Optimal receptor response functions for the detection of pheromones by agents driven by spiking neural networks

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Abstract

The goal of the work presented here is to find a model of a spiking sensory neuron that could cope with small variations in the concentration of simulated chemicals and also the whole range of concentrations. By using a biologically plausible sigmoid function in our model to map chemical concentration to current, we could produce agents able to detect the whole range of concentration of chemicals (pheromones) present in the environment as well as small variations of them. The sensory neurons used in our model are able to encode the stimulus intensity into appropriate firing rates.

1 Introduction

In this study, we want to investigate the encoding of information about pheromones in spiking neural networks controlling artificial agents. Initially, the pheromones are diffused symmetrically from a point source (Figure 1). In order to create pheromone sensing agents, we need to decide which kind of sensory neurons we want to use. To model the sensory neurons in a biological plausible way and to be able to explore different encoding strategies, we used spiking neurons. One challenge of using a spiking neural network is to decide the coding to use in order to map information received by a sensor that will transform these stimuli into spikes.

Different coding strategies can be used [Floreano and Mattiussi, 2001]:

a) Mapping stimulus intensity to the firing rate of the neuron.
b) Mapping stimulus intensity onto the number of neurons firing at the same time.
c) Mapping stimulus intensity onto the firing delay of the neuron.

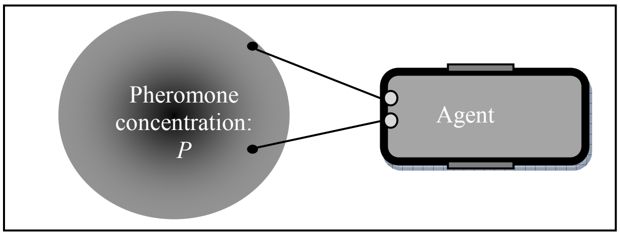

Figure 1. An agent equipped with two wheels and two antennae linked to two sensory neurons used to detect pheromones.

In order to use one of these encoding schemes, one needs first to decide how the input current of a sensor should represent its stimulus intensity. The current received by a sensor will be different from the one received by a non-sensory neuron because it will be based on the external stimulus intensity and not the activity of other neurons or sensors. We want an agent to be able not only to detect small variations of pheromone concentration but also the whole range of concentrations. Therefore, the agents must be equipped with sensory neurons that can produce spike trains at different frequencies depending on the pheromone concentration. The ideal case would be to have a linear relationship between the pheromone concentration and the firing rate of the sensory neuron. Such relationships exist in biological systems. For example in humans, the relationship between the frequency of firing of sensory neurons and pressure on the skin is linear [Kandel *et al.*, 2000]. We tried to find out how to implement such a relationship by carrying out different experiments using different expressions for the sensory neuron's current.

2 Experiments

We modelled a sensory neuron as a leaky integrate-and-fire neuron and tried different equations to calculate its input current. The sensory current I was always calculated depending on the pheromone concentration P. If the membrane potential, which depends on the current I, reaches a certain threshold θ the sensory neuron emits a spike. Therefore, the firing rate of the sensory neuron depends on the relation between pheromone concentration and current (Figure 2). In our experiments, we tried many different functions relating the pheromone concentration P to the current I in order to obtain a desired quasi-linear relationship between the pheromone concentration and the firing rate of the sensory neuron.

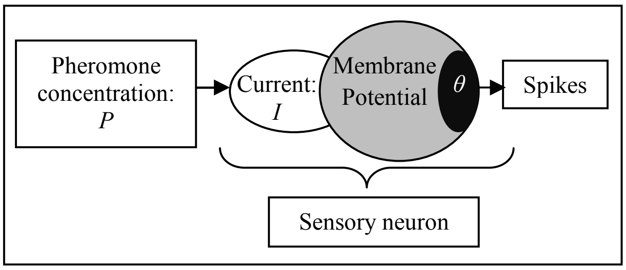

Figure 2. Mapping pheromone concentration into spikes.

