Adaptive concept learning in honeybees using spiking neurons

Abstract: *Learning is one of the most essential skills for an organism even if it is at a very low level. It facilitates foraging, communication, adaptivity, and the overall survival of the organism. It is important to understand the inner workings of the learning mechanism to increase its efficiency. A plethora of ongoing research dating back to the 1900s has helped shed some light on the empirical front of learning in animals. In this report, I study the empirical results of concept learning and adaptivity in honey bees and propose a biologically inspired spiking neuronal model of the mushroom body in their brain to fit the data. The model is based on the equations proposed by Sir Alan Hodgkin and Sir Andrew Huxley that are regarded as the most accurate depiction of spiking neurons. Studying spiking neurons through modelling or simulation is very important as they are the basis of a biological neural network and it will help provide a deeper understanding of the inner mechanism of learning. The bee model is able to learn the concept of similarity/difference presented as stimuli and adaptively perform optimally on novel stimuli without re-learning it.*

Introduction

Any agent that is robust to changing environments and flexible enough to optimally respond to novel stimuli is adaptive. Insects have been shown to portray this form of adaptivity in a number of studies. This report focuses on one such study where honeybees are shown to learn the concept of 'sameness' and 'difference' with the help of visual stimuli and rewards [1]. These studies are essential as they provide insights into the abilities shared by humans and other species, and a motivation to understand how our brain works. Finding similarities in less complex species than our own is beneficial as it is easier to map their functioning mechanisms.

In [1], the authors train the honeybees to learn the concept of 'sameness'/'difference'. They set up a Y-Maze with two circular discs coloured blue and yellow or gratings of horizontal or vertical lines. In the coloured stimuli, the bee was shown a coloured disc before entering the maze, then, it entered the maze and saw the two discs. In 'sameness' learning, if the bee moved toward the disc shown in the initial step before entering the maze, they rewarded the bee with a sucrose solution. They call this delayed matching to sample or DMTS as there is some delay after the initial stimulus and the final stimulus. In 'difference' learning, if the bee selected the other stimulus present in the maze that is different from the initial stimulus, it was rewarded with sucrose. This is called delayed non-matching to sample or DNMTS. The same setup was tested with discs covered in horizontal or vertical gratings.

The bees were able to learn from this setup and substantially choose the rewarding stimulus depending on the learned method after training. Also, they demonstrated adaptive nature as they were able to transfer their learning to novel stimuli and efficiently select the rewarding stimulus that they haven't seen or trained on before even across stimuli modalities like visual to olfactory. This is evidence of higher-order cognition which is observed in humans and other complex organisms [2]. A possible explanation for the evidence is the presence of mushroom bodies in honeybees.

Mushroom bodies are multisensory processing structures in bee brains. They can receive multimodal inputs such as visual, olfactory, gustatory, and mechanosensory [3, 4]. A mushroom body consists of about 170,000 Kenyon cells which are arranged in parallel. These cells are capable of integrating stimuli across modalities [5]. This might be the reason for the adaptive behaviour where the bees are able to transfer learning between visual and olfactory stimuli. Furthermore, mushroom bodies facilitate both reward and inhibition/punishment as they are closely connected to octopaminergic for reward and dopaminergic neurons for punishment [6, 7]. A stimulus resulting in no reward or 'punishment' results in decreased neural activity for that particular stimulus when it is presented again. The inhibition is achieved from protocerebral-calycal tract or PCT neurons which are connected to the mushroom body. PCT neurons are gamma-aminobutyric acid or GABAergic which are inhibitors and they act as a feedback mechanism to the mushroom body. They modulate the dopamine activity for aversion learning by inhibiting the neural response. While PCT neurons also inhibit the neural response for a repeated stimulus regardless of the reward, the neural activity of the rewarded stimulus is less prone to inhibition as compared to the non-rewarded stimulus [8]. Though it can be fruitful to use artificial neural networks, Q-Learning, etc. for modelling such empirical data and theorizing the working mechanism of cognition, a much more biologically plausible method of modelling is with the use of spiking neurons, especially in the empirical results which demonstrate higher-order cognition.

The Hodgkin-Huxley model is a set of non-linear differential equations that describes the initiation and propagation of action potentials in neurons [9]. An action potential is the spike generated when a stimulus is large enough to cross the action potential threshold.

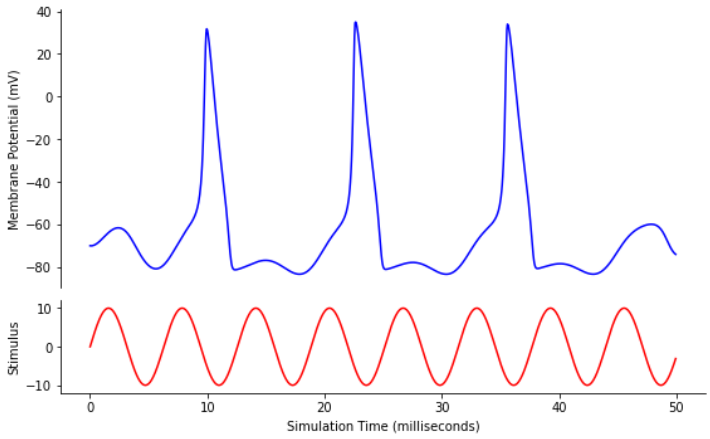


Fig1: Action potentials generated from a sine wave as the stimulus.

