ROBOT MODELS OF CRICKET AUDITORY BEHAVIOUR

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1 INTRODUCTION

> “I am never content until I have constructed a mechanical model of the subject I am studying. If I succeed in making one, I understand; otherwise I do not.” (Lord Kelvin, Baltimore Lectures on Molecular Dynamics and The Wave Theory of Light, 1904)

One way to test our understanding of the functioning of a natural system is to attempt to replicate it. By implementing the mechanisms that we believe should account for an observed phenomenon, we can test the coherence, completeness and adequacy of our current hypotheses. More commonly, we might implement an analog of the mechanism, e.g., in the form of a mathematical or computational model. But sometimes additional insight can be gained from embedding such models in hardware to evaluate their capabilities in the real world. In cases where the hardware used is a robot, and the aim of the evaluation is to explain the behaviour of some biological system, this modelling approach has been termed ‘biorobotics’ [1, 2].

In the field of bioacoustics, the biorobotic approach has been applied principally in models of auditory localisation based on owls e.g. [3] or humans e.g. [4, 5]; and also in investigations of bat sonar e.g. [6, 7]. The complexity of these vertebrate examples makes it very difficult to implement complete systems: models that represent the precise neural circuitry, close the loop from sensing to action, and can be run on real-time behaving robots. We have focussed instead on building a robot model of a ‘simpler’ animal with interesting acoustically guided behaviour, the cricket (figure 1, left). Female crickets can locate conspecific males by moving towards the species-specific calling song the males produce. Typical male songs, produced by moving their wings, consist of groups of short sound bursts (e.g. for *Gryllus bimaculatus*, four 20 ms ‘syllables’ of 4.7 kHz sound make up a ‘chirp’) produced several times a second. Females appear to be selective for both the carrier frequency of the song and the temporal pattern of sound bursts, particularly the repetition rate of syllables within each chirp. The neuroethology of this system has been extensively studied (see reviews in [8–10]). In this paper we describe how this data is currently incorporated in a robot model and which aspects of the cricket’s behaviour it is able to reproduce.

2 HOW IS CRICKET CALLING SONG LOCALISED?

2.1 THE PERIPHERAL AUDITORY SYSTEM

The wavelength of the calling song (around 6-7cm) compared to the separation of the crickets ears (1-2cm) produces a problem for localising the sound to which evolution has provided an elegant solution, one that was independently discovered by engineers and called a pressure difference receiver (figure 1, right). The cricket’s ears consist of a pair of tympani, on each front leg, and associated vibration receptors that appear to have evolved from proprioceptive chordontonal organs [11]. The tympani are connected to each other and to a pair of spiracles on either side of the prothorax by a set of tracheal tubes; thus their vibration is determined by the combination of filtered delayed and direct sounds [12]. We have mimicked this auditory morphology in an electronic circuit that can be used on a robot [13].

