

## The Insect Mushroom Bodies: a Paradigm of Neural Reuse

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### Abstract

This paper is devoted to discuss the implementation of models, which are inspired by the fly *Drosophila melanogaster* and able to handle open problems in the field of robotics such as attention, expectation and sequence learning. The role of the Mushroom Bodies (MBs) in solving these tasks is analyzed in detail and a unifying plausible biologically inspired model is proposed. The developed neural structure is able to show different capabilities in line with the paradigm of neural reuse. The same neural circuit can be exploited to accomplish multiple tasks showing interesting capabilities such as attention, expectation and delayed match-to-sample. The simulation results here reported suggest at the same time new neurobiological experiments suited to better understand the underlying mechanisms, to verify the hypotheses formulated and to prove the biological significance of the results.

### Introduction

Efforts to build efficient and adaptive machines stimulated a lot of researchers to take inspiration from Nature for designing, modeling and implementing bio-mimicking circuits and systems able to reproduce specific biological behaviors: locomotion, learning, recognition and others. Since the beginning of this scientific wave, which dates back to the early part of the last Century, two main approaches were established. The first one belongs to the field of artificial intelligence; it took the high level capabilities of living beings as starting point and aimed at designing abstract, yet sometimes very well performing computational models. The second one, called connectionism, started from modeling the structure of the brain at different levels of resolution, with the claim that a good model of the low-level topology and function should lead to the emergence of behaviors well mimicking the biological counterpart, even with regard to high-level functions (Rumelhart and McClelland, 1986). Very recently this second research field successfully exploited innovative tools and methodologies from neurobiology and neurogenetics, with an effectiveness impossible to predict only two decades ago. These new tools opened the way to novel insight into the brain and tremendously contributed to unravel a lot of surprising functions of neural tissues. One of these findings is the so-called *neural*

*reuse*. The term refers to a very common property of neural assemblies, i.e. neural circuits established for one purpose are exploited, recycled, redeployed, during evolution or individual development for other different purposes, often without losing their original functions (Anderson, 2010). This research field is widely supported both by physiological observation and by imaging experiments (i.e. fMRI), where in a considerable number of cases especially high-level cognitive functions are involving the concurrent activation of different areas of the brain otherwise (and well known to be) involved in completely different functions. Insects possess a much simpler brain structure than mammals: their brains were miniaturized during evolution in response to constraints like energy consumption. Notwithstanding their much scaled-down brain size, insects are able to show an impressive number of adaptive behaviors, until a few years ago ascribed only to higher animals (Chittka L., 2009): the smaller brain size did not prevent important capabilities. Considering the fruit fly *Drosophila melanogaster*, one of its first-studied forms of learning is related to olfaction. This learning process has been localized in the Mushroom Bodies (MBs), one of the two prominent insect brain neuropiles of the protocerebrum; the other one is the Central Complex (CX). MBs are commonly considered as a model system for the biochemistry and the connectivity of how synaptic networks can form memory and store information. MBs are responsible for both the short-term and long-term component of olfactory memory. Several different experiments demonstrated how, through classical conditioning, flies can associate a meaning to olfactory inputs after pairing them with positive and negative reinforcement signals (Gerber et al., 2004). Compared to the rest of the insect brain, MBs have attracted a lot of attention witnessed by the recent specialized literature, since, besides olfactory processing and learning, recent studies identified MBs as also responsible for other learning processes (Scherer et al., 2003; Liu, 2006) and choice behaviors (Gronenberg and Lopez-Riquelme, 2004; Tang and Guo, 2001; Brembs, 2009). By modeling the MBs as a pool of spiking neurons divided into different lobe systems and introducing the synaptic connec-

tions identified between the MB intrinsic Kenyon cells and the other structures directly involved like Projection Neurons (PN), Antennal Lobes (AL) and the Lateral Horn (LH), it is possible to investigate the emergence of interesting neural activities that can establish specific behaviors shown in flies, like attention (Arena et al., 2012b), expectation (Arena et al., 2012a) and delayed-matching to sample tasks (Arena et al., 2013) that have been recently proposed. The role of MBs in motor learning is also known from fly experiments: in particular the short-term memory component is not obtained if MB plasticity is inhibited in mutant flies. MBs can be modeled as a reward-driven parameter adapter that improves the fly performance while a task like climbing over a chasm is continuously repeated for multiple times (Pick and Strauss, 2005).

