Miniature cognitive architectures: Modeling the honey bee's mushroom bodies in delay and trace conditioning

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Abstract:

Despite having a brain with less than a million neurons, honey bees demonstrate higher-order cognitive functions, being able to solve non-elemental forms of learning and abstract tasks. Experimental studies showed that honey bees successfully perform trace and delay conditioning tasks, associating a conditioning stimulus (CS) with an unconditioned stimulus (US). In humans, trace conditioning requires higher-order functions such as attention and memory, and it has been even suggested to relate to conscious perception. Here, taking inspiration from the honey bee's neurobiology, we investigated the cognitive architectural ingredients necessary to perform trace conditioning tasks. Specifically, we modeled a population of 560 Kenyon cells in the honey bees' mushroom bodies (MB), a structure involved in associative learning and memory. We demonstrated that MB neurons learn to associate an olfactory CS with a sucrose US via spike-time-dependent plasticity (STDP). Additionally, we modeled an attentional mechanism that allows disregarding distractors stimuli, in line with recent experimental findings. Our results matched the experimental observations on olfactory trace conditioning in honey bee, corroborating our approach. Overall, our results give new insights into the neural mechanisms involved in trace conditioning, providing a computational benchmark to test future predictions and unveil the mechanisms of these miniature cognitive architectures.

Keywords: Trace Conditioning, Olfactory Conditioning Spiking Networks, Honey Bees, Cognitive Architectures

Introduction

Insects' behaviors and neurobiology can provide valuable insights into diverse cognitive processes and their neural mechanisms. For example, several experimental studies showed that honey bees solve complex tasks, such as judging whether two items are the same (Giurfa et al., 2001), and simple mathematical operations, including the concept of zero, addition, and subtraction (Giurfa, 2019). Therefore, investigating and modeling honey bees' cognitive architecture can prove a powerful tool for understanding higher-order cognitive functions. In this work, we consider two types of Pavlovian learning: trace and delay conditioning. In both tasks, honey bees learn the association between a conditioned stimulus (CS, e.g., an odor) and the unconditioned stimulus (US, e.g., a sucrose reward), but while in delay conditioning the two stimuli overlap, in trace conditioning these are separated by a gap of several seconds (figure 1A). Interestingly, trace conditioning in humans has been related to conscious perception and attention, proving that such tasks involve non-trivial cognitive functions to be successfully learned (Droege et al., 2021). Here, we implement a computational model to test whether an architecture inspired by the honey bee brain can perform such a task. Specifically, we test the hypothesis that the mushroom bodies (MB), a multimodal structure involved in learning and memory, play a crucial role in learning such association. As shown in figure 1B, the MB's Kenyon cells (KC) receive the olfactory information from the projection neurons (PN) for the CS. Information on a possible distractor from the same modality may also be conveyed via PNs while information on distractors from different sensory modalities may be conveyed by other neural tracts reaching the MBs. Via spike-time-dependent-plasticity (STDP), Kenyon cells associate the olfactory CS to the appropriate motor response (i.e., the Proboscis Reflex Extension to get the sucrose reward), here represented by the extrinsic output neuron (EN). Our results show that such honey bee-inspired architecture can learn both the delay and trace conditioning tasks, also in the presence of the distractor, matching our experimental data with real bees. In addition, we demonstrate the importance of the serotonergic system, enacted by the dorsal paired medial neurons (DPM) discovered in fruitflies, which act as a sort of attentional mechanism, driving the learning of relevant stimuli, by maintaining their neural trace during the gap, while ignoring the distracting ones (Zeng et al., 2023).

Methods

Our architecture and computational simulations. The model's architecture is shown in figure 1, inspired by Wessnitzer et al. (2012). The network is composed of two layers: 78 projection neurons (PN) constitute the first layer, which receives input from sensory receptors (not modeled here) and directs it into 560 Kenyon cells (KC). These KC cells compose the mushroom bodies and eventually project into a single motor neuron (EN), involved in the control of the Proboscis Extension Reflex (PER), i.e., the response to the sucrose solution.

