Modeling the Insect Mushroom Bodies: Application to a Delayed Match-to-Sample Task

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Abstract

Despite their small brains, insects show advanced capabilities in learning and task solving. Flies, honeybees and ants are becoming a reference point in neuroscience and a main source of inspiration for autonomous robot design issues and control algorithms. In particular, honeybees demonstrate to be able to autonomously abstract complex associations and apply them in tasks involving different sensory modalities within the insect brain. Mushroom Bodies (MBs) are worth of primary attention for understanding memory and learning functions in insects. In fact, even if their main role regards olfactory conditioning, they are involved in many behavioral achievements and learning capabilities, as has been shown in honeybees and flies. Owing to the many neurogenetic tools, the fruit fly *Drosophila* became a source of information for the neuroarchitecture and biochemistry of the MBs, although the MBs of flies are by far simpler in organization than their honeybee orthologs. Electrophysiological studies, in turn, became available on the MBs of locusts and honeybees. In this paper a novel bio-inspired neural architecture is presented, which represents a generalized insect MB with the basic features taken

from fruit fly neuroanatomy. By mimicking a number of different MB functions and architecture, we can replace and improve formerly used artificial neural networks. The model is a multi-layer spiking neural network where key elements of the insect brain, the antennal lobes, the lateral horn region, the MBs, and their mutual interactions are modeled. In particular, the model is based on the role of parts of the MBs named MB-lobes, where interesting processing mechanisms arise on the basis of spatio-temporal pattern formation, paradigm already investigated in robot control applications (Arena et al., 2008b, 2009c). The introduced network is able to model learning mechanisms like olfactory conditioning seen in honeybees and flies and was found able also to perform more complex and abstract associations, like the delayed matching-to-sample tasks known only from honeybees. A biological basis of the proposed model is presented together with a detailed description of the architecture. Simulation results and remarks on the biological counterpart are also reported to demonstrate the possible applications of the designed computational model. Such neural architecture, able to autonomously learn complex associations is envisaged to be a suitable basis for an immediate implementation within an robot control architecture.
Key words: neuroscience, insect brain, insect mushroom bodies, spiking neurons, learning, neural model

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1. Introduction

Despite the small number of neurons in their brains, insects show interesting capabilities to learn, categorize and recall associations and contextual information in order to solve tasks that can, in the case of honeybees, even require a complex level of abstraction (Menzel & Giurfa, 2006; Chittka & Niven, 2009; Liu

et al., 1999; Tang & Guo, 2001). Insect brains are becoming a primary source of inspiration for the design of powerful autonomous machine learning architectures and control algorithms. Within the insect brain the mushroom bodies (MBs) have attracted a lot of research attention regarding their architecture and behavioral functions for modeling artificial neural networks (Smith et al., 2008). MBs are well known in bees and flies for their role in performing associative learning and memory in odor conditioning experiments (Menzel & Muller, 1996; Menzel , 2001; de Belle & Heisenberg, 1994; Szyszka et al., 2005; Scherer et al., 2003; Liu & Davis, 2006), but they are also involved in the processing of different sensory modalities like for example visual tasks (Menzel , 2001; Liu et al., 1999; Tang & Guo, 2001), other forms of learning, and in choice behavior (e.g. Gronenberg & Lopez-Riquelme (2004); Tang & Guo (2001); Brembs (2009)). We refer primarily to the architecture of the MBs in *Drosophila melanogaster* which is simpler than in the honeybee and can be divided into substructures, called *calyx, peduncle* and five *lobes* of the lobe system. The major intrinsic neuron type is the Kenyon cell and those cells make up the MBs, the substructures of which correspond to their dendritic regions, their axons and their axonal branches, respectively. Olfactory information is projected to the calyx regions of the MBs from the antennal lobes (ALs). Recently, also feedback connections from the MBs back to the ALs have been found (Hu et al., 2010); a functional role of such connections in filtering input information is hypothesized here. MBs interact with the lateral horn region (LHs), presumably to provide a sparse representation of odors.

The ALs are modeled as a lattice of neurons, in which each neuron codifies a particular odor component. Moreover, a locally competitive topology is implemented here, as suggested by neurobiology (Sachse & Galizia, 2002). The

AL layer randomly projects connections to the MB calyx, which is composed of the dendritic arborizations of three different Kenyon cell types namely the $\alpha - /\beta-$neurons, the $\alpha^{'} - /\beta^{'}-$neurons and the γ-neurons. The $\alpha - /\beta-$ and the $\alpha^{'} - /\beta^{'}-$lobes are connected through plastic connections and demonstrate capabilities in clustering information. The LH model, as suggested by neurobiology (Perez-Orive et al., 2002), has been thought as an input-triggered system that provides a delayed global inhibition to the MB network. The actual model builds upon a previous, much more limited version, successfully used to model processes of expectation (Arena et al., 2011, 2012). The upgraded model is able to reproduce, beside the olfactory classical conditioning, more complex tasks, like delayed matching-to-sample tasks, which represent capabilities found in honeybees (Giurfa et al., 2001).

The proposed artificial neural network of the MBs provides the possibility for modelling autonomous and complex decisions with application in controlling tasks which involve different sensory modalities within the insect brain, with particular attention to honeybees and flies. In honeybees prominent visual inputs to the MBs are anatomically evident and behaviorally most relevant (Menzel , 2001); in flies there is behavioral evidence for the involvement of the MBs in visual tasks like visual context generalization and resolving contradictory visual cues (Liu et al., 1999; Tang & Guo, 2001).