This paper revisits a recently introduced low-level model of the fruit fly *Drosophila melanogaster* MBs under the aspect of neural reuse. It will be shown how the same neural structure can concurrently give rise to a number of different adaptive behaviors, which are also encountered in the biological counterpart. Neural reuse in action will be shown referring to behaviors ranging from classical conditioning, to attention, expectation, consolidation and delayed-matching-to-sample. All these last capabilities can be easily transferred to robotic structures for the implementation of real-time adaptive behaviors.

### Neural Reuse Theory

Various general theories were proposed on the overall functionality of the brain. Among them are two main lines of research worth to be considered in the context of this paper: *Massive Modularity* and *Neural Reuse*. The first theory is mainly drawn from Evolutionary Psychology (Sperber, 2001) and claims that brain processing can be studied by decomposing it into dissociable functional components that vary independently of one another (Carruthers, 2006). Indeed this is a very useful approach, especially when it comes to dealing with complex brains: decomposing and localizing modular blocks in some cases allowed focalizing on specific brain functions. On the other hand, the Neural Reuse theory of brain processing appears to be radically different. It starts from the fact that brains are complex dynamical systems. It refrains from the idea to functionally break a complex function in sub-functions and to assign these functions to specific parts, but rather applies a holistic and somehow heuristic approach to brain functions, which has a lot in common with the complex dynamical system theory. It is grounded on the concepts of *network thinking* and pays attention to higher order brain functions as patterns of neural activity emerging from the overall behavior of a complex system, caused by the spatio-temporal, self-organised, synchronized activity of different parts of the brain working as an orchestra. This concept has been recently studied from the physical point of view especially in simple brains, like the one of the worm

*C. elegans*. These studies demonstrated that network theory can topographically and dynamically address brain dynamics, at least in those small neural assemblies (Dunn et al., 2004). According to the complex system approach, brain behavior can be described in the language of Patterns, and it is most powerful when several, particularly higher brain areas are involved. The decomposition approach is powerful when specific, mostly sensory-input related processing can be broken up into specialized functions. On the other hand decomposition can be too restrictive when looking for much higher functions, like learning, decision making, multisensory processing and complex sensory-motor loops. Within this perspective of complex tasks, if multiple brain areas are involved, it directly derives that various behavioral purposes have to be achieved concurrently. This means that the same spatial temporal patterns emerging from one neural lattice are exploited at the same time in multiple behaviors. This is the core of the *Neural Reuse Theory* (Anderson, 2010). This concept appears to be radically different from the massive modularity concept, even if also neural reuse accepts some functional bias within individual brain regions, especially for those dealing with specific sensory features; it poses a specific distinction between the concept of *work* and that of *use* (Bergeron, 2008). The former is related to the fixed low-level functions of specific brain regions whereas the latter refers to the way these workings are arranged together for many different and concurrent uses of those same regions. The concept of neural reuse can be considered in a phylogenetical and ontogenetical perspective: phylogenetically driven, in the sense that evolutionary processes are biased toward using already functioning circuits over introducing new ones; ontogenetically driven, since learning, with the addition of neural wiring, is one powerful possibility to connect different brain regions and creates cross-over associations. Along these lines, the *Massive Redeployment Hypothesis* (Anderson, 2007) assesses neural lattices that are massively re-used in different high-level functions, since they can be connected in different ways, leading to very different functions. We'll try to apply the introduced neural reuse paradigm on a specific example, a multifunctional structure of the insect brain called Mushroom Bodies. Cittka and Niven (Niven and Chittka, 2010) already asserted that insect brains have the suitable size to try to investigate neural reuse in action, since in these small brains, the relatively low number of neurons and mainly short-distance connections are candidate elements for neural reuse, even if circuits are composed of different brain areas. For example, a retention of aversive olfactory memory from larvae to adult flies (Tully et al., 1994) suggests a reuse of particular neural structures through metamorphosis. The smaller the brain, the larger the need for neural reuse. Even if anatomical modularity is clearly given in such small brains, it is also true that a lot of sensory-motor behaviors involve different brain sectors. The insect brain thus appears to be a net-

work mainly composed of locally connected circuits, which however are connected through rare, even single-unit made, long-range links. Whereas modularity increases energy efficiency, the presence of long-range connections appears to promote neural reuse. Therefore invertebrates are a suitable class of animals for neural-reuse investigation, and also for finding an expected compromise between massive modularity and reuse.

