/ β -lobes
W_{inh}	-10	fixed inhibitory weight in the α -/ β -lobes
W_{exc-AL}	0	fixed excitatory weight in the Antennal Lobes
W_{inh-AL}	-40	fixed inhibitory weight in the Antennal Lobes
W_{loop}	5	fixed excitatory weight of the feedback synapses between the α -/ β and the α' -/ β' -lobes
W_{in}	30	fixed excitatory weight between the Antennal Lobes and the α -/ β -lobes
$W_{AL-to-Inh}$	30	Synaptic weight of the synapses between the Antennal Lobe and the interneuron used to stimulate the end neuron (Inhibitory neuron model)
$W_{\alpha/\beta-to-Context}$	30	Synaptic weight of the synapses between the α -/ β -lobes and the Context Layer
W_{exc-C}	11	maximum value of the excitatory weight in the Context Layer (gaussian shape)
W_{inh-C}	-7	fixed inhibitory weight in the Context Layer
$G_{current}$	1	Gain in the calculation of the current for the synapses
$G_{\alpha-\beta}$	0.5	Gain in the calculation of the current for the synapses between the α -/ β -lobes and the α' -/ β' -lobes
$G_{\alpha-\beta-to-input}$	2	Gain in the calculation of the current for the STDP synapses between the α -/ β -lobes and the Antennal Lobes
$G_{Context}$	2	Gain in the calculation of the current for the synapses of the Context Layer
W_0	0.05	initial condition for the synapses subject to learning
W_+	8	upper saturation for the synapses subject to learning
W_-	0.05	lower saturation for the synapses subject to learning
$\Delta I_{Persistence}$	8	Increment/decrement of the α -/ β -lobes winning neuron bias current in presence of persistence
Lattice characteristics		
Parameter	Value	Description
$n \times n$	9x9	number of neurons in the α -/ β -lobes
m	4	number of different features used in the Antennal Lobes
p	4	number of different values for each feature used in the Antennal Lobes
$m_c \times p_c$	12x12	dimension of the Context Layer
f_{loop}	2000Hz	Threshold in spiking rate used for the sameness detection
f_{end}	150Hz	Threshold in spiking rate used for the end sequence detection
p_{conn}	25%	Probability used to create synapses between the Antennal Lobes and the α -/ β -lobes
p_{conn2}	25%	Probability used to create synapses between the α -/ β -lobes and the Context Layer
n_{clu}	5	number of neurons considered in a winning cluster
N_r	1	Neighbourhood radius
Time constants		
Parameter	Value (time steps)	Description
k_{sim}	2500	Number of steps in each epoch

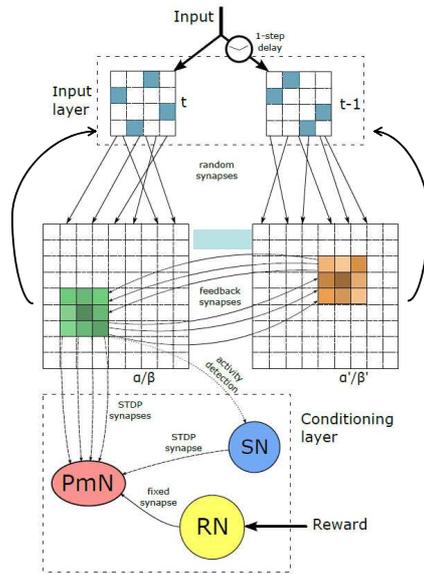


Figure 2: Computational model of the MB-inspired network, the synapses present inside each layer are not depicted. The input layer is randomly connected with the α -/ β and α' -/ β' -lobes that are themselves interconnected each other using synapses subject to learning. The conditioning layer is finally needed to exploit the information embedded in the lobes, through reward-based association mechanisms with the motor system.

the α -/ β and α' -/ β' -lobes. The topology of the two lattices is similar even if they fulfill different functions: the α -/ β layer receives in input the fresh information from the ALs whereas the α' -/ β' layer receives a delayed input that refers to the previously presented object. The model includes feedback connections between the α -/ β layer and ALs whereas for the α' -/ β' only feedforward connections are present as supported by the biological investigations.

A first scheme of the proposed architecture is reported in Fig. 2. The α -/ β -lobes model consists of a lattice of $n \times n$ neurons where $n = 9$ in the following simulations. The chosen dimension is a compromise between the larger number of neurons constituting the MBs and the computational time that was reduced

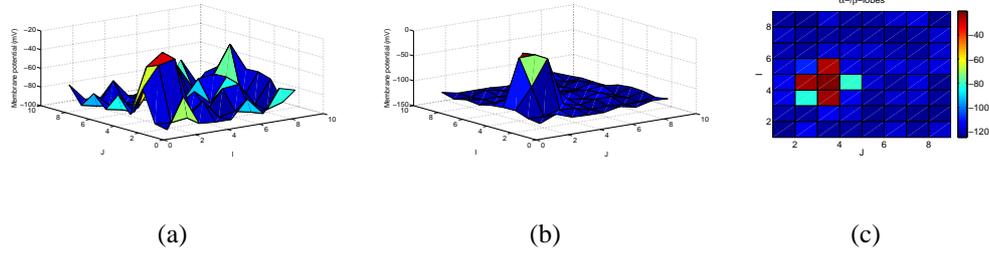


Figure 3: Cluster formation in the α -/ β -lobes. The mean value of the membrane potential in a window of 300 steps is reported at the beginning of the simulation (a) and at the end (b)-(c). The whole simulation needs 2500 simulation steps.

without losing those emergent capabilities we want to focus on.

The α' -/ β' -lobes model presents the same characteristics as the previous lattice. Each lattice presents a toroidal shape and synaptic connections link neurons within the lattice, following the paradigm of local excitation and global inhibition (Arena *et al.*, 2012). The neighbourhood size is set to 1, so each cell excites the 8 neighbouring cells. The connection shape and the weight distribution allow the network to create clusters of activities as shown in Fig. 3; the formation of a cluster of activity in the α -/ β -lobes neurons is shown in time. Extensive simulations showed that the chosen network size was enough to allow the formation of multiple distinct classes also thanks to the toroidal boundary conditions which facilitate the spatio-temporal evolution of the neuron activity avoiding singularities in the boundary of the lattice. The cluster of spiking activity, even if limited to a cross-like shape, is enough to discriminate a winner in the process.

The presence of a second lobe structure (i.e. α' -/ β' -lobes) allows the formation of a pattern related to a delayed input that can be compared with the current one to implement mechanisms like delayed match-to-sample and expecta-

tion: these require only a one step memory whereas for multiple-step correlation another memory structure has to be considered as detailed below.

The input layer representing a simplified AL, was implemented through two $m \times p$ lattices of neurons: $m = 4$ represents the number of input features whereas $p = 4$ is related to the possible value that each feature can assume. When an object is presented, the neurons in the input layer associated to the object features are excited with an external current. The connections between the input layer and the lobes are randomly generated with a fixed probability and weight (see Table 1). Within the input layer there are also internal synapses. The different neurons associated to the same feature inhibit each other, in details this allows noise due to the presence of multiple objects in the scene to be filtered out. At the same time the different feature classes can excite each other: when an object is presented, the connections among the neurons associated to the extracted features are strengthened to store the relation among these characteristics in a detected object.

The different phases that constitute the process at a given cycle of the simulation are here described:

Phase A An input is presented and is used to elicit a cluster in the α -/ β -lobes. This phase is completed after 1000 simulation steps.

Phase B The α -/ β -lobes are subject to both the input stimulus and to the influences coming from the other layers. A comparison between the actually emerged cluster and that one obtained during the previous phase is performed: in this step expectation is formed and/or reinforced (duration 1000 simulation steps).

Phase C Feedback between the α -/ β -lobes and α' -/ β' -lobes is activated. Depending on the lattice activity in terms of mean frequency, the presence of a matching with the previous object (delayed-match-to-sample task) is evaluated (duration 500 simulation steps).

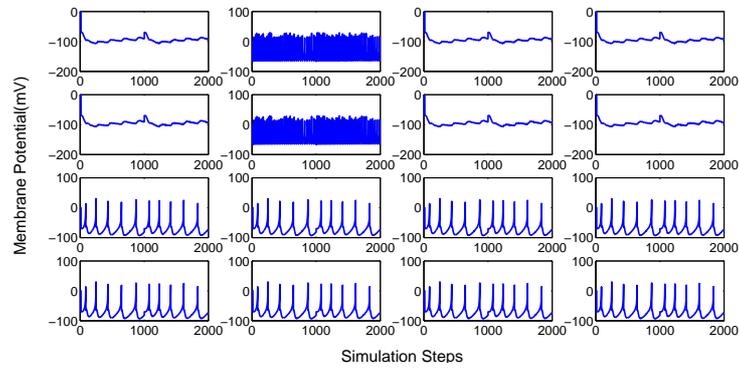
The three phases indicated were used to explain the sequence of neural processing that arise in the architecture after the presentation of an external input. The overall dynamics is generated from the interaction among input driven dynamics which generates bumps of neural activation in the lobes (Phase A), and feedback loops from higher brain areas (Phase B). In our model we hypothesised also the additional contribution of alpha'-beta' lobes for addressing the basis of the sameness concept (Phase C).

