

Learning expectation in insects: a recurrent spiking neural model for spatio-temporal representation

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Abstract

Insects are becoming a reference point in Neuroscience for the study of biological aspects at the basis of cognitive processes. These animals have much simpler brains with respect to higher animals, showing, at the same time, impressive capability to adaptively react and take decision in front of complex environmental situations. In this paper we propose a neural model inspired by the insect olfactory system, with particular attention of the fruit fly *Drosophila melanogaster*. This architecture is a multilayer spiking network, where each layer is inspired by the structures of the insect brain mainly involved in the representation of the olfactory information, namely the Mushroom Bodies, the Lateral Horns and the Antennal Lobes. The Antennal Lobes layer is based on a competitive topology between sets of neurons. Its function is to transform the sensorial information into a pattern, projecting such information to the Mushroom Bodies layer. Here a competitive reaction-diffusion process leads to a spontaneous emerging of clusters. The Lateral Horns have been modeled as a delayed input-triggered resetting system. Using plastic recurrent connections with the addition of simple learning mechanisms, the structure is able to realize a top-down modulation at the input level. This leads to the emergence of an attentional loop as well as to the arousal of expectation based behaviors in case of subsequently presented stimuli. Simulation results and analysis on the biological plausibility of the architecture are provided and the role of noise in the network is reported.

Key words: insect brain, spiking neurons, olfactory model, attention, expectation

1. Introduction

In the last few years an increasing interest has been paid to study simple animal brains, at the aim both to deeply understand the neurobiological details, and to exploit the derived knowledge to build efficient bio-inspired sensing-perceiving-acting machines. Particular attention is being devoted to the insect world, since insects are being recognized not only as reflex-driven automata: even if their brain structure is very small, most of them are indeed able to show such complex behaviors that, since a few years ago, were believed to be possible only in higher animals like mammals or even humans. In contrast with what assumed in the last decades, even social insect swarms capabilities are not merely related to the concept of distributed intelligence: the complex social behavior is largely due to the intelligence and adaptive behavior shown by individual agents in the colony (Dornhaus & Franks, 2008; Webb & Consi, 2001). Insects clearly show such distinct features as learning and memory; they are able to solve tasks that require numerosity, capability to show the “sameness versus difference” concept in action, and others (Chittka & Niven, 2009). The worker honeybee is certainly a well-known organism for studying the fundamental principles of color vision, pattern recognition, learning and memory, flight control, and navigation, (Menzel & Giurfa, 2006; Srinivasan & Zhang, 2004; Srinivasan et al., 2006; Wehner, 1981). The enhanced tools recent adopted in insect Neurophysiology allowed to shed light on the details of neural signal processing in some specific parts of insect brain responsible for complex behaviours like attention. The insect brain areas responsible for these processes are the *Mushroom Bodies* (MBs) that, together with the *Lateral Horns* (LHs) are primarily devoted to olfactory learning. The spatio-temporal olfactory information coming out from a neural structure named Antennal Lobes (ALs), is processed and stored in spatial patterns (Huerta & Nowotny, 2009; Liu & Davis, 2006). MBs are well known for their capability to perform associative learning for odor conditioning (Scherer et al., 2003). Recently neural models inspired by the *Drosophila melanogaster* and locust brain anatomy were proposed using roughly the same number and connectivity as the olfactory biological counterpart. 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 was implemented. In that paper the structure exploited autonomous clustering capabilities and no learning algorithms were taken into consideration. In order to include specific learning capabilities into the system, the proposed architecture is based on models of spiking networks where characteristics like visual features, learning, recalling and forgetting were considered (Arena

& Patané, 2009; Arena et al., 2010). These structures were successfully applied to enhance the capabilities of an autonomous robot, but they were really far from the insect skills, which are able to show other interesting capabilities like attention and expectation based behaviors. Novel tools from Neurophysiology are continuously advancing the knowledge about neural activity even in such small brains as the fruit fly. In particular, regarding the attention process, in van Swinderen (2007) interesting clues of the presence of attention processes were found analyzing the registered local potential field (LPF) within the fly brain. They in fact were able to show increased LPF activity when the fly is positioned in a rotating cylinder with two alternating different objects, whereas no LPF variation was observed when displaying twice the same object in the same setup. Moreover learning mutants in the cAMP cascade, showing deficits in short-term memory, did not show such neural evidence. Of course specific tests excluded that such behavior was due to a lack of visual cues responsiveness. To host such skills, the traditional model, mainly based on feedforward connections from the sensory to the classification layer, should also include other kinds of feedback connections, able to affect the input sensitivity to particular expected sensory features. Recently feedback connections from MBs to the ALs have been found (Hu et al., 2010). Here a functional role of such connections in filtering input information is hypothesized and proposed in the developed model. This new interesting feature allows to refine the models previously presented, adding new capabilities to the system.

Starting from the already introduced neurobiological findings, in this paper a new artificial model of the insect olfactory system with enhanced capabilities is introduced. This model could explain how sophisticated attention and expectation mechanisms arise in insects when facing with complex environments. Learning to know in advance the input stimulus correlated with the actual one is a fundamental ability in living beings, useful to take the appropriate action, sometimes life-saving. The possibility to make predictions and to modulate sensorial inputs through expectations is the key point that the model introduced in this work does allow. The proposed model is a multi-layer spiking neural network basically inspired to Nowotny et al. (2003), and including the recent findings in Hu et al. (2010). The first layer represents the Antennal Lobes model: inputs are decomposed in main *features*, represented by feature-specific groups of neurons within the input layer. Here a locally competitive topology is implemented, as suggested in Neurobiology (Sachse & Galizia, 2002). This layer randomly projects connections to the second layer, which models the functionalities of the Mushroom Bodies, mainly constituted by Kenyon Cells (KCs layer). Each neuron in this layer

is connected through fast excitatory synapses to its neighborhood and, within the same layer, through fast inhibitory synapses to the rest of the network. In order to have a symmetric set of connections, a toroidal shape was implemented. The KCs layer shows interesting clustering capabilities and represents the core of the system in terms of spatio-temporal pattern formation. Recurrent connections are present from KCs to the ALs. The Lateral Horns model, as suggested from Neurobiology (Perez-Orive et al., 2002), has been thought as an input-triggered system that provides a delayed global inhibition to the Mushroom Bodies network. The model, originally presented in Arena et al. (2011), is here further assessed, both from the design and from the experimental point of view. In particular, specific considerations that served as guidelines to derive the model, based on neurophysiological details, are reported. Moreover, through new experimental results, the role of noise was assessed in a twofold aspect: the former is related to the clustering robustness, whereas the latter, more interesting, exploits the possibility to use the positive role of noise when no input activity is registered at the ALs layer, to give rise to a spontaneous learning activity, mimicking the phenomenon of consolidation during sleep, well known to take place in the fly, as well as in humans.