### Mushroom Bodies: Neurobiological aspects

The MBs of the fruit fly *Drosophila melanogaster* MBs are a paired structure of the protocerebral hemispheres. The most important constituents of the MBs are the 2500 Kenyon cells (KCs) per side which run in parallel from the input-region calyx through the peduncle and, after a bifurcation, to specific appendices, called lobes. These possess roughly the same topology, but are differently connected to the other neural structures. Among them are the  $\alpha - \beta$ - and the  $\alpha' - \beta'$ -lobes. In flies, there is a prominent olfactory input from the antennal lobes into the calices (Masse et al., 2009). Input from other sensory modalities is not topologically identified in *Drosophila*, but the role of MBs in tasks related to vision, decision making and behavioral adaptation have been reported e.g. in Liu et al. (1999) and Tang and Guo (2001). In the insect brain, MBs interact with Lateral Horns (LHs) and Antennal Lobes (ALs). Recent studies have shown that mutations affecting olfactory-memory formation in *Drosophila* also produce distinct defects in visual attention-like behaviors (van Swinderen and Flores, 2007), suggesting that parts of MBs are reused in several different behavioral contexts and across several sensory modalities. MBs and LHs codify the spatio-temporal information coming from the glomeruli of the ALs. Connections between LHs and MBs have been found, whose entity in *Drosophila* is not well known, but in locusts, which produce an inhibitory effect to the MBs neurons (Perez-Orive et al., 2002); in *Drosophila* they are not yet identified. Not anatomically obvious in *Drosophila*, but in honeybees, MBs receive inputs from other sensory modalities but olfaction like vision, gustation and mechanosensation. In flies and bees, the MB lobe region receives information on sugar reward or electric shock through octopaminergic and dopaminergic neurons, respectively. There is an output of the MBs to pre-motor areas of the brain.

A general block scheme of the interactions among the different neural structures involved in the proposed model is depicted in Fig. 1.

Inside the MBs the flow of information is through the Kenyon cells from the calyx towards the lobes. Neuroanatomical studies in *Drosophila* revealed arborizations of extrinsic and intrinsic MB neurons across the peduncle and mainly in the lobe systems. The lobes are the output region of the MBs and also a region for modulatory inputs (Krashes et al., 2009). Intrinsic neurons provide an alterna-

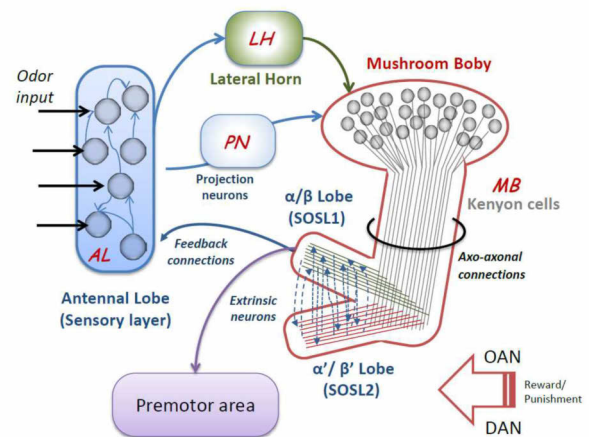


Figure 1: MBs and their interactions with other insect brain centers. MBs, together with the antennal lobes (ALs) and the lateral horn (LH), are the place for odor representation and learning. The presence of axo-axonal connections between the Kenyon cells, feedback connections between the lobes and the AL layer and the reward or punishment signals mediated via octopaminergic (OAN) and dopaminergic (DAN) neurons, respectively, are important elements that allows the emergence of patterns of neural activity responsible for multiple complex behaviours.