Referring to Fig. 2 the Conditioning layer includes neurons related to the reward mechanism (RN), to the sameness recognition (SN) and to the premotor area (PmN): the network includes both fixed synapses and learnable ones. In details, the reward neuron receives a fixed current (i.e. I_{rew}) when an unconditioned rewarding stimulus occurs; the sameness neuron (SN) similarly receives an input (I_{sam}) when the α -/ β -lobes activity is beyond a given frequency threshold (Arena *et al.*, 2013). Both RN and SN are linked to the Pre-motor neuron (PmN) through fixed excitatory synapses for RN and via STDP for SN respectively. Other STDP connections are present between the α -/ β -lobes and PmN to implement a conditioned learning mechanism. The response of the input layer, after the presentation of an object is shown in Fig. 4 (a). As can be noticed the recognized object contains features that excite the second neuron of the first and second row of the lattice, whereas the other two characteristics are not defined. The inhibitory mechanism is visible for instance in the first row, where the winner neuron suppress the

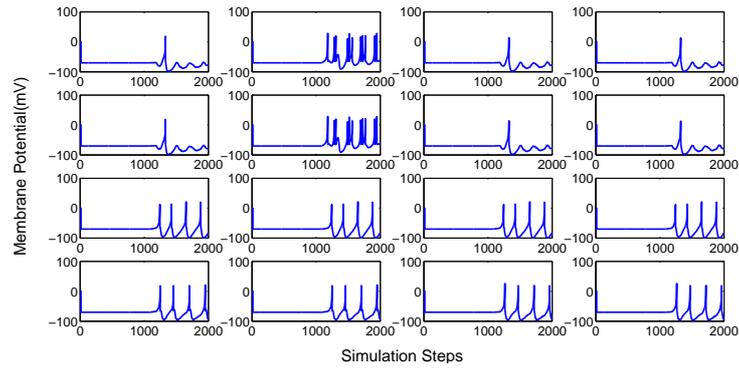
activity of the others. As illustrated in Fig. 2 another set of synapses were introduced between the α -/ β -lobes and the input layer. Their role is to associate that specific object featured in the input layer to a cluster formed in the α -/ β -lobes. This feedback is at the basis of the expectation mechanisms outlined in Phase B above. An example is shown in Fig. 4 where in (a) the input layer response is shown in presence of object A characterized by two features reported in the first two rows; in (b) during the second part of the simulation after step 1000, the object is no longer given to the input and the neurons associated to the features of object A are excited by the feedback synapses from α -/ β -lobes, learned to create an expectation, in this case for the same object.

Expectation is the capability to predict the next element depending on the last presented one. This one step memory could not be enough to discriminate complex sequences: a memory layer, here called Context layer should be included. Experimental results using data from the real-world problem domain demonstrate that the use of context has three important benefits: (a) it prevents destructive interference during learning of multiple overlapping sequences, (b) it enables the completion of sequences from missing or noisy patterns, and (c) it provides a mechanism to selectively explore the space of learned sequences during the recall phase (Berthouze, 2006).

A first attempt to create a Context layer was inspired by the path integration models using the principles of a virtual vectorial sum on the previously emerged clusters creating a spatio-temporal map of contexts. The Context layer was here modelled with a pool of independent neurons spatially distributed in a lattice as schematically shown in Fig. 5. The horizontal axis indicates the time evolution whereas the vertical axis represents the internal states sequence, forming the con-



(a)



(b)

Figure 4: Membrane potential evolution in the input layer. (a) The object A, characterized by two features ($f_{1,2}$ and $f_{2,2}$) is presented to the network, (b) when the input is no longer provided, the feedback synapses coming from the lobes create an expectation effect depolarizing the input neurons depending on the features of the expected object.

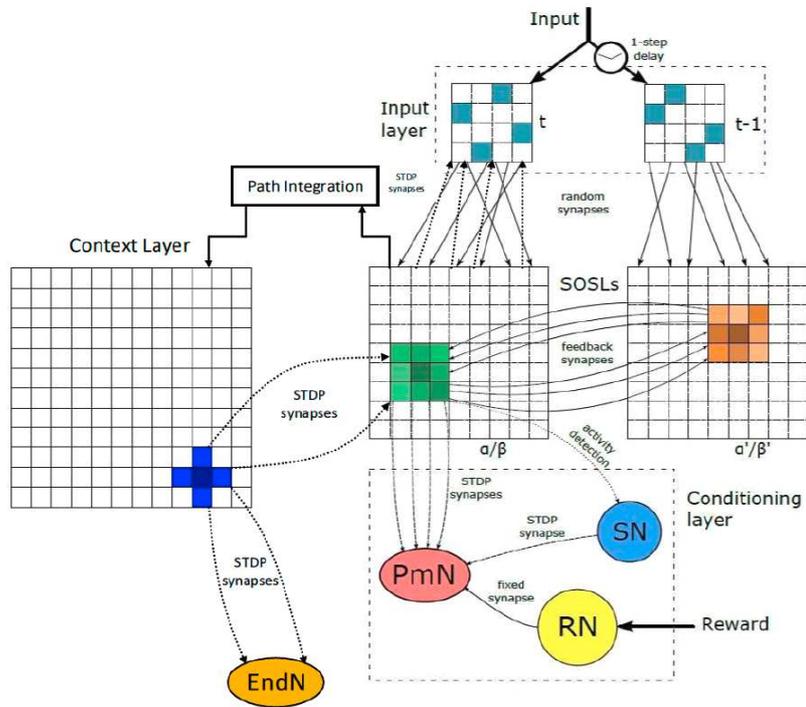


Figure 5: Block scheme of the MB-inspired computational model with the inclusion of the Context layer where the history of the sequence is stored through a mechanism similar to the path integration. STDP synapses link the context with the next cluster in the α/β -lobes and the End neuron is used to identify the conclusion of a sequence.

text at each time step. The links between the Context layer and the α/β -lobes are obtained through STDP synapses: each neuron of the Context layer is connected to each neuron in the α/β -lobes. These synapses are activated using a conditional gating mechanism, only during the second phase (i.e. Phase B) of the simulation.

Fig. 6 shows the trend of the synaptic weights connecting the context layer with one generic neuron of the α/β -lobes. A cross-like pattern of neurons active beyond a given spike rate threshold is formed in the Context layer to maintain the history of the previous events: the synapses connecting the neuron pattern

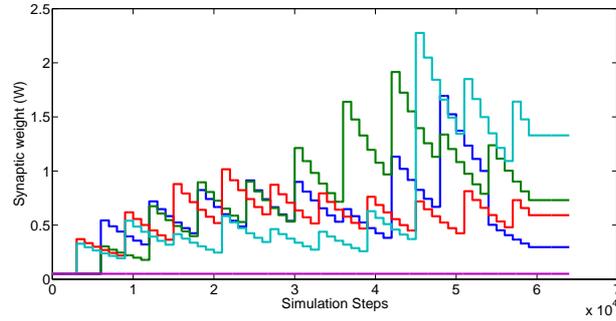


Figure 6: Trend of the synaptic weights between the Context layer and one neuron in the α -/ β -lobes that is part of a winning cluster associated to an object included in two different positions in the sequence that has been presented ten times to be learned. The largest weight is associated to the central neuron of the winning cluster whereas the others are related to the four neurons with neighbourhood one.

formed in the Context layer to the winning cluster in the α -/ β -lobes emerging in the following input presentation are strengthened through STDP. The cluster shape depends on the lattice size and neighbourhood radius. Experiments with different size and radius (e.g. lattice 20x20 with neighbourhood radius $Nr=2$) were performed obtaining comparable functional results. For these reasons, to reduce the processing time for robot experiments, we preferred to consider a minimal number of neurons (i.e. 9x9 lattice).

The cross-like cluster in the Context layer will be reduced to a single active neuron in the successive implementation of the model as will be presented below.

Another important element introduced in the architecture is the *End Neuron* (EndN in Fig. 5) used to introduce the information about the length of the sequence during the learning phase. In the testing phase the context is reset when the End neuron is activated by the Context layer.

Two possible strategies were used to activate the End Neuron. The first was to

associate it to a reward event that can elicit the EndN and, through STDP learning, relate the last activated element of the Context with the end of the sequence. The second strategy includes an indirect connection between the Input layer and the EndN through an inhibition induced spiking neuron: in this way it is possible to stimulate the EndN when no further inputs are provided to the system, in a defined time window, during the sequence learning process. In any case, whenever a cluster in the lobes arises, either for the effect of an input signal or for the feedback contribution descending from the Context Layer, the EndN is inhibited (see Fig. 8). For instance, if the sequence ABC is stored in the system, the C element will stimulate the EndN. If a new Sequence ABCDE is also stored, the presentation of the third element C of the sequence will stimulate the EndN but concurrently will still stimulate also the arousal of a cluster in the α -/ β -lobes as a predictor of the fourth element D. In our model, the presence of this activity cluster strongly inhibits the EndN, allowing the reconstruction of the longer sequence ABCDE. This inhibition could be more graceful, allowing a competition. In this case the activation of the EndN will depend on the number of presentations of the two sequences.