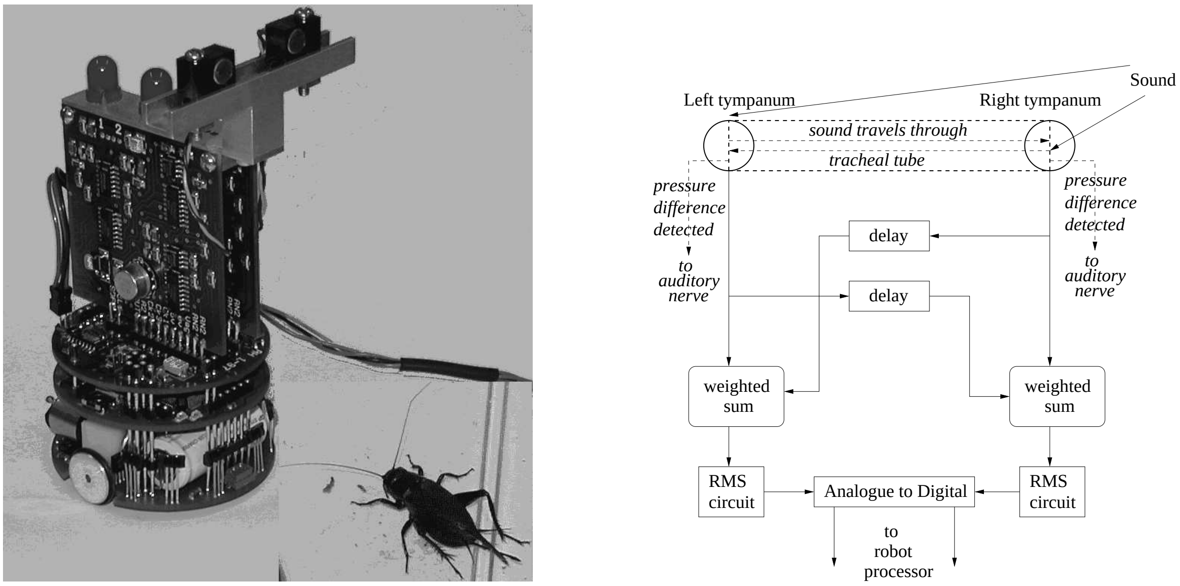

Figure 1: Left: a robot used to model a cricket. Right: the cricket's peripheral auditory system acts as a pressure difference receiver, and can be modelled on the robot using delay lines.

In a simplified approach, which illustrates the principle, two microphones are used, and each input is delayed (representing time for sound to travel through the tracheal tube) and then subtracted from the other (representing sound on opposite sides of a tympanum). The distance between the two microphones is set at $18\ mm$, and the delay to $53\mu s$ that is, approximately $1/4$ of the wavelength of the Gryllus bimaculatus song carrier frequency of $4.7kHz$. Thus for lateral sound, the direct and delayed inputs to the composite response will be 180° out of phase on the side the sound is coming from and in phase on the opposite side; the relative phase will vary between these two extremes as the sound direction changes. By differencing the direct and delayed inputs, the electronic analogue of the tympani has an output amplitude that corresponds to the direction of the sound source. Of course, this directionality is frequency dependent; but this might be advantageous for the female cricket as it will implicitly limit localisation to biologically relevant stimuli. When two simultaneous songs with different carrier frequencies are presented to our robot, it consistently 'prefers'—is more likely to approach—the $4.7kHz$ song [13] although there is no explicit frequency filtering or choice mechanism.

2.2 NEURAL PROCESSING

The directional response produced by the peripheral auditory system can be used in an obvious way by the female cricket to approach the sound:

> "she follows the simple rule turn towards the ear more strongly stimulated. We use the word simple because a two-eared robot programmed to obey this rule (if suitable noise were incorporated) could be made to track a sound source in a manner like that of the female." [14]

But how exactly is this implemented? Could there be a direct effect of ear stimulation to slow the stepping speed on that side of the cricket? Or are the ear inputs internally compared in some way? Does this produce a fixed size or rate of turn, or a graded response relative to the angle of the sound source? Is the comparison instantaneous or does the cricket integrate the input over some time interval before producing the response? Despite the large number of studies of this behaviour e.g. [15–23] there is surprisingly little consensus on any of these issues.

The cricket has around 50-60 sensory units innervating the tympanal organ, which have varied thresholds and amplitude ranges [24]. Their axons form the tympanal nerve which innervates a number of

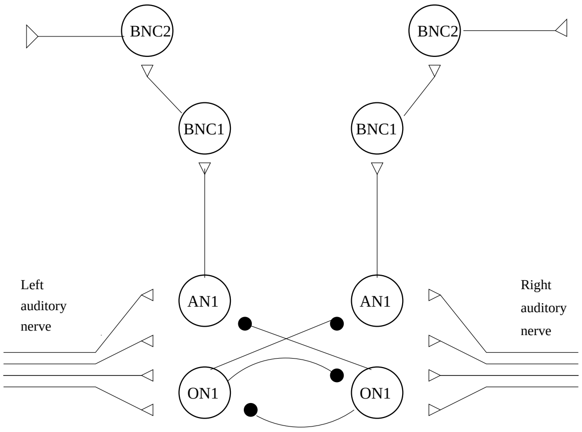

Figure 2: A neural model for phonotaxis, based on identified neurons in the cricket, that has been implemented on the robot.

auditory interneurons in the prothoracic ganglion (part of the central nerve cord of the insect), the most prominent being the pairs of omega neurons (ON1 and ON2) that make inhibitory cross connections to contralateral auditory neurons [25, 26]. Two pairs of interneurons that have axons ascending to the brain (AN1 and AN2) have been relatively well studied. Ablation [27] or hyperpolarisation [28] of AN1 has been shown to strongly affect the phonotaxis response, whereas AN2 appear to be critical in the cricket's escape response to bat ultrasound [29].

We can model this initial sound processing circuitry on the robot using simple simulated spiking neurons, e.g. the 'leaky integrate and fire' model, based on the RC circuit description of neurons in [30], or the two factor quadratic model proposed by Izhikevich [31]. Neurons are connected by synapses which model the conductance change induced in the post-synaptic neuron by spiking in the presynaptic neuron. Several dynamic effects are included in our synapse models, such as short-term facilitation and depression mechanisms and variable synaptic delays, which enable a richer representation of real neural network behaviour than can be obtained in typical artificial neural nets.