2. Biological Background on Mushroom Bodies - *Drosophila* as an Example

Classical aversive or reward odor conditioning experiments in the fruit fly *Drosophila* (Schwaerzel et al., 2003; Schroll et al., 2006) have shown that acquisition of a memory, its stabilization and retrieval all require intact MBs (Kasuya et

al., 2009; Liu & Davis, 2006). Their neuroarchitecture, their input/output relations and biochemistry are worked out in quite some detail (e.g. Gerber et al. (2004); Liu & Davis (2006)). Over the years, behavioral evidences accumulated for additional pivotal roles of the MBs in non-olfactory behaviors. Liu et al. (1999) reported a function in discriminating between visual background and objects to be avoided in classical aversive conditioning experiments. Tang & Guo (2001) found a role for the MBs in disentangling contradictory visual cues when it came to decisions which object to avoid. The visual pathway to the MBs of flies is not anatomically known to date.

Mutations affecting olfactory and visual memory formation in *Drosophila* are also affecting short-term visual processes relevant to selective attention. A common component of these systems appears to be the MBs that might be involved in generating oscillatory brain activity required for attention-like processes in the fly brain (van Swinderen, 2007; van Swinderen et al., 2009). We will therefore concentrate on the neuroanatomical details of the olfactory learning and memory pathway of the fruit fly assuming that the MBs, first serving olfaction, had turned out in evolution to be a "universally useful" learning network. Thus other sensory modalities may have been fitted into a very similar neuroanatomical structure pre-existing for olfaction-related behaviors.

The computational MB-model shown in Figure 1 takes into account the actual biological organization of the olfactory pathway in flies consisting of the antennal lobes (AL), projection neurons of the antennal lobes (AL-PNs), the lateral horn (LH), the MB intrinsic Kenyon cells (KC), and extrinsic MB neurons (MB-EN1-4) as well as octopaminergic neurons (OAN) and dopaminergic Neurons (DAN). Olfactory sensory neurons (ORN) are excited by different odorant components and

project, depending on their odor-receptor type, to one of the about 62 glomeruli of the AL (Fishilevich & Vosshall, 2005).

About 150 excitatory projection neurons (cholinergic) emerge from the AL (Tanaka et al., 2008), and deliver their preprocessed information to the calices (the input region of the MBs) and the lateral horn region (responsible for congenital behavior and direct responses to olfactory stimuli). At the level of the AL excitatory and inhibitory interneurons interact in the first preprocessing of olfactory information and the AL-PNs convey this pattern of activation. On average, each of the 2500 KCs receives input from ten AL-PNs (Turner et al., 2008) so that single KCs represent different combinations of odorants.

Detailed studies on the post- and presynaptic organization of the KCs at the level of the calices revealed that $\alpha - /\beta -$ and $\gamma -$neurons can form post- and presynaptic areas, whereas $\alpha' - /\beta' -$neurons exhibit just postsynaptic sites at their dendritic branches (Christiansen et al., 2011). Synaptic input and output areas are organized in calycal microglomerular elements. Claw-like postsynaptic endings of several KCs enclose a given presynaptic projection neuron bouton. Therefore, one projection-neuron is able to contact different classes of KCs in perfect synchrony (Leiss et al., 2009). For instance, two copies of the same information might exist in different systems for differential processing. Christiansen et al. (2011) suggested that the synaptic organization is suited for dendro-dendritic (i.e. bi-directional) communication between different KCs at the level of the calyx. Perez-Orive et al. (2002) reported inhibitory input from the lateral horn into the calyx in locusts. This input leads to 20Hz-oscillations within the calyx and seems to shut off projection neuron input every 50ms (Nowotny et al., 2003). In addition to the sparseness in time there is a sparse code implemented in the way

how projection neurons converge onto individual KCs (Turner et al., 2008). Respective connections between the lateral horn and MB calices are known also in *Drosophila*, but their direction is up to date undetermined. According to Turner et al. (2008) sparse activity is useful in structures involved in memory in part because sparseness tends to reduce representation overlaps.

Neuroanatomical studies in *Drosophila* revealed arborizations of extrinsic and intrinsic MB neurons across the peduncle and mainly the lobe system. KCs have their dendritic specializations in the calyx, their axons run through the peduncle of the MB and bifurcate at its end into different MB-lobes. The γ-neurons run into the medial γ-lobe (and some bifurcate into a very small "heel"), α-/β-neurons bifurcate into the medial β- and the vertical $\alpha-$lobe. The $\alpha'-$/ β'-neurons bifurcate into the medial β'- and the vertical $\alpha'-$lobe (Crittenden et al., 1998). The lobes are the output region of the MBs and also a region for modulatory inputs (Krashes et al., 2009; Riemensperger et al., 2011).

Intrinsic neurons provide an alternative modulation pathway between different KCs and/or KCs and other protocerebral brain areas. Extrinsic neurons, on the other side, may be able to bind sensory information processed earlier in different lobes before or after any kind of modulation (see Fig. 1 EN-MB1-4).

MB modulation is one of the most interesting computational features for understanding olfactory-memory formation, consolidation and retrieval. To this end the MB model by Tanaka et al. (2008) offers a possible explanation by allocating MB substructures to different modulation units. The model takes the three different KC types and their specific neuroanatomy into account and considers the organization of the MB-lobes into segments. Those segments are defined by the arborization of extrinsic MB neurons. The $\beta-$ and β'-lobes are subdivided into

two and the $\alpha-$ and $\alpha'-$lobes into three segments per strata. Via these functional units the behavioral output of the MBs can be modulated. From here, for example, specific extrinsic MB neurons arborise, which are involved in the formation of a labile aversive memory (Aso et al., 2010), whereas some others help to integrate the internal state of hunger and appetitive memory in the fashion of a motivational switch (Krashes et al., 2009).