More in details, the development of the Context follows mechanisms typical of the reaction-diffusion processes. In particular the α -/ β -lobes are randomly connected to the Context layer. This is composed by groups of neurons topologically organized in lines. This topology resembles not only the linewise arrangements on the MB fibers, but also recalls the granulate cells in the cerebellum that are responsible for encoding, not only a pattern of activations (that identifies the unique input pattern), but also the time elapsed from the onset of the input pattern, creating a context that is then used by the Purkinje cell to generate the corresponding

output response (Buonomano and Mauk, 1994).

Functionally, the context formation process is schematically depicted in Fig. 7. It starts when the first presented input generates a winning cluster in the α -/ β -lobes, say at time t_0 : the lobes randomly excite the Context layer. At this time only the first column of context neurons (Col_{t_0}) is receptive and through a winner-takes-all strategy one neuron emerges over the others as representative for the current state. After a resetting due to the Lateral Horn, a new presented element (at time t_1) generates a second cluster in the lobes that randomly excites the Context layer (Col_{t_1}). Here in the mean time, the previous winner in Col_{t_0} already started to diffuse with a gaussian shape towards Col_{t_1} in the context layer. The interaction between these two mechanisms allows the choice of a second winner neuron in Col_{t_1} of the Context, that is related to the history of the previously presented elements. All the neurons in the context are massively connected with the α -/ β -lobes with synapses subject to the STDP learning. Therefore the synapses connecting the active neuron in Col_{t_0} that generates the diffusion process, and the current winner in the α -/ β -lobes are strengthened. After multiple presentations of the same sequence, the synapses between the Context layer and the α -/ β -lobes are strong enough to allow the reconstruction of a learned sequence in the recall/testing phase.

Terms like Learning and Testing are here used to distinguish two different times of the system processing. Of course it is not the case in real life scenarios, but in biological experiments performed in lab often the protocol used follows this artificial distinction. However we considered a continuous learning process where the synaptic connections are strengthened or weakened according to the neuron activity. The process of learning is therefore incremental and we do not need to

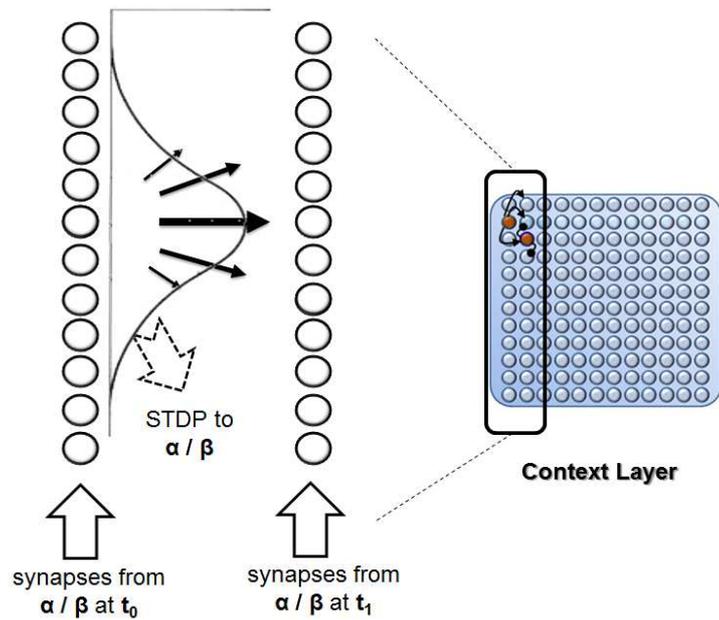


Figure 7: Scheme of the activation mechanisms triggered in the Context layer. The first winning cluster in the α -/ β -lobes excites the first column in the context where a winner-takes-all topology allows the choice of a representative neuron that start to diffuse exciting the second group of neurons. When the second presented element is classified in the α -/ β -lobes, the new stimulus provided to the context is shaped by the diffusion to determine a second neuron in the context that takes care of the previously elements of the presented sequence.

make a sharp distinction between learning and test. Consolidation arises from the multiple presentations of specific sequences that will be statistically discriminated from other considered irrelevant.

5. Network applications

To summarize the capabilities of the developed architecture, all the different behaviours that can arise from this unique structure as shown in Fig. 8 are outlined in Table 2.

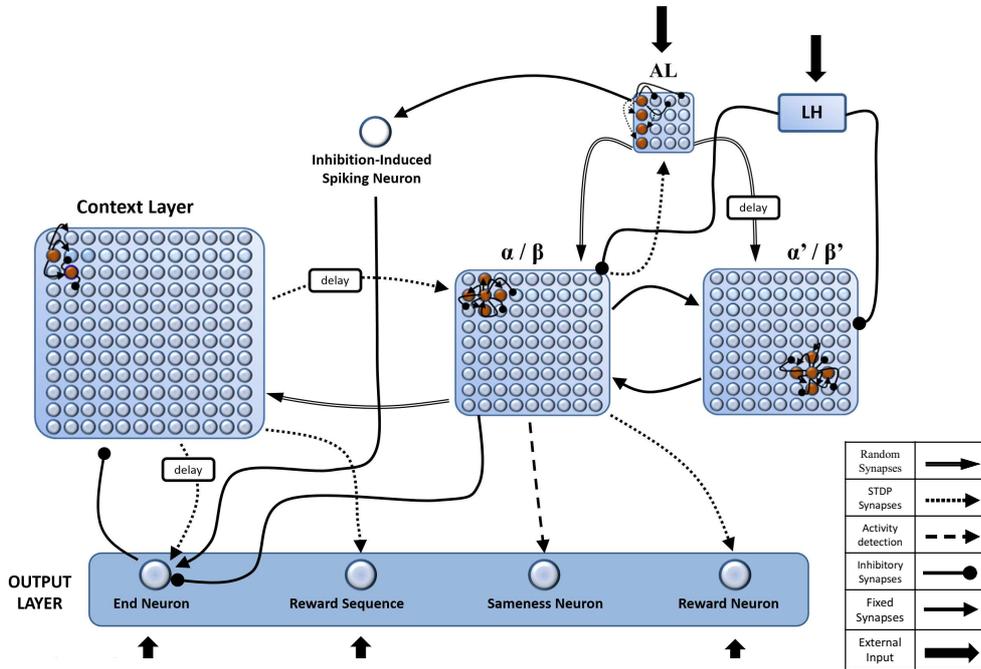


Figure 8: Scheme of the complete architecture where the interaction among the different neural structures is depicted.

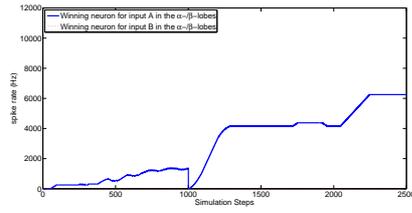
In details, starting from the basic capabilities of the system, the persistence /distraction mechanisms can be identified. The wild-type insect shows the capability to focus on a target avoiding flickering behavior that can be caused by the presence of distracters. As shown in several experiments with the *Drosophila melanogaster*, MB-defective mutant flies lose this capability, continuously switching the target of interest with a considerable waste of energy. Looking at the proposed model, this attentional capability is assured by the presence of feedback connections which produce a memory effect at the level of the KCs in the α -/ β -lobes. If such links are suppressed, we can replicate the results obtained with the mutant animal.

Behaviours	Neural Structures involved	Plasticity
Persistence	Antennal Lobe (AL) α -/ β -lobes	(1) STDP from α -/ β -lobes to AL (2) Memory effect in the α -/ β -lobes
Distraction	Antennal Lobe (AL) α -/ β -lobes	(1) STDP from α -/ β -lobes to AL (2) No memory effect in the α -/ β -lobes
Delayed match-to-sample	Antennal Lobe (AL) α -/ β -lobes α' -/ β' -lobes Sameness Neuron	(1) STDP from α -/ β -lobes to AL (2) Feedback synapses from α -/ β -lobes to α' -/ β' -lobes lobes and viceversa (3) Activity Detection by the Sameness Neuron
Expectation	Antennal Lobe (AL) α -/ β -lobes Context layer	(1) STDP between one feature to other features within the AL (2) STDP From α -/ β -lobes to AL (3) STDP from Context Layer to α -/ β -lobes
Sequence Learning	Antennal Lobe (AL) α -/ β -lobes Context Layer Output Layer	(1) STDP From α -/ β -lobes to AL (2) STDP from Context Layer to α -/ β -lobes (3) STDP from Context Layer to Output Layer (4) STDP from α -/ β -lobes to Output Layer

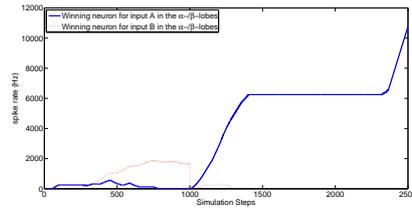
Table 2: Different behaviors that can be shown by the proposed architecture. For each behavior the relevant neural structures involved are reported together with the elements subject to learning.