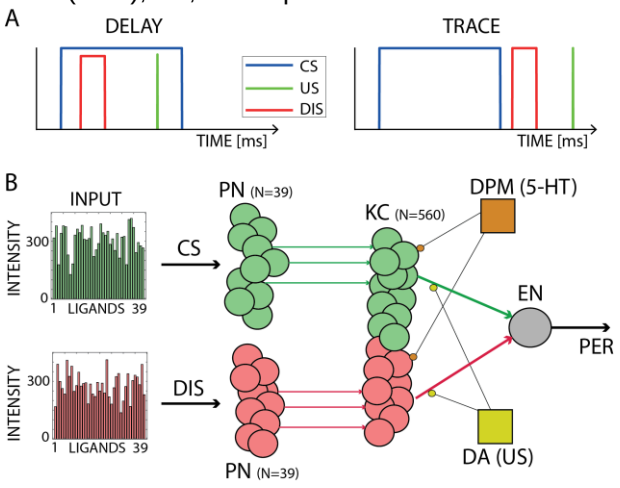

Figure 1: A) Delay and trace conditioning learning scheme, with CS, US, and distractor (DIS). B) Graphic representation of our architecture. See text for details and abbreviations.

Each neuron is modeled by the biologically plausible dynamics proposed by Izhikevich et al. (2004). Specifically, the membrane potential v is modeled as :

$$C\dot{v} = k(v - v_r)(v - v_t) - u + I$$

Where u represents the recovery current:

$$\dot{u} = a(b(v - v_r) - u)$$

If the membrane potential reaches the threshold v_t, both the current and the membrane potential are set to: $v = c$ and $u = u + d$.

Importantly, $a, b, c, d,$ and k are model parameters determining the neurons' dynamics and firing rate. We set the neurons' parameters to model the firing rate of honey bee KCs (Wüstenberg et al., 2004). Specifically, we set $a = 0.01,\ b = -0.3,\ c = -65, d = 8,\ k = 0.015,$ $C = 4, v_t = -25$ and $v_r = -85$. The learning occurs via STDP mechanisms, as described in (Izhikevich, 2007), mimicking the learning via octopaminergic neuromodulators (octopamine in honey bees is the equivalent of dopamine in flies). In short, the synapses w between pre-and post-neuron are modulated by the octopaminergic concentration d and an eligibility trace:

$$\dot{s} = c * d$$

where the eligibility trace c is defined as:

$$\dot{c} = -\frac{c}{\tau_c} + STDP(\tau)\delta(t - t_{pre/post})$$

Intuitively, the eligibility trace is a memory signal that decay over time with time-constant τ_c. Lastly, we included the effect of the serotonergic DPM neurons, which modify each Kenyon cell's eligibility trace decay (i.e., τ_c), acting as an attentional system. We trained the model for 12 trials, each composed of 1000-time steps (each representing a millisecond). In each trial, after 100ms, a CS was presented for 500ms. In delay conditioning, the US was delivered within the last 200ms of the CS. In trace conditioning, the US was given 200ms after the end of the CS. If the distractor was presented, it occurred randomly before the US (in trace conditioning, it always happened after the end of the CS).

Experimental results. We trained N=46 and N=56 honey bees to perform the delay and trace conditioning tasks, respectively. Another set of N=46 and N=61 honey bees were trained to perform the same tasks with distractors (visual stimuli) delivered randomly during the inter-stimulus interval. The CS was an odor stimulus in all experiments, whereas the reward (US) was a sucrose solution. Learning was quantified as the % of animals responding to the CS alone during conditioning trials (%PER on the y-axis of figure 2A).

Results

Figure 2A reveals that honey bees learn the CS-US association in the delay conditioning within a few trials, irrespective of the distractor's presence. However, %PER dropped in trace conditioning and even more in the presence of a distractor. As shown in figure 2B, our simulations replicate empirical observations. After exposing the model to the stimuli in each condition (delay/trace, with/without distractors), we tested the activation of the motor neurons when giving only the CS or the distractor. Our results show that the model successfully learns the CS-US association in the delay conditioning but less so in the trace one, matching the experimental data. In addition, as in the real data, the effect of the distractor becomes more significant in trace conditioning. We next performed a 'lesion study' by removing the attentional mechanisms implemented by the DPM neurons. Interestingly, in this case, the model learns to associate not only the CS to the US but also the distractor, as shown in the rightmost column of figure 2. We propose in the discussion a possible interpretation of this result.