Some of the MB-ENs specified as octopaminergic neurons (OAN; Busch et al. (2009)) and others as dopaminergic neuron (DAN; Mao & Davis (2009)). The OANs are known to mediate the unconditioned stimulus in the reward processing (Schwaerzel et al., 2003; Schroll et al., 2006). The reward neuron orthologous to the well-known VUMmx1-neuron in honeybees (Hammer , 1993) is the OA-vUMa2 neuron in flies (Busch et al., 2009).

The DANs play important roles in the acquisition of aversive and appetitive olfactory memory in flies (Fig.1 OAN and DAN; Kim et al. (2007)). Their input to the MB subdivisions is weighing the processed information in the KCs, so that the behavioral outcome differs depending on the association of the stimulus with punishment or reward.

And last but not least KCs of the $\beta-$ and $\gamma-$lobes give rise to a functional feedback from these lobes centrifugally out to the antennal lobes via extrinsic MB neurons as shown in Fig. 1: EN-MB3 (Hu et al., 2010). Hu et al. (2010) reported a gain increase in the antennal lobes caused by this modulatory influence which may account for the formation of expectations.

Up to date there is no information on the extrinsic neurons connecting the MBs with premotor areas of the fly brain. Evidence comes from behavioral studies. Flies with ablated MBs show neither olfactory conditioned avoidance nor condi-

tioned appetitive locomotor behavior and abnormal variations in their locomotor activity, suggesting premotor pathways which can be strengthened by learning and a general regulation of premotor areas by the influence of the MBs (Martin et al., 1998; Serway et al., 2009).

Taking inspiration primarily from the fly system and from the different computational and learning capabilities of insect MBs, here a neural architecture is proposed which is useful also for visual tasks to be integrated with models of the Central Complex responsible for visual orientation. Involvement of the fly MBs in respective tasks is based on behavioral evidence. However, the much more elaborate honeybee MB system does have known visual inputs to the calyces (Ehmer & Gronenberg, 2002). Also the organization of the visual inputs to the fly MB might be not so dissimilar to the olfactory system, as parallels in the glomerular organization of the visual input at the transition from the optic lobes to the lateral protocerebrum of flies are described (Mu et al., 2012; Strausfeld et al., 2007).

The dimension of the network of the proposed computational model, in terms of a specific number of neurons and connections, does not match one to one with its biological counterpart. It indeed represents a scaled version ready for direct implementation in hardware for robot control applications (Arena et al., 2007, 2008). However, the neural architecture and biological structure have been maintained in our model.

For the learning algorithms we propose that information reaching the $\alpha^{'} - /\beta^{'}-$lobes is delayed during the path, so that the neural activity within the two lobe systems represents the current input ($\alpha - /\beta-$lobes) and the previous one ($\alpha^{'} - /\beta^{'}-$lobes). The whole neural network is modeled using lattices of spiking neurons. Moreover, learning mechanisms based on the Spike-Timing Dependent

Plasticity (STDP) are used to associate the KCs activity to a premotor area (Arena et al., 2009). Similar structures Central Pattern Generators have been already developed and can be integrated for a complete control of legged robots (Arena et al., 2003, 2005).

3. The Proposed Neural Architecture

The spiking networks used to model the insect brain blocks are based on the Izhikevich spiking neuron, proposed in Izhikevich (2003). Izhikevich neural model is well known in the literature and offers many advantages from the computational point of view. The model is represented by the following differential equations:

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

with the spike-resetting

$$\texttt{if } v \geq 0.03\texttt{, then} \begin{cases} v \leftarrow c \\ u \leftarrow u + d \end{cases} \tag{2}$$

where v is the membrane potential of the neuron, u is a recovery variable and I is the synaptic current. The value used for the parameters are different between ALs and MBs. In the first case the 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 as explained in the next sections.

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:

$$\varepsilon(t) = \begin{cases} Wt/\tau \exp(1 - t/\tau), & \texttt{if } t > 0 \\ 0 \ , & \texttt{if } t < 0 \end{cases} \tag{3}$$

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

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

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, whereas positive constants A_+ and A_- represent the maximum variation of the synaptic weight. Applications of this learning paradigm to robot control, together with details on the parameters, are reported in Arena et al. (2009b). All the equations are solved using the Euler method with an integration time of 0.08 ms.

3.1. Antennal Lobe Model

Inspired by the insects' ALs, we can assume to have a layer able to codify the odor components (i.e. odorants) or, moving to the visual domain, the extracted

features of objects. As in the insect ALs each glomerulus is able to detect a specific odorant (or a specific side chain of different odorants), in our model each neuron in this layer encodes a particular aspect related to a detected object. Neurons within the AL model are organized in groups. Each group codifies a kind of feature or odorant, and neurons in the same group codify different values or intensity of that feature. Neurons in the same group are linked together through inhibitory synapses. This topology implies that, when the AL 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. Therefore, when an odor is presented to the network, it is decomposed within the AL in its relevant odorant features, and the corresponding neuron of each feature group remains excited.

In the proposed simulations, the AL layer is constructed of a 4x4 lattice. In particular, there are four groups of neurons (f_1, f_2, f_3 and f_4), and each group is made of four neurons (for instance, the neuron j in the group f_i will be called f_{ij}). Neurons in the same group are connected to 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, are increasing the efficiency of the synaptic connection 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 encoding the features of that object are excited with an input current $I_{AL} = 70pA$.

The AL 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 realize the primary odors representation. Each neuron in the AL layer

has a probability P = 0.25 of being connected to the KCs. The choice of the sparse connections between the first and the second layer is directly drawn from the sparse connections in the biological counterpart (Perez-Orive et al., 2002). The main issue is related to the design of connections within each layer. The synapses between the first and second layer have a fixed efficiency of $W^{AL,KC} = 10$.