The persistence behaviour, typical of wild-type fly, can be reproduced in the architecture as reported in Fig. 9 where the trend of the spiking rate in the winning neurons of the α -/ β -lobes is analyzed. After multiple presentations of object A, a distracter B is presented but the system persists on the previous object thanks to the contribution of the α -/ β -lobes layer which produces a kind of integral effect. A fading memory takes place and only after a significant number of presentations of the same object B (this number can be tuned in the model) the corresponding cluster will win and the system will loose persistence on object A. This behaviour coexists in the same neural structure with the other network capabilities.

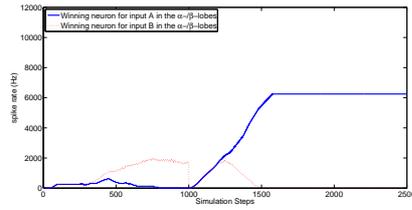
In experiments involving MB-defective mutant flies, the persistence behaviour disappears and a continuous switching toward the currently presented object is observed. This defect can be reproduced cancelling the feedback contribution from the α -/ β -lobes to the AL layer, obtaining the behaviour shown in Fig. 10. It



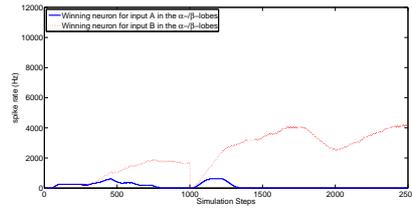
(a)



(b)



(c)



(d)

Figure 9: Trends of the spiking rate in α/β -lobes during the different epochs when a sequence of 20 object is presented. (a) Spiking rate of the winning neuron in the α/β -lobes after 11 presentations of object A; (b) at step 12 a new input B is presented, as easily visible in Phase A (first 1000 simulation steps). After the MB contribution which acts as an integration effect in Phase B, the network persists in following the object A. (c) At step 16 the strength in following A decreases and finally (d) at step 18 the system follows the new input B.

depicts the spiking rate for the winning neuron during the switching between two different presented objects.

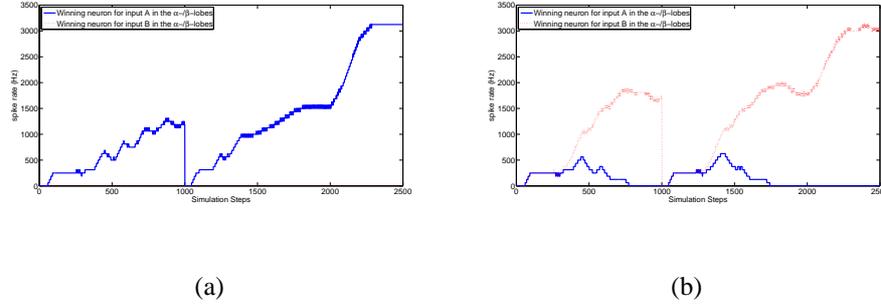


Figure 10: Distraction simulations: trends of the spiking rate in α -/ β -lobes during the different epochs when a sequence of 20 objects is presented. (a) Spiking rate of the winning neuron in the α -/ β -lobes after 11 presentations of object A, (b) at 12 steps a new input B is presented and the system is immediately distracted and follows the new object.

Another interesting capability consists in solving the delayed match-to-sample task. As illustrated in details in *Arena et al. (2013)*, the introduction of the α' -/ β' -lobes in the architecture allows to identify the presence of two successive presentations of the same element through the detection of an increase the α -/ β -lobes frequency activity as shown in Fig. 11. The acquired information can be also used to elicit, after conditioning, a behavior that can be triggered by a matching detection.

The potentialities of the developed MB-inspired architecture are here increased with the introduction of the Context layer that could be related to the γ -lobe. This layer, as previously discussed, is used to store information about the chain of events previously acquired by the system. Exploiting this capability, the structure is able to extract information about the neurally encoded causality between

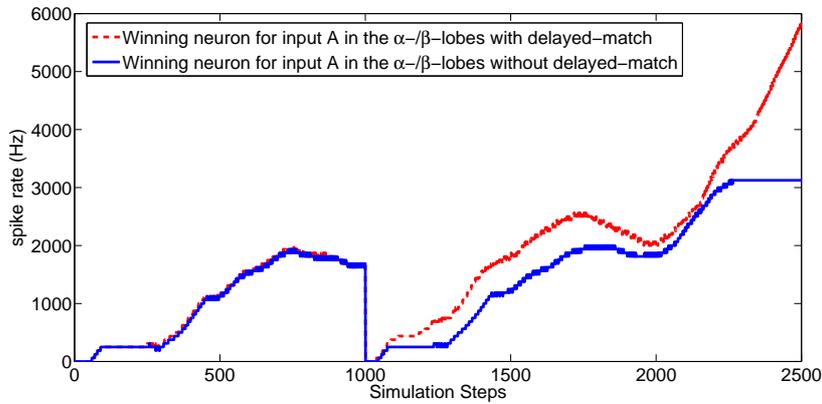


Figure 11: Effect of a delayed-match to sample in the spiking rate of the winning neuron. The comparison between the behavior of the winning neuron in absence and in presence of a match is reported.

consecutively presented objects, to create expectations on the successive presentation (Arena *et al.*, 2012). The presence of a Context layer allows to perform not only one-step predictions but also to reproduce sequences of objects, solving also potential ambiguities, exploiting information on the context of each object. The Context layer is arranged in a toroidal shape thus improving the length of sequences that can be memorized. At the same time that allows to loop in the lattice. This solution can create ambiguities justified by the actual size of the context memory and can be improved increasing the dimension of the lattice.

Finally either rewarding or punishing signals can be associated to the ending element of a sequence and this information can be used to choose the most rewarding sequence to be followed when different choices are provided to the system.

To illustrate the activity of the architecture during the presentation of a complex sequence, the result of a simulation is shown in Fig. 12. Here the sequence *ABCBC* is provided as input and triggers the activity of the different process-

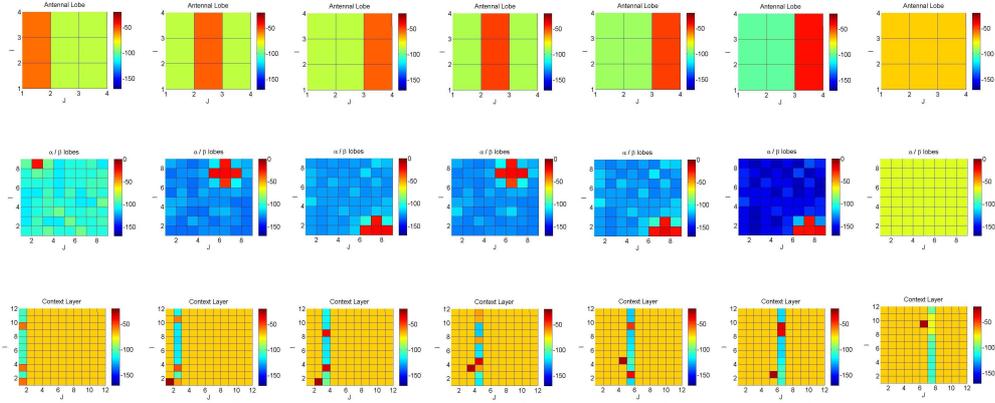


Figure 12: Behavior of the network when a sequence of objects is provided in input to the AL (input) layer (i.e. ABCBCC). The activity of the AL layer is reported in the first row, the emerged cluster in the α -/ β -lobes and the activity in the Context layer are depicted in the second and last row, respectively. The colours indicate the average membrane potential in mV evaluated in the last 200 steps of the simulation. In the last row both the actual activation coming from the α -/ β -lobes and the context neuron performing the diffusion process are shown. The features associated to each object are: $A(f_{11}, f_{21}, f_{31})$; $B(f_{21}, f_{22}, f_{32})$; $C(f_{13}, f_{23}, f_{33})$. An absence of any input stimuli represents the end of the sequence: this is recognized by the End neuron.

ing layers in the MB-inspired model. It can be noticed that the sequence presents multiple ambiguous elements that could not be correctly predicted using a simple one-step-ahead expectation mechanism. The role of the Context layer is crucial to correctly recognize, learn and reproduce this complex sequence.