We first set the sensor's input to a concentration of 1 and we recorded at what time a spike was emitted in order to determine the frequency (firing rate). We applied the same method to study the firing rate of the sensors over the whole range of pheromone concentration up to some maximum (that we chose to be 300). We did not want the sensory neuron to fire if the concentration was equal to 0 so only the presence of pheromones could stimulate a sensor. Afterwards, we modelled each different kind of sensory neuron as part of an agent and looked at the agent's behaviour.

2.1. Linear relationship between current and pheromone concentration

We first carried out experiments implementing a simple linear relationship, expressed by Equation (1), between the pheromone concentration P and the current I (Figure 3.a) and studied the sensor's firing rate (Figure 3.b.).

$$I = KP \qquad (1)$$

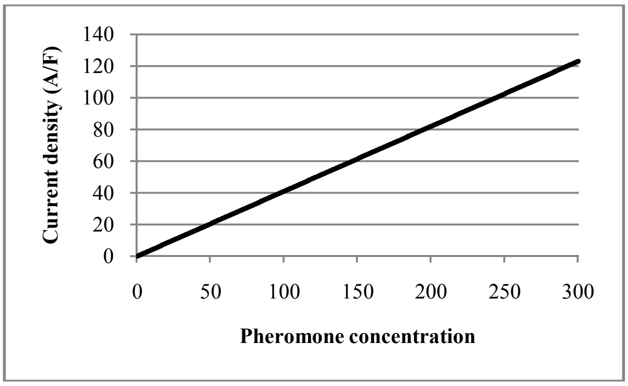

Figure 3.a. Current density (in Ampere per Farad) input to sensory neuron using Equation (1) with K=0.41.

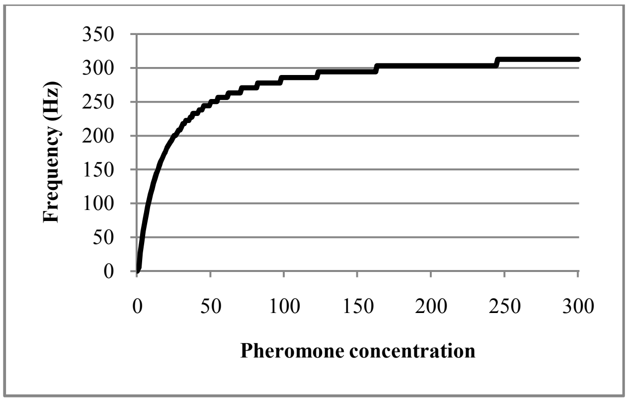

Figure 3.b. Resulting firing rate of sensory neuron. The maximum firing rate of a neuron is around 300 Hertz.

After a few experiments using different values for K, we realized that the sensor was saturating (Figure 3.b) due to the nature of the sensory neuron (leaky integrate-and-fire [Koch, 1999]). In fact, above a small value of pheromone concentration, the current produced was too high and the sensor fired at its maximum rate. After implementation in the agent, we saw that it was not able to detect the difference between a concentration of 200 and 250 for example.

2.2. Linear relationship with offset between current and pheromone concentration

Then, we tried to use the same equation but with an added baseline current and a much smaller slope (K_2) (Equation (2) and Figure 4.a). We made these changes knowing that our sensor responds to a small range of currents with a large bandwidth.

$$I = K_1 + K_2 P \qquad (2)$$

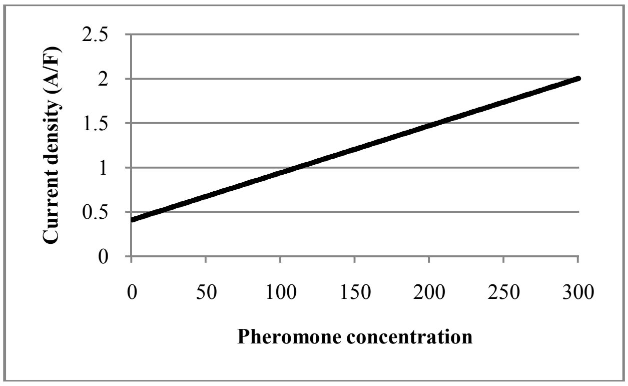

Figure 4.a. Current density input to sensory neuron using Equation (2) with K_1 = 0.41 and K_2 = 0.0053. Note that in this graph, the ordinate scale is different than in Figure 3.a and the current density is very low.