tive 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. This is very interesting for our modeling purposes. Very recently, recurrent connections between MBs and ALs have been found (Hu et al., 2010). The presence of this functional feedback from the MBs to the ALs suggests top-down modulation of olfactory information processing in *Drosophila*. The presence of dynamically changing conditions and noise in the environment leads animal to develop attention-like processes. Attention facilitates focusing on the attended events, while filtering out irrelevant information. These interesting processes have been studied in *Drosophila*. In particular, results by Xi et al. (2008) suggest that MBs in flies behave like an adaptive sensory gain controller, allowing the processing of salient cues, filtering out the background noise and distracting signals. More information from neurobiology, essential to develop an efficient, flexible and multi-functional neural model, concerns the presence of axo-axonal connections among the kenyon fibres, whose role could not be clearly unraveled in experiments, but give us the possibility to add to the computational model efficient diffusion phenomena, which are at the basis of the spatial-temporal clustering capabilities.

### Mushroom Bodies: a computational model

The proposed computational model is directly inspired by the MB structure, including top-down connections to the Antennal lobes, the global inhibitory effect of the Lateral Horn and the axo-axonal diffusive connections among the KC fibers. The proposed neural architecture is a two layers recurrent network in which each neuron is an Izhikevich's class one spiking neuron with spike resetting, (Izhikevich, 2003), which offers many advantages over other neuron models from the computational point of view. Neurons are connected through synapses, modeled as first-order dynamical systems which transform the pre-synaptic voltage spike trains into a post-synaptic current. There are sites where learning is added to the basic dynamics of the synapses. These adaptive sites are areas where neural reuse is prominent: reuse exploits the dynamics arising at sites (which correspond to the working sites in (Anderson, 2010)) where learning is not present, but synaptic and neural dynamics concur to the emergence of clusters of neural activity. Learning is implemented through a correlation based, Hebbian rule called Spike Timing Dependent Plasticity (STDP) (S. Song, 2000, 2001) which has been used in different application, including robot learning (Arena et al., 2009). The algorithm acts on the synaptic weights, modifying them according to the temporal sequence of occurring spikes (Arena et al., 2011). An output layer can be added in order to link the behavior of the second layer to a motor or pre-motor area. The developed neural structure, even if inspired by the insect olfactory system, can be used for stimuli of different sensory modalities (e.g visual features can be easily used in robotic scenarios).

The Antennal Lobes model, as shown in Fig. 1, receives input from the olfactory sensory system (i.e. Antennas). We can assume that each AL neuron, when active, codifies the presence of a particular value for a specific feature of the input. Neurons in the ALs are organized in groups, each group presenting the different values of a given input feature. A competitive topology is implemented between neurons within each group, whereas plastic excitatory synapses link neurons belonging to different groups. When the AL layer is stimulated, after a short transient time, only one neuron in each group remains excited, owing to a Winner Takes All (WTA) topology. The ensemble of all the active neurons encodes the presented object. The adaptive connections between groups of neurons bias the network toward temporarily retaining the presented objects through all its features or to reconstruct lacking features in case of incomplete or noisy detection. Non-learning synapses from the AL model to the MB model are randomly established, with a given probability of connectivity. The MB model is made-up of two twin lattices representing the two-lobes system, here called Self Organizing Spiking Layer (i.e. *SOSL1* and *SOSL2*). They have a toroidal geometry, with local excitatory and global inhibitory synapses. Each neuron within them is connected

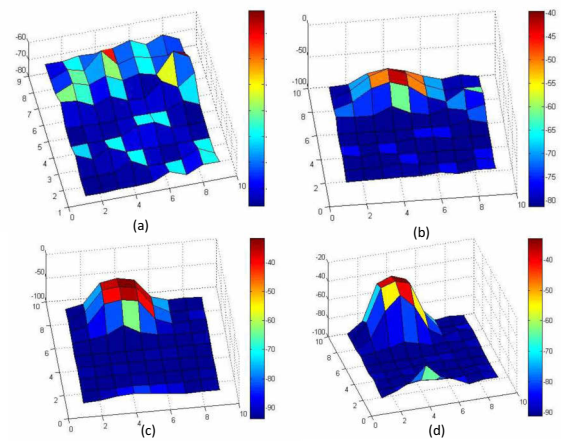


Figure 2: Time evolution of the neural activity in the Self Organizing Spiking Layer (SOSL) lattice. The network topology allows the emergence of a winning cluster. This example is related to a lattice of 9x9 neurons (represented in the x-y plane) and reports the mean potential of each neuron in the lattice (z axis) evaluated by dividing the simulation in four time windows. The clustering is obtained after 80 ms of simulation.

