

A neural model of cross-modal association in insects

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Abstract. We developed a computational model of learning in the Mushroom Body, a region of multimodal integration in the insect brain. Using realistic neural dynamics and a biologically-based learning rule (spike timing dependent plasticity), the model is tested as part of an insect brain inspired architecture within a closed loop behavioural task. Replicating in simulation an experiment carried out on bushcrickets, we show the system can successfully associate visual to auditory cues, so as to maintain a steady heading towards an intermittent sound source.

1 Introduction

A large body of evidence suggests that the Mushroom Body (MB), a distinct region in the insect brain, plays a cardinal role in adaptive behaviour (see [1] for a review). We propose a minimalist architecture, based on this neural circuit, able to modulate reflex behaviours in closed-loop conditions i.e. where the system's output influences the system's inputs. We test it for the simulated task of using visual cues for maintaining a course towards a sound source, as observed in the bushcricket *Poecilimon affinis* [2].

Male bushcrickets are able to maintain a straight course to a female, by coupling visual cues to an acoustically detected direction [2]. Stabilising effects of visual information on course maintenance are found in other insects (c.f., [3]), but in this case it was also shown that optical cues could *stand in* for (temporarily absent) auditory signals. In particular, the animal could quickly learn to walk at an arbitrary angle to a visual landmark, corresponding to the sound direction. In the absence of sound it would follow the displacement of the landmark with an appropriate change in walking direction. In a comparable task, the MB of the cockroach have been shown to play a role in place memory relating distant visual cues to an invisible target [4]. Here we show how the neural architecture of the MB can account for such capabilities, using a biologically plausible neural representation and learning rule.

2 Model description

2.1 Neuron model

We chose the neuron model proposed by Izhikevich [5] since it exhibits biologically plausible dynamics, similar to Hodgkin-Huxley-type neurons, but is com-

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putationally less expensive and thus, suitable for large-scale simulation. Change in membrane potential v (mV) is modelled as:

$$C \frac{dv}{dt} = k(v - v_r)(v - v_t) - u + I + [\xi \sim N(0, \sigma)] \quad (1)$$

$$\frac{du}{dt} = a(b(v - v_r) - u), \quad (2)$$

where u is the recovery current and I the synaptic input. $a = 0.3$, $b = -0.2$, $c = -65$, $d = 8$, and $k = 2$ are model parameters. $C = 100$ (pF) is the capacitance, $v_r = -60$ mV is the resting potential, and $v_t = -40$ mV is the instantaneous threshold potential. ξ is a Gaussian noise term with standard deviation $\sigma = 1$. The variables v and u are reset if membrane potential exceeds a threshold ($v \geq +35$ mV):

$$\begin{cases} v \leftarrow c \\ u \leftarrow u + d \end{cases} \quad (3)$$

Synaptic inputs are modelled by:

$$I(t + \Delta t) = gS(t)(v_{\text{rev}} - v(t)), \quad (4)$$

where v_{rev} (mV) is the reversal potential of the synapse and g (nS) is the synaptic conductance. The reversal potential of excitatory synapses is 0mV, whereas that of inhibitory synapses is -90 mV. $S(t)$ is the amount of neurotransmitter active at the synapse at time t and is updated as follows:

$$S(t + \Delta t) = \begin{cases} S(t)e^{\frac{-\Delta t}{\tau_{\text{syn}}}} + \delta & , \text{ if presynaptic spike} \\ S(t)e^{\frac{-\Delta t}{\tau_{\text{syn}}}} & , \text{ otherwise} \end{cases} \quad (5)$$

where $\delta = 0.5$ is the amount of neurotransmitter released when a presynaptic spike occurred, τ_{syn} (ms) is the synaptic timescale, and the simulation timestep Δt was set to 0.25ms.

2.2 Neural architecture

The neural architecture for the agent is based on the insect brain; in particular, on evidence that the MB is involved in modulating more basic, reflexive behaviours [1]. Insect behaviour is often viewed as collections of parallel, highly specialised sensorimotor loops, and such loops form the basis of our proposed architecture (such as the phonotaxis loop in figure 1). However, collections of reflex-loops are insufficient for explaining the behavioural complexity of insects [6]. Higher brain centers, such as the MB, act to modulate the direct sensorimotor loops in context-dependant and heterarchical manner (c.f., [6, 7]). Indirect secondary pathways via the MB, which form a parallel route for sensory inflow, are used to place information from various sensory modalities or

other domain-specific sensorimotor loops into context, and to form associations between different inputs.