The paper is divided into five sections: Section II presents the biological background of the work and the state of the art regarding artificial models of insect brains. In Section III the proposed architecture is introduced and described whereas Section IV presents some simulation results and also introduces preliminary potential applications for the model. Finally, Section V draws the conclusions.

2. Biological Background

The most deeply studied neural centers in the fly brain are the MBs, that, together with the LHs are widely recognized to play a fundamental role in processing the spatio-temporal information coming from the glomeruli of ALs. Mutual inhibitory connections among the ALs glomeruli have been found very recently in neurobiological studies on the fruit fly, as discussed in Sachse & Galizia (2002). This competitive topology allows the creation of odor-evoked patterns of excited and inhibited glomeruli that are sent out to the higher brain structures like MBs and LHs. MBs are a paired structure within the protocerebral hemispheres. They play a primary role in olfactory learning: this was unambiguously proven thanks to specific experiments with MB-defective mutant flies (de Belle & Heisenbergh, 1994). In the fly *Drosophila melanogaster*, each side of the MBs is constituted by 2500 Kenyon cells which run in parallel from the *calyx* through the *peduncle* and

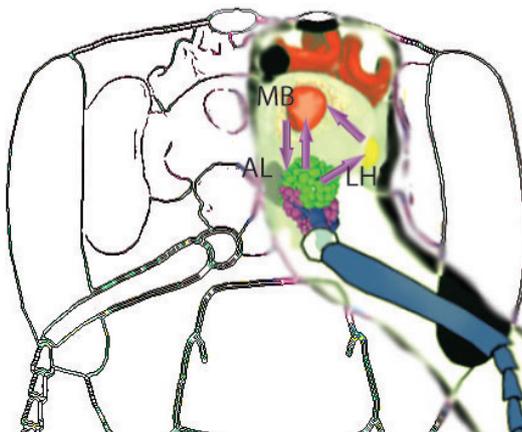


Figure 1: Circuit for olfactory processing. The Antennal Lobes (ALs) project olfactory information to the Mushroom Bodies (MBs) and Lateral Horns (LHs) through the Projection Neurons (PNs). In locusts, the LHs inhibits the MBs activity.

to the *lobes*. There is a prominent olfactory input from the Antennal Lobes into the calices. Input from other sensory modalities is not obvious in *Drosophila*, even if high level tasks dealing with the choice behavior in front of contradictory visual cues and involving MBs are described for flies (Tang & Guo, 2001). In other insect species MBs are a fundamental neural center where multimodal sensory integration for learning was found: for example honeybees MBs receive prominent visual (Gronenberg & Lopez-Riquelme, 2004), gustatory, and mechanosensory input (Schrter & Menzel, 2003). There is also an output of the MBs to pre-motor areas of the brain. The information flow through MBs was formerly considered as prominently feedforward, i.e. from the Kenyon cells to the calyx and towards the lobes. Very recently, recurrent connections between MBs and ALs have been found. The presence of this functional feedback from the MBs to the ALs opened the way to suggest a model including top-down modulation of olfactory information processing in *Drosophila* (Hu et al., 2010). The scheme of the architecture proposed is depicted in Fig. 1, where the different involved neural centers are outlined. Olfactory information flows in parallel from the ALs to the MBs and LHs. Connections from LHs to MBs have been found, but their entity in *Drosophila* is not well known. Further information comes from locusts, where LHs play an inhibitory effect to the MBs Kenyon Cells (Perez-Orive et al., 2002). A model which takes into account this inhibitory role was implemented in Nowotny et al. (2003). In this model each Kenyon cell is strongly connected with the cells of its neighborhood, and in this architecture the Antennal Lobes layer randomly projects

to the Kenyon cells layer. A coincidence detection mechanism allows the model to codify sequences of events in spatial patterns of firing neurons. No learning is implemented in the model proposed in Nowotny et al. (2003), whereas the system architecture discussed in this paper includes also learning mechanisms to allow pattern reconstruction and expectation capabilities.

3. Insect inspired neural model

The neural model here proposed (Fig. 2) combines behavioral evidences in insects, including flies, concerning attention capabilities, with the state of the art on the neural structures responsible for these processes, including also a biologically relevant learning rule which boosts the system capabilities: expectation is the emergent aspects of this new architecture. The model is directly inspired to the olfactory system of the *Drosophila melanogaster*, including the new enhanced top-down connections from MBs to the ALs, and considering the global inhibitory role played by LHs. The overall neural structure is configured as a two layer recurrent network endowed with artificial spiking neurons. Presently the model capabilities were analyzed referring to the clustering, attention and expectation learning processes. Of course a natural evolution of the model proposed could include an additional layer, of the type already implemented elsewhere by the authors (Alba et al., 2010), and connected to the motor area for behavioral motion control. As previously outlined, the developed neural structure was inspired by the insect olfactory system. At the aim to build a computational model useful for a number of different applications, the same structure can be used for processing different sensorial artificial stimuli (e.g visual features can be easily used in robotic scenarios). In insects the MBs are involved in a huge number of tasks and completely different aspects of learning and memory (Chittka & Niven, 2009). For this reason in the rest of the paper generic object features will be taken into consideration.

3.1. The Neuron and Learning Models

The neural network is built around a cluster of spiking neurons organized in layered lattices. Each unit is an Izhikevich spiking neuron (Izhikevich, 2003). The model is represented by the following differential equations:

$$\begin{aligned} \dot{v} &= 0.04v^2 + 5v + 140 - u + I \\ \dot{u} &= 0.02(-0.1v - u) \end{aligned} \quad (1)$$

with the spike-resetting

$$\text{if } v \geq 0.03, \text{ then } \begin{cases} v \leftarrow -0.055 \\ u \leftarrow u + 6 \end{cases} \quad (2)$$

where v is the membrane potential of the neuron, u is a recovery variable and I is the synaptic current. Izhikevich neural models are well-known in literature and offer many advantages from the computational point of view.