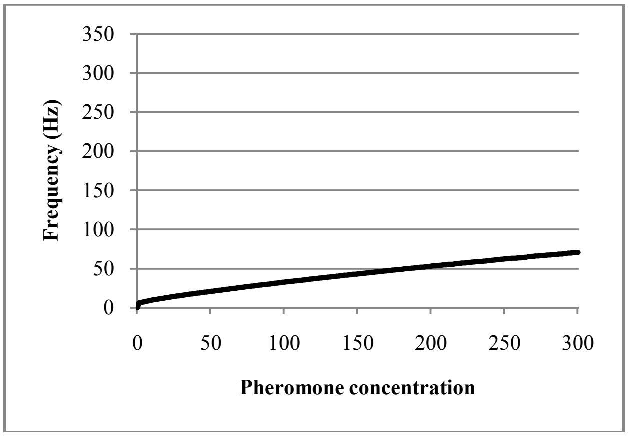

Figure 4.b. Resulting firing rate of sensory neuron.

With this equation, we had a more linear relationship between pheromone concentration and the firing rate of the sensor (Figure 4.b) so the agent should have been able to detect smaller variations. Unfortunately, the sensor did not use its whole bandwidth and its resolution was relatively poor. Therefore, another kind of functional relationship had to be tried.

2.3. Non-linear relationship between current and pheromone concentration

Concerning the neurons we are using, we know the limits of currents and the corresponding firing rate. For every cell (motorneurons, sensors, and interneurons):
$I_{min} \approx 0.4\ (f \approx 0.6\ Hz)$
$I_{saturation} \approx 20\ (f \approx 300\ Hz)$

We also know that the firing rate of a leaky integrate-and-fire neuron is given by [Koch, 1999]:

$$< f > = \frac{1}{t_{th}+t_{ref}} = \frac{1}{t_{ref}-\tau ln\left(1-\frac{V_{th}}{IR}\right)} \quad (3)$$

Where:

- t_{th} is the mean time to reach the threshold value
- V_{th} is the threshold voltage (a spike is emitted if the membrane potential is above this value).
- t_{ref} is the refractory period.
- I is the current
- R is the resistance (constant)
- C is the capacitance (constant)
- $\tau = RC$ (time constant)

Given that our sensory neuron is modelled as a leaky integrate-and-fire neuron, we rearranged Equation (3) to find an equation (4) for the current (Figure 5.a) that would always produce a linear relationship between the pheromone concentration and the firing rate of the sensory neuron (Figure 5.b).

$$I = \frac{V_{th}}{R}\left[\frac{1}{1-exp\left(\frac{t_{ref}}{\tau}-\frac{1}{<f>\tau}\right)}\right] \quad (4)$$

To get a linear relationship between the current and the pheromone concentration, we replaced $< f >$ by P and to make sure the frequency was between 0 and 300, we needed:

- $\frac{V_{th}}{R} = 0.4\ mV/\Omega$
- $t_{ref} = 3/1000 = 0.003\ s$
- $\tau = 1/20 = 0.05\ s$

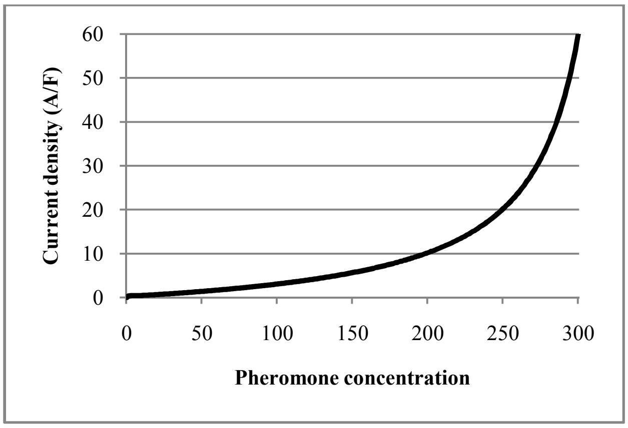

Figure 5.a. Current density input to sensory neuron using Equation (4).