Moreover to generalize the results also with larger lattices the same simulation was performed changing the α -/ β -lobes to a 20×20 lattice of neurons with a neighbourhood radius $N_r = 2$, as shown in Fig. 13. The emerged clusters are very robust to noise, involve more neurons and generate a different chain of activation in the Context layer that however is uniquely associated to the presented sequence

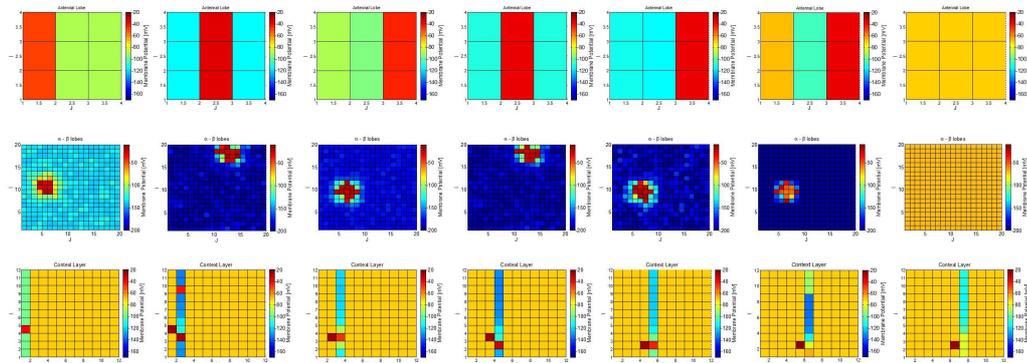


Figure 13: Behavior of the network obtained with the same set-up of Fig. 12 when the α/β -lobes size is 20x20 instead of 9x9 and the neighbourhood size is 2 instead of 1. The input are the same therefore the AL layer activity is identical to the previous case; the cluster generated in the α/β -lobes are larger and smoother with respect to the smaller size lattice and the sequence is stored in the Context layer in a different neuron chain.

of elements. The presence of a repetition in the sequence (the last part contains two consecutive C symbols) modifies the activity of the α/β -lobes increasing the average spiking rate due to the positive feedback with the α'/β' -lobes.

5.1. Robotic experiments

To evaluate the performance of the designed architecture, a series of experiments were carried out with a roving platform.

Even if the most suited robotic architecture should have been a legged machine, for which sophisticated controllers were already developed (Arena *et al.*, 2003, 2005), the simpler mechanical structure of a wheeled platform was here preferred to focus attention on the architecture developed.

The selected robot is equipped with a on-board PC that communicates with a series of micro-controller-based boards used for the motor control. Moreover two ultrasound sensors are used to detect obstacles and an omnidirectional camera is

included to identify the presence of specific shapes in the environment used as objects of interest.

We considered the following time windows for each part of the processing and execution stages: (a) Sensory information gathering (e.g. the time needed to acquire the panoramic image and extract the relevant objects in the scene). This time is software/hardware dependent; (b) the network performs the 2500 steps of elaboration (200ms of simulation that correspond to a few seconds in the actual robot setup, depending on the data logging) using the gathered sensory input even if no objects are present in the scene; (c) depending on the obtained results an action/behaviour is performed. (d) The robot is able to perform again the step (a) repeating the procedure. Following this structure the new objects have to be present at step (d). Basically the assumption is that the actions performed by the robot are relevant for the next object presentation as occurs in typical experimental set-up (e.g. multiple T-maze experiment) so when the behaviour is completed we can look for other information in the scene.

The first proposed experiment is directly related to the persistence behavior as shown in Fig. 14. The robot is attracted by the objects shown on the monitors placed in an arena and is able either to filter out the distracter, like in the wild-type insect, or to switch among the presented objects, like in the MB-defective case as reported in Fig. 15.

Experiments with sequences where some objects are missing or with multiple objects presented simultaneously were performed to evaluate the capability of the system to reproduce an already learned sequence. If an object is missing, the input layer is not stimulated by exogenous inputs, but thanks to the feedback connections coming from the Context layer, a cluster can be elicited to cover the gap in

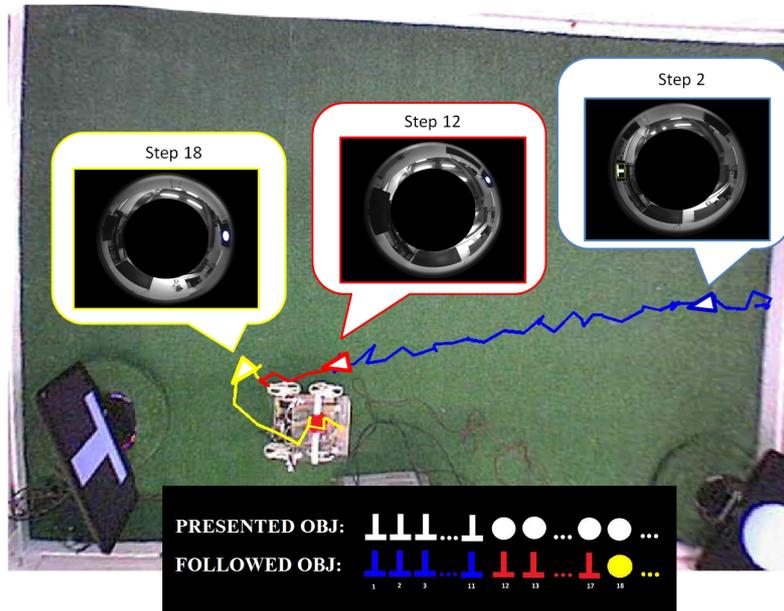


Figure 14: Persistence experiment with a roving robot. Trajectory followed by the robot during the experiment. The images acquired from the on-board fish-eye camera are shown in three different steps. The robot is able to persist moving in the direction of the inverted T also when a distracter is presented (i.e. the circle). After multiple presentations, the memory associated to the inverted T fades down and the robot follows the circle.

the sequence. Similarly when multiple objects are simultaneously present, both the filtering mechanisms at the input level and the effect of the context (that concurrently guides the cluster formation) allow the emergence of the correct element stored in the learned sequences. An experiment related to sequence learning was performed with the roving robot in the arena reported in Fig. 16. The learned sequence was presented about ten times to allow a stable storing in memory encoded in the synaptic weights of the network. During the recall phase the robot received visual stimuli from the two monitors placed in the opposite sides of the arena and,

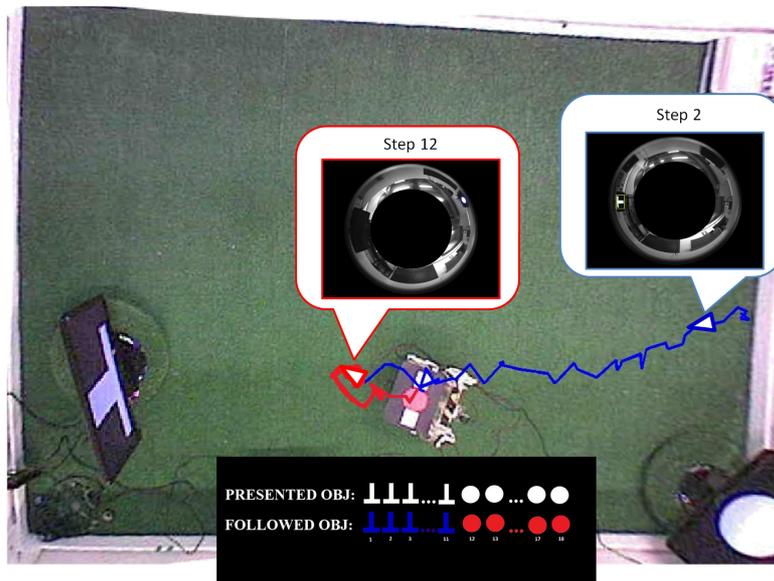


Figure 15: Distraction experiment with a rover. The presentation of a new object at step 12 is enough to change the robot behavior independently of the time/energy already invested in following the previous target.

depending on the learned sequence, it tried to orient towards the correct element expected and to approach it. Fig. 16 contains the evolution of the gaze direction of the robot, even in presence of noisy conditions (i.e. multiple stimuli are simultaneously presented to the robot), the system was able to filter out the disturbances and to follow the stored sequence generating, each epoch, the expected behaviour.

Multiple sequences can be stored thanks to the effort provided by the Context layer to disambiguate the potential overlapping. An example is shown in Fig. 17 where the chain of neurons activated in the Context layer for different sequences is reported with different colored circles: (a) *ABCD*, (b) *DBCA* (c) *BBD* (d) *CCA*. It can be noticed that a simple expectation mechanism that takes into account

only the previous element cannot be used to perform a correct prediction because elements like *B* can be followed by a *B*, a *C* or a *D*.

The learning process generates, after multiple presentations of the four sequences, the strengthening of a series of synaptic connections from the Context layer to the α -/ β -lobes as shown in Fig. 17. So, if the neuron corresponding to input *A* is active in the Context layer, its synapses stimulate the arousal of object *B* in the α -/ β lattice and so on. These synapses contain all the information needed to autonomously generate the learned sequences when one of the first elements is provided in input.

Taking one of the learned sequences as example (i.e. *ABCD* in Fig. 18 (a) and *DBCA* in Fig. 18 (b)) it is possible to distinguish the path followed by the signals coming from the α -/ β -lobes to the Context layer. Here, diffusion, matched with the incoming new clustered input, leads to the emergence of a winning neuron in the Context layer, which, in turn, projects back to the lobes. This allows to learn the association between the actual context and the successive element in the sequence.