We have used this architecture in previous modelling of non-elemental associative learning [8]. In the current experiment, the reflex pathway represents a response to sound (see figure 1). Each spike of the output (left or right) neurons of the phonotaxis (sound localising) circuit (based on [9]) cause the agent to turn by 1 degree in the direction of the sound source and also excite the extrinsic neurons (EN). The visual position of the landmark is mapped onto projection neurons (PN) that activate the Kenyon cells (KC) that form the mushroom body. These converge on the extrinsic neurons. During conditioning, the sound is on and the agent moves towards it. After conditioning, the agent should have associated the required movements with a particular landmark direction, and thus be able to control its course using only visual cues.

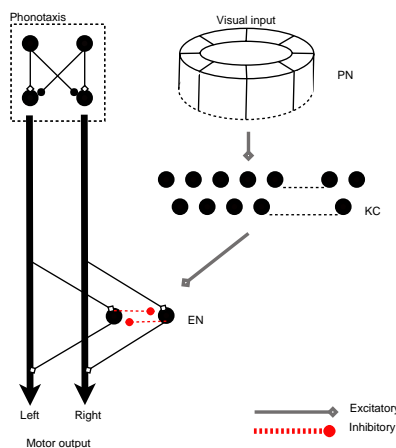


Fig. 1: The implemented MB network receives sensory cues from the visual field via projection neurons (PN), which make direct excitatory connections to the Kenyon cells (KC). The MB output converges on a small number of extrinsic neurons (EN), which are also excited by the underlying direct reflex pathways, and can activate these pathways. Learning occurs between the KC and EN.

PN layer. This layer consists of 72 neurons giving a visual resolution of $\frac{360}{72} = 5$ degrees. We assumed preprocessing of visual information and that receptive fields are not overlapping. Each PN encodes a particular relative angle towards the landmark. The neurotransmitter release (at a PN when the landmark is in view at its particular relative angle) is calculated as follows: $S(t + \Delta t) = S(t) + \delta$.

KC layer. The KC layer consists of 72 neurons. The topographical organisation of the PN layer is maintained, i.e. each KC only receives input from one PN. The synaptic strength of PN-KC synapses ($g_{PN,KC}$) were set at random in the interval [20,30].

EN layer. The EN layer contains 2 neurons and each EN is connected to all

KC, i.e., every KC-EN pair is connected ($\tau_{\text{KC,EN}} = 5\text{ms}$). Learning occurs only through modulation of the KC-EN connections. However, the synaptic conductance $g_{\text{KC,EN}}$ for all synapses is initialised to 0, and is subsequently modified as described below. The EN neurons also receive excitatory input from the underlying reflex pathways, thus the learning reflects the coincidence of activity in these pathways and the activity in the KC layer.

2.3 Spike Time-Dependent Plasticity (STDP)

Synapses are modified using STDP which has been observed in biological neural systems (e.g., [10]). In STDP, synaptic change depends on the relative timing of pre- and post-synaptic action potentials. Synaptic conductances are adapted by the following STDP rule:

$$\Delta g = \begin{cases} A_+ e^{-\frac{t_{\text{pre}} - t_{\text{post}}}{\tau_+}} & , \text{ if } t_{\text{pre}} - t_{\text{post}} < 0 \\ A_- e^{-\frac{-(t_{\text{pre}} - t_{\text{post}})}{\tau_-}} & , \text{ if } t_{\text{pre}} - t_{\text{post}} \geq 0 \end{cases} \quad (6)$$

where t_{pre} and t_{post} are the spiking times of the pre- and postsynaptic neuron respectively. $A_+ = 20$, $A_- = -20$, $\tau_+ = 10\text{ms}$, and $\tau_- = 5\text{ms}$ are parameters. If this modification rule of synaptic conductances g pushes the values out of the allowed range $0 \leq g \leq g_{\text{max}}$, g is set to the appropriate limiting value ($g_{\text{max}} = 50$).

A ‘forgetting’ factor is introduced in the form of a slow decay of g . At each timestep,

$$g(t + \Delta t) = g(t) e^{-\frac{\Delta t}{\tau_{\text{decay}}}} \quad (7)$$

where $\tau_{\text{decay}} = 10^5$ (ms). The coupling of visual cues to auditory signals should only be temporary (c.f., [2]).

3 Results

The model was tested in two scenarios. In one, the agent walks on a treadmill so that it can only change its orientation - this is directly comparable to the original behavioural experiments on the bushcricket. In the other, the agent moves in an arena towards the sound source, which is more like the natural interaction of the insect with the environmental cues. In each case the conditioning trials (with constant sound) lasted a total of 120s, with the agent starting at a random heading. The conditioning trials were repeated and reset as follows. In the ‘treadmill’ scenario the heading was randomly reset every 10s, whereas in the ‘arena’ scenario if it arrived within a small radius of the sound source it was returned to its starting position (with a random heading) and repeated its approach.