Our simulated auditory nerve consists of eight parallel fibres, each with differing sensory threshold, and with neural time constants in the order of a millisecond. This results in clear copying of time varying patterns, with some adaptation within the first few milliseconds of response to a sound burst. The fibres connect to one pair of 'AN1' and one pair of 'ON1' neurons (see lower part of figure 2) . The ON1 are mutually inhibitory and also inhibit the opposite AN1. The most obvious function of these cross connections is to increase the difference in activation between the two sides, to emphasise the directionality of the response. Experiments have shown that inhibition from the opposite side makes a difference of several spikes per chirp to the AN1 response [26], an effect we can replicate in our model. Another effect of this circuitry might be gain control. For varying amplitudes of sound (experienced as the cricket or robot approaches the sound source) the amplitude of the response adapts, because the inhibitory signal increases proportionally to the level of excitation. This allows the circuit to encode the relevant difference between the ears within a similar range of firing rates, without saturation.

How is this difference used to drive behaviour? As mentioned above, the activity of the AN1 pair seems to be essential for phonotaxis, and the turning of the animal can be controlled by manipulating the relative response of these neurons [27,28]. However, turning to sound based simply on the relative firing rates of AN1 neurons (e.g. by proportional steering) would not be selective for different sound patterns, as these neurons fire to any input pattern, including continuous tones. One possibility is that the neural system compares onset latency to sound bursts, rather than firing rate per se, to determine the turning direction. As described further in the next sections, this provides a simple mechanism for introducing some pattern selectivity and has been used in earlier versions of the robot [32]. One clear prediction from this model is that if the animal is presented with simultaneous sound from both sides, then a small onset difference should induce turning in the direction of the leading sound pulse. However, this was not observed to be the case when tested on the cricket [33].

An alternative hypothesis is that turning is dependent on how clearly the relevant pattern is present in AN1 output. This was suggested by an experiment [21] in which a song was played to the cricket from above, providing similar input to both sides, and then a continuous tone was added from one side. Despite the higher sound amplitude on that side, produced by the sum of the song and the tone, the animal turned in the opposite direction, i.e., towards the side where the song pattern was less masked by the tone. Another line of evidence for this hypothesis was in choice tests [34] which showed that if different songs are presented from different sides, the AN1/ON1 neurons encode only the song pattern on their respective side, and the animal turns towards the pattern most like the conspecific song. If turning depends on the pattern, then to implement localisation, we first need to model sound pattern filtering.

3 HOW IS THE SOUND PATTERN RECOGNISED?

A highly characteristic feature of the male cricket song is the rate at which syllables repeat (each syllable is a single sound pulse produced by closure of the wings). Female crickets show a band-pass preference for the syllable rate in male cricket songs [15, 17]. They appear less sensitive to the duty cycle or to higher order pattern features such as chirps (groups of several sound bursts separated by pauses) although some studies have shown that these can influence taxis in some cricket species, e.g. [19, 20, 22, 33]. Thus neurophysiological investigations have focussed on finding a neural circuit that produces a bandpass output comparable to the cricket's behaviour [35].

3.1 HIGHPASS AND LOWPASS FILTERING BY SYNAPSE DYNAMICS

The prothoracic interneurons (AN1 and ON1) already described above do not appear to meet the bandpass criteria, at least when their response is described in terms of overall spike rate in response to different sound patterns. However alternative characterisations of the response are possible. In particular, if changes in firing rate, such as sudden onsets, are considered, then already at this processing level there is potentially enough information to distinguish patterns. A classic paradigm for testing cricket behaviour is to vary the syllable repetition interval (SRI) from 10ms to 90ms while holding constant the total length of the chirp (figure 3, left). As can be seen in the model neuron results (figure 3, right), for the faster patterns, the onsets tend to be obscured in the AN1 response because the synaptic time constants act as a low pass filter. For the slower patterns, there are simply fewer onsets as the SRI increases. A cricket (or robot) that turns only for each *onset* in AN1 spiking will turn most to the fastest pattern that is still slow enough to reveal syllable onsets, i.e., produce a bandpass preference in phonotaxis.