Looking to this experimental results, an important aspect, relevant to suggest new experiments in biology is the co-existence of different behaviours within the same neural structure. For instance persistence/distraction behaviour is deeply studied in insects as a stand-alone characteristic but rarely in relation with other behaviours like sequence learning. From our simulation we can identify that the two behaviours can co-exists and compete together to determine the system overall behaviour. When the same object is presented multiple times, any new one is filtered (i.e. considered as a distractor), to persist in the on-going behaviour. However the new objects could be part of a long sequence of presentation (e.g.

AAAAAB). Depending on the network parameters the final behaviour can be tuned accordingly, posing more emphasis on one or the other behavioural strategy. Focused biological experiments can be designed to better understand memory/forgetting processes.

5.2. Sensitivity analysis

The network parameters as reported in Table 1 in the paper, were tuned to guarantee the co-existence of the different described behaviours in a whole structure. The reported values are the results of previous works where a huge amount of simulations were performed to numerically identify the best configuration within a well constrained searching space (Arena *et al.*, 2012). Finally an hand-tune process was actuated to optimize the system for solving conflictual situations. A sensitivity analysis was performed to underline a series of aspects concerning the robustness of the network to noise and the role of specific parameters in obtaining the desired expected behaviour provided by the architecture.

Concerning the effect of the noise in the system, the robustness of the network was evaluated introducing a white noise in the input current of each neuron both in the case of external input and for the current generated by the synaptic connections with other neurons. All the simulations were performed adding a noise that dynamically changes in each integration step, in a range of $\pm 5\%$. The result is that all the behaviours are robust to this disturbance; the effect of the noise on a neuron in the α/β -lobes is shown in Fig. 19. If the level of noise is further increased to about $\pm 20\%$ the clustering capabilities at the level of the α/β -lobes are reduced and sometimes completely destroyed, also because we are limiting the simulation windows and, to filter-out the noise, the network needs more processing time. Furthermore, the noise effect is also related to the number of presentations needed

for each sequence to be stored in the structure. In fact, the strength of the memory trace should be strong enough to compete with noise corrupted neuron activities due to the high level of noise.

The behavioural response of the system is also robust to the variation of important parameters involved in the neural processing. The network contains multiple synapses with fixed weights, whose values are reported in Table 1. To analyse the robustness of the network behaviours to the selected values a noise of $\pm 5\%$ was included during the creation of the synapses. The obtained results show that in most cases the network is solid this disturbance and, even if the activity in the Context layer could change with respect to the default value, the context activation is robustly associated to a specific sequence, obtaining the same behavioural results. Also in this case a larger level of noise (about $\pm 10\%$) can destroy the network behaviour. In particular, the activity in the α/β -lobes is disturbed and sometimes the Context layer is not able to guide the arousal of the correct winning cluster as expected by the learned sequence.

Going deeper into analysing the sensitivity of the network to the selected parameters an important aspect is related to the co-existence of different behaviours in the same architecture that needs a balancing between the parameters involved. An interesting example can be found considering the persistence behaviour: when the same input is the co-existence of these mechanisms and to further refine and tune the model that now hypothesizes the presence of dynamical mechanisms with different time scales for the repetitively presented to the network an integral effect is generated at the level of the winning cluster neuron. The effect is obtained adding a hyper-polarization current that either increases if the presented object is equal to the previous one or decreases for the same quantity otherwise with

$\Delta I_{Persistence}$	MaxCP
0	No persistence behaviour
0.5	7
1	5
10	4
20	3
30	Dominance of persistence

Table 3: Relation between the $\Delta I_{Persistence}$ used to take care of the persistence effect due to the presentation of the same element multiple times and the maximum number of equal presentations that can be learned in a sequence before the effect of the persistence will be predominant (i.e. MaxCP).

an lower limit of 0. This increment/decrement ($\Delta I_{Persistence}$) was set to 8 in the proposed experiments but this value can be changed to either reduce or increase the strength of the persistence behaviour versus the expectation/sequence learning mechanism. The selected value allows a predominance of the expectation over the persistence if the number of consecutive presentations of the same symbol is less than 6, otherwise the system will prefer to persist in the previous object instead of following the indication coming from the Context layer that will lose the competition to generate the expected winning cluster. The numerical analysis of this competition between behaviours is reported in Table 3 where changing the $\Delta I_{Persistence}$ from 0 to 30 it is possible to obtain either a complete absence of persistence behaviour or a complete dominance of the persistence behaviour on the sequence generation.

The last element taken into consideration for the analysis is the balancing between the synaptic weights from α -/ β -lobes to the Context layer and the excitatory/inhibitory connections in the Context layer. The Context layer is the key element for the storing and further generation of sequences. The α -/ β -lobes are connected to each column of the Context layer with a probability of 25% and a

weight $W_{\alpha/\beta\text{-to-Context}} = 30$. The diffusion process in the Context layer that transfers the information in time from one column to the next one, is controlled by a series of synaptic connections with a Gaussian distribution for the weight (the gain is 11 and the standard deviation is 2). The ratio between these two classes of weights is a critical parameter to be defined. In Table 4 and 5 a series of configurations has been tested and the behaviour of the network has been evaluated. It can be noticed that the network dynamics is very robust to a parameter variation if the ratio between the synaptic weights is maintained within a certain range. Critical situations can be identified when the strength of the diffusion effect (W_{Exc-C}) is too strong with respect to the new stimuli coming from the α/β -lobes; in this case the new winning cluster in the lobes is irrelevant because the Context activation always degenerates into the same row of winning neurons (see Table 4).

Another problem was identified when the spiking activity of the Context neurons is reduced due to the small value for the $W_{\alpha/\beta\text{-to-Context}}$ so the synapses $W_{Context\text{-to-}\alpha/\beta}$, updated through STDP, grow slowly. In this case, to obtain a robust storage for a sequence, the number of presentations needed should be increased. Moreover the correct balance between excitatory and inhibitory mechanisms is crucial for the system. In fact, as reported in Table 5, when the inhibitory effect is not well balanced, the network activity is completely destroyed and it is not possible to find a winning neuron in the Context layer.

6. Conclusions

The ability to understand the environment is a dynamic process. The context in which events occur can be even more important than the events themselves. On the basis of the biological evidences concerning insect capability to learn se-

$W_{\alpha/\beta-to-Context}$	W_{Exc-C}	Ratio	Behaviours
30	11	2.72	✓
15	5.5	2.72	✓
60	22	2.72	✓
60	11	5.44	✓
30	5.5	5.44	✓
15	11	1.36	✓
30	5.5	1.36	✓
90	11	8.16	✓
30	3.66	8.16	✓
10	11	0.90	<i>ContDeg</i>
30	33	0.90	<i>ContDeg</i>
30	30	1	<i>ContDeg</i>
11	11	1	<i>ContDeg</i>

Table 4: Robustness of the network behaviours when the synaptic weights involving the Context layer ($W_{\alpha/\beta-to-Context}$ and W_{Exc-C}) are modified. All the network functionalities are maintained in most of the cases, the first row represents the default configuration, except when the strength of the diffusion effect (W_{Exc-C}) is too high and the new winning cluster is irrelevant: the Context activation always degenerate into a row of winning neurons (ContDeg).

quences and the identification of candidate neural structures responsible for these processes, in this work a new model for sequence representation and learning, inspired by the Mushroom Bodies structure, is proposed. The idea was to include in the same architecture a series of functionalities that, from biological experiments, can be associated to MBs. Starting from basic capabilities like attention, expectation and others, the model was extended to include sequence learning that is a fundamental process shown also by insects. In this paper it is shown that the basic neural circuits and learning functions needed for sequence learning are indeed contained in the *Drosophila melanogaster* brain. The results suggest to try to find new experiments where these capabilities should better emerge. Therefore, during the modelling phase, several hypotheses were identified to take care of the still unknown biological information and the obtained results can be of interest in order to further assess future experiments on the insect behaviours. Simulation

$W_{\alpha/\beta\text{-to-Context}}$	W_{inh-C}	Ratio	Behaviours
30	-7	4.28	✓
60	-14	4.28	✓
15	-3.5	4.28	✓
60	-7	8.56	✓
30	-3.5	8.56	✓
15	-7	2.14	✓
30	-14	2.14	✓
90	-7	12.84	✓
30	-2.33	12.84	✓
10	-7	1.42	P_1
30	-21	1.42	✓
7.5	-7	1.07	✓
30	-28	1.07	P_2

Table 5: Robustness of the network behaviours when the synaptic weights involving the Context layer ($W_{\alpha/\beta\text{-to-Context}}$ and W_{inh-C}) are modified. All the network functionalities are maintained in many configurations for the weights, the first row represents the default case. The problem identified are: P_1 - the spiking activity of the Context neurons is reduced due to the small value for the $W_{\alpha/\beta\text{-to-Context}}$ so the learnable synapses ($W_{Context\text{-to-}\alpha/\beta}$), updated through STDP, grow slowly and, to obtain a robust storage for a sequence, the number of presentations needed should be increased; P_2 - when the inhibitory effect is too strong, the network activity is destroyed and it is not possible to find a winning neuron in the Context layer.

and experimental results demonstrate the effectiveness of the proposed architecture that represents a key element for the development of a complete insect brain computational model.