Figure 1 shows an example of an action potential. Spikes are generated when the stimulus which is a sine wave in this case pushes the current to cross a threshold. The threshold value depicted here is -55mv which is generally the true threshold value for neurons [10]. A pattern of repeated spikes is referred to as a 'spike train'. The Hodgkin-Huxley model is regarded as the most accurate model of spiking neurons to this day. It accounts for most of the biological properties of neurons such as the conductance and electrochemical gradient of Sodium (Na), Potassium (K), and leakage ion channels along with a representation of Sodium and Potassium gated-ion channels. All of these channels work to initiate, stabilize, and propagate action potentials.

In this report, I use this model to simulate a biologically inspired mushroom body with spiking neurons to fit the empirical data presented in [1]. Further, I discuss the biological relevance of the model, its parameters and why is it important to study in the future.

Methods

Starting with the Hodgkin-Huxley equations [9]:

$$\frac{dV_m}{dt} = \frac{I}{C_m} - \frac{\bar{g}_K n^4}{C_m}(V_m - V_K) - \frac{\bar{g}_{Na} m^3 h}{C_m}(V_m - V_{Na}) - \frac{\bar{g}_l}{C_m}(V_m - V_l)$$
$$\frac{dn}{dt} = \alpha_n(V_m)(1-n) - \beta_n(V_m)n$$
$$\frac{dm}{dt} = \alpha_m(V_m)(1-m) - \beta_m(V_m)m$$
$$\frac{dh}{dt} = \alpha_h(V_m)(1-h) - \beta_h(V_m)h$$

Where,

C_m = membrane capacity per unit area (1 μF/cm^2)

$\bar{g}_{Na}$ = conductance per unit area for Sodium (Na) ion-channel (120 μS/cm^2)

$\bar{g}_K$ = conductance per unit area for Potassium (K) ion-channel (36 μS/cm^2)

$\bar{g}_l$ = conductance per unit area for leak channels (0.3 36 μS/cm^2)

V_K = potential of Potassium (-12 mV)

V_{Na} = potential of Sodium (115 mV)

V_l = leak potential (10.613 mV)

V_m = 0.0 (initial)

The constants are kept according to the original paper which effectively sets the resting potential at V=0. To calculate $\alpha_n,\ \beta_n,\ \alpha_m,\ \beta_m,\ \alpha_h,\ \beta_h$, the following equations are used :

$$\alpha_n(V_m) = \frac{0.01(10 - V_m)}{e^{(1.0 - 0.1V_m)} - 1}$$
$$\beta_n(V_m) = 0.125e^{-\frac{V_m}{80}}$$
$$\alpha_m(V_m) = \frac{0.1(25 - V_m)}{e^{(2.5 - 0.1V_m)} - 1}$$
$$\beta_m(V_m) = 4e^{-\frac{V_m}{18}}$$
$$\alpha_h(V_m) = 0.07e^{-\frac{V_m}{20}}$$
$$\beta_h(V_m) = \frac{1}{e^{(3 - 0.1V_m)} + 1}$$

After specifying the constants and the equations, they are procedurally integrated to get the output spikes. The first equation $\frac{dV_m}{dt}$ is the action potential output. $\frac{dn}{dt}$, $\frac{dm}{dt}$, and $\frac{dh}{dt}$ are the probability of each channel opening (i.e. Sodium and Potassium.) Notice there are two terms in $\frac{dn}{dt}$, $\frac{dm}{dt}$, and $\frac{dh}{dt}$. The first term accounts for closed channels that open and the second

accounts for the open channels that are closed. The visual stimulus is presented as a sinusoidal encoded light wave with the formula:

$$y(t) = A\sin(2\pi f t)$$

Here, f=6.66Hz for blue light and 5.16Hz for yellow light which is scaled down from the physically accurate frequency values for both the colours in the visible spectrum. For horizontal and vertical gratings, arbitrary f values of 8 and 10 are taken respectively.