How, neurally, could this variation in onset rate be detected? One suggestion [36] is based on neural recordings that show that the onsets of syllables actually cause peaks in the firing rate of ON1 (and it is assumed, AN1). That is, the first two or three spikes in response to a syllable occur closer in time than the remaining spikes during the syllable. In theory, a subsequent neuron could be tuned with a threshold and time constant that make it respond only at these peak rates. However, in attempting to implement such mechanism in the neural model on the robot, we encountered some difficulties. In particular, it must be very sensitive to small (sub-millisecond) differences in the gap between spikes, and is thus not robust against reasonable expectations of noise. It is also unclear how changes in signal amplitude, which will also alter the spike rate, can be dealt with in such a system.

Our alternative proposal for the filtering is based on simple synapse dynamics, and also draws on some data from brain neurons in the cricket. Schildberger [37] identifies two main classes of auditory responsive cells in the brain: BNC1 which appears to get direct input from AN1; and BNC2 which get input via BNC1 (see upper part of figure 2). These neurons vary in their response to the sound pattern, with different neurons appearing to act as low-pass, highpass and bandpass filters for the syllable rate. A lowpass filter could be produced by having a depressing synaptic connection from AN1 to

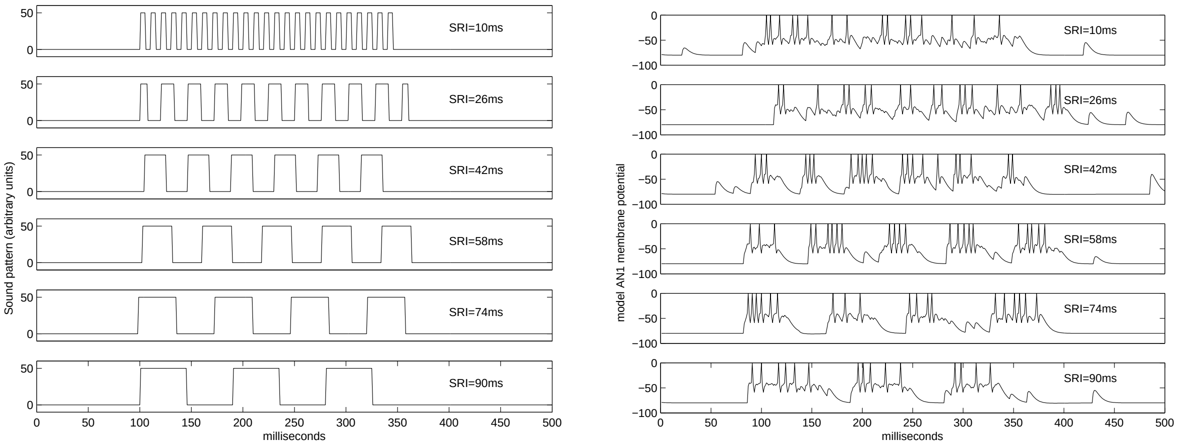

Figure 3: Left: varying the sound pattern played to the robot by changing the syllable repetition interval (SRI) while holding chirp duration approximately constant at 250 milliseconds. Crickets prefer SRI=42ms. Right: the response of a simulated thoracic interneuron (AN1). The pattern is obscured for fast SRI; slow SRI have fewer syllables per chirp; SRI=42ms produces the most clear spiking onsets per chirp.

BN1, that is, the amount of excitation of BN1 by a spike in AN1 decreases for each subsequent spike, and only recovers after a gap in AN1 firing. Fast patterns thus fail to produce any spiking in BN1, and slower patterns result in at most a few spikes at each syllable onset. A second depressing synaptic connection from BN1 to BN2, with a relatively slow time constant, effectively performs temporal summation of the BN1 output. Slower patterns fail to produce enough onsets within the time interval to summate, with the result that BN2 acts as a highpass filter. In figure 4 we show the response of our simulated BN1 and BN2 neurons to different song patterns.

One useful way to characterise the cricket's behaviour more thoroughly is to consider how it responds to songs varied systematically on two dimensions, the pulse length and the length of the gap between pulses (figure 5, top left). If these are varied with $pulse = gap$, we have the standard experiment in which different syllable rates are compared. If varied with $pulse + gap = constant$, we are testing sensitivity to duty cycle. Or we can examine what happens with varing pulse and constant length gap, or varying gap and constant length pulse. We can also look at the response with different sound amplitudes. The comparative results for the cricket and the model are shown in figure 5.