Acknowledgement

This work was supported by EU Project EMICAB, grant no. 270182 and the MIUR project CLARA (CLoud plAtform and smart underground imaging for natural Risk Assessment).

References

- Anderson, M. L. (2010). Neural reuse: a fundamental organizational principle of the brain. *Behav. Brain Sci.*, **33(4)**, 245–266.
- Arena, P. and Patané, L. (2009a). *Spatial Temporal Patterns for Action-Oriented Perception in Roving Robots*. Springer, Series: Cognitive Systems Monographs, Vol. 1.
- Arena, P. and Patané, L. (2009b). Simple sensors provide inputs for cognitive robots. *IEEE Instrumentation and Measurement Magazine*, **12(3)**, 13–20.
- Arena, P. and Patané, L. (2014). *Spatial Temporal Patterns for Action-Oriented Perception in Roving Robots II: an insect brain computational model*. Springer, Series: Cognitive Systems Monographs, Vol. 21.
- Arena, P., Fortuna, L., Frasca, M., Patané, L., Vagliasindi, G. (2005). CPG-MTA implementation for locomotion control. In *IEEE International Symposium on Circuits and Systems*, pages 4102–4105.

- Arena, P., Fortuna, L., Frasca, M., and Patané, L. (2003). Sensory feedback in CNN-based central pattern generators. *International journal of neural systems*, **13(6)**, 469–478.
- Arena, P., Fortuna, L., Lombardo, D., and Patané, L. (2008). Perception for action: Dynamic spatiotemporal patterns applied on a roving robot. *Adaptive Behavior*, **16(2-3)**, 104–121.
- Arena, P., De Fiore, S., Patané, L., Pollino, M., and Ventura, C. (2009a). STDP-based behavior learning on TriBot robot. In *Proceedings of SPIE - The International Society for Optical Engineering*, art. no. 736506.
- Arena, P., Fortuna, L., Lombardo, D., Patané, L., and Velarde, M.G. (2009b). The winnerless competition paradigm in cellular nonlinear networks: Models and applications. *International Journal of Circuit Theory and Applications*, **37(4)**, 505–528.
- Arena, P., Patané, L., and Termini, P. (2011). Decision making processes in the fruit fly: a computational model. In *Frontiers in Artificial Intelligence and Applications - Proceedings of the 21st Italian Workshop on Neural Nets*, volume 234, pages 284–291, Seville, Spain.
- Arena, P., Patané, L., and Termini, P. (2012). Learning expectation in insects: a recurrent spiking neural model for spatio-temporal representation. *Neural Networks*, **32**, 35–45.
- Arena, P., Stornanti, V., Termini, P., Zaepf, B., and Strauss, R. (2013). Modeling the insect mushroom bodies: Application to a delayed match-to-sample task. *Neural Networks*, **41**(), 202–211.

- Berthouze, L.; Tijsseling, A. (2006). A neural model for context dependent sequence learning. *Neural Process. Lett.*, **23**(1), 27–45.
- Billard, A. and Hayes, G. (1999). DRAMA, a Connectionist Architecture for Control and Learning in Autonomous Robots. *Adaptive Behavior*, **7**(1), 35–63.
- Buonomano, D. V. and Mauk, M. D. (1994). Neural network model of the cerebellum: Temporal discrimination and the timing of motor responses. *Neural Comput.*, **6**(1), 38–55.
- Chameron, S., Schatz, B., Pastergue-Ruiz, I., Beugnon, G., and Collett, T. (1998). The learning of a sequence of visual patterns by the ant *cataglyphis* cursor. *Proc. R. Soc. Lond. B*, **265**, 2309–2313.
- Christiansen, F., Zube, C., Andlauer, T., Wichmann, C., and Fouquet, W. (2011). Presynapses in kenyon cell dendrites in the mushroom body calyx of *drosophila*. *The Journal of Neuroscience*, page 9696.
- Collett, T., Fry, S., and Wehner, R. (1993). Sequence learning by honeybees. *J. Comp. Physiol. A*, **172**, 693–706.
- de Ibarra, O., Howard, L., and Collett, T. (2011). Do wood ants learn sequences of visual stimuli? *The Journal of Experimental Biology*, **214**, 2739–2748.
- Elman, J. L. (1990). Finding structure in time. *Cognit. Sci.*, **14**, 179–211.
- Farris, S. M. (2011). Are mushroom bodies cerebellum-like structures? *Arthropod Struct Dev.*, **40**(4), 368–379.

- Foucaud, J., Burns, J.G., and Mery, F. (2010). Use of Spatial Information and Search Strategies in a Water Maze Analog in *Drosophila melanogaster*. *PLoS ONE*, **5**(12).
- Freeman, W. J. (1987). Simulation of chaotic EEG patterns with a dynamic model of the olfactory system. *Biol. Cybern.*, **56**, 139–150.
- Freeman, W. J. (2004). How and why brains create meaning from sensory information. *International Journal of Bifurcation and Chaos*, **14**(2).
- Glenn, C., Maxim, B., and Gilles, L. (2007). Olfactory representations by drosophila mushroom body neurons. *Journal of neurophysiology*, page 734.
- Gronenberg, W. and Lopez-Riquelme, G. (2004). Multisensory convergence in the mushroom bodies of ants and bees. *Acta. Biol. Hung.*, **55**, 31–37.
- Gupta, N. and Stopfer, M. (2012). Functional analysis of a higher olfactory center, the lateral horn. *The Journal of Neuroscience*, page 8138.
- Harter, D. and Kozma, R. (2005). Chaotic neurodynamics for autonomous agents. *IEEE Trans. Neural Netw.*, **16**(3), 565–579.
- Heinrich, B. (1976). Foraging specializations of individual bumblebees. *Ecol Monogr*, **46**, 105–128.
- Huerta, R.N.; Nowotny, T. (2009). Fast and robust learning by reinforcement signals: Explorations in the insect brain. *Neural Computation*, **21**, 2123–2151.
- Izhikevich, E. M. (2004). Which model to use for cortical spiking neurons? *Neural Networks, IEEE Transactions on*, **15**(5), 1063–1070.

- Janzen, D. (1971). Euglossine bees as long-distance pollinators of tropical plants. *Science*, **171**, 203–205.
- Janzen, D. (1971). Serial Order: A Parallel Distributed Processing Approach. *ICS Report 8604, Inst. Cognit. Sci., University of California San Diego*.
- Junko, K., Hiroshi, I., and Toshihiro, K. (2009). Neuronal mechanisms of learning and memory revealed by spatial and temporal suppression of neurotransmission using shibire, a temperature-sensitive dynamin mutant gene in *Drosophila melanogaster*. *Molecular Neuroscience*, pages 1–4.
- Liu, X. and Davis, R. (2006). Insect olfactory memory in time and space. *Curr. Opin. Neurobiol.*, **6**, 679–685.
- Macquart, D., Latil, G., and Beugnon, G. (2008). Sensorimotor sequence learning in the ant *Gigantiops destructor*. *Animal Behaviour*, **75**, 1693–1701.
- Manning, A. (1956). Some aspects of the foraging behaviour of bumblebees. *Behaviour*, **9**, 164 – 201.
- May, R. and Wellman, A. (1968). Alternation in the fruit fly *Drosophila melanogaster*. *Neuroscience and biobehavioral reviews*, **12**(Psychonomic science), 339–340.
- Mronz, M. and Strauss, R. (2008). Visual motion integration controls attractiveness of objects in walking flies and a mobile robot. In *International Conference on Intelligent Robots and Systems*, pages 3559–3564, Nice, France.
- Murphey, R. (1965). Sequential alternation behavior in the fruit fly *Drosophila*

- melanogaster*. *Neuroscience and biobehavioral reviews*, **60**(Journal of Comparative Physiology and Psychology), 196–199.
- Nowotny, T., Rabinovich, M., Huerta, R., and Abarbanel, H. (2003). Decoding temporal information through slow lateral excitation in the olfactory system of insects. *Journal of Computational Neuroscience*, **15**, 271–281.
- Rabinovich, M., Volkovskii, A., Lecanda, P., Huerta, R., Abarbanel, HDI, and Laurent, G. (2001). Dynamical encoding by networks of competing neuron groups: winnerless competition. *Physical Review Letters*, **87**(6), 068102-1.
- Rubin, D. and Wenzel, A. (1996). One hundred years of forgetting: A quantitative description of retention. *Psychological Review*, **103**, 734–760.
- Schroter, U.; Menzel, R. (2003). A new ascending sensory tract to the calyces of the honeybee mushroom body, the subesophageal-calycal tract. *Journal of Comparative Neurology*, **465**(2), 168–178.
- Song, S. and Abbott, L. (2001). Cortical development and remapping through spike timing-dependent plasticity. *Neuron*, **32**, 339–350.
- Song, S., Miller, K., and Abbott, L. (2000). Competitive hebbian learning through spike-timing-dependent plasticity. *Nature Neurosci.*, **3**, 919–926.
- Stocker, R., Lienhard, C., and Borst, A. (1990). Neuronal architecture of the antennal lobe in *drosophila melanogaster*. *Cell Tissue Res*, pages 9–34.
- Sun, R. and Giles, C., editors (2001). *Sequence Learning: Paradigms, Algorithms, and Applications*. Springer-Verlag, Heidelberg, Germany.