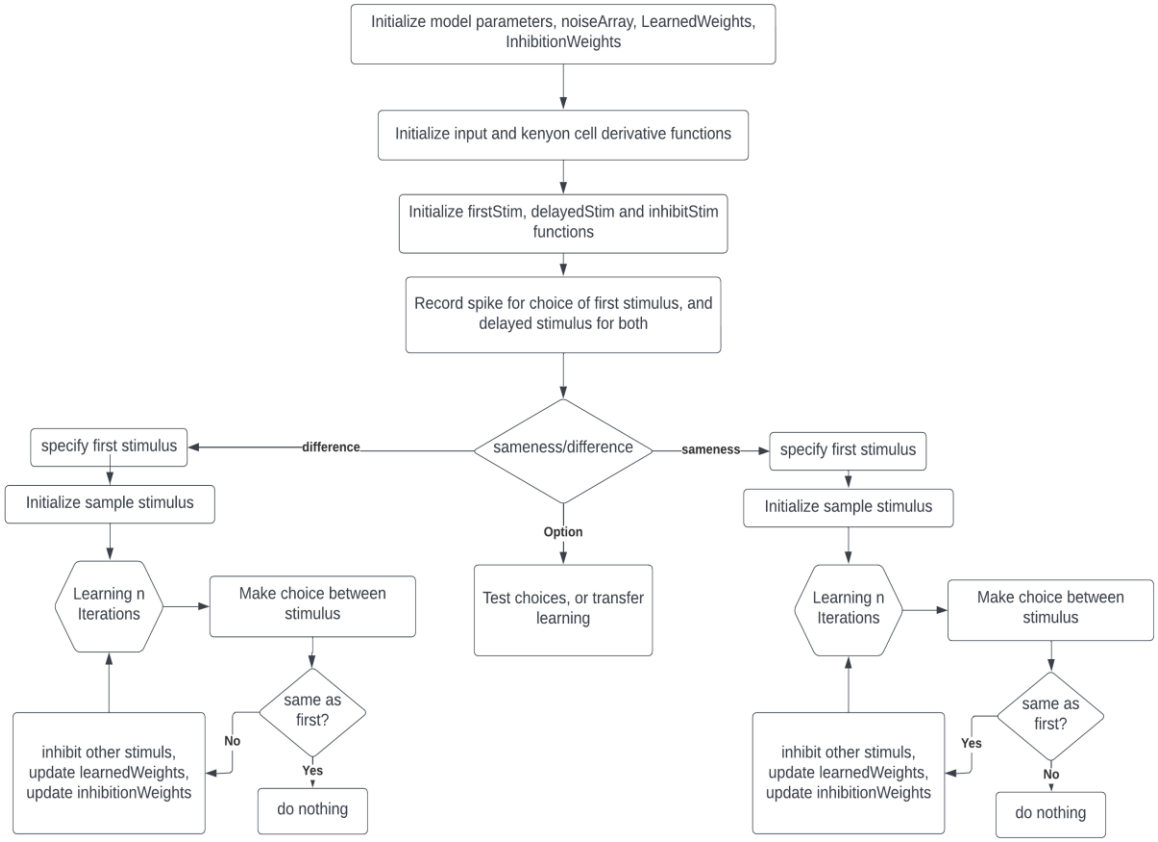


Fig2: Model Algorithm

Model Summary:

- The structure of the model is input stimulus neuron ⟶ Kenyon cell neuron (with inhibition feedback analogous to having PCT neurons) ⟶ output.
- Kenyon cell derivative function uses an inhibition constant to generate sparsity and inhibition due to repeated stimulus. It takes input from the output of the stimulus input neuron.
- The firstStim function is analogous to the stimulus shown at the entrance of the maze. It integrates the equations for an input stimulus twice. The output of the first integration when the stimulus is presented, is the input to the second integration function which is the Kenyon cell derivative function. The output of the second integration is the final output which is the Kenyon cell output. This is the ground truth.

- The delayed stimulus is analogous to the bee entering the maze after some delay due to which some noise is introduced in the Kenyon cell output. It accepts learned weights as a parameter to reduce the effect of noise during testing or transfer learning after the model is trained.
- The inhibitStim function punishes by inhibiting the non-rewarding stimulus during training. It essentially scales down the spike train of the Kenyon cell output more aggressively than the delayedStim function.
- A noise array is used in the delayedStim and inhibitStim function to decrease the neural activity due to delay and punishment. This is analogous to forgetting.
- During training, a choice between stimuli is made depending upon the probability weights which is the sum of the output of delayedStim array. Initially the probability weights are close which is why the model might choose incorrectly. As the training progresses, the probability weights of the non-rewarding stimulus starts decreasing due to inhibition while the rewarding stimulus remains constant. This provides more weight to the rewarding stimulus and compels the model to choose it in the next iterations.
- The learnedWeights captures the value of noise for the time step where the choice was correct during training. This is used in transfer learning to reduce the effect of noise when a novel stimulus is presented so that it can be closer to the ground truth.
- The inhibitionWeights array is used in transfer learning to scale down the non-rewarding stimulus. Using the combination of learned stimulus and inhibition stimulus, the model will have optimal probability weights which will help it to make the correct choice.

