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Modelling the insect Mushroom Bodies: Application to sequence learning

Paolo Arena [a,b], Marco Calí [a], Luca Patané [a,*], Agnese Portera [a], Roland Strauss [c]

[a] Dipartimento di Ingegneria Elettrica, Elettronica e Informatica, University of Catania, Italy
[b] National Institute of Biostructures and Biosystems (INBB), Viale delle Medaglie d'Oro 305, 00136 Rome, Italy
[c] Institut für Zoologie III (Neurobiologie), University of Mainz, Germany

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ABSTRACT

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

1. Introduction

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

The problem of sequence learning has been faced in the literature using different approaches based on artificial models (Stocker, 2001), most of them derived from Jordan and Elman's recurrent networks (Elman, 1990; Janzen, 1971b). Hebbian learning schemes were proposed in Wang and Arbib (1990) where neural networks eliciting short term memory (STM) were able to learn and recognize temporal sequences. Later on Billard and Hayes (1999) proposed a connectionist architecture, DRAMA (Dynamical Recurrent Associative Memory Architecture), for dynamic control and learning of autonomous robots. This is a time-delay recurrent neural network, using Hebbian update rules able to learn spatio-temporal regularities in discrete sequences of noisy inputs.

Nowadays the study of animal brains and the modelling of relevant neural structures on the basis of behavioural experiments continuously improve the knowledge about learning mechanisms. Several attempts can be found in the literature related to the development of algorithms or bio-inspired networks able to model the functionalities expressed by specific brain centres of mammals, molluscs and insects (Webb & Consi, 2001). Looking in detail inside the insect world, there are very interesting species where, in spite of the relative small number of neurons, the complexity of their behaviour repertoire is impressive.

Discovering where and how sequence learning is formed, retained and extracted, is a hard task, however insects can represent a good starting point. In fact in insects there are neurobiological evidences of processes related to spatio-temporal pattern formation and time-dependent learning mechanisms that can be used to solve tasks that include sequence learning. The most plausible brain structures involved in these processes are the *Mushroom Bodies* (MBs) that, together with the *Lateral Horns* (LHs), are

* Corresponding author.
E-mail address: lpatane@dieei.unict.it (L. Patané).

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principally devoted to olfactory learning (Liu & Davis, 2006). The spatio-temporal olfactory information coming out from the Antennal Lobes (ALs) are processed and stored in spatial patterns that can evolve in time and can be associated to specific behavioural responses (Huerta & Nowotny, 2009). 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 has been implemented. Taking into consideration this spatio-temporal pattern formation process that has been unravelled from a different prospective in other works (Arena, Fortuna, Lombardo, & Patané, 2008), we investigated the possibility to extend the processing capabilities of the MBs system to model an artificial bio-inspired structure for sequence learning.

The olfactory model of locusts illustrated in Nowotny et al. (2003) clearly underlines the inhibitory effect of the LH circuit on the MB cells. Each Kenyon cell is strongly connected with the cells of its neighbourhood, and connections between this layer and the Antennal Lobes-like layer are randomly generated. A coincidence detection approach allows the model to codify sequences of events in a spatial pattern of firing neurons. However no learning is implemented in the model even if successive works started to introduce classification mechanisms to the network with the support of reinforcement learning mechanisms used to associate the MBs sparse activity to predefined classes (Huerta & Nowotny, 2009).

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

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

Another model for sequence learning was proposed in Berthouze and Tijsseling (2006) where a neural network was developed to implement context-dependent learning of complex sequences. The model utilizes leaky integrate-and-fire neurons to extract timing information from its input and modifies its weights using a learning rule with synaptic noise. The context layer is used to solve ambiguities where identical inputs should be associated to different outputs in the sequence depending on the previous provided elements. Similarly we started from unravelling the functionalities of the insect MBs trying to extend the neural model basic capabilities, mainly devoted to olfactory learning, to perform more complex tasks related to sequence learning. The idea is to create a unique neural structure able to show multiple functionalities as demonstrated in several experiments in which the MBs are involved (Glenn, Maxim, & Gilles, 2007; Gronenberg & Lopez-Riquelme, 2004). This is very next to the concept of Neural Reuse, another additional characteristics of biological neural networks (Anderson, 2010). The architecture here proposed is a multilayer spiking network based on *Izhikevich's* neuron model (Izhikevich, 2004), in which the interaction among the different layers, similarly to its biological counterpart, allows the generation of different capabilities that range from the classical odour learning to other more complex behaviours like attention, expectation and sequence learning.

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

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

2. Sequence learning in nature

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

Sequence learning is a difficult task also for ants and preliminary studies indicate that ants perform conditional discriminations reliably when stimuli are simultaneous, but they usually fail when stimuli are sequential (de Ibarra, Howard, & Collett, 2011). However other studies showed that ants can learn stereotyped foraging routes guided in part by the visual features that they encounter along the route (Macquart, Latil, & Beugnon, 2008). Ants could then sequence together the successive basic motor programs into a site-specific serial program as a kind of signature route. Such a procedure would facilitate animals reducing cognitive needs imposed by learning and remembering numerous visually identified landmarks when directing towards a target. Therefore ants can learn to negotiate a maze using the shapes for guidance rather than a fixed motor strategy. Trained ants could not only discriminate positive from negative shapes, but also learn the correct sequence of choices. Experiments described in Chameron, Schatz, Pastergue-Ruiz, Beugnon, and Collett (1998) show that the contextual signal must come from previous events in the sequence and be stored internally. However, the experiments cannot clarify whether ants store the whole sequence, or internal linkages extend only one step back in the chain.

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

The experiments reported in May and Wellman (1968) and Murphey (1965) represent a first attempt to test the fruit fly behaviour in a multiple T-maze scenario where a sequence of choices