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. Here is the mathematical response of the synapses to a pre-synaptic spike:

$$\varepsilon(t) = \begin{cases} Wt/\tau \exp(t/\tau), & \text{if } t > 0 \\ 0, & \text{if } t < 0 \end{cases} \quad (3)$$

where t is the time lasted from the spike, τ is the time constant and W is the efficiency of the synapse. This last parameter can be modulated with experience.

Hebbian learning, introduced by Donald Hebb in 1949, is a mechanism where the synaptic efficiency increases through coincident stimulations of the postsynaptic and presynaptic cell.

The Spike Timing Dependent Plasticity (STDP) can reproduce Hebbian learning in biological neural networks (Song et al., 2000; Song & 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 in biorobotics of this learning paradigm, together with details on the parameters are reported in Arena & Patané (2009); Arena et al. (2009a).

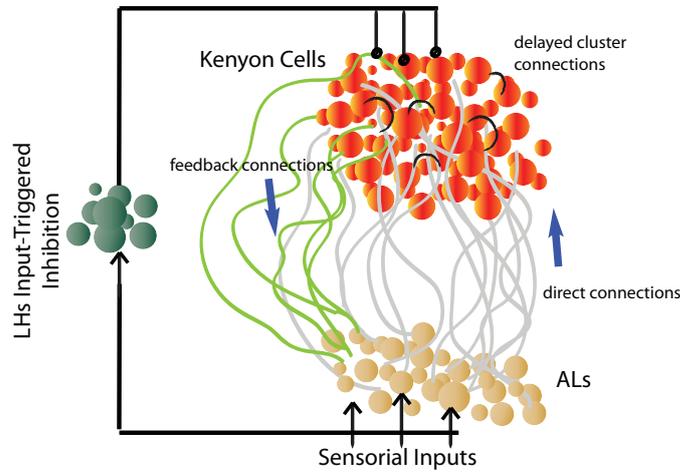


Figure 2: The Antennal Lobes model is directly connected to the sensorial system (Antennas). We can assume that the activity of each neuron codifies the presence of a particular value for a specific feature. Neurons in the ALs are organized in groups. Synapses from the Antennal Lobes model to the KCs layer are randomly chosen, with a given probability of connectivity. The KCs layer is a toroidal lattice, with local excitatory and global inhibitory synapses. The Lateral Horns periodically inhibit the KCs neurons. Feedback plastic connections link clusters in the MBs to the ALs neurons. Local connections within the ALs and the KCs are not reported. The delayed plastic synapses in the KCs layer allow a temporal link between subsequent object presentations.

3.2. Antennal Lobes Model

Inspired by the ALs of the *Drosophila melanogaster*, we can assume to have a layer able to codify the interesting *features* of objects. In the insect ALs each glomerulus is able to detect a peculiar component of an odor: in our model each neuron in this layer encodes a particular aspect related to a detected object. Neurons within the ALs model are organized in groups, as illustrated in Fig. 3. Each group codifies a kind of feature (examples of features could be color, shape, etc.), and neurons in the same group codify different values of that feature (i.e. different colors or shapes). Neurons in the same group are linked together through inhibitory synapses. This topology implies that, when the ALs layer is stimulated, after a short transient time, only one neuron in each group remains excited, according to a Winner-takes-all topology. Neurons in different groups are linked together through plastic synapses, reinforced when neurons are firing together, according to the Hebbian rule. This process reinforces organization among the neurons representing the different features of a presented object, leading them to reach a phase locked firing state. These mechanisms have several analogies

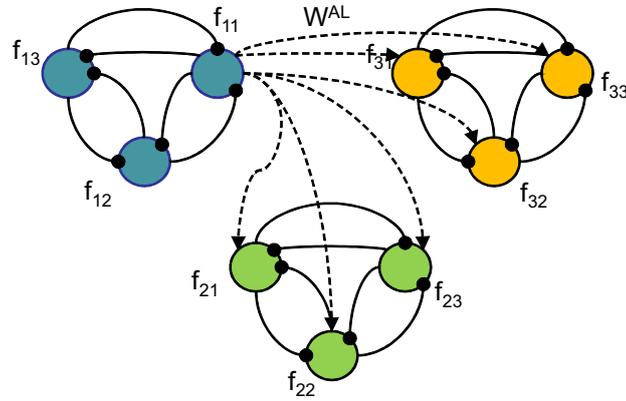


Figure 3: Connection scheme of the ALs neural model where three different features and three different classes within them are considered. The neurons associated to the same feature class are mutually inhibited whereas they excite neurons of other sets through plastic excitatory connections that are subject to learning (only the excitatory connections for neuron f_{11} are reported in figure).

with the Winnerless competition principle (Rabinovich et al., 2001; Arena et al., 2009b), modelled after ALs studies. Therefore, when an object is presented to the network, the ALs model decomposes that object in its relevant features, and the corresponding neuron of each group remains excited. The ALs model topology is inspired by the biological case (Masse et al., 2009), in which excitatory and inhibitory connections allow the interaction between glomeruli in order to have the primary odors representation. The ALs layer projects excitatory direct connections to the MBs network, constituted by a number of neurons which represent the Kenyon Cells (KC) in the fly MBs. Each neuron of the ALs is connected to each KC model with a given probability of connection, recalling the sparseness of connections in the corresponding areas of the fly brain.

3.3. Mushroom Bodies and Lateral Horn Models

MBs model is configured as a complex recurrent neural structure. It is made up of a number of KCs which receive afferent input from the ALs and send feedback synapses back to the ALs. More in details, a competitive topology was designed for the KCs layer. Each KC is a spiking Izhikevich neuron and the whole KCs lattice, thanks to the connections among KCs and ALs neurons, undergoes a spatial temporal wave, which leads to the emergence of a cluster of neural activity. This spatial temporal activity represents the crucial aspect of the overall network. The KCs layer was conceived as a toroidal lattice where each neuron is connected through fast excitatory synapses with all the neurons of its neighborhood, and