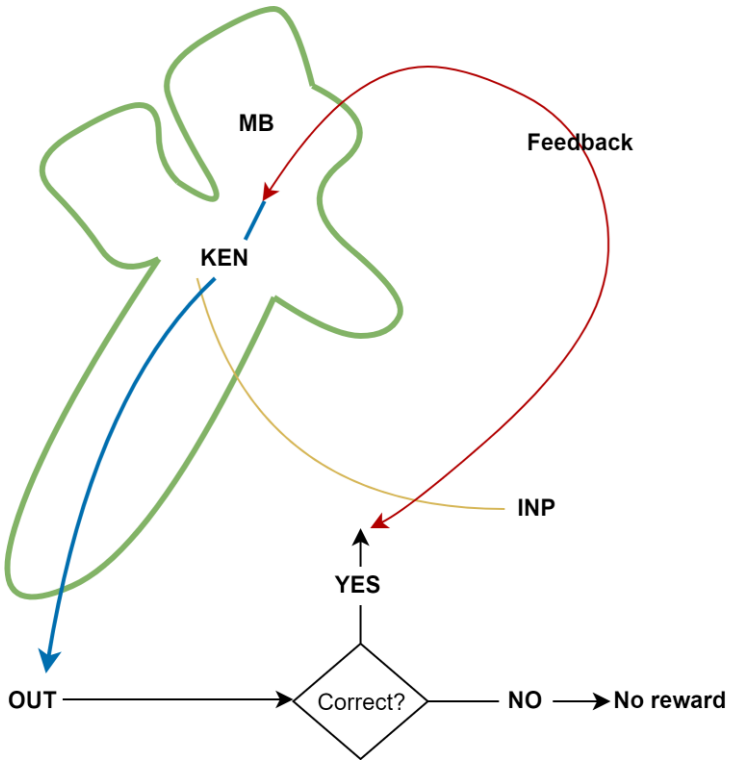
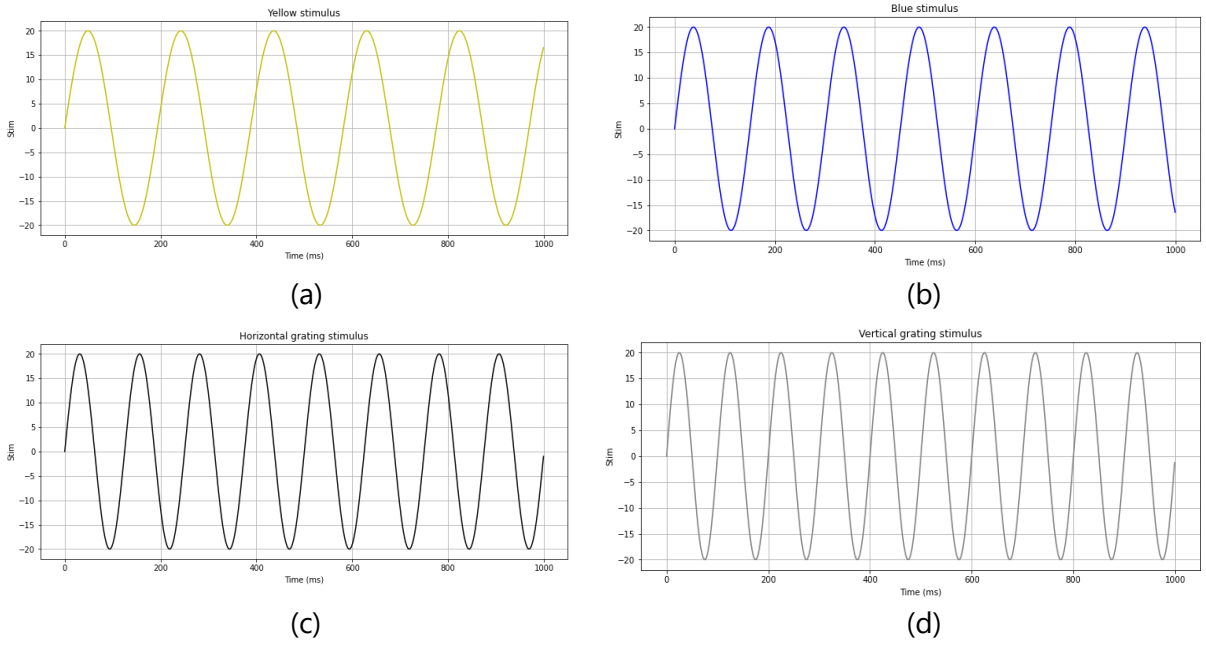


Fig3: Model state diagram

Results and analyses

The input stimuli were encoded with a sinusoidal wave using the sine wave equation. Figure 4 shows the stimuli.



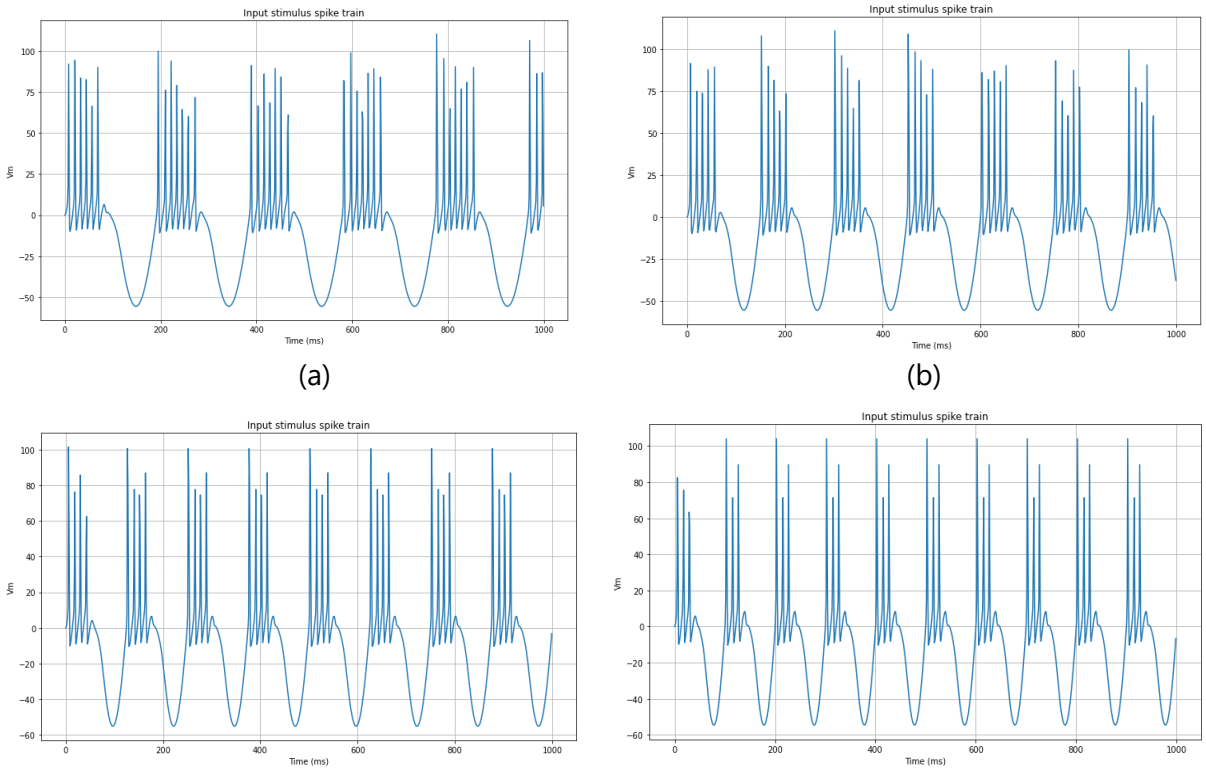
(a) (b)

