

## Real neurons in real networks

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**Abstract:** A dynamic model of spiking neurons is used to simulate a hypothesised neural control circuit for phonotaxis in crickets. The six-neuron system exploits specific temporal properties of the membrane potential to effectively turn only towards sounds with appropriate temporal patterns. This demonstrates how low-level neural properties, not normally included in artificial neural nets, may contribute directly to successful behaviour in real biological systems.

### 1. Introduction

Artificial neural networks are typically related only in an abstract fashion to the neural networks that control the behaviour of biological creatures. In particular their uniformity of structure, while computationally appealing, does not reflect the diverse properties and connections of neurons in real nervous systems. As a consequence, the solutions to behaviour control problems produced by training an ANN may be radically different to those existing in biology.

Our aim is to gain an understanding of how biological neural circuits control behaviour. Our approach is to model networks of neurons to investigate their control properties. In doing so, we seek to represent at an appropriate level of detail the known characteristics of and connections between neurons. Where possible we embed the neural models in real-world sensorimotor systems to fully test their efficacy.

As yet, directly linking neural circuitry to behaviour is only possible for invertebrate models, where neuroethological investigations have led to the identification of specific neurons and how their activity affects a particular behaviour. In this paper we look at the neural underpinnings of phonotaxis behaviour in the cricket. In previous work (Webb, 1994, 1995), a simplified model of this system was tested in a robot and it was demonstrated that the basic mechanism could control the behaviour as hypothesised. Here, the hypothesis is fleshed out using a neuronal circuit model (Scutt & Dampner, 1991) that includes temporal properties of neural activity that may be essential to the behavioural control.

### 2. The neurons

The neuronal circuit model described in this paper is an object-oriented program (Scutt & Dampner, 1991, 1992) using a flexible parameter system to cater for differences between neurons and to keep track of the changing state of each neuron over time. These parameters represent features of the neuron at a higher level than ionic concentration, but which have obvious correlates in the real neuron (e.g. base membrane potential, threshold, time constant). The use of such a system allows

circuits of heterogeneous neurons modelled on real data to be constructed with a minimum of effort.

The model neurons generate spikes like real neurons, rather than using the continuous activation functions typically associated with ANNs. The model uses an approximate state-system for simulating the changes in each neuron's membrane potential; the exact nature of this state-system depending on the type of neuron involved. A neuron is treated as being in one (or, occasionally, more than one) of six states, depending on whether the cell has just fired, the present membrane potential, the threshold etc. For example, if the membrane potential is above the threshold, and the cell is not already in the process of firing, then the neuron will start to generate a spike and will initiate synaptic transmission. The weight of a synapse and the breadth of the spike determines the strength of the signal received by the postsynaptic neuron. As with an ANN, the sign (positive or negative) of the synapse's weight indicates whether the connection is excitatory or inhibitory.

### 3. The network

Cricket phonotaxis - the ability of females to locate males by walking towards their calling song - has been well studied both behaviourally and physiologically. Important facets of the behaviour are that the response is selective and reactive. That is, the female only approaches songs of the males of its species, the main 'recognition' cue being given by the syllable repetition interval (SRI) in the song. Also, the female changes direction whenever the song direction changes and will continue walking for hours on a treadmill getting no nearer to the sound source.

**Identified neurons:** The input side of the neural circuitry is relatively well studied. The axons of around 50 auditory receptors make up the auditory nerve which forms synapses in the prothoracic ganglion. A number of pairs of auditory interneurons have been identified in this ganglion: two pairs of 'omega' neurons (ON1 and ON2) that receive ipsilateral excitation, and inhibition from their contralateral pair; and two pairs of ascending neurons (AN1 and AN2) which receive excitatory input from the ear ipsilateral to their dendrites (Wohlers & Huber, 1982). There are also identified descending neurons in this ganglion. In the brain, several types of auditory neurons have been identified (BNC1 and BNC2) which appear to be connected to AN1 and AN2 (Schildberger, 1988). Descending neurons sensitive to sound have been found but their connectivity is not well understood (Bohm & Schildberger, 1992).

The AN1 pair have been closely studied because they are considered critical to phonotaxis. They connect principally to the auditory receptors tuned to the male calling song frequency. Hyperpolarizing one of the pair causes reversible effects on the walking direction of the female. They have no background activity; excitatory input causes a rise in postsynaptic potential with superimposed spikes; and firing is maintained with little adaptation for the duration of the signal. The rate of decay of potential after cessation of excitation determines the 'critical pause length' at which gaps in the input pattern can be detected in the neural response; decay to 50% takes around 15ms. Thus normal song patterns (in which e.g. 30ms syllables are repeated at 15Hz) can be seen in the firing pattern. The intensity of the excitatory signal is coded

by both the firing rate (0-10spikes per syllable) and latency before firing (38-16ms) in the AN1 reponse.