3.2 NEURAL RESONANCE

More recently we have considered another possible mechanism, neural resonance, based on behavioural experiments on the bushcricket *Tettigonia cantans* [38] that show phonotaxis to non-natural songs that resonate at the natural pulse rate. We adopted a simple model proposed in [39] for a 'resonate-and-fire' neuron. The activity of the neuron is described as a damped oscillator, represented as a complex variable z whose time evolution is determined by the following differential equation:

$$\dot{z} = I + (b + 2\pi i\omega)z \tag{1}$$

where I is the input current, ω is the resonant frequency, and b the rate of attraction to rest. The neuron 'fires' when the imaginary part (considered as membrane potential) exceeds a threshold a_{thresh}. Using the parameters $b = -30$, $\omega = 25$ (the preferred pulse frequency for *T. cantans*), and $a_{thresh} = 0.12$, we simulated different input patterns, I, to the neuron to represent different songs, and counted the output spikes.

This simple model reproduces all the 'resonant' properties of the bush cricket behaviour described in [38]. Pulses of a constant duration ($= 18ms$) played at rates from 8 Hz to 67 Hz, produce the

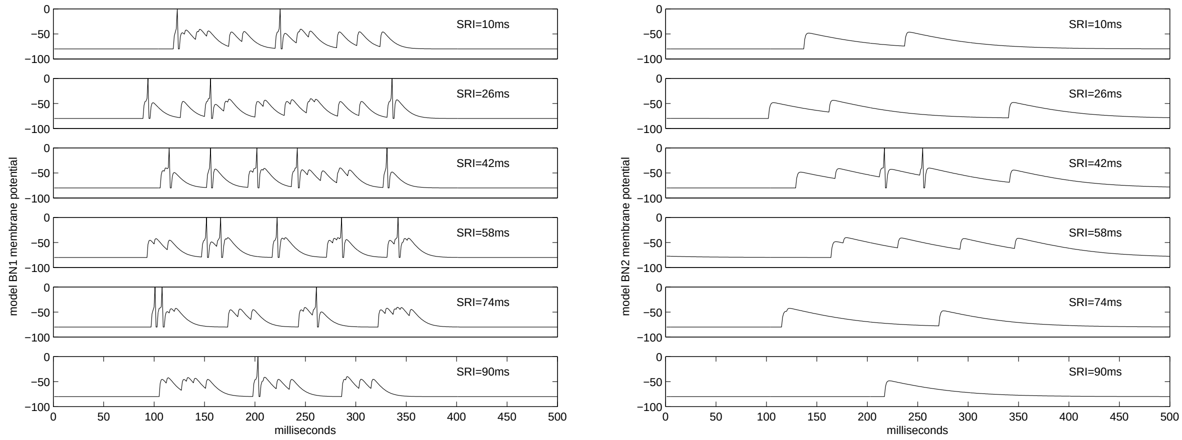

Figure 4: The response of simulated brain neurons (left, BN1; right, BN2) to the sound patterns shown in figure 3. Left, BN1 gets input from AN1 and responds best to onsets after a clear gap in firing. Right, BN2 gets input from BN1 and requires spikes to occur close in time to summate above threshold. As a result only SRI=42ms produces output spikes in BN2.