(c) (d)

Fig4: Input stimuli: (a) Yellow, (b) Blue, (c) Horizontal grating, (d) Vertical grating

The frequency values for Yellow, Blue, Horizontal, and Vertical gratings are 5.16(Hz), 6.66(Hz), 8(Hz) and 10(Hz) respectively.

Moving on to the initial stimulus which is analogous to the bee entering the maze, Figure 5 shows the spike train for each of the input stimuls.



(a) (b)

(c) (d)

Fig5: Input spike train: (a) Yellow, (b) Blue, (c) Horizontal grating, (d) Vertical grating

Note that in Figure 5, the spike train portray the actual biological behaviour of a neuron during action potential. A stimulus first causes sodium channels to open. Because there are more sodium ions on the outside, the inside of the neuron becomes negatively charged which is why the sodium ions shoot into the neuron. Since sodium has a positive charge (Na^+), the neuron experiences depolarization. Meaning, the potential is increased and we get an action potential. When the potassium channels open, potassium rushes out of the cell, which reverses the depolarization. At about this time, the sodium channels start to close. Which causes repolarization, meaning, the action potential descends to the resting potential 0mV in our case. It can be observed that the action potential also goes below the resting potential. This state is called hyperpolarization. This is due to the potassium channels staying open for longer than usual. Eventually, the neuron returns to the resting state and the whole process is repeated for each action potential. It was really fascinating to see unique spike trains for different stimulus. This spike train is passed as an input to the Kenyon cells which are sparse and inhibitory in nature. Figure 6 shows the spike train of the Kenyon cells for each stimulus. This is the final output.

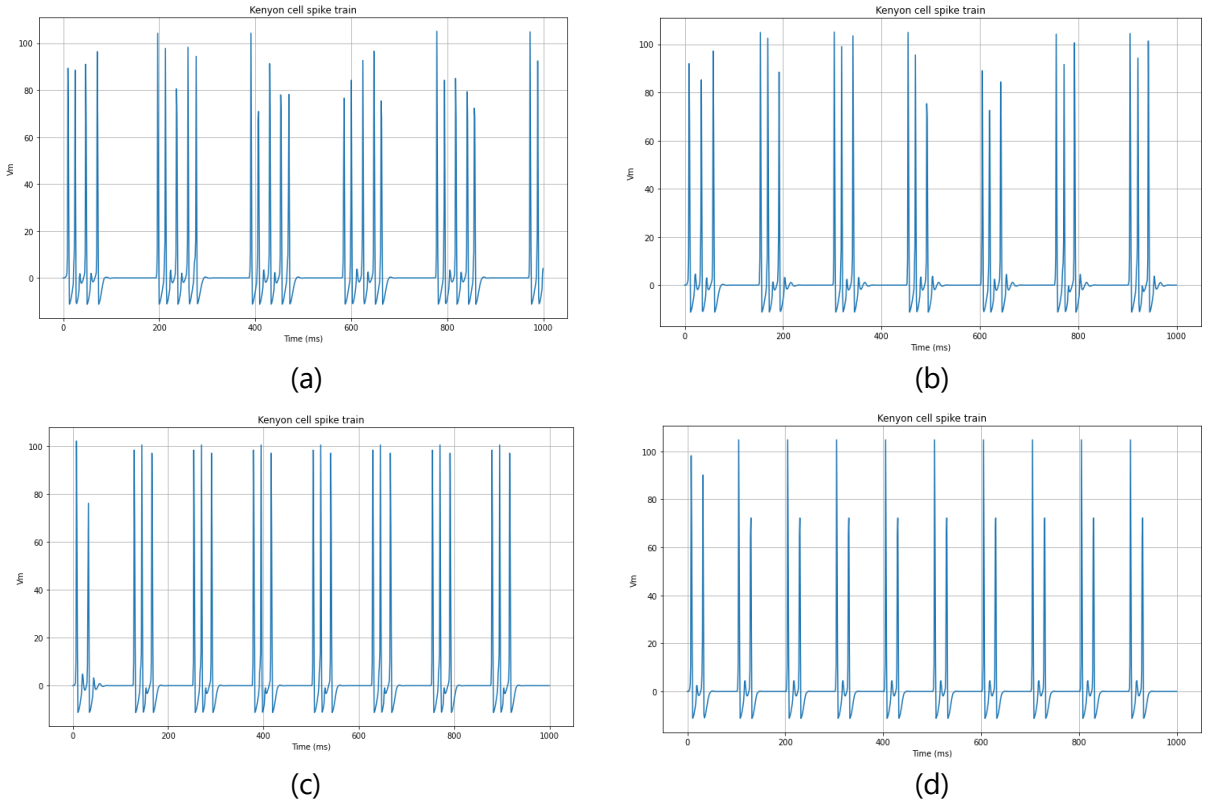


Fig6: Kenyon cells spike train: (a) Yellow, (b) Blue, (c) Horizontal grating, (d) Vertical grating

It can be observed from Figure 6 that the Kenyon cells produce sparser outputs for each stimulus. Since this is the output from the initial stimulus presentation, **it is the ground truth** and the delayed stimulus spike train should aim to come close to the above result depending on the training scenario. For example, if the yellow stimulus is learnt, the spike train of the

yellow delayed stimulus should be stronger along the lines of the ground truth. Of course, since the noise might even diminish a few spikes, usually, rest of the spikes are along the lines of the ground truth. This should be clearer from Figure 7 which shows how the delay introduced some noise in the ground truth which is the output of the delayed stimulus function.