**Hypothesis:** It was hypothesised that these specific properties of AN1 might explain the selectivity of the female's behaviour without further processing for her to 'recognise' the signal. The relative onset time of the left and right members of the AN1 pair can be used to decide which way to turn, as whichever fires first will be the direction of the source relative to the the cricket<sup>1</sup>. However, if the signal is unpatterned or repeats too rapidly, both neurons will fire continuously, and so "which fired first" will not be an effective signal. If the signal repeats too slowly, decisions to turn will also be slowed down and path correction become less efficient. Between these extremes there should be a band of repetition rates for which the system works well - which is what has been observed in the behaviour of the animal.

**Robot model:** The robot model (Webb 1994,1995) implemented this hypothesis using simple summation functions to represent the response-latency relationship and the decay rate. The subsequent processing stage - identifying the first onset and causing a turn - was not neurally based (though neurally plausible). Even with this simple control network it was possible to show succesful taxis - in the real world - to specific sound sources, selectivity, and the ability to approach one of two sound sources. The behaviour was surprisingly robust in noisy environments.

**The neuron model:** Our main objective was to reimplement the basic hypothesis using model neurons and synapses to implement the summation, comparison and supression functions. The model simulated a cricket on a treadmill, i.e. at a fixed distance from the sound source but able to vary its direction relative to the source. The auditory input, or response of each ear, was calculated from the sound source amplitude and direction as a cardioid ( $a(1 + \cos\theta)$  for each ear where  $\theta = 0^\circ$  at right-angles to that ear).

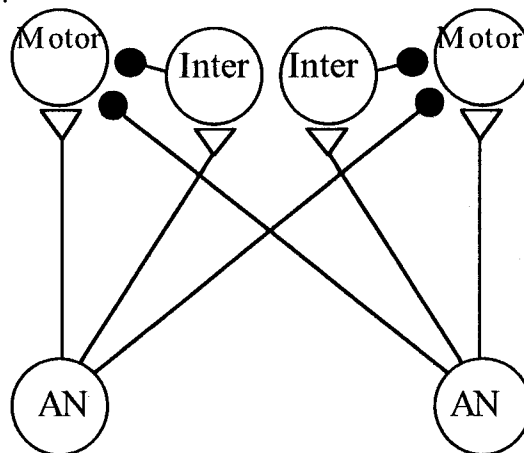


Figure 1: The six neuron circuit to model the cricket response to sound.

<sup>1</sup> It is beyond the scope of this paper to explain how the auditory system of the cricket is directionally responsive to sound - see eg. Michelson et al (1994).

The neural circuit consisted of three pairs of neurons (see figure 1). The AN neurons, and inhibitory Interneurons were of type *plateau*. Neurons of this type can generate spikes as long as they remain above threshold and continue to receive excitatory signals. Those of type *noisy* (the Motor neurons) produce a constant amount of self-generated stochastic noise which produces slight fluctuations in the neuron's membrane-potential. Also, unlike *plateau* neurons, once a *noisy* neuron spikes it cannot generate *another* spike until it has undergone a hyperpolarising afterpotential. Apart from the neuron type, all other neuronal parameters (such as base membrane potential, threshold, time constant, etc.) were constant across all neurons. Each AN made a direct excitatory connection to the ipsilateral motor neuron, and a direct inhibitory connection to the opposite motor neuron. Consequently the motor neuron would tend to fire only if its ipsilateral AN started to fire before the opposite AN. Each AN also made an indirect connection to its ipsilateral motor neuron via an inhibitory Interneuron. The relative delay caused by this link meant the motor neuron would fire once after AN started firing, and subsequently be suppressed until AN had ceased firing. Each spike produce by a motor neuron caused a 5 degree 'turn' of the simulated animal.

Although there is no obvious 'unit' for synaptic strength, the relative weightings of connections were as follows: From AN to ipsilateral Motor: 12; AN to opposite Motor: -5; From AN to Interneuron: 9; From Interneuron to Motor: -9. These weights did not require much fine tuning. A change in weights made the circuit responsive to different SRI's

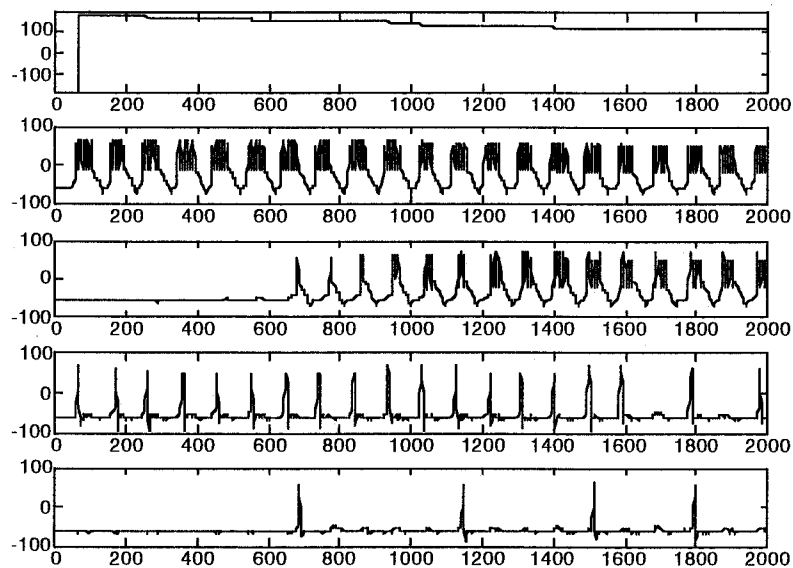


Figure 2: Traces of membrane potential as the simulated cricket moves to face the sound source (direction shown in upper plot). Second and third plot show AN right and left; fourth and fifth show respective Motor neurons. See results.