3.2. Model of the Mushroom Body Lobes and their Interaction with the Lateral Horn

Like in the biological counterpart, and as outlined in the previous section, the KCs of the MBs project, through the peduncle, to five main appendices, called lobes. They possess roughly the same topology, but were shown to serve different functions. Our architecture is restricted to model the structure and functions of the $\alpha - /\beta -$lobes, and the $\alpha^{'} - /\beta^{'} -$lobes, divided into two main networks. The two networks representing the KCs, project random dendritic arborizations to the ALs. Each network is designed so as to show a cooperative-competitive dynamics: if excited, the neurons in the AL layer begin a competition and, after a transient, only one cluster of neurons will remain active and stable. The LH model resets both the networks each 120 ms.

In our architecture each lobe is a 9x9 lattice of neurons with a toroidal topology. The neurons in this layer are all connected to 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 $W^{KC}_{near} = 50$. It is also connected with the other neurons of the lattice through inhibitory synapses with an efficiency of $W^{KC}_{far} = -30$. This set of connections gives the network its clustering capabilities (Arena et al., 2011). The time constant

used for fast excitatory and inhibitory synapses in the network is $\tau_{fast} = 1ms$.

The lobes are connected to each other through two sets of plastic synapses, one from the $\alpha-/\beta-$lobes to the $\alpha^{'}-/\beta^{'}-$lobes and the other set from the $\alpha^{'}-/\beta^{'}-$ to the $\alpha-/\beta-$lobes. It is known from neurobiology that the neurons belonging to the two clusters are morphologically different. Moreover, whereas $\alpha-/\beta-$ neurons give information back to the ALs, generating feedback at the sensory stage, the $\alpha^{'}-/\beta^{'}-$ neurons provide no output signals back into the system, at the level of the calices. So we can assume that the information which arrives to these lobes is retained there and used as a kind of backup copy for memory purposes. In particular this is analogous to hypothesize that the signals coming from the ALs through the calices are delayed while arriving in the $\alpha^{'}-/\beta^{'}-$lobes. The implementation of this concept implies that the winning cluster in the $\alpha-/\beta-$lobes represents the odor presented to the ALs at the actual step, whereas the winning cluster in the $\alpha^{'}-/\beta^{'}-$lobes represents the odor presented to the ALs at the previous time step. The synapses between the lobe systems are reinforced when two clusters in different lobes are concurrently active. This structure can be used to detect whether the object presented to the ALs remains the same in two subsequent steps. In fact, if this is true, the plastic synapses between the lobe systems create a positive loop between the clusters in the two lobe systems: this allows the networks to increase the spiking rate of the active neurons. We will assume also to have a neuron sensitive to the firing activity of the $\alpha-/\beta-$lobes network. The sequence of the network evolution is schematically shown in Fig. 2 where, in the first step, two subsequent presentations of the same object generate a positive loop between the two lobe systems and a corresponding increase of spiking rate, whereas during the following presentation, a different object is identified as a con-

sequence a loop is no longer generated and the spiking activity within the lobes is no longer boosted. During the first 1000 integration steps, the winning clusters are able to emerge independently in the two lobe systems. Soon after the synaptic connections between the winning clusters are strengthened and the effect of the connections is evaluated for another 500 integration steps. Only if the cluster associated with the first object in the $\alpha' - /\beta'-$lobes and that one associated with the second object in the $\alpha - /\beta-$lobes are the same (see Fig. 2 second column, the yellow and red dot indicating the winning clusters are in the same position), a positive loop can be created. If the two active clusters in the two lobe structures are not associated with the same object, the positive recurrent connections are not able to create a loop as shown in the last case examined in Fig. 2. In our model the mean spiking activity of the $\alpha - /\beta-$lobes is encoded in a neuron used to discriminate the matching/no-matching events.

3.3. Premotor Area

Biological experiments revealed that context generalisation, visual attention, salience based fixation and decision making are all MB mediated behaviors (Liu et al., 1999; van Swinderen et al., 2009; Tang & Guo, 2001; Xi et al., 2008; Zhang et al., 2007). Furthermore, aspects of the control of motor activity are also linked to the MBs. For example, initial motor activity in MB-ablated flies is high, whereas long-term measurements show a decrease in motor activity (Serway et al., 2009; Martin et al., 1998).

In the proposed model the activity of the KCs in the MB-lobes is finally used to control the system behavior, making a link to the Premotor Area primarily useful for robot control puerposes. Let us consider a simple choice: the agent can decide if the presented object is attractive and worth to be followed or not. The MBs

and the Premotor Area are connected via an associative structure that uses the STDP paradigm for a positive/negative-based reinforcement learning. In particular, four different neurons were considered: the *Reinforcement Neuron* (RN), the *Matching Neuron* (SN), the *No-Matching Neuron* (DN) and the *Premotor Neuron* (PmN). The network topology is depicted in Fig. 3. When the reward signal is active, an input current of $I_{RN} = 100pA$ is provided to the RN. The RN is connected to the PmN through a fixed synapse, $W_{RN} = 40$, representing the unconditioned response to the reward. The SN is a special neuron that we will assume to be sensitive to the mean spiking activity of the $\alpha-/\beta-$lobes. In particular, if the activity of these lobes is larger than a given threshold, the SN is active, excited through a constant current $I_{SN} = 40pA$. The SN is connected to the PmN through a plastic synapse, as well as the DN that is spontaneously active but can be inhibited by the SN. Moreover, another set of plastic STDP synapses links the $\alpha - /\beta-$ neurons to the PmN for a classical associative learning purpose.

4. Simulation Results

Inspired by the biological background, a set of experiments on learning in MBs are proposed in this section. The setup is able to learn to associate a targeting behavior to specific odors, depending on the specific odorant features, using a classical conditioning mechanism. At the same time, a more complex kind of learning, based on the delayed matching-to sample task has been considered.

