



## Directional hearing in a silicon cricket

Richard Reeve<sup>a</sup>, André van Schaik<sup>b</sup>, Craig Jin<sup>b</sup>, Tara Hamilton<sup>b</sup>,  
Ben Torben-Nielsen<sup>c</sup>, Barbara Webb<sup>a,\*</sup>

<sup>a</sup> *Institute of Perception, Action and Behaviour, School of Informatics, JCMB, University of Edinburgh, Mayfield Road, Edinburgh, UK*

<sup>b</sup> *School of Electrical and Information Engineering, University of Sydney, New South Wales, Australia*

<sup>c</sup> *Institute for Knowledge and Agent Technology, Universiteit Maastricht, The Netherlands*

Received 28 February 2005; received in revised form 8 July 2006; accepted 15 July 2006

### Abstract

Phonotaxis is the ability to orient towards or away from sound sources. Crickets can locate conspecifics by phonotaxis to the calling (mating) song they produce, and can evade bats by negative phonotaxis from echolocation calls. The behaviour and underlying physiology have been studied in some depth, and the auditory system solves this complex problem in a unique manner.

Experiments conducted on a simulation model of the system indicated that the mechanism output a directional signal to sounds ahead at calling song frequency and to sounds behind at echolocation frequencies. We suggest that this combination of responses helps simplify later processing in the cricket. To further explore this result, an analogue, very large scale integrated (aVLSI) circuit model of the mechanism was designed and built; results from testing this, agreed with the simulation. The aVLSI circuit was used to test a further hypothesis about the potential advantages of the positioning of the acoustic inputs for sound localisation during walking. There was no clear advantage to the directionality of the system in their location. The aVLSI circuitry is now being extended to use on a robot along with previously modelled neural circuitry to better understand the complete sensorimotor pathway.

© 2006 Published by Elsevier Ireland Ltd.

**Keywords:** Field cricket; *Gryllus bimaculatus*; Phonotaxis; Auditory hardware; Neuromorphic aVLSI circuit

### 1. Introduction

Understanding how insects carry out complex sensorimotor tasks can help in the design of simple sensory and robotic systems. Often insect sensors have evolved into intricate filters matched to extract highly specific data from the environment which solves a particular problem directly with little or no need for further processing (Wehner, 1987), for example flight stabilisation in the fly, in which wide-field visual neurons are tuned to detect the specific optical flow patterns that correspond to specific flight deviations (Krapp and Hengstenberg, 1996). Another example is phonotaxis in crickets.

Phonotaxis is the ability to orient towards or away from sound sources. Crickets can locate conspecifics by phonotaxis to the distinctive calling song produced by the males (Huber and Thorson, 1985). They can also evade bats by negative phonotaxis from echolocation calls (Nolen and Hoy, 1986). The behaviour and underlying physiology of both behaviours have been studied in some depth.

Because of the size of the cricket body (less than 1 cm), the interaural time difference (ITD) for sounds arriving at the two sides is very low (10–20  $\mu$ s). Even with the tympanal membranes (eardrums) located, as they are, on the forelegs this only reaches about 40  $\mu$ s, which is too low to detect directly from timings of neural spikes. Because the wavelength of the cricket calling song is significantly greater than the body width, little shadowing of the sound is done by the body either, so the interaural

\* Corresponding author. Tel.: +44 131 651 3453;  
fax: +44 131 651 3435.

E-mail address: [bwebb@inf.ed.ac.uk](mailto:bwebb@inf.ed.ac.uk) (B. Webb).

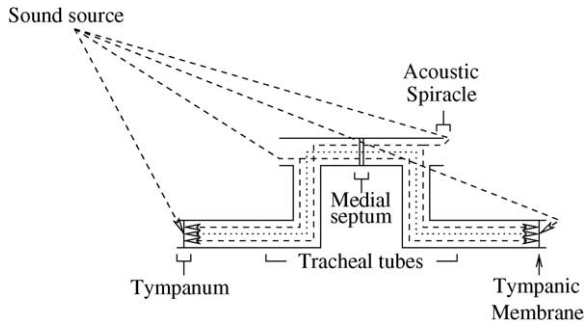


Fig. 1. The cricket auditory system consists of two sound receivers (tympana) on the legs, with four acoustic inputs (the external tympanic membranes and two spiracles on the body) channelling sounds directly or through tracheal tubes onto each sound receiver. Sound from contralateral inputs has to pass a (double) central membrane (the medial septum), inducing a phase delay and reduction in gain. Although all four inputs are illustrated here, the sound transmission from the contralateral tympanum is very weak, making each eardrum effectively a three input system.

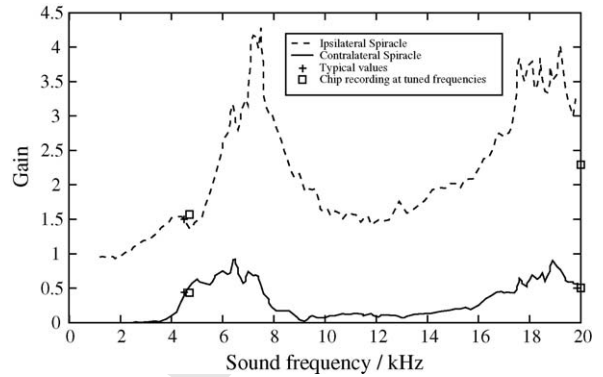


Fig. 2. Absolute values of gains of sounds entering through spiracles when they arrive at the inside of the tympanum for a single field cricket (along with “typical” values) from (Michelsen et al., 1994) with points showing corresponding values on the aVLSI chip. An amplitude of 