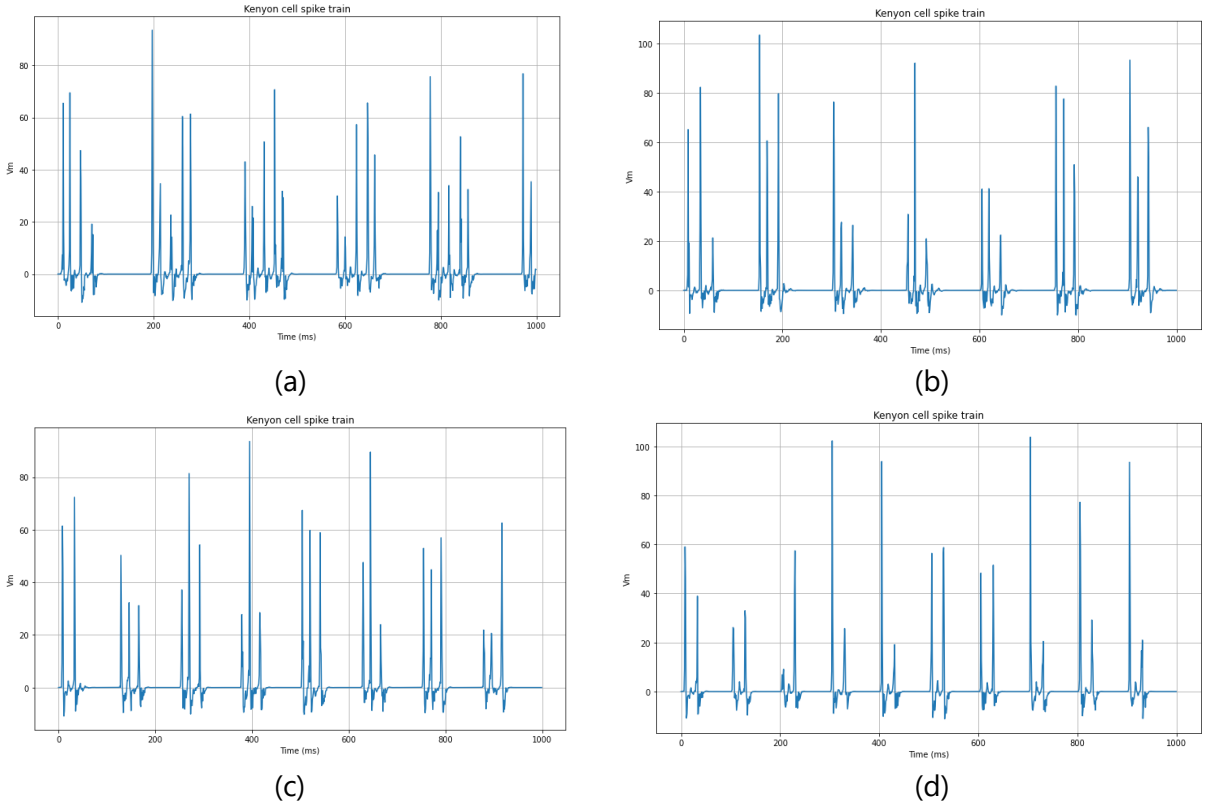


Fig7: Delayed Kenyon cells spike train: (a) Yellow, (b) Blue, (c) Horizontal grating, (d) Vertical grating

Notice the inhibitions in spike train due to noise in Figure 7. Take for example Figure 6(a) and Figure 7(a), they are the ground truth and the delayed stimulus output for the yellow stimulus. If you count the number of spikes in both of them, it is conserved but a bit diminished in the delayed stimulus output Figure 7(a). Now, if the yellow stimulus is learnt, it will remain as it is and the other stimulus will diminish even more due to punishment. Hence, when you pass the sum of their output array as the probability weights, the model will choose the learnt stimulus substantially more often as we can see from Figure 7(a) that it is closer to Figure 6(a). Figure 8 shows how punishment inhibits the stimulus even more.