In a first experiment the capability of the network to solve a classical conditioning task is shown. The simulation is divided into two phases, a learning and a test phase, and it has been repeated with two different testing setups. In particular, in the learning phase a sequence of ten odors (here simulated through abstract ob-

jects) is presented to the network. We are assuming to have three different odors: A, B and C. We assume that odor A is represented by odorant features associated with neurons f_{11}, f_{21}, f_{31} and f_{41} of the AL layer, odor B is represented by neurons f_{12}, f_{22}, f_{32} and f_{42} and odor C by the neurons f_{13}, f_{23}, f_{33} and f_{43}. We associate a positive reinforcement signal to odor A and so, whenever odor A is presented, the reinforcement neuron is also excited. The STDP is then used to establish the correlation between odor A, represented by a cluster in the $\alpha - /\beta-$lobes, and the PmN. During the subsequent test phase, no reward is given and the network must use the stored experience to make a choice that is visible in terms of level of activation of the PmN. In a second experiment the capability of the architecture to implement a more sophisticated kind of learning is investigated. In this case, the architecture should learn to activate the PmN only if two matching objects are presented in sequence, according to the matching-to-sample paradigm. In order to avoid possible ambiguities, we indicate as *simulation step* the interval between two different presentations of objects (1500 integration steps), whereas the integration step corresponds to 0.08 ms. The STDP is then used to establish the connection between the SN, active only when the loop interaction between lobes indicates the presence of a persistent object, and the PmN. As it is possible to notice from Fig. 4, the presence of loop connections between the lobes increases the spiking activity. In particular, Fig. 5 indicates that it is possible to find a threshold in the neural activity of the $\alpha - /\beta-$lobes to distinguish the activity in the case of loop and no-loop connection between the lobe systems.

Fig. 6 shows the evolution of the membrane potential of the PmN and reward signal provided during the learning phase in the first and second experiment. During the learning phase the PmN follows the reward: in the first case associated

with odor A and in the second case associated with the Matching event. The evolution of the synaptic weights subject to STDP is shown in Fig. 7 where only the trend of the winning neurons in the $\alpha - /\beta -$lobes is shown. It is evident from the weights evolution: in the first case the system learns the correlation between the reward and the odor A, whereas in the second case the initial ambiguity between odor A and a Matching event due to the particular sequence of presented objects is solved around the end of the simulation, when the correlation between reward and Matching event is well established. However the STDP learning rule is not only applied to the winning neuron (i.e. the most active one) but also to the other active neurons in the winning cluster of the $\alpha - /\beta -$lobes lattice. Finally, the behavior of the network was tested after the learning phase, without presenting a reward signal (see Fig. 8). The knowledge, acquired in the form of synaptic weights, is able to correctly activate the PmN either when the preference for odor A is learned or when the preference for Matching is formed. In this last case the network is able to identify Matching events even if odors never presented before are given as input (i.e. new odor C).

5. Discussion and Conclusions

Insects are a point of reference in neuroscience and their autonomous learning capabilities are amazing considering their tiny brain dimensions and their neuronal connectivity. Physiology and biochemistry of these intriguing architectures have been deeply investigated in these last years both to understand the sources of these astonishing capabilities and to design powerful autonomous machines and control algorithms. Inspired by biological evidences in honeybees and flies, a neural architecture has been designed and tested in simulations. The architec-

ture derives from the olfactory and learning system primarily of flies and was found able to solve classical conditioning but also more complex tasks, not yet discovered in flies, like the delayed matching-to-sample tasks. The network was suitably scaled, in terms of dimensions, with respect to the biological counterpart, to provide both an efficient and rapid design using conventional computer architectures, and a direct shortcut to an efficient hardware implementation, in view of controlling, in the near future, one of the robot prototypes available in our labs.

To understand neural circuits in insect brains, several approaches can be followed concurrently: both behavioral and neurophysiological experiments, and the realization of computational models at different levels of complexity.

Interesting examples of MB modeling are available in the literature. A well-known model for olfactory associative learning was proposed by Scherer et al. (2003). This model addresses the larval stage, reproducing the effect of positive and negative reinforcements in olfactory conditioning. On the basis of these biological evidences, other ideas were developed to design biologically plausible models of the MBs. A more detailed analysis was performed by Turner et al. (2008) who addressed the olfactory representation in *Drosophila* on the basis of KC in-vivo recordings.

Smith et al. (2008) designed a high-level computational model of MBs for associative learning using simplified models of neurons and synapses and a learning rule based on activity dependent pre-synaptic facilitation. The developed model, in order to fill the gaps in existing knowledge, acquired some information from invertebrate studies and in particular the synaptic mechanisms underlying learning and memory in *Aplysia*. This procedure has been followed also in our present study, where knowledge on the MB functions was taken from bees and other in-

sects and transferred to *Drosophila*. The feedback mechanisms used in Smith et al. (2008) to stabilize the learning procedure allow to increase synaptic strength at an initial level appropriate for an association and to prevent strength increase for established associations. Our model uses STDP and Hebbian learning to create associations between stimuli and we hypothesized that the matching of similar samples can be obtained through resonance using a positive feedback loop. However, the feedback mechanisms used in Smith et al. (2008) to avoid the further increase of synaptic weights for established associations will be considered to further refine the proposed model at the level of the pre-motor area for behavior selection.

Self-organization properties of the MBs are discussed in Nowotny et al. (2005). Their model is based on spiking neurons and synaptic plasticity, distributed through different layers. It is able to show consistent recognition and classification of odors. In their study the MBs are assumed to be multi-modal integration centers combining olfactory and visual inputs. As in our current model, their system capabilities are independent of the type and source of information processed in the MBs.