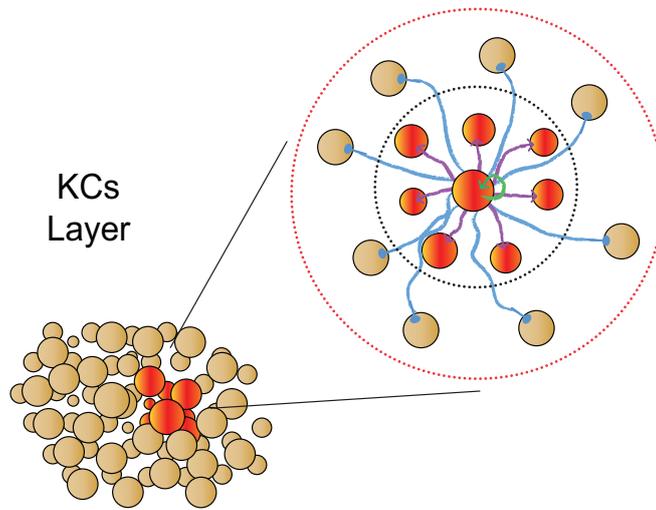


Figure 4: The KCs layer is a toroidal lattice, with local fast excitatory and global fast inhibitory synapses. Another set of plastic delayed synapses links each neuron of the KCs layer to the other neurons of the same lattice, in order to have the possibility to temporally link different clusters, allowing short term prediction and expectation capabilities of the neural architecture. In figure, the inner circle indicates the locally excitatory neighborhood, whereas the outer circle includes all the KCs layer network where a global inhibitory effect takes place.

through fast inhibitory synapses with all the other neurons of the lattice, as shown in Fig. 4. The main capability of the KCs layer is a spontaneous clustering of spiking activity, driven by a Winner takes all-like structure. In this way, information coming from the ALs is compressed together into a cluster of neurons spiking at a given frequency. In addition to this process, a slow and delayed diffusion of the neural activity within the KCs layer is also included in our model. More in details, another set of plastic delayed synapses links each neuron of the KCs layer to the other neurons of the same lattice, in order to have the possibility to temporally link different clusters. These synapses are subject to the STDP learning algorithm, that allows to discover and retain temporal causality among clusters. These connections have the interesting capability to generate, within the KCs layer, expectation and short term prediction capabilities. Plastic feedback connections are also present, as already outlined, from the MBs model to the ALs layer. These connections, recently discovered in Biology (Hu et al., 2010), were never considered in any bioinspired model up to now. Their role is precious to boost the model performance and two main functions have been identified: they are useful to create an expectation-based depolarization of the neurons in the ALs; they are

also essential to reconstruct the expected object. When a cluster is elicited in the KCs layer, the synaptic connections between the neurons of the MBs cluster and those neurons which are firing in the AL (due to the synchronous presence of the corresponding input) are increased, according to the Hebbian paradigm.

Lateral Horns, after the neurobiological evidence of connections to the fly MBs, and according to their mainly inhibitory role in locusts (Nowotny et al., 2003), have been modeled as a event-driven resetting system, that generates an inhibitory wave to the MBs, defining a processing time window for the system. In this way, the KCs layer integrates the information coming from the ALs in a given time window and, after the emergence of a cluster, the neural activity of the network is inhibited by the LHs wave.

4. Network design and simulation results

In this Section the behavior of the whole network is analyzed through a series of simulations. The obtained results are useful to understand the basic principles that rule the network and its parameters.

4.1. Network Parameters

An important aspect of a multi-layer spiking network consists in the tuning of parameters. The guidelines used for this proposed model are here discussed. While the morphology of the insect brain structure is well known, the details of the topological organization and above all the peculiarities of the network connections are largely unknown. Only in some particular cases light is being shed and the features of specific neural structures were unraveled, thanks also to the support of behavioral Neurogenetics. Only very recently modern tools allowed reliable neurophysiological measurements in specific brain regions. This is the case of locust and, to a lower extent, of the fly. As a consequence, the network considered in this work was designed drawing considerations from a number of different cues. As regards the structure and the number of neurons in each subpart of the network, we know from Biology that the odorant components, through the olfactory glomeruli, stimulate 250 neurons for each AL, which project to 2500 KCs. In our model we maintained roughly the same ratio, even if the actual architecture has a much scaled topology and connectivity with respect to the biological counterpart, and has to be considered as a proof of concept for the basic and enhanced capabilities ascribed to the olfactory insect neural architecture. In our case, 9 neurons in the ALs layer are connected to 81 KCs; each neuron in the ALs layer has a probability $P = 0.012$ of being connected to a KC neuron. The choice of the

sparse connections between the first and the second layer is directly drawn by the sparse connections in the biological counterpart (Perez-Orive et al., 2002). In the proposed simulations, the first layer is made by a 3x3 lattice. In particular, there are three groups of neurons (f_1, f_2, f_3), and each group is made of three neurons (for instance, the neuron j in the group f_i will be called f_{ij}), as previously shown in Fig. 3. Neurons in the same group are connected each other through inhibitory synapses, with a synaptic efficiency $W^{AL} = -3$. Neurons in different groups that, after the presentation of an object, fire together, increment the efficiency of the synaptic link with a $\Delta W^{AL} = 2$. The initial value of such synapses is zero. When an object is detected, the neurons of the first layer that encode the features of that object are excited with an input current $I_{AL} = 70$. The synapses between the first and second layer have fixed efficiency of $W^{AL,KC} = 10$.

Concerning the KCs layer, a 9x9 lattice with a toroidal topology has been considered. The neurons in this layer are all connected each other according to the paradigm of local excitation and global inhibition. A neighborhood of radius $r = 1$ is defined. In this way, each neuron is connected to the neurons in its neighborhood and with itself through excitatory synapses with an efficiency of $W_{near}^{KC} = 50$. It is also connected with the other neurons of the lattice through inhibitory synapses with an efficiency of $W_{far}^{KC} = -30$. This set of connections gives the network its clustering capabilities. Moreover, a second set of synapses is implemented, which allows the linking of sequences of winning clusters. Each neuron is connected to each other neuron in the lattice through a time-delayed synapse, subjected to learning. In this case, the most active neurons of two clusters activated sequentially in time reinforce the synapses among them according to the STDP rule. Feedback connections are initially set to zero. When a cluster in the KCs layer is firing together with neurons in the AL layer, the corresponding synapses are raised, $\Delta W^{KC,AL} = 1$. The time constant used for fast excitatory and inhibitory synapses in the network is $\tau_{fast} = 1ms$. All the equations are solved using the Euler method with an integration time of 0.08 ms. Synapses time constants have been chosen in order to have a plausible matching with respect to the biological counterpart. Furthermore the learning coefficients for the network (e.g. $\Delta W, A^+$ and A^-) are chosen in order to obtain a robust association after a few presentations of consecutive objects, similarly to the biological counterpart (Gerber et al., 2004; Scherer et al., 2003). In order to demonstrate the robustness of the structure and to mimic realistic situations, noise has been introduced during the simulations. In particular, each parameter has been altered adding a gaussian noise with zero mean and variance equal to the 10% of the mean value of the same parameter.