through fast excitatory synapses with all the neurons of its neighborhood and through fast inhibitory synapses with all the other neurons of the lattice. The main peculiarity of these SOSLs is a spontaneous clustering, due to the competitive topology: information coming from the ALs is compressed into a cluster of spiking activity, which can arise in different positions in the SOSL1 and SOSL2 due to the random connectivity of the SOSLs with the input layer. A typical neural activity leading to the emergence of a cluster in the SOSL is shown in Fig. 2.

Only in the SOSL1, representing the  $\alpha - \beta$ -lobes, a slow and delayed diffusion of the neural activity links each neuron to the other neurons of the same lattice, in order to have the possibility to temporally link different clusters. These synapses are subjected to the STDP learning algorithm, that allows discovering and retaining temporal causality among clusters. These connections have the interesting capability to generate, within the SOSL1 layer, expectation and short-term prediction capabilities, whereas the SOSL2 layer has the main function of working as a back-up copy. Feedback connections able to learn link clusters in SOSL1 to the ALs neurons.

The two lobes (SOSLs) 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  $\alpha - \beta$ - neu-

rons give information back to the ALs, by that generating a feedback at the sensory stage, the  $\alpha' - /\beta'$  neurons were found to provide no output signals back into the system, but they just receive sensory input in the last place at the level of the calices. Arena et al. (2013) therefore assumed that the information which arrives at these lobes is retained there and used as a kind of backup copy for memory purposes. Further details on the model are reported in (Arena et al., 2012a).

To summarize this paragraph, input coming from the ALs is clustered into feature-based objects. This information is sent, without learning, to the SOSLs where a clustering effect arises in terms of self-organized spiking activity. The SOSLs concurrently integrate the information coming from the ALs in a given time window: in particular after the emergence of a cluster the neural activity of the network is inhibited by the LH wave. Clusters of spiking in SOSL1 are temporally linked, thanks to synapses that are able to learn, and concurrently, a cluster-induced depolarization of the AL layer is emerging like in Fig. 3. Moreover, a cluster corresponding to the previous input provides information on the past experience of the network for sequence learning purposes. One crucial issue is the synchronization between the delay of the synaptic cluster-linking connections in the SOSLs and the LHs induced inhibitory action onset time. The output layer connects the model to a motor or premotor area. Neurons in the output layer are linked to the SOSL neurons through synapses subject to an associative learning.

### Behavioral repertoire

The concept of neural reuse is applied to the MB architecture that is able to show different behaviors in a unique dynamical system.

#### Conditioning in MBs

The model works for conditioning purposes exploiting the feedforward processing of the network. Clusters emerging in the SOSL1 after presenting a given input stimulate an output associative output neuron. When a rewarding unconditioned stimulus is given to the network, a Reward Neuron (RN) becomes active. This is connected to the output neuron through a fixed synapse, representing the unconditioned response to the reward. That way the output neuron is forced to fire, and the synapse connecting this neuron to the SOSL1 cluster is trained. The mechanism guides classical and operant conditioning through hebbian learning: the output neuron takes the role of a premotor neuron, in case of applications to tactic or phobic reactions following learned attractive or repulsive signals, respectively, in robotic applications.

#### Modeling attention using the Mushroom Body structure

The attention capability was well assessed experimentally by van Swinderen (2011). Attentional capabilities are ob-

tained by exploiting the feedback synapses, which reuse the dynamics formed into the  $\alpha - /\beta$  lobes lattice (SOSL1) to provide an input to the AL layer. The role of feedback connections in the insect olfactory system model has been analyzed by Arena et al. (2011), on the basis of the biological evidences found by Hu et al. (2010). Feedback synapses are updated according to the STDP learning algorithm. When a cluster is elicited in the SOSL1, the synaptic connections between these neurons and those neurons which are firing in the AL (due to the synchronous presence of the corresponding input) are strengthened, according to the Hebbian paradigm. This produces a pre-polarization of the AL layer and acts as a filter for the sensory input, leading to an attention-like phenomenon. Two major aspects are worth mentioning: the first one is that the spatio-temporal dynamics assumed to link the different internal representations of objects in time is modeled as a specific function of the SOSL1 lobe. The second aspect is that the output of the feedback synapses is delayed; the postsynaptic current influences the input layer only after the lobes have been reset via the LHs. This is equivalent to assume that the action of these feedback connections, being focused to enhance attention loops, is able to persist also after the inhibition coming from the LHs. The actual model hypothesizes massive feedback connections from SOSL to ALs neurons, even if a probability distribution could maintain the same performance in case of a large-scale implementation.