Wessnitzer et al. (2012) investigated the interaction of MBs and ALs in non-elemental learning. Different levels of learning and reinforcement mechanisms were considered at the stage of the KCs to create a coincidence detector and non-elemental learning. Our present study considers learning at the KC layer and also plasticity at the level of the AL as suggested by Sachse & Galizia (2002). They had applied important filtering mechanisms to reduce noise and reconstruct missing features directly at the input level. Moreover, the different roles of specific lobes in the MBs, not considered in Wessnitzer et al. (2012), has been addressed

in our current computational model.

According to the authors, the learning capacity of the model by Wessnitzer et al. (2012), which is a simplification of the fly MBs, seems to be larger than the capacity shown by flies in shock-odor association experiments. Our current model has not been compared to fly experiments, which do not exist to date. However, the model shows that the MB structure is well suited for performing matching-to-sample tasks.

In the actual model, as previously outlined, single objects are consecutively presented to the network, which has to decide if the actually presented object matches or not the previously presented one. Our model does neither take notice of the type of features shown by the objects, nor of the fact that multiple objects could be contemporarily present in the environment, but considers the object presented to the network as the results of a segmentation. Moreover, the network parameters were designed to allow a learning convergence within a few reward cycles. This last choice was adopted in view of a robotic implementation of the network. However, the network reported here shows the key ingredients for modeling a generalization of the matching-to-sample task: the concept of sameness. In fact, biological experiments in honeybees present learning campaigns involving much longer series of presentations and reward cycles before the animals grasp the concept of sameness. Moreover, several sensory modalities are commonly involved. All these aspects could be considered in a generalization of our network, which therefore could be useful to model the concept of sameness.

In conclusion, the model architecture discussed here represents a fundamental building block toward an artificial neural processing structure unifying different functionalities, and performing different behaviors, that biological counterparts

are able to show.

Acknowledgement

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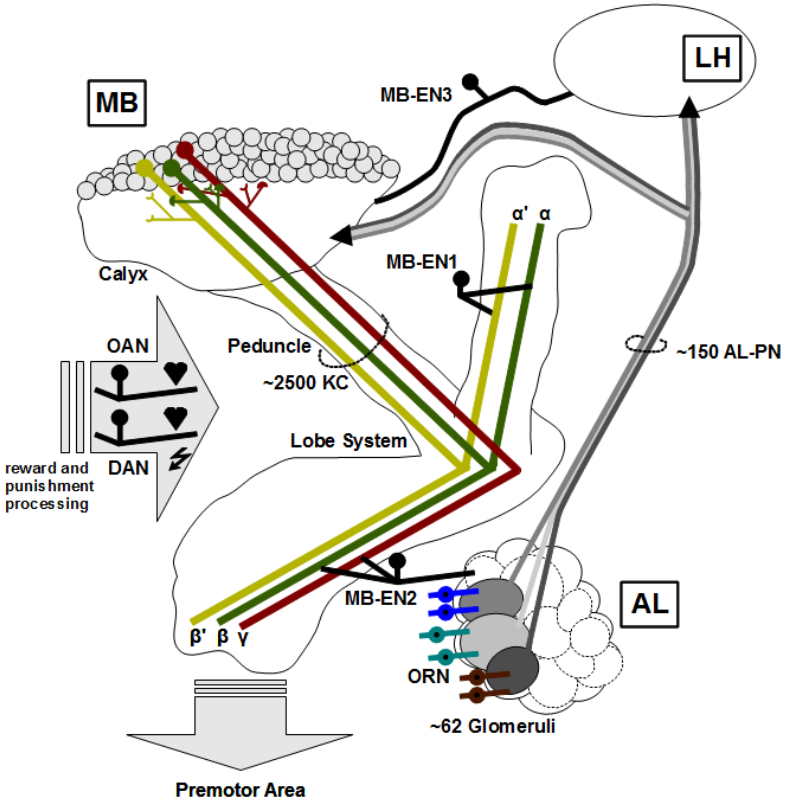


Figure 1: Block scheme of the processing of odor stimuli in insects. Olfactory receptor neurons (ORN) transfer information to the Antennal Lobes (AL). Each of the 62 glomeruli there is specific for a particular odor receptor. The ALs' activity is transferred through the Projection Neurons (AL-PN) to 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 mixed synaptic terminalia (postsynaptic (open semicircle) and presynaptic (full semicircle) allowing for inter-KC traffic. The peduncle of the MB is composed of KC axons which project into five different lobes of the lobe system: ($\alpha - /\beta-$neurons (green) bifurcate in the $\alpha-$ and $\beta-$lobe, $\alpha' - /\beta'-$neurons (yellow) bifurcate in the $\alpha'-$ and $\beta'-$lobe, γ-neurons (red) project in the 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 a direct neuronal link is unknown to date.