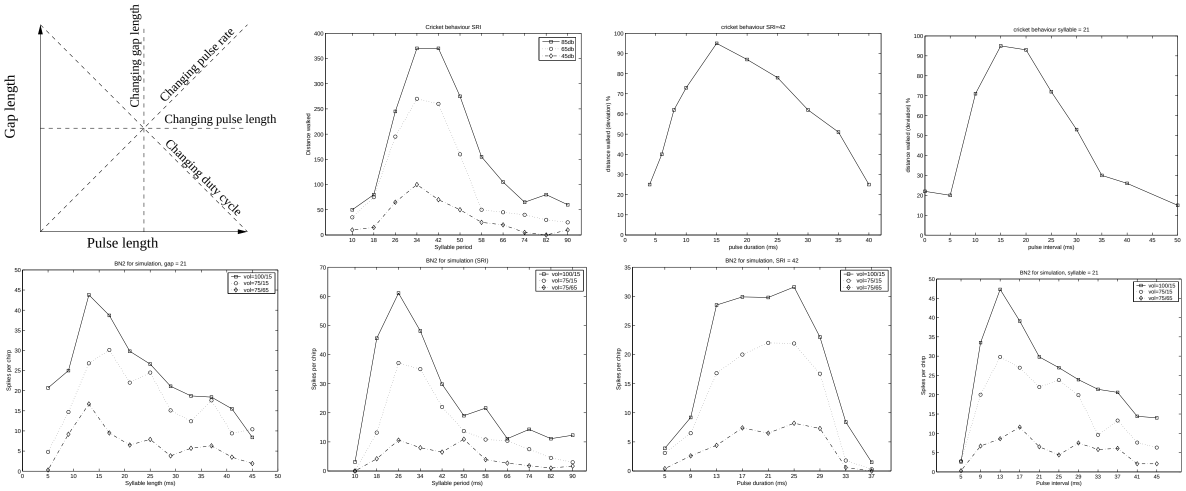

Figure 5: Top left, the space of stimuli for testing the pattern filtering properties of insect behaviour and neural models. Top row, behaviour of the cricket: changing the syllable repetition interval ($pulse = gap$); duty cycle ($pulse + gap = 42ms$); and gap length. Bottom row, output from the neural model (number of spikes in BN2): changing the pulse length (comparable cricket data not available); syllable repetition interval; duty cycle; and gap length. Cricket data from James Poulet and Berthold Hedwig.

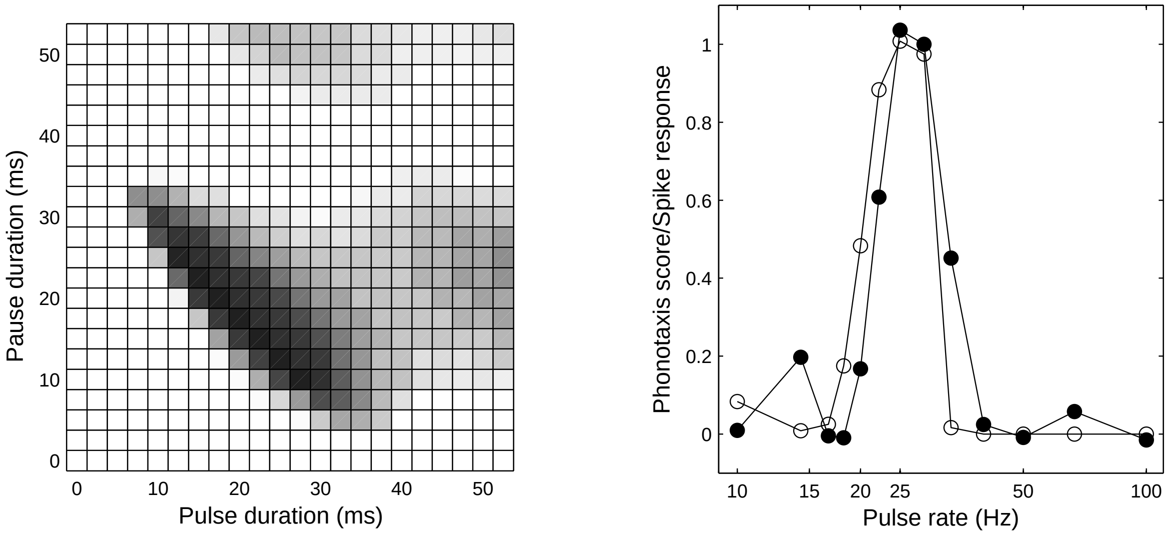

Figure 6: Left: response of the resonance model to varying the pulse and pause length. Darker squares indicate a stronger response. Response of the bush cricket (dark circles) and the model (open circles) to varying the pulse rate with a constant duty cycle. From [40]

expected peak at 25 Hz, a second peak of half the size at 12.5 Hz, and a smaller increase at 8 Hz. Using songs that vary systematically in pulse and pause duration (figure 6) we find a good response over a large range of songs where $pulse + pause = 40ms$, a pattern of preference that has also been shown for *T. cantans*. As before, the diagonal $pulse = pause$ is equivalent to varying the frequency of pulses with a constant duty cycle of 50%. Comparing the simulation result to the behaviour of the animal tested with a 50% duty cycle stimulus, we can see that the overall shape of the tuning curve is very similar.

There is some evidence that an identified neuron in the auditory system of the cricket *Teleogryllus oceanicus* shows a resonant response [9]. However it should be noted that experiments on the cricket *Gryllus bimaculatus* have not revealed the same pattern of behavioural results as the bush cricket (B. Hedwig, personal communication). Thus it is not currently clear which, if any, of the above models accurately describes the sound pattern filtering process in the cricket. Nevertheless, assuming some mechanism of this kind does exist, we can return to the question of how the turning response to the (correct) sound is generated.

4 HOW ARE LOCALISATION AND RECOGNITION COMBINED?

At the end of section 2 we suggested that the interaction of localisation and recognition is a serial process. The peripheral auditory system and the AN1-ON1 circuit produce a stronger response on the side of the cricket nearer to the sound. The output of each AN1 is fed through neural filters (BN1 and BN2, or a resonant neuron) to produce an output that reflects the presence of a particular syllable rate in the input. This output could be used directly to control the turning behaviour of the robot. But how does the cricket actually use such a signal to alter its course?