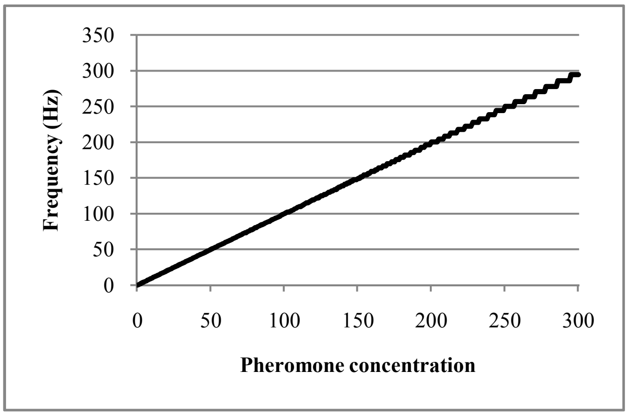

Figure 5.b. Resulting firing rate of sensory neuron.

With this equation, an agent is able to detect a small variation in the pheromones concentration using its whole bandwidth. We created Equation (4) artificially but we can use it as a guide to look for an equation commonly found in biological systems that describes a similar relationship and a graph similar to Figure 5.a.

2.4. Hill functions

We know that pheromones and other odours bind to receptor proteins situated in an animal's olfactory sensory neurons [Wyatt, 2003]. The current generated by the sensory neurons depends on their binding capacity. We first investigated an equation used by biochemists describing the binding of ligand molecules to proteins: a Hill function [Stryer, 1988].

$$h(x, k, m) = \frac{x^m}{k^m + x^m} \qquad (5)$$

Where:

- k is the concentration of molecules when h is equal to 0.5
- m is the Hill coefficient and is considered as an estimate of the number of binding sites of a protein.
- x is the concentration of ligands

Archibald Hill used this equation in 1910 to describe the binding of oxygen to Hemoglobin. It seems appropriate to use Hill functions to describe the shape of the current produced by the sensor as they are very similar to Equation (4).

The first Hill function (6) we used was too simple to fit the function (4). An example with m = 1, K_1 = 50 and K_2 = 100 is given in Figures 6.a. and 6.b. Once again, we realized that the sensor was saturating quite rapidly.

$$I = K_1 \left(\frac{P^m}{K_2^m + P^m}\right) \qquad (6)$$

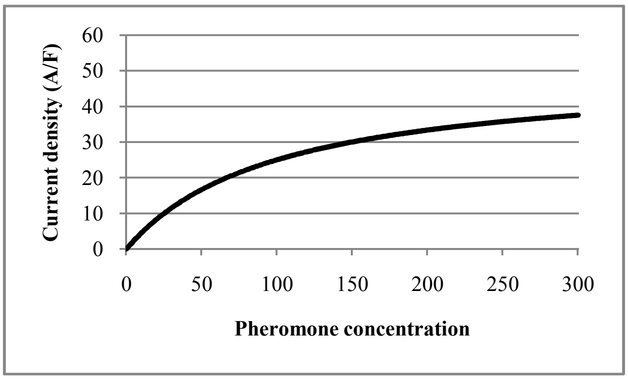

Figure 6. Current density input to sensory neuron using Equation (6).

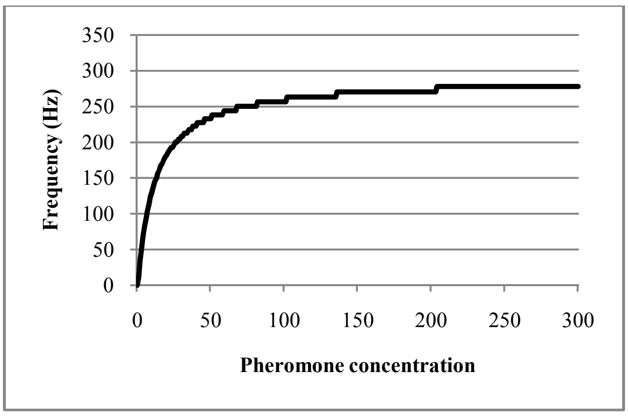

Figure 6.b. Resulting firing rate of sensory neuron.