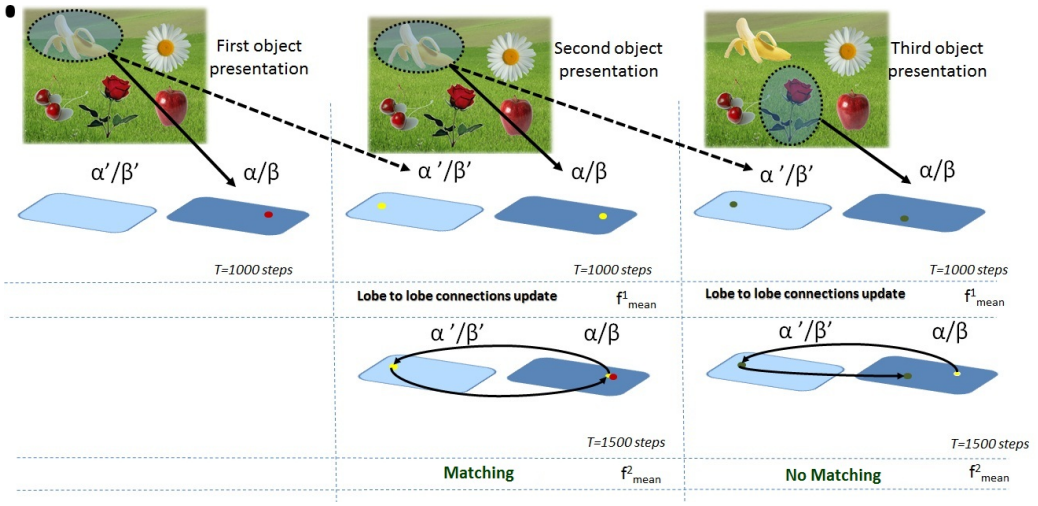


Figure 2: Processing steps executed by the network during the presentation of a series of odors (here presented through objects). When the first object is presented information about its characteristics are transferred to the $\alpha-/\beta-$lobes of the MBs and a cluster arises in the lattice (represented here by objects). During the presentation of a second object the same process for the $\alpha-/\beta-$lobes is performed whereas the $\alpha^{'}-/\beta^{'}-$lobes are exited by the previously presented object. These presentations lead to the emergence of two clusters in both of the lobe systems (i.e. after T=1000 simulation steps) and the plastic synaptic lobe-to-lobe connections are increased: the connection between the previously winning neuron of the $\alpha-/\beta-$lobes and the current winning neuron of the $\alpha^{'}-/\beta^{'}-$lobes is strengthened together with the synapses between the current $\alpha^{'}-/\beta^{'}-$winner and the current $\alpha-/\beta-$winner. The mean spiking activity of the $\alpha-/\beta-$lobes (f^2_{mean}) computed in the interval [1000 - 1500] integration steps is then compared with the activity without the lobe-to-lobe connection (f^1_{mean}). If a loop has been created (i.e. the winning neuron in the $\alpha-/\beta-$lobes is in the same position) a relevant increase in the spiking rate is obtained allowing the matching/no-matching discrimination.

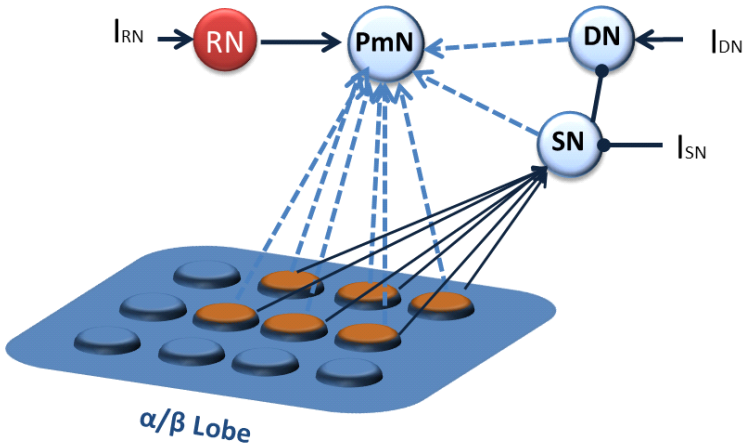


Figure 3: Scheme of the interaction between the $\alpha - /\beta-$lobe layer in the MBs and the Premotor Area. Plastic synapses (dashed lines) connect the lobe layer with the Premotor Neuron (PmN) as well as the Matching/No-Matching Neurons (SN and DN) with PmN. Fixed synapses are shown as solid lines (for the sake of clarity only a subset of connections coming from the $\alpha - /\beta-$lobe layer is visible in the scheme). If the spiking activity of the lobe layer is high enough, the generated current is able to activate the SN that otherwise is inhibited by the current I_{SN}. The SN inhibits the DN that is excited by a constant current I_{DN}.

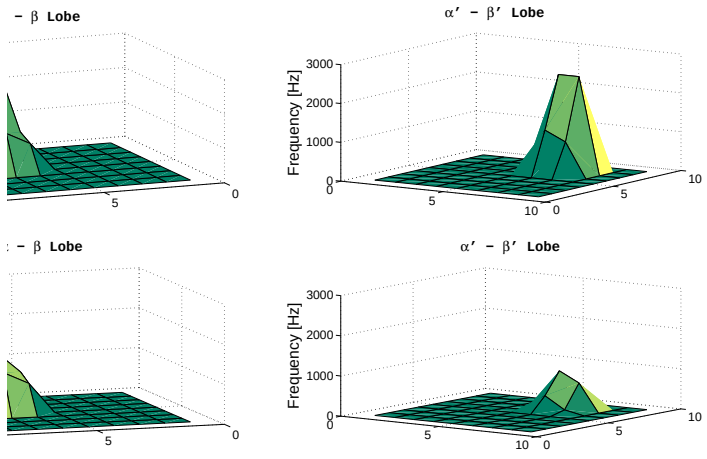


Figure 4: Clusters of spiking activity in the $\alpha - /\beta -$ and $\alpha^{'} - /\beta^{'} -$lobes in the case of loop and no loop connection between lobes. In the first case the activity of the networks is raised. The color indicates the level of activity in terms of frequency following the level reported in the frequency axis; warmer colors represent higher activity.