Unfortunately the connectivity from brain neurons via descending neurons to motor neurons for phonotaxis is largely unknown. Some data on the response of neurons descending from brain is available [41–43] but the circuit is unclear. Another way to approach this question is to provide a more detailed characterisation of the dynamics of the cricket's response, e.g., how long is sound integrated before a turn is produced, how large a turn is made, and how often? It is only relatively recently that cricket experiments that use a high time resolution (milliseconds) to analyse the behaviour have been performed, and the results were rather surprising [23, 33, 44]. It was observed that there is a small but significant steering response to every pulse of sound within the song, within a short time interval (around 50 ms). This can be seen most clearly when the cricket is presented with ‘split-song’: alternate syllables in a chirp are presented from alternate directions, and the animal steers back and forth for each sound pulse. In fact the legs can be observed to change trajectory within a step cycle as soon as the sound direction changes [45].

This strongly suggests that the basic turning response does *not* include a stage for filtering the temporal pattern in the song, as the pattern (the syllable rate) cannot be detected from the first sound burst alone. This was confirmed by testing the cricket with single chirps of the wrong syllable rate in the midst of correct song — the cricket would turn towards these normally unattractive stimuli [33]. From examining the start and end of bouts of phonotaxis, it appears that a fast and unselective localisation reflex is modulated, over a much longer time scale (2-5 seconds), by an independent recognition process that filters for the temporal pattern [33].

Consequently our most recent experiments on robot phonotaxis incorporate a change to the basic hypothesis about the mechanisms in the cricket (figure 7, top left), based on this data. We suggest that there is a relatively direct, or ‘fast’ connection from the AN1 neurons to the motor control of turning. This connection is usually inhibited (by a hypothetical ‘gate’ neuron), but this inhibition is itself inhibited by output from brain neurons which filter for the temporal pattern in the sound in the same way as before. Thus the robot will produce a turn to every pulse of a split song, with the size of turn increasing at the onset of a correct pattern (figure 7, top right). A 100 ms test pulse will produce a stronger response after a song pattern has been presented, with the response decreasing over several seconds after the end of song (figure 7, bottom right). Inserting chirps of different SRIs into normal song will produce a stronger response than the same chirps presented alone (figure 7, bottom left).

Although we can thus produce most of the observations on the cricket, some unresolved issues remain. It is difficult to obtain identical dynamics in the robot as observed in the cricket by varying the synaptic parameters within plausible ranges, suggesting that the modulation mechanism may have a different basis, such as gradual neuromodulator release, not currently included in our neural simulator. It is not clear from the cricket data so far whether there is likely to be bilateral recognition, as in the current model, or whether the input from the two sides is combined in a single recognition process.

A final issue that requires further investigation is that although this mechanism on the robot can qualitatively match the the behaviour of the cricket in a tethered treadmill paradigm, it does not seem to produce comparable behaviour in an arena paradigm. The tracks of freely walking crickets towards sound are characterised by straight or slightly curved segments interrupted by pauses and relatively sharp turns. The robot tested in the same paradigm, using the control mechanism shown in figure 7 produces very smooth curving trajectories towards the sound. This difference may indicate a difference in cricket behaviour under closed loop feedback rather than in open loop on the treadmill. It may also relate to how the precise leg movements made when turning towards sound are translated into body position. We are carrying out ongoing studies into these issues.

5 CONCLUSION

Cricket acoustic behaviour is an interesting model system for understanding neural circuits for recognition and localisation of sound. It is possible to model the complete sensorimotor loop, at the level of identified single neurons. Such models have brought new insights into the underlying mechanisms of sound processing, and suggested novel experiments for better understanding these processes in biology.

It has long been recognised that mathematical and computational modelling are important means to enforce theoretical rigour, both in defining terms and mechanisms explicitly, and in formally demonstrating the conclusions that follow (sometimes counter-intuitively) from certain hypotheses. One distinctive feature of the biorobotic approach described here is that it involves moving from purely software simulations to simulations that involve at least some hardware as part of the technology for implementation. This can have both advantages and disadvantages when it comes to the problem