#### Modeling expectation

During the efforts spent in delivering an MB model able to elicit both traditional odor conditioning features and attention processes, a behavior emerged, which is related to our concept of expectation. Indeed, this capability is not yet found in insects, but nevertheless the computational results can open the way to a new wave of insect experiments in this direction. The MB neural lattice (SOSL1) is reused for creating expectation by means of the set of plastic delayed synapses (providing a kind of second order diffusion effect) linking each neuron of the SOSL1 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 discovering and retaining temporal causality among clusters. Simulation results show that these connections have the interesting capability to generate expectation and short-term prediction features within the SOSL. The plastic feedback connections, present from the SOSL1 to the AL model and exploited for attention, have here a precious role (this can be also considered a kind of reuse) to boost the model performance. Two main functions have been identified: they are useful to create an expectation-based depolarization of the neurons in the ALs and they are also essential to reconstruct the expected object.

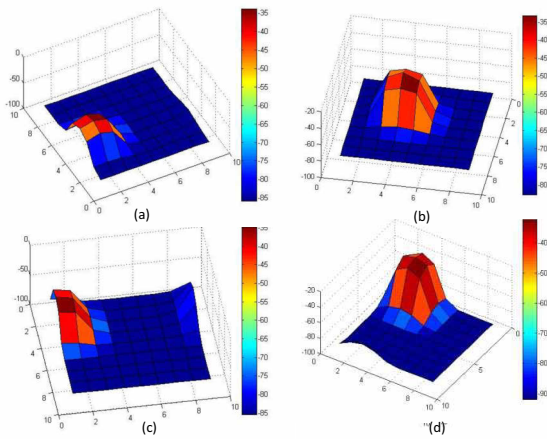


Figure 3: Time sequence of evoked winning clusters obtained during memory consolidation. Each plot represents the mean potential of the voltage in a 9x9 lattice in a steady state condition. The role of noise is important to give to the lattice enough energy to allow the rise of a cluster (a) that activates in time the different clusters (b-d) in a previously learned sequence; this consolidates the memory.

### Memory consolidation

By exploiting the presence of noise in the system (Arena et al., 2012a), an interesting property of the network can emerge. In fact, the contribution of noise can be useful to consolidate the acquired knowledge during a resting phase, when the network is not physically connected to any input signal. In this phase that can be thought of as sleeping condition, the network is simulated no longer by real-world signals used for training, but by noise. The simulation aimed at showing this effect consists first of a learning phase, in which the network creates the association between clusters and objects. As discussed in (Arena et al., 2011) at the end of the training phase no physical input is presented at the ALs layer, but it is assumed that the SOSL1 is subject to noise. These disturbances onset transients in the SOSL1 neurons until a cluster will emerge over the others. If this cluster had formerly been trained to represent a given object, this is recalled at the AL layer, like an “evoked object”. An example of sequence of evoked clusters is reported in Fig. 3.

A new learning cycle will then arise, in which not only this object will be consolidated, but also all the other objects expected after this one in an already learned sequence. During this simulation phase, the network is reused: new imagined solutions could also be experienced during this “sleeping phase”; the system could even create new or longer sequences starting from what it already learned during the “awake phase”.