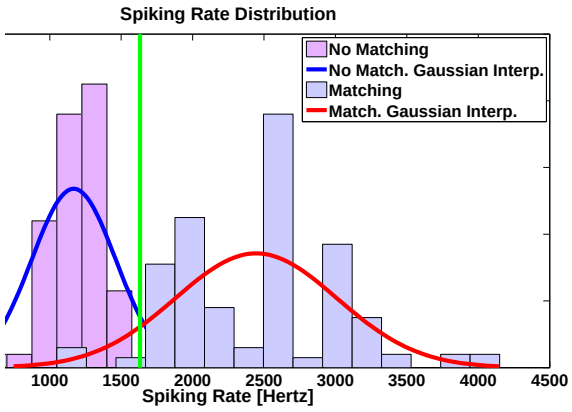
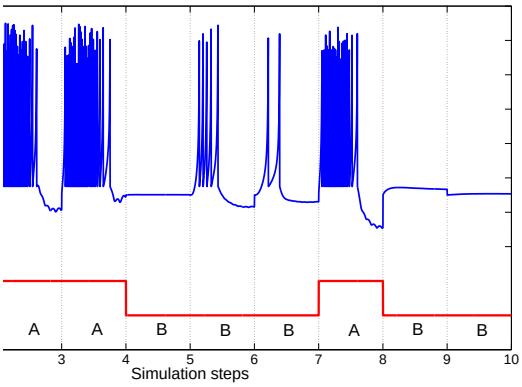
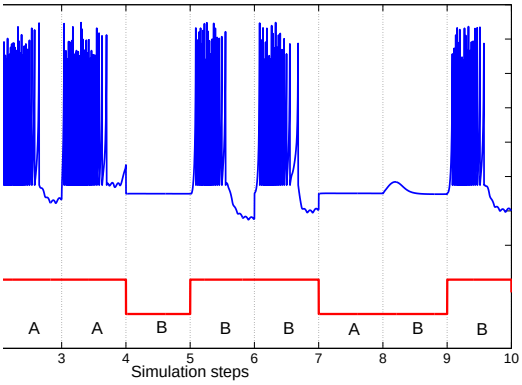


Figure 5: Statistical distribution obtained over 500 simulations of the mean spiking activity of the $\alpha - /\beta -$lobes after the increase of the feedback connections between lobes. When a loop arises, the spiking rate is significantly increased and choosing a threshold at f = 1632 Hz it is possible to distinguish the Matching/No-Matching of two consecutive presented objects, with an error of about 3%.

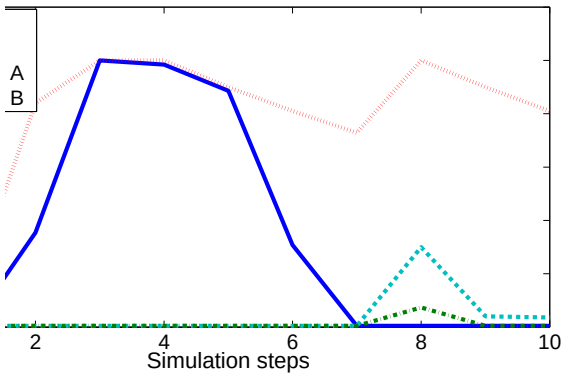


(a)

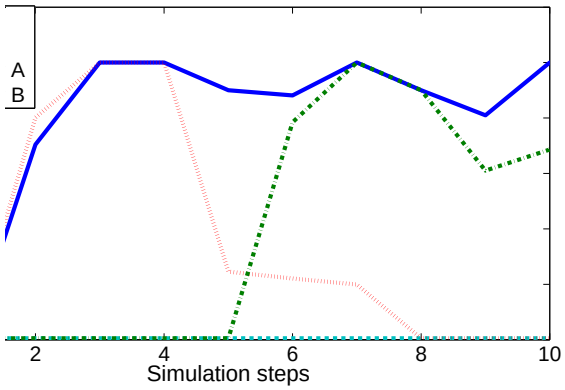


(b)

Figure 6: Evolution of the membrane potential of the PmN and reward signal provided during the learning phase. In simulation (a) the object A is rewarded whereas in (b) the same sequence of objects is presented as in simulation (a), but the Matching is reinforced. When the PmN is active the system indicates its preference for the presented object and a following behavior is elicited.



(a)



(b)

Figure 7: Evolution of the synaptic weights to the PmN, when the object A is rewarded (a) and when the Matching event is reinforced (b). Only the weights associated with the winner neuron (i.e. the most active one) are shown even if all the active neurons in the winning cluster are subject to the STDP learning.

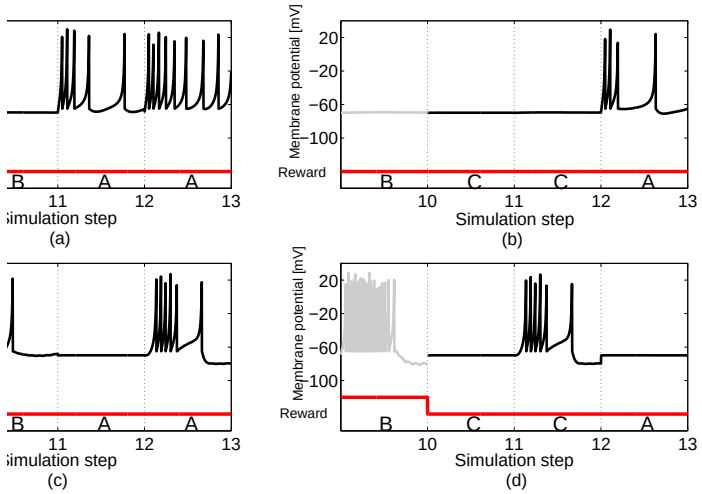


Figure 8: Results of the testing phase when the reward in no longer provided to the system and an autonomous decision has to be taken. The last simulation step of the learning phase (grey lines) and three new steps for the test phase (black lines) are shown. After learning, in which object A was rewarded (Fig. 6(a)), the system is able to follow A also during the test phase (a) and does not show any preference when new objects are presented (b). After learning, during which each Matching event is reinforced (Fig. 6(b)), the system is able to recognize autonomously successive presentations of the same object (c) even if it was never shown before to the network (d).