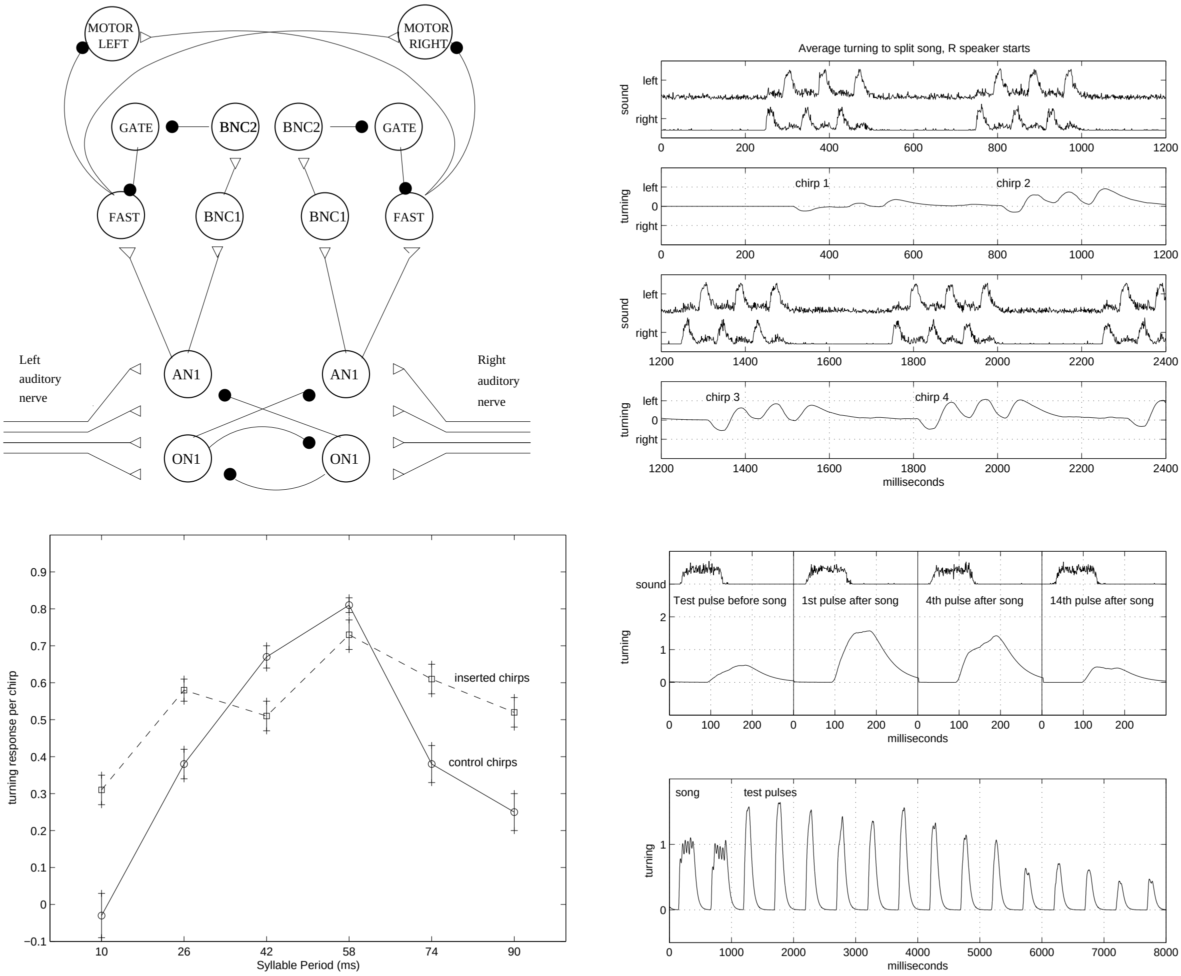

Figure 7: Upper left: Neural circuit to produce a fast steering response modulated by slower recognition filtering. Upper right: Behaviour of the robot to split song onsets. Lower right: Behaviour of the robot to tone pulses before or after song. Lower left: change in the preference curve from normal SRI stimuli (solid line) to SRI chirps inserted within standard song (dotted line).

of whether the implementation correctly represents the hypothesis. For example, we can test the robot directly under the same acoustic conditions as the cricket, rather than having to simulate the sound propagation in a virtual environment. We can even test it in more naturalistic sound conditions, e.g., outdoors [46]. However, this imposed additional constraints on the robot mechanics, in this case reducing the possibility of obtaining similar paths to the cricket due to the robot's increased turning circle.

Our current research aims include closer replication of the cricket's actuation, using a six-legged robot, and further investigation of the brain and descending neural circuitry involved in this behaviour. In addition, we are interested in how the cricket combines phonotaxis with other sensorimotor behaviours, such as visual reflexes and escape responses, and the role of self-generated feedback in co-ordinating control.

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