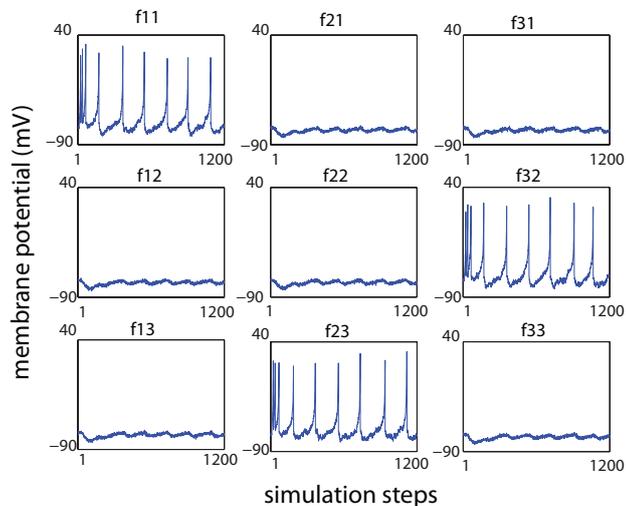


Figure 5: Evolution of the membrane potential of the neurons in the first layer, during the presentation of the first object. In this case, no competition is present between neurons, due to the absence of the contribution coming from the expectation feedback. However, it can be noticed the inhibitory effect of the excited neurons on the others. Input neurons project information to the KCs layer.

4.2. Analysis of the clustering properties

To test the clustering properties of the neural model an object with three different features is presented to the first layer of the network; three neurons are excited, one for each group of input neurons (Fig. 5). The ALs projects the information to the second layer (KCs layer), exciting its neurons. After a transient of 1200 simulation steps, the network is able to elicit a winning cluster. Fig. 6 depicts the trend of the mean potential of the KCs neurons in given time windows, clearly showing the clustering arousal. The emerged cluster tends to remain stable during time. It is important to notice that some of the main properties of the KCs layer model remain constant with respect to the variation of the dimensions of the lattice. For example, in Fig. 7, a simulation of a 20x20 lattice is presented. The behavior of the network is similar to the 9x9 one. The main difference stands in the time needed to elicit a winning neuron. A larger lattice needs more time to converge, since more connections are involved. However, the mean frequency of the oscillations in the membrane potential of the winning neuron remains within the same range. That is in line with the neurophysiological measurements performed in the locust ALs (Nawrot et al., 2011). So we designed the neuron parameters, the input current amplitudes and the time constants taking into consideration these guide-

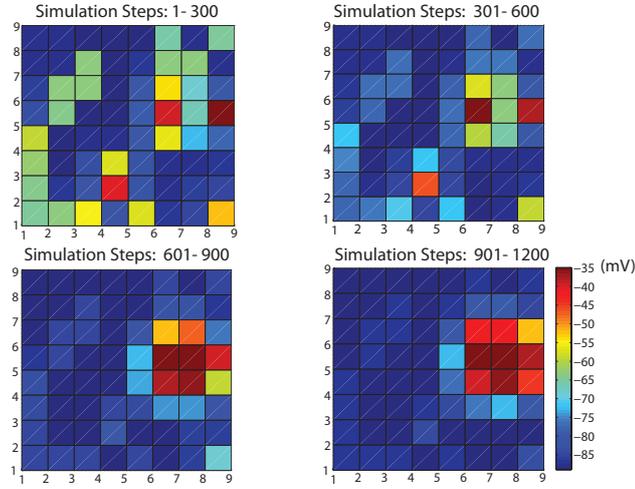


Figure 6: Evolution of the mean potential of the neurons in the 9x9 KCs layer. The network has been simulated for 1200 steps with an integration time of 0.08ms. The membrane potential is averaged every 300 simulation steps. At the end of the simulation, only one cluster of neurons remains active.

lines from Biology. Also the mean membrane potential of the neurons remains unaffected from the network scaling. It is to be noticed that the transient time is also related to the connectivity level between the ALs and the KCs layer. The increase of wiring probability leads to a longer transient to reach a steady state condition in the KCs layer. In any case the clustering capabilities are preserved. It could be also noticed that the clustering capability of the network depends on the ratio between the efficiency of the local excitatory synapses and the inhibitory ones. In particular, maintaining the chosen ratio to about 5 : 3, the clustering capabilities are preserved. However, high values of efficiency increase the robustness to noise. For example, with the parameters $W_{far}^{KC} = -3$ and $W_{near}^{KC} = 5$ the network maintains its functionality with zero noise but its clustering performance are not robust if a noise of 10% is introduced during the simulations. For this reason we prefer to use larger weights, as already introduced, obtaining a more robust and stable clustering capability during the pattern formation process in the KCs layer. In the following the main capabilities of the proposed network are outlined through a series of key simulations.

4.3. Attention through top-down modulation

The network structure can be trained to show attentive capabilities, which consist in filtering out, from a previously presented and learned object, all the other

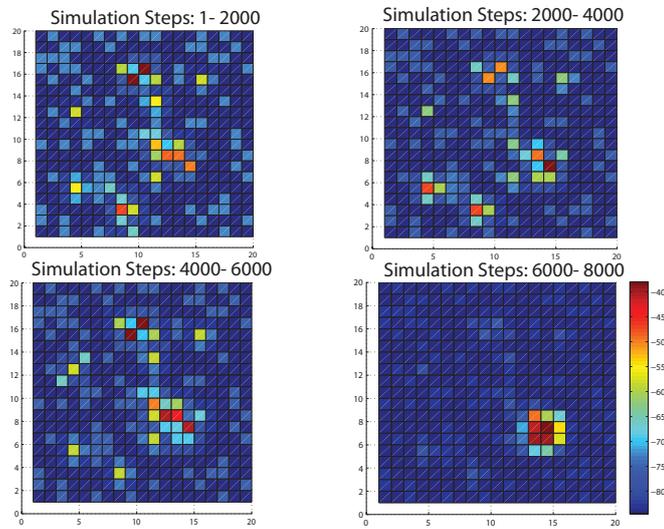


Figure 7: Evolution of the mean potential of the neurons in the 20x20 KCs layer. The network has been simulated for 8000 steps with an integration time of 0.08ms. The membrane potential is averaged every 2000 simulation steps. At the end of the simulation, only one cluster of neurons remains active.