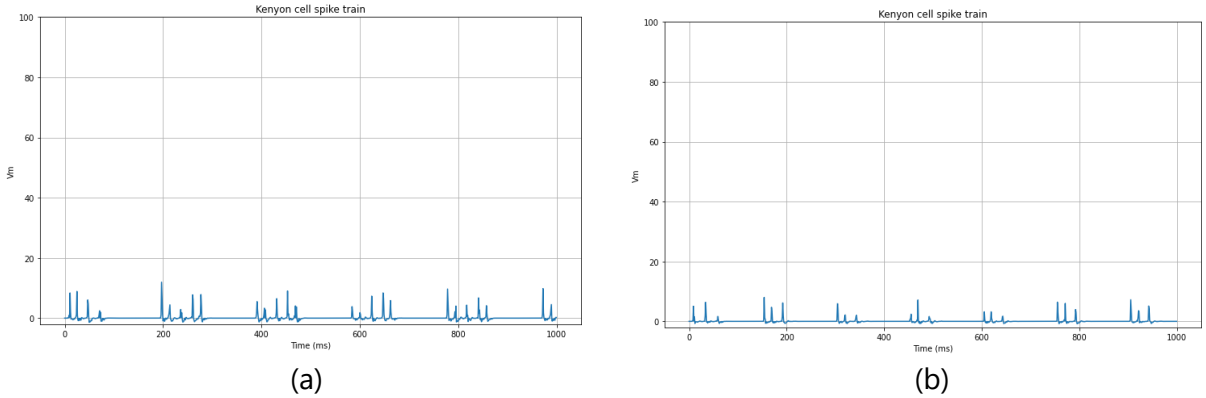


Fig8: Inhibited Kenyon cells spike train due to punishment: (a) Yellow, (b) Blue

During testing, of the yellow learnt stimulus for example, Figure 8(a) is compared to Figure 7(a) by taking the sum of the final output of both the arrays and passing it as the probability weights. Naturally, it can be observed that Figure 7(a) is much closer to Figure 6(a) than Figure 8(a). Hence the model will choose the correct stimulus much more often. While the whole training process helps the model to select the rewarding stimulus, it also records the learned weights that are the values of noise at the time steps when the model predicted correctly and the inhibition weights array that is the final output of the punishment stimulus. For example, again, if the yellow stimulus is learnt, the inhibition weights will be the final output of the blue array after punishment which is represented in Figure 8(b). These arrays are used in transfer learning by passing the learned weights array in the delayed stimulus function to reduce the effect of noise and scaling the non-desired stimulus with the inhibition array. For example, when transferring the learned weights in sameness learning from yellow and blue stimulus to horizontal and vertical gratings, if the horizontal grating is showed before entering the maze, when the bee receives the delayed stimulus output when it enters the maze, the horizontal grating will benefit from the learned weights while the vertical grating will be scaled by the inhibition weights.

Finally, Figure 9 shows the results of how the proposed model fits with the empirical data.