In the ‘arena’ scenario, coupling visual cues to phonotactic behaviour has a stabilising effect on course maintenance. As a measure we used the Vector

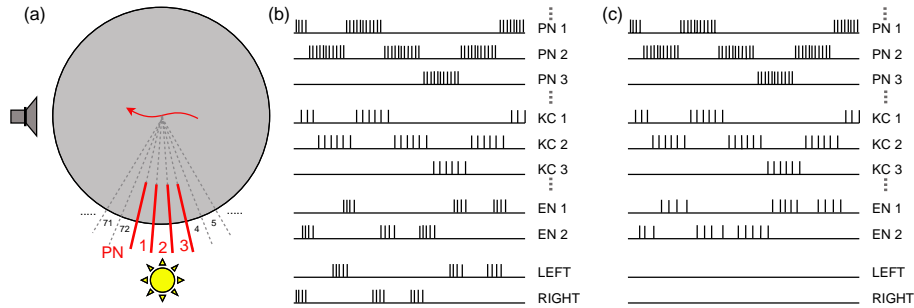


Fig. 2: Schematic drawing of neural activity. As the agent zig-zags towards the sound source (a), turning is controlled by the output (left, right) of the phonotaxis network (b) activating the extrinsic neurons (EN). During these movements, the visual stimulus activates several different projection neurons (PN) which activate their respective Kenyon cells (KC). The system learns to associate KC and EN firing, so that after conditioning (c) the visual stimulus alone is able to control turning.

Length (VL) defined as the quotient of the distance from start position to the position of the source and the actual path length. The mean VL was 0.59 (s.d.=0.1) before conditioning and 0.818 (s.d.=0.182) after conditioning. More importantly, the landmark could now be used to stand in for the sound. This was tested by looking at the mean angle that the agent moved with sound off when the landmark was displaced. As shown in figure 3, the agent's direction is appropriate to the conditioning angle and follows the landmark displacement consistently, for both the 'treadmill' scenario (figure 3a, closely comparable to the biological data seen in figure 9 in [2]) and the more naturalistic 'arena' scenario (figure 3b). The system has associated each possible visual position of the landmark with the movement required to re-orient so that the landmark falls into the visual position it occupied during walking towards the sound.

4 Discussion and future work

Animal behaviour is a continuous closed loop, with sensory events transformed by the agent into motor actions, and these actions transformed by the environment into new sensory events. Neural learning mechanisms should thus be evaluated in a closed loop context if they are to be considered biologically relevant. A fundamental role of learning for behaving animals is associating the reflex response to one cue with another cue that can refine, predict or substitute for the original cue. In the bushcricket example used here, the visual information can stabilise auditory localisation behaviour and be used to maintain the correct heading when the sound is turned off. We have replicated this capability in a simulation, using a plausible model of insect brain circuitry.

In future work we will evaluate the system using more realistic modelling of

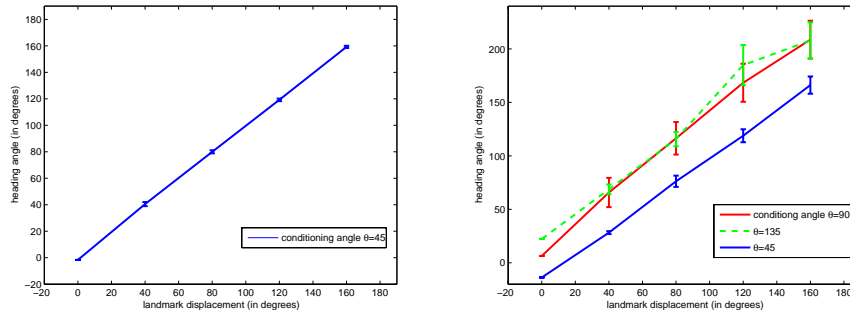


Fig. 3: Mean heading angle plotted versus landmark displacement. (a) The agent can turn but does not move forward, simulating an insect on a treadmill. (b) The agent can move through the environment. In each case the agent maintains the appropriate relative heading as the landmark is displaced.

the input (auditory and visual) and output (motor) functions, with the eventual aim of illustrating the same learning capabilities on a real robot. The same neural architecture will also be tested for the related task of place memory, in which a particular home location is associated with an array of landmarks, a behaviour known to be dependent on the Mushroom Body in insects [4].

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