stimuli, being them other objects or noise, that could be presented concurrently with the reference object. Such attention capability, recently discovered in the fly (van Swinderen, 2007), is a simple emerging property of our structure which derives from the presence of recurrent top-down connections. In fact, if a given object is repetitively presented to the network input, a particular cluster emerges, and concurrently, the feedback connections to the ALs neurons corresponding to the presented object are reinforced. If the presented object is disturbed by the presence of additional distracting inputs (being these noise or other objects), the feedback connections bias the ALs neurons associated to the current cluster, to be much more excited than those ones elicited by the distracter inputs. As a result, internal ALs connections, with the addition of the feedback ones, cooperate in such a way as to efficiently filter out the exogenous signals, enhancing the attentional process. If the top-down connections were absent, the WTA processing in the ALs layer would not be able, by itself, to filter out distracters and a new cluster would emerge, showing a clear example of distraction process, as found in cAMP-cascade learning mutant flies, which show attention deficits (van Swinderen, 2007). If such an attentional process is extended to subsequently stimulated clusters, expectation-based processes emerge, as described and experimen-

tally shown in the following.

4.4. *Expectation through top-down modulation*

The expectation capabilities of the MBs structure can be modeled exploiting the synaptic modulation of the feedback connections between the Kenyon Cells and the Antennal Lobes when objects are presented in sequence. To better explain this process a simulation is here reported, where two subsequent objects are presented to the network. In particular, the first object is characterized by features that stimulate f_{11}, f_{21}, f_{31} ALs neurons whereas the second object is identified by other features (f_{11}, f_{23}, f_{32}). During the presentation, the KCs layer elicits two consecutive clusters and links them through the delayed synapses. Moreover, the connections between the two clusters and the corresponding input neurons at the ALs layer are learned. Several scenarios are presented in the following, to outline various interesting features of the proposed architecture.

1. A first simulation consists in the presentation of a first object, followed by another object with an incomplete feature set presented at the second step. In particular, information about the feature related to the second group of neurons in ALs (f_{2j}) is missing. In this case, thanks to the previous learning cycles, the KCs layer is able to reconstruct the lacking feature: feedback connections from the MBs excite the ALs neurons that codify that object and synaptic connections among neurons in different ALs groups allow the reconstruction of the complete object. No competition does take place in the ALs layer, but top-down connections allow the recalling of the lost information. An example of this reconstruction mechanism is shown in Fig. 8. The expectation capability herewith presented can be further exploited for modelling a simple sequence learning paradigm. In fact, if during the learning phase a short number (say three) of objects is presented, three winning clusters are subsequently elicited and the central neuron for each cluster reinforces its connection to the central neuron for the winning cluster associated to the subsequent object. So, during the testing phase the presentation of the first object is able to elicit the sequence of winning clusters in the KCs layer, which reconstruct at the AL layer, the sequence of corresponding objects. The sequence of formed clusters following this procedure is depicted in Fig. 9. At the end of each phase, the network is reset by the LHs.
2. In a second test, after the presentation of the first object, the second object is presented again. In this case, the feedback system acts as an expectation-based filter that enhances the response of the whole architecture. The cluster

elicited by the first object stimulates, through the delayed connections, the second cluster and then the ALs neurons speeding up the response to the second object.

3. Finally the behavior of the network in case of unexpected situation is evaluated. After the presentation of the first object, a second object is presented to the network, but it is different from the second object presented in the learning phase. In this case, a competition takes place. The top-down connections enhance the response of the neuron representing the common features between the object just presented (and unexpected) during the test phase and the second object shown in the learning phase. At the end of the competition, a new cluster is elicited in the KCs layer, as shown in Fig. 10. This cluster represents the new object, creating a new sequence. The network is then able to store multiple short competing sequences and the most reinforced one will be finally stored. It has to be considered that the structure is not conceived to act as a sequence generator, but it contains the same ingredients and, suitably modified and scaled up, could be the starting point for an efficient bio-inspired sequence generator. From the biological point of view we have clear evidence for sequence learning in bees, but until now the neural circuits giving rise to such capability are unknown.

4.5. Consolidation during Sleep

An interesting property of the network can emerge, exploiting the presence of noise in the system. In fact the contribution of noise in can be useful to consolidate the acquired knowledge during a resting phase, in which no sensorial inputs are given to the network. A simulation divided in two phases is prepared; the first one is a learning phase, in which the network creates the association between clusters and objects. In particular, four sequences of two objects have been presented to the network. At the end of the training phase no physical input is presented at the ALs layer, but it is assumed that the KCs layer is subject to noise which was supposed as gaussian with zero mean and variance $\sigma_{noise} = 10$. This noisy disturbance will onset a dynamical transient in the KCs neurons until a cluster will emerge over the others, as shown in Fig. 11. If this cluster had formerly been trained to represent a given object, this will be recalled at the ALs layer, like an “imagined object”. A new learning cycle will then arise, in which not only this object will be consolidated, but also all the other objects eventually expected after this one in an already learned sequence (see Fig. 12). New imagined solutions could also be experienced during this “sleeping phase” and, in more complex

networks including also more environmental details, the system could discover new strategies to efficiently solve difficult situations starting from what already learned during the “awake phase”.

