Neural Networks 32 (2012) 35–45

Contents lists available at SciVerse ScienceDirect

Neural Networks

journal homepage: www.elsevier.com/locate/neunet

2012 Special Issue

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

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ARTICLE INFO

Keywords:
Insect brain
Spiking neurons
Olfactory model
Attention
Expectation

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 decisions in front of complex environmental situations. In this paper we propose a neural model inspired by the insect olfactory system, with particular attention to 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 olfactory information processing, namely the Mushroom Bodies, the Lateral Horns and the Antennal Lobes. In the Antennal Lobes layer olfactory signals lead to a competition among sets of neurons, resulting in a pattern which is projected 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 basic expectation 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.

1. Introduction

In the last few years simple animal brains have attracted an increasing interest, at the dual aim to deeply understand the neurobiological details, and to exploit the derived knowledge in order 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 a repertoire of behaviors that, since a few years ago, were believed to be possible only in higher animals like mammals or even humans. In contrast with the last decades' assumptions, 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 (Dornhous & Franks, 2008; Webb & Consi, 2001). Insects clearly show distinct features such 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, Zhang, & Reinhard, 2006; Wehner, 1981). The enhanced tools recently adopted in insect Neurophysiology have allowed to shed light on the details of neural signal processing in some specific parts of insect brain responsible for complex behaviors 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, Stocker, & Gerber, 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, Rabinovich, Huerta, and Abarbanel (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

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0893-6080/$ – see front matter
doi:10.1016/j.neunet.2012.02.034

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, De Fiore, Patané, Pollino, & Ventura, 2010). These structures were successfully applied to enhance the capabilities of an autonomous robot, but they were really far from the skills of insects, 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, 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. The author was 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 cue 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, Zhang, & Wang, 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 they face complex environments. Learning to know in advance which incoming input stimulus is correlated with the actual one is a fundamental ability in living beings, useful in taking appropriate action, sometimes life-saving. The possibility to make predictions and to modulate sensorial inputs through expectations is the key point of the model introduced in this work. 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 the 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, Patané, and Termini (2011), is here further assessed, both from the design and 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 interestingly, exploits the possibility to use the positive role of noise when no input activity is registered at the ALs layer. Noise produces a spontaneous learning activity, maintaining the phenomenon of consolidation during sleep, well known as occurring in the fly, as well as in human beings.

The paper is divided into five sections: Section 2 presents the biological background of the work and the state of the art regarding artificial models of insect brains. In Section 3 the proposed architecture is introduced and described whereas Section 4 presents some simulation results and also introduces preliminary potential applications for the model. Finally, Section 5 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 recently in neurobiological studies on the fruit fly, as discussed in Sachse and 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 & Heisenberg, 1994). In the fly *D. melanogaster*, each side of the MBs is constituted by 2500 Kenyon cells which run in parallel from the *calyx* through the *peduncle* and 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 (Schröter & 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 to 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.