#### 4. Results

Figure 2 shows a segment of the neural traces when presented with a sound of ideal syllable rate. Initially the sound is  $90^\circ$  to the right of the cricket, which starts turning towards it. The right AN1 is firing rapidly and causes a spike per syllable to occur in the right motor neuron. As the animal turns, the response in the left AN1 increases although initially it still falls behind the right AN1. As the sound direction comes to the front, the left and right AN1 fire at around the same level; sometimes cancelling each other out; sometimes one or the other firing first and causing a corresponding burst in the motor neuron. Note the raised potential during firing of the AN1 neurons and the slow decay back to resting potential. When rapidly repeating syllables are used, this slow decay means that AN1 neurons fire almost continuously and the motor neurons almost never (because of the inhibitory connections). In figure 3 the direction of the cricket relative to the sound source during three trials at differing SRIs are shown. With ideal syllables (30ms) it turns towards the sound (at 0) and oscillates around it. With slow syllables (60ms) it takes longer to turn, never reaching 0. With fast syllables (10ms) it makes very few turns. It is also interesting to note that the oscillation for the correct sound occurs between  $\pm 30$ , which corresponds quite well to the cricket. With the longer syllables there are more errors (i.e. turns away from zero) in the 30-60 range, than for the ideal. These effects are the same as those found using the robot; and the same as those taken as evidence for 'recognition' of correct syllable rates by the cricket (Webb,1995).

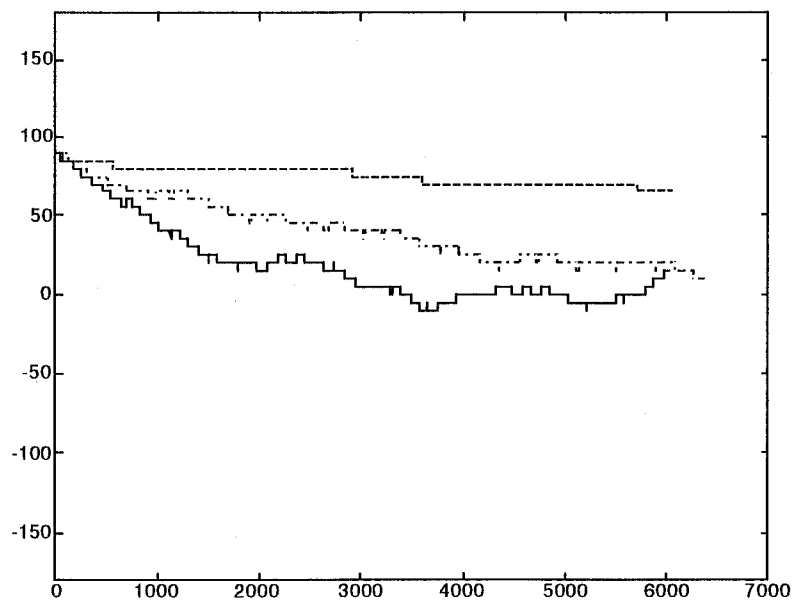


Figure 3: Traces of the orientation of the simulated cricket during 6000ms of movement. The solid trace is with an ideal syllable rate of 30ms; the dotted trace with 60ms syllables and the dashed trace with 10ms syllables.

## 5. Discussion

The results presented demonstrate that the hypothesised mechanism for taxis can be implemented by realistic neural processes, complementing the previous demonstration that it can work when linked to the real sensors and actuators of a robot. Clearly a useful further step would be to use the realistic neural model on a robot. We plan to investigate this next, but it may require some redesign of the functions used in the neural simulation software so that it could run quickly enough for real-time control. Neither the robot nor the simulation currently uses a particularly close parallel of the motor system of the cricket. One difficulty with doing so is the paucity of information about the control of turning in six-legged walking; nevertheless more realistic temporal dynamics (i.e. turning rate relative to syllable rate) could be introduced. In addition the simulation could be improved by more closely mimicking the auditory response properties of the cricket ears and including some noise in the effects of the 'environment' on the system and the system on the environment. Such additions are planned, to allow more complex facets of the behaviour to be addressed. The circuit implemented was simple - consisting of six neurons - but the detailed properties of these neurons and their connections gave rise to some interesting complexity of behaviour. In particular, being able to explicitly utilise the temporal properties of these neurons was exploited to make comparison of input strengths occur through a few excitatory and inhibitory connections, in a straightforward and rapid manner. It also allowed 'recognition' of temporal patterns to occur as a side-effect. Heterogeneity in neural properties and temporal processes in firing patterns are not generally included in artificial neural nets, yet turn out to be the key to understanding this particular biological system. We believe that without such properties it may be difficult to draw useful connections between biological and computational explorations of neural controllers.

## References

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