5. Conclusions

Inspired by specific parts of the insects brain, we proposed a neural model for expectation-based learning. The neural architecture is a multi layer structure in which the first layer consists of sensory neurons inspired by the insect Antennal Lobes. The neurons of this layer are able to detect the presence of characteristic features in objects. The information coming from the sensorial system is then projected to the second layer, that is a self-organizing layer inspired by the insects Mushroom Bodies. The competitive topology of this network is focalized to the emergence of clusters, and it is periodically reset, simulating the LHs effect found in locusts. The basic principle of the architecture is that the expectation for objects can be translated into a sequence of winning clusters in the KCs layer, that projects back to the ALs. Simulation results show the suitability of the proposed network as a bio-inspired architecture, in which drawing inspiration by simple beings, emergent capabilities, like attention, expectation and simple sequence recalling tasks can be found. The network capabilities can be exploited in robotic applications like landmark recognition, behavioral choices in front of expected situations versus unexpected ones, and sequence learning for maze solving. Regarding the network topology, the random probability-based connections between the first and the second layer improves the clustering capabilities of the network. This enables the birth of new clusters in presence of slightly different objects, decreasing, on the other side, the memory capacity of the network that can be improved by scaling-up the network dimensions, reaching configurations similar to the biological case. Moreover, a really added value provided by this simple network is the possibility to reconstruct an expected object. In fact the top-down information stimulates the AL neurons that are considered as representative of the single features that constitute the expected object. The expected object is then projected down at the sensing layer filtering out the other objects eventually present in the scene. So, in case of multiple presented objects, the network will “pay attention” only to the expected one. Finally, the network could learn even without a real input presented: if a suitable level of noise is added in the network in absence of input, for example simulating the overnight autonomous behavior, the noise will excite the KCs layer, which will give rise to sequences of network iterations. This phenomenon could suitably model the overnight memory

consolidation effect, well known in insects. Of course the simulation results here presented have to further be refined, together with the model itself in a more and more strict accordance with the biological case.

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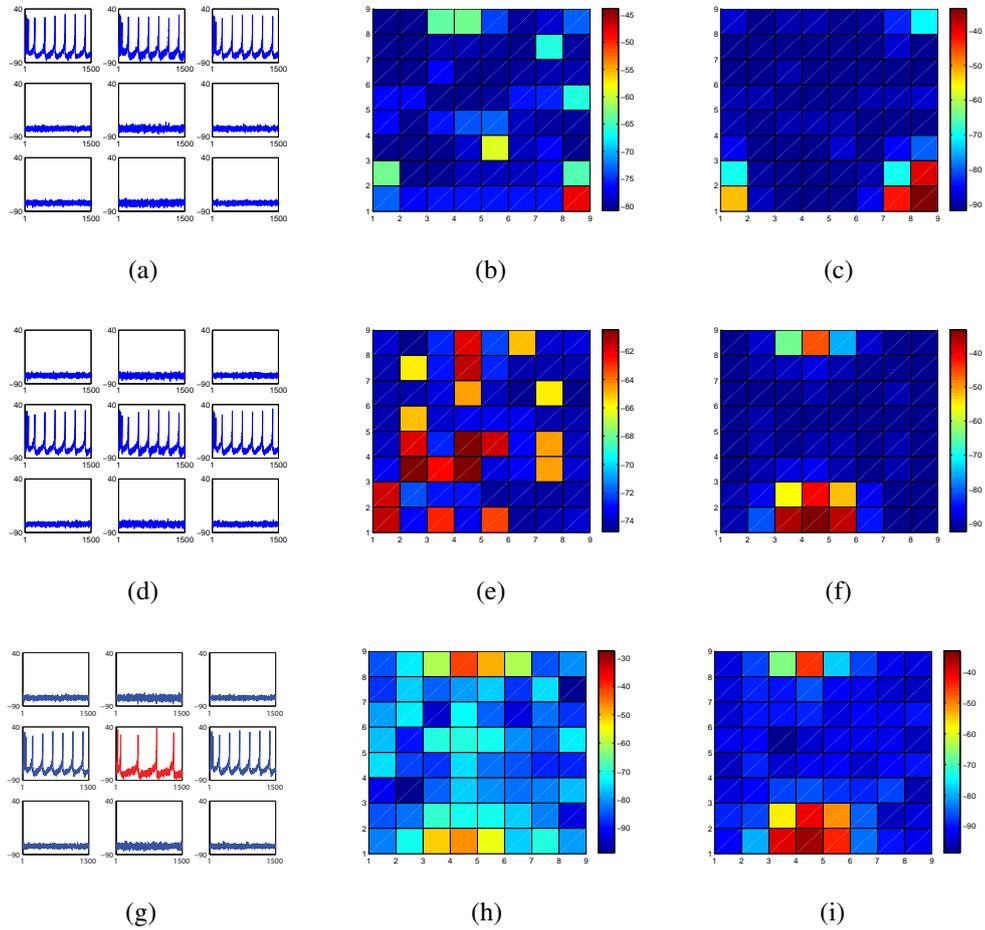


Figure 8: The network is able to reconstruct the missing feature using expectation mechanisms. When the first object is presented the ALs layer is stimulated (a) and a cluster emerges in the KCs layer. The mean of the KCs membrane potential at the beginning (b) and the end of the simulation (c) (for a total of 1500 simulation steps) is reported. During this process the plastic synapses in the ALs change according to the Hebbian rule as well as the feedback connections from KCs to ALs. When a second object is presented again, the ALs process the new features information (d) and the KCs layer converges to a new cluster (e)-(f). During this process the delayed connections in the KCs layer are modulated accordingly and the two consecutive clusters (c) and (f) will be linked together. Finally, after the learning phase, if the first object is presented, it is possible to reconstruct the missing feature (f_{22}) of the second object using the acquired knowledge (g) and the correct cluster emerges (h)-(i).

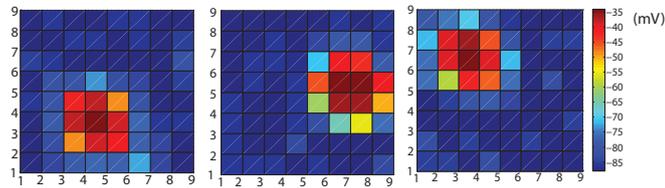


Figure 9: During the learning phase, three objects are presented to the network. In the test phase each cluster representing a given object excites the cluster that represents the following object in the sequence. Objects can be reconstructed thanks to the feedback connections from the KCs layer to the ALs.