We used a MATLAB fitting routine to find appropriate constant values for a second Hill function using Equation (6), to minimize the difference between the two functions (6) and (4) (as shown in Figure 5.a.) in order to have a function that would create a near linear relationship between the pheromone concentration and the firing rate of a sensory neuron like the function (4) (Figure 7).

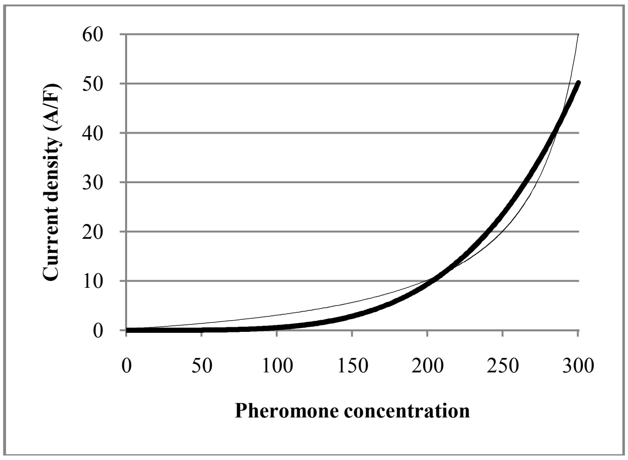

Figure 7. Current density input to sensory neuron using Equation (6) with $K_1 = 2.38*10^7$, K_2 = 7104 and m = 4.13. The thin curve is Equation (4) and the thick one is Equation (6).

Unfortunately, this function was not as good as (4). In fact, the sensor could not detect a pheromone concentration of 1. So we decided to add an offset to the function.

2.5. Hill functions with offset

$$I = K_1 \left(\frac{P^m}{K_2^m + P^m}\right) + b \qquad (7)$$

This time, the MATLAB routine found a value for b too high so the sensor could fire even if it did not perceive any pheromones (Figure 8). So we tried to constrain the value of b to be less than 0.4 (Figure 9). Unfortunately, the current produced was the same (= 0.4) for a large range of small pheromone concentration so the agent could not detect differences of concentration in this range. We concluded that it was difficult to use a Hill function for the sensors' current so that the agents would be able to detect a very small and very high pheromone concentration. Hill functions with coefficients > 1 are sigmoidal so we decided to use a more general sigmoidal function.

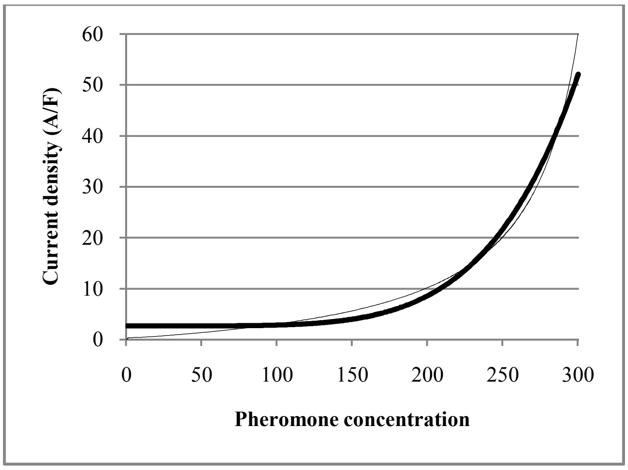

Figure 8. Current density input to sensory neuron using Equation (7) with $K_1 = 2.33*10^6$, $K_2 = 2348$, $m = 5.23$ and $b = 2.65$. The thin curve is Equation (4) and the thick one is Equation (7).