### The delayed matching-to-sample task

The previously introduced model has been extended to include the role of the MB-lobes in solving problems like the delayed matching-to-sample task: the capability to recognize successive presentations of the same object (Arena et al., 2013). For the first time now this behavior directly exploits the presence of two different lobes structures:  $\alpha - / \beta -$  and  $\alpha' - / \beta' -$  lobes. It is known from neurobiology that the neurons belonging to the two clusters are morphologically different: whereas  $\alpha - / \beta -$  neurons give information back to the ALs, by that generating a feedback to the sensory stage, the  $\alpha' - / \beta' -$  neurons were found to provide no output signals back into the system, but they just receive sensory input at the level of the calices. It was therefore assumed by Arena et al. (2012a) that the information arriving at these lobes is retained there and used as a kind of backup copy for memory purposes. As presented in the previous section, each lobe is modeled as a toroidal lattice with clustering capabilities. In addition to the delayed feedback synapses from the  $\alpha - / \beta -$  lobes to the input layer, and useful for attention capabilities, 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. The overall process dynamics develops as follows. Each SOSL network shows a cooperative-competitive dynamics: if excited, the neurons in both SOSL networks begin a competition and, after a transient, only one cluster of neurons will remain active and stable in each lobe. The LH inhibits both networks after every time window. The resetting effects only the soma, but not the spike responses of the synapses; in particular, those ones between the lobes are reinforced when two clusters in different lobes are concurrently active. This creates a positive loop which increases the spiking rate in the SOSL1 active cluster. We assumed also to have a neuron sensitive to the firing activity of the  $\alpha - / \beta -$  lobes network to detect this situation. This structure was used in (Arena et al., 2012a) to detect whether the object presented to the input layer remains the same in two subsequent steps. In fact, the successive presentation of a different object does not cause the closing of the loop and therefore prevents any increase of the synaptic activity in the lobes.

### Towards other behaviors

Insect MBs are involved in a lot of different behaviors: we are in the process of integrating most of these behaviors into a unique model. First of all sequence learning, a capacity of bees, can be considered as an iterated form of the expectation process. Moreover, the concept of sameness, found also in the behavioral repertoire of bees, can be seen as an augmented form of the delayed matching-to-sample-task: we are not so far from showing also these features within the proposed architecture. Even more complex behaviors, within which MBs have a clear role as in decision making

(Tang and Guo, 2001) and motor learning, are presently being deeply investigated. We already have working models that can explain each one of these capacities, but our aim is to use as much as possible information from neurobiology to devise a unified model for all of them, as it is done in the biological counterpart.

### Conclusions

Insects show a complex behavioral repertoire and, in recent years, are becoming a reference point in neuroscience. Their tiny brains must serve all the survival operations despite their really small mass: the surprise is that also a lot of behaviors that are summarized briefly in this paper and traditionally ascribed to the brains of higher animals, are experimentally found in insects as well. Mushroom bodies, the most studied neural assemblies in the insect brain, have several times been functionally compared to mammalian brain centers like the hippocampus (because of their involvement in learning and memory) and the cerebellum (for their involvement in motor learning). MBs play an important role in a large number of behavioral capacities and it is apparent that they serve different low- and high-level functions concurrently: therefore, in accord with the theory of neural reuse, MBs are a paradigmatic case of reused neural networks in action. The role of extrinsic neurons appears to be fundamental, some of which have connections to the KC fibers at the level of the MB calices and others at the level of the lobes and at the same time to other brain centers like premotor areas, ALs and LHs. They appear as the natural candidates to exploit the neural dynamics within the MB cells to boost the insect brain functionality.

In this manuscript we presented a model that has been recently introduced, but has been revisited here in terms of multi-functionality and neural reuse. This model was built in a connectionist manner, obeying, although in a scaled version, the neurobiological topology. The model was initially built for showing basic learning and conditioning capabilities; subsequently it was found able to show other interesting behaviors, like attention, expectation, sequence learning, consolidation during sleep and delayed-matching-to sample tasks. All of the just-mentioned features emerge from the same spiking neural lattice, which is reused in different ways. An interesting fact is that, while most of these behaviors were experimentally found in fly experiments, others, like expectation, were not yet considered as a capability of the fly. The fact that the model built here is able to show such additional capacities, opens the way to design experiments for finding these behaviors in flies. This is a win-win example in which neurobiology and computational modeling can mutually help one another to advance knowledge in both fields. There are other complex behaviors that these tiny insect brains are able to show, like decision making, motor learning and so on, in which MBs are known to be involved. Particular efforts are ongoing to see if and to

what extent the actual model might be able to represent also these additional behaviors; these efforts will further enhance our understanding of the concept of neural reuse and multi-functionality.

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