- Tang, S. and Guo, A. (2001). Choice behavior of drosophila facing contradictory visual cues. *Science*, **294**, 1543–1547.
- Tanji, J. and Shima, K. (1994). Role for supplementary motor area cells in planning several movements ahead. *Nature*, **37**, 413–416.
- Wang, D. and Arbib, M. (1990). Complex temporal sequence learning based on short-term memory. *Proceedings of the IEEE*, **78**(9), 1536–1543.
- Webb, B. and Consi, T. (2001). *Biorobotics : methods and applications*. Menlo Park, CA : AAAI Press/MIT Press.
- Wehr, M. and Laurent, G. (1996). Odor encoding by temporal sequences of firing in oscillating neural assemblies. *Nature*, **384**, 162–166.

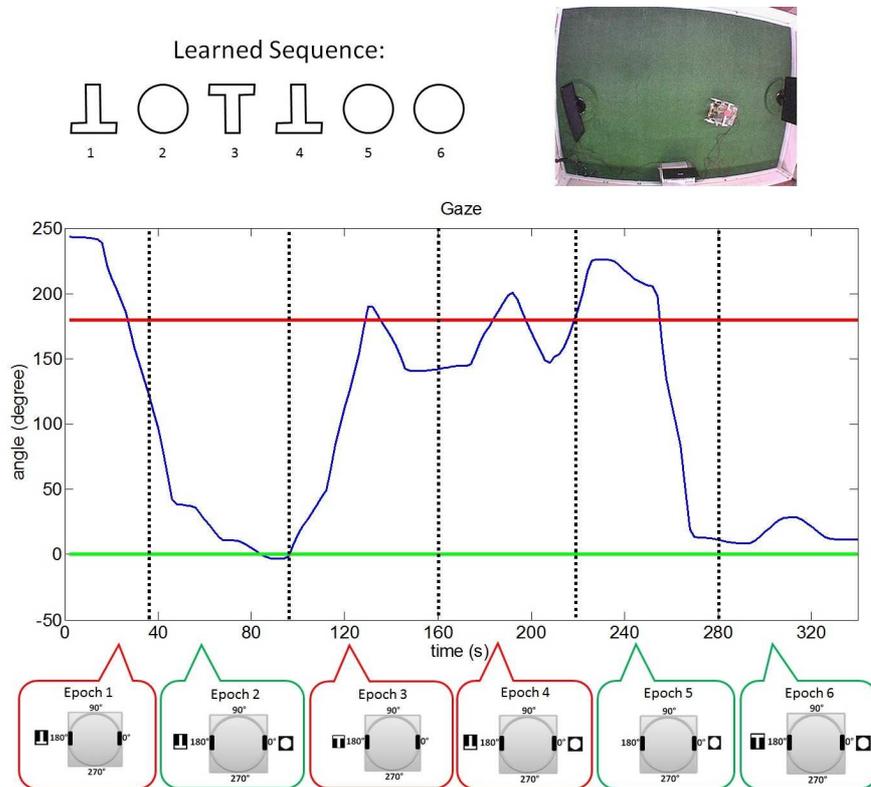


Figure 16: Behaviour of the robot while reconstructing a learned sequence when noisy inputs are provided. The arena is depicted on the top right side, the learned sequence on the top left side, the snapshots at the bottom side depict the objects presented at each epoch of the sequence, whereas the graph shows the time evolution of the gaze direction of the robot. When two visual stimuli are simultaneously presented (epoch 2, 4 and 6) the disturbance is filtered out and the robot orients towards the monitor where the correct expected symbol is shown.

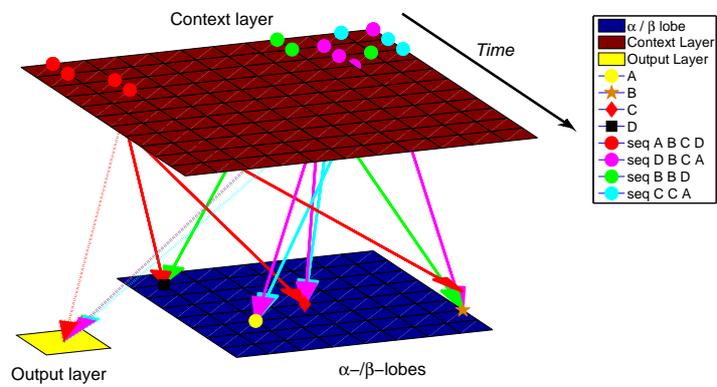
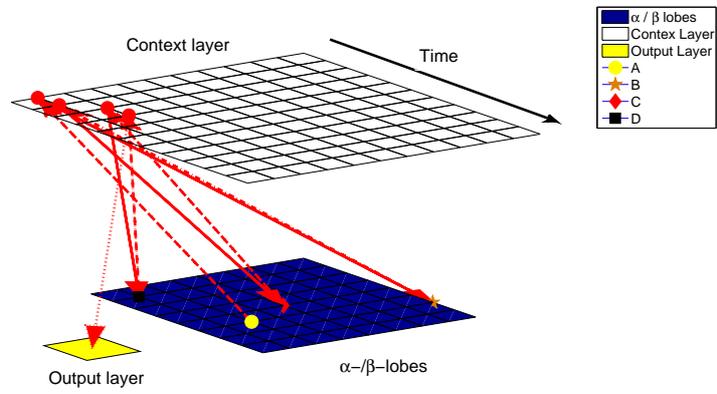
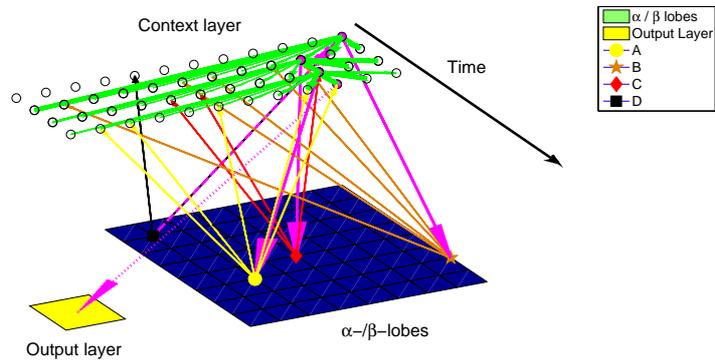


Figure 17: Synapses connecting the neurons of the Context layer to the α -/ β -lobes winning neurons for various sequences. The synapses learned through STDP induce the generation of a sequence. The last element of each sequence is connected to the end neuron in the output layer.



(a)



(b)

Figure 18: Activity in the α -/ β -lobes and in the Context layer during the learning phase for the sequence (a) *ABCD* (b) *DBCA*. The connections between the α -/ β -lobes and the Context layer are indicated together with the diffusion activity produced by the winning neurons in the context.

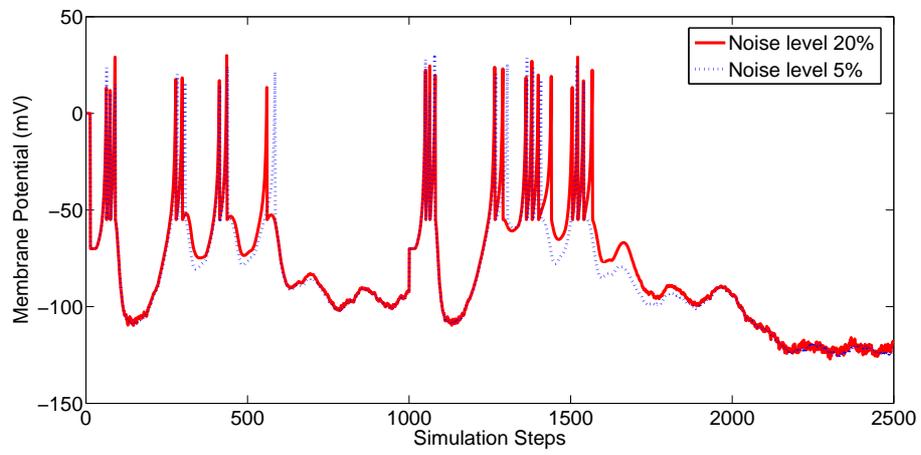


Figure 19: Trend of the membrane potential of a neuron in the α -/ β -lobes when the level of noise in the input current is $\pm 5\%$ and of $\pm 20\%$.