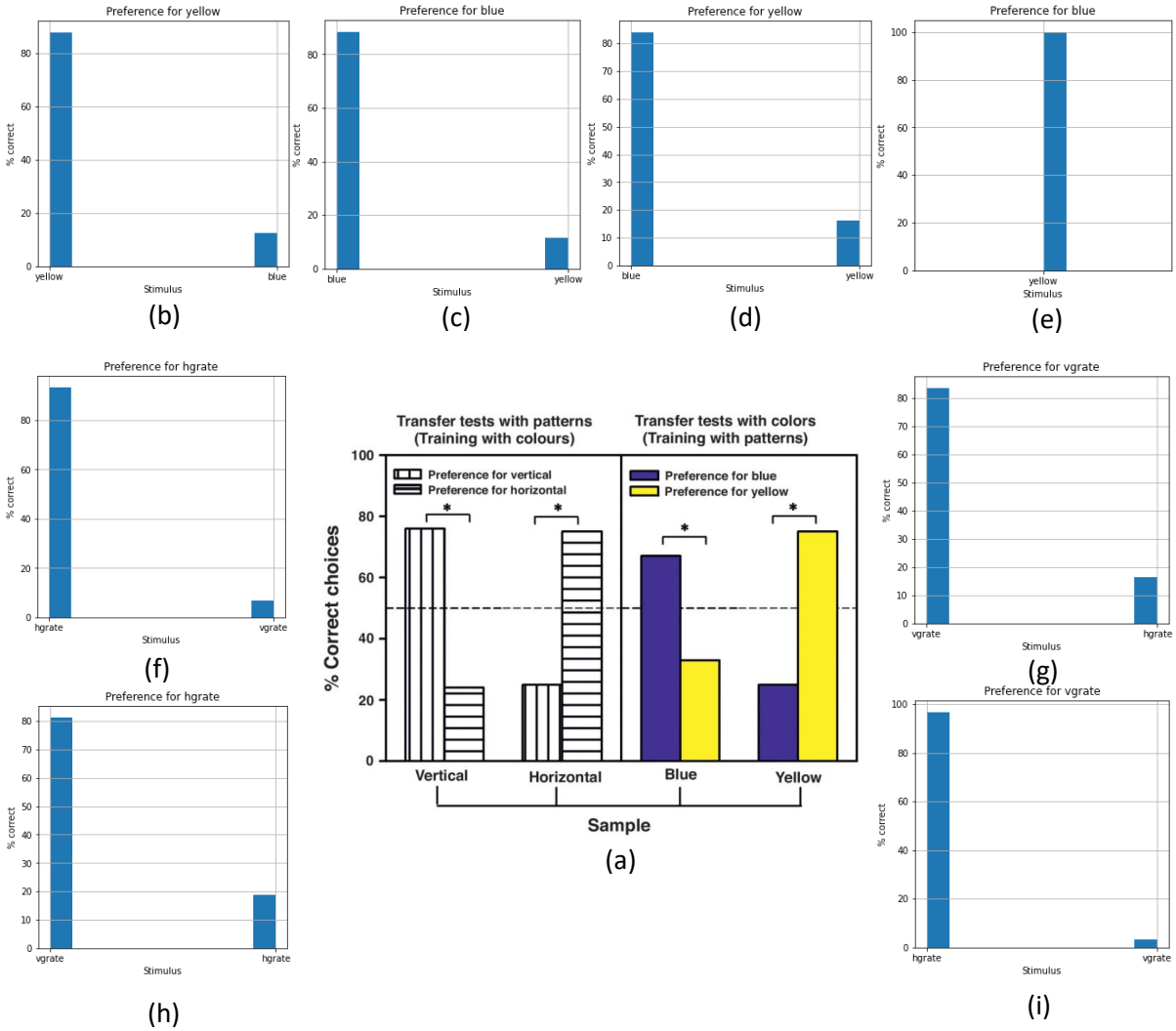


Fig9: Empirical results compared to the model output: (a) Empirical results from Girfua et al. [1] , (b) Sameness learing of yellow stimulus, (c) Sameness learing of blue stimulus, (d) Difference learing of yellow stimulus, (e) Difference learing of blue stimulus, (f) Transferred learning of sameness in horizontal grating stimulus, (g) Transferred learning of sameness in vertical grating stimulus, (h) Transferred learning of difference in horizontal grating stimulus, (i) Transferred learning of difference in vertical grating stimulus

From Figure 9(a) it can be observed that when the bees were trained for example, on yellow stimulus, they preferred the yellow stimulus substantially more than the blue stimulus when trained for 'sameness'. The proposed model produced similar results which can be observed in Figure 9(b). This similarity is retained when 'difference' is learnt. Though the authors did not show the graphs of difference learning, the written explanation agrees with the results of the proposed model. Figure 9(d) shows the bees learning the yellow stimulus but giving preference to the blue stimulus. These results are conserved across stimuli. Figure 9(f,g) show transfer learning of sameness in horizontal and vertical gratings. Again, the results are similar to the empirical data. Lastly, Figure 9(h,i) show transfer learning of difference in horizontal and vertical gratings which agrees with the written text.

Discussions

To summarize what we have seen so far, honey bees have been shown to be capable of concept learning and higher-order cognition skills. The report proposed a biologically inspired mushroom body model with spiking neurons to train and fit the empirical data in [1]. The model consists of an input neuron which connects to a Kenyon cell to process the stimuli and a choice between two stimuli is received as output based on the type of the learning task and the initial stimulus. The visual stimuli for blue and yellow colours were presented in the form of physically accurate sinusoidal encoded waves scaled in frequency. We saw how each stimulus produced a unique spike train in the neuron. The results show that the model is capable of learning the concept of similarity/difference from visual stimuli and adaptively transfer it to perform optimally in novel stimuli without the need for relearning them. Hence, the model is robust to changing environments and flexible enough to optimally respond to novel stimuli.

The reason behind using spiking neurons is simply because they are the 'real deal'. The brain is a complex arrangement of spiking neurons which embody the day-today actions and behaviour of an organism. To understand the mechanism for higher-order cognition, it is very essential to study the dynamics of biological neurons. Also, the brain is extremely efficient in terms of power consumption which is why extensive research in SNNs is necessary to build good neuromorphic hardware. Fortunately, the Hodgkin-Huxley equations seems to be a really good starting point.

The goal for this report was to be as biologically plausible as I could which is why parameters such as the inhibition constant is introduced and the stimulus was presented as a sinusoidal wave. Kenyon cells produce sparse representation of the stimulus due to their connection with the GABAergic PCT neurons. This was confirmed when GABA reduction drugs were administered and the Kenyon cells showed more activity in the mushroom body [11]. The inhibition constant accounts for this property of sparsity and repetition related inhibitory response in neural activity of a stimulus. The optimal value of the inhibition constant was

identified through trial and error and it is multiplied by the membrane capacity C_m in the Kenyon cell derivative function due to the fact that the speed of the action potential propagation is inversely proportional to the membrane capacity [12]. Hence the more the inhibition constant is increased, the less the neural activity output. The stimulus was presented as a sinusoidal wave as two of the stimuli were specific colours. Colours have a defined frequency value in the visible spectrum and a monochromatic light i.e. of single frequency exhibits sinusoidal oscillation [13]. Granted that the real world coloured light waves are not pure sinusoidal, since the authors did not mention the physical properties of the stimulus, a monochromatic light wave worked well for the simulation.

The structure of the model also takes into account the actual arrangement of neurons in the mushroom body. Simply, the input neurons are connected to the Kenyon cells which are connected with PCT neurons for inhibition and reinforcement and lastly, they process everything and pass it to the output neurons. For simplicity, the inhibition calculations are done mathematically in the model during the training process rather than acquiring values from an external neuron.

Apart from the Hodgkin-Huxley model, there are other models such as the Leaky-integrate and fire model which shows nonlinear discontinuous dynamical behviour. Essentially, it mimics the Hodgkin-Huxley model output by following the leaky channel. This model also fires an action potential when the input can push the current above threshold. It is much less compute intensive than the Hodgkin-Huxley models but it is not that biologically accurate. However, this models can be interesting to look at when we are concerned with a very lower level cognition. Nevertheless, there is a lot of future scope for models like the one proposed in this report. The dynamics of more complex arrangement of neurons should fit the empirical evidences even more. A much more closely modelled network of neurons that are present in the mushroom bodies might provide some insights about the manner in which the brain waves are generated during learning. Honey bees have been shown to use alpha waves as humans and other mammals [14]. Modelling less complex brains than ours to understand this sort of shared abilities will open completely new pathways for research.

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