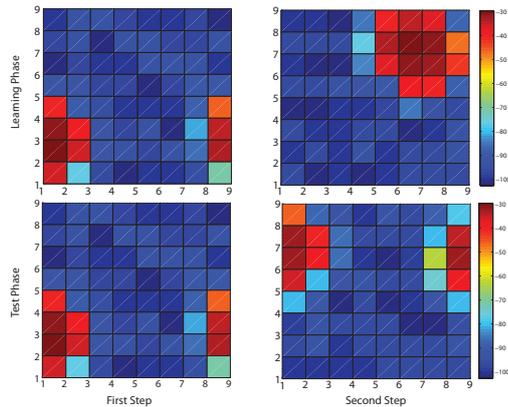


Figure 10: Behavior of the network in the case of non satisfied expectation. During the learning phase, after the presentation of two consecutive objects, the KCs layer elicits two clusters and links them through the delayed synapses. During the test phase, after the presentation of the first object, an object that does not follow the previous stored sequence is presented. In this case, at the second step the network tries to recall the second object, but the competitive topology in the first layer corrects the prediction and a different cluster is formed in the KCs layer.

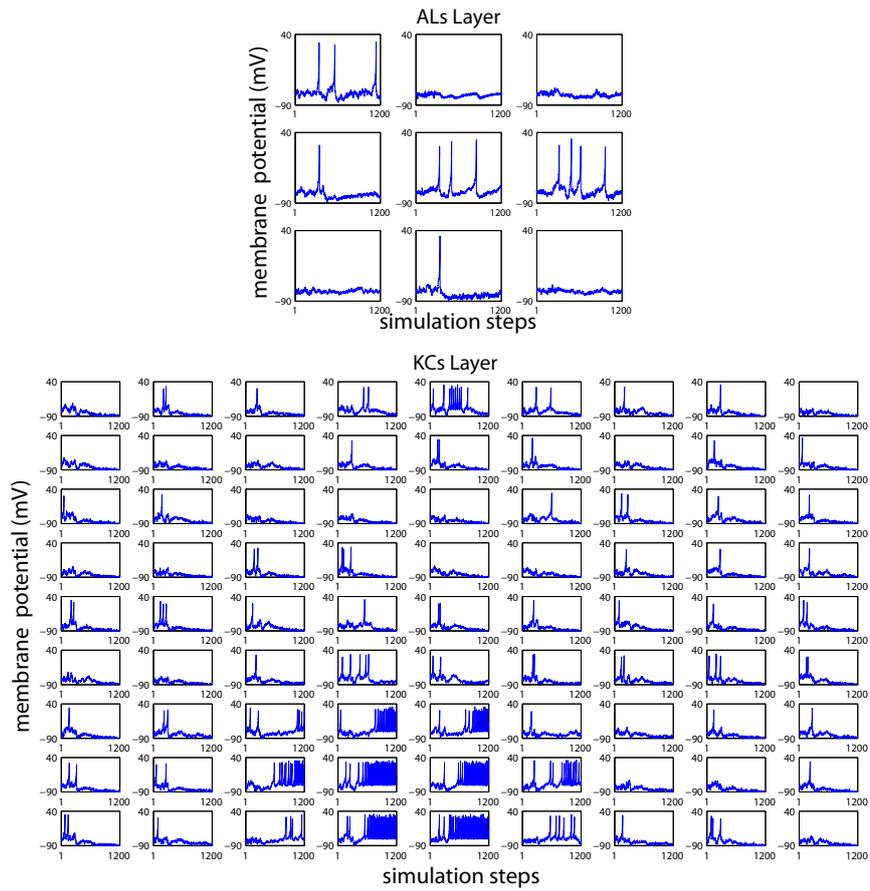


Figure 11: After the learning phase, noise can excite the KCs layer leading to the emergence of a cluster. It can be noticed the competition in the ALs layer during the transient in the KCs layer. The relative object features (f_{11} , f_{22} , f_{32}) are reconstructed in the ALs layer through the feedback connections.

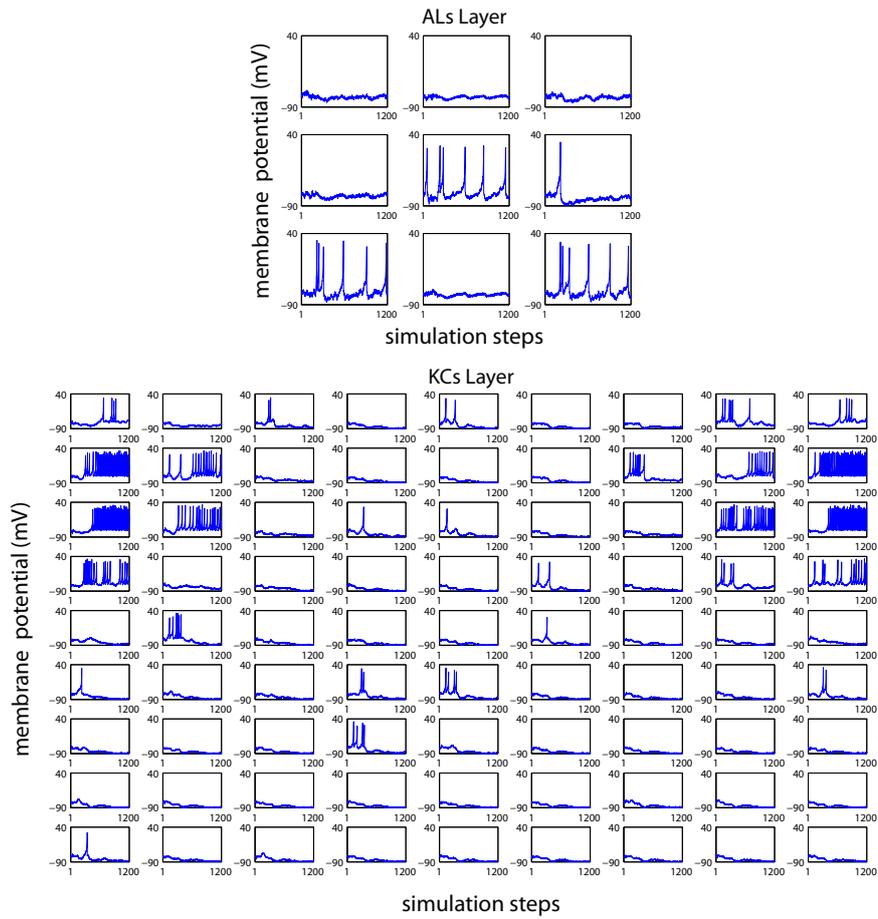


Figure 12: During the second step of the consolidation experiment the network autonomously recalls the second object. The connection between the two clusters is strengthened and the second cluster, in turn, stimulates the ALs layer, eliciting the corresponding object (f_{13} , f_{22} and f_{33}).