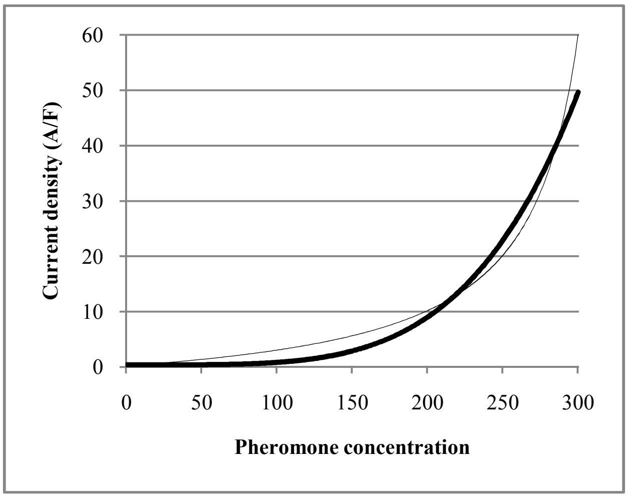

Figure 9. Current density input to sensory neuron using Equation (7) with $K_1 = 3.45*10^4$, $K_2 = 1378$, $m = 4.297$ and $b = 0.4$. Dashed curve is Equation (4) and the other one is Equation (7).

2.6. Sigmoid function

Due to the fact that the function (4) (Figure 5.a) resembles the first part of a sigmoid function, we decided to investigate general sigmoid functions.

$$I = K_1 \left(\frac{1}{1+exp\left(\frac{h-P}{K_2}\right)} \right) \quad (8)$$

We also fit this function to (4) (Figure 10). Unfortunately, the sensor could not detect 1 unit of pheromone so we added an offset to the function.

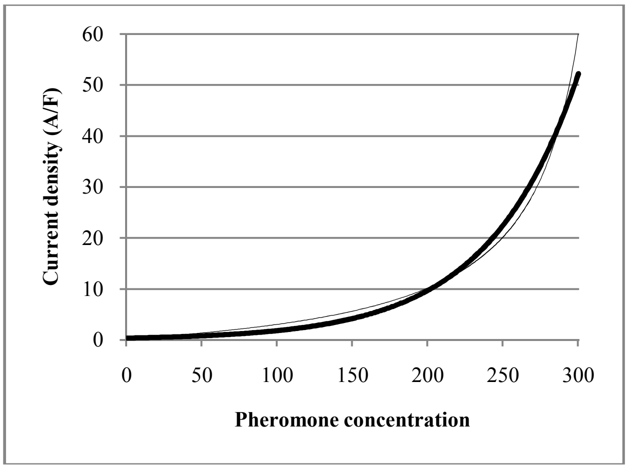

Figure 10. Current density input to sensory neuron using Equation (8) with $K_1 = 2.38*10^8$, $K_2 = 59.35$ and $h = 1210$. The thin curve is Equation (4) and the thick one is Equation (8).

2.7. Sigmoid function with offset

$$I = K_1 \left(\frac{1}{1+exp\left(\frac{h-P}{K_2}\right)} \right) + b \quad (9)$$

We found a function very similar to (4) but with an offset too high (Figure 11). So the sensor was firing even when it did not receive any information. We therefore constrained b to be less than 0.08 and found a very similar function with a small offset (Figure 12.a). After modelling a sensor using this function, we finally produced a relationship between the pheromone concentration and the sensor's firing rate (Figure 12.b) that was less linear than by using (4) but perfectly adequate to allow the agent to detect small and large variation of pheromone concentration.

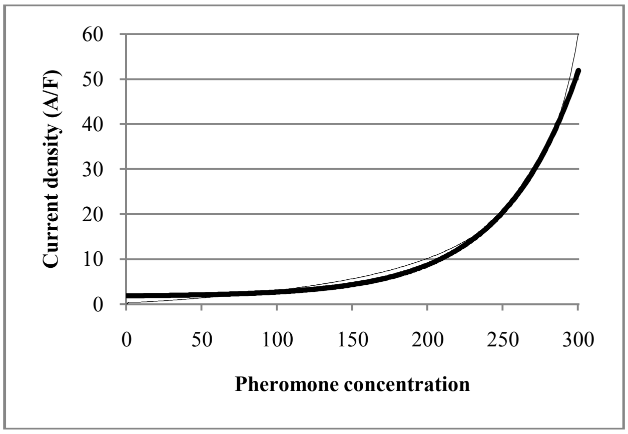

Figure 11. Current density input to sensory neuron using Equation (9) with $K_1 = 2.7*10^7$, $K_2 = 51$, $h = 973$ and $b = 1.7$. The thin curve is Equation (4) and the thick one is Equation (9).