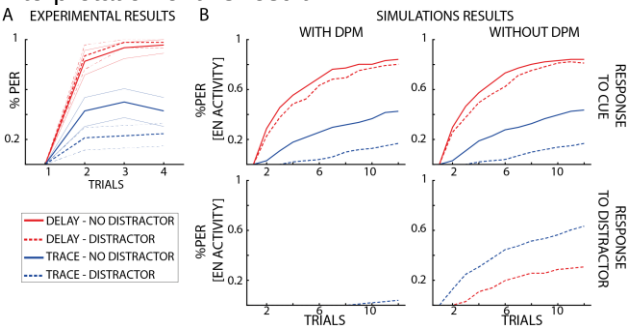

Figure 2: A) average and 95% CI of experimental data. B) Results of the simulations. In each condition, we trained a distinct model ex-novo.

Discussion

In spite of their relatively small brains, honey bees show remarkable skills in solving complex tasks and learning, becoming an essential inspiration for bio-inspired autonomous robots and control algorithms. Here, we implemented a simplified architecture of the honey bee mushroom bodies to investigate the occurrence of delay and trace learning. Overall, our simulations matched the experimental data in real honey bees, thus corroborating our modeling efforts. Interestingly, our simulations shed new light on the role of the DPM neurons and provided a novel interpretation based on attentional control of trace conditioning: how does the honey bee manage to learn the appropriate trace CS while ignoring the distractor? We suggest that the DPM serotonergic system acts as an attentional mechanism, enabling the honey bee to focus on ecologically relevant stimuli while ignoring distracting ones. This interpretation aligns with the experimental evidence provided by Zeng et al. (2023), where genetic manipulation of the DPM neurons revealed their inhibitory role in modulating the KC time window involved in associative learning. Future experimental studies will be required to confirm such new interpretations. All in all, our study reveals the key ingredients to learning a complex task, such as trace conditioning, and it sheds some light on the cognitive architectures of these remarkable, miniature brains.

Acknowledgments

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References

Droege, P., Weiss, D. J., Schwob, N., & Braithwaite, V. (2021). Trace conditioning as a test for animal consciousness: a new approach. *Animal Cognition*. https://doi.org/10.1007/s10071-021-01522-3

Giurfa, M. (2019). An Insect's Sense of Number. In *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2019.06.010

Giurfa, M., Zhang, S., Jenett, A., Menzel, R., & Srinivasan, M. V. (2001). The concepts of "sameness" and "difference" in an insect. In *Nature* (Vol. 410, Issue 6831, pp. 930–933). https://doi.org/10.1038/35073582

Izhikevich, E. M. (2007). Solving the distal reward problem through linkage of STDP and dopamine signaling. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhl152

Izhikevich, E. M., Gally, J. A., & Edelman, G. M. (2004). Spike-timing dynamics of neuronal groups. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhh053

Wessnitzer, J., Young, J. M., Armstrong, J. D., & Webb, B. (2012). A model of non-elemental olfactory learning in Drosophila. In *Journal of Computational Neuroscience*. https://doi.org/10.1007/s10827-011-0348-6

Wüstenberg, D. G., Boytcheva, M., Grünewald, B., Byrne, J. H., Menzel, R., & Baxter, D. A. (2004). Current- and voltage-clamp recordings and computer simulations of Kenyon cells in the ~~honeybee~~honey bee. *Journal of Neurophysiology*. https://doi.org/10.1152/jn.01259.2003

Zeng, J., Li, X., Zhangren, Z., Lv, M., Wang, Y., Tan, K., Xia, X., Wan, J., Jing, M., & Li, Y. (2023). Local 5-HT signals bi-directionally modulate the coincidence time window of associative learning. *Neuron*. https://doi.org/10.1016/j.neuron.2022.12.034