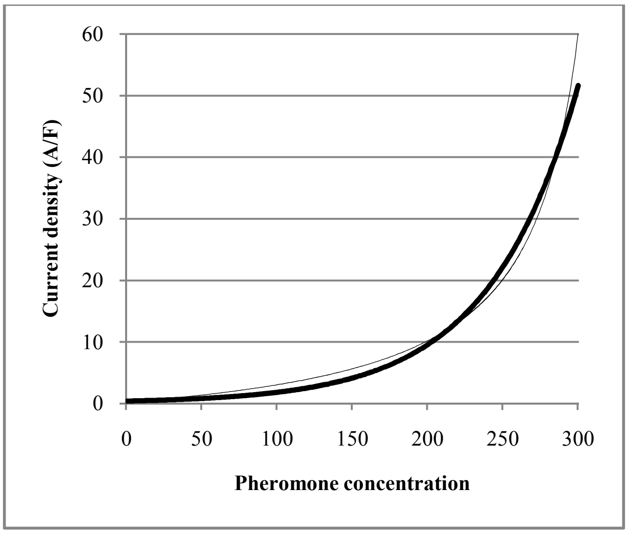

Figure 12.a. Current density input to sensory neuron using Equation (9) with $K_1 = 3.9*10^4$, $K_2 = 59$, $h = 691$ and $b = 0.08$. The thin curve is Equation (4) and the thick one is Equation (9).

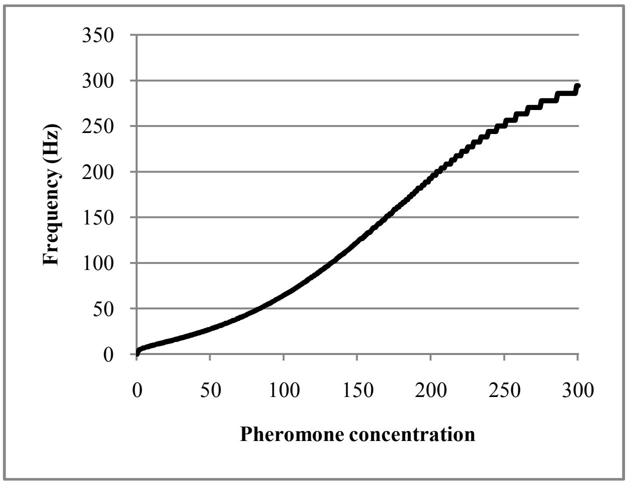

Figure 12.b. Resulting firing rate of sensory neuron.

3 Conclusion

The long-term goal of our research that sets the context for this study is to create agents able to find and interact to pheromones diffused symmetrically from a point source. In order to achieve this goal, we had to find a model of spiking sensory neuron that could cope with small variations of pheromone concentration and also the whole range of concentrations. We tried many different functions to map the pheromone concentration onto the current of the sensory neuron in order to produce a linear relationship between the concentration and the firing rate of the sensor. After unsuccessful trials using linear currents, we created an equation that would by definition achieve this task and used it as a model to help us find a similar function that is also used in biology. We concluded that by using a biologically plausible sigmoid function in our model to map pheromone concentration to current, we could produce agents able to detect the whole range of pheromone concentration as well as small variations. The sensory neurons used in our model are able to encode the stimulus intensity into appropriate firing rates. Moreover, using this model of sensory neurons, we managed to create a simulated robot capable of chemotropotaxis. We are currently studying how an agent can use two different types of information encoding strategies depending on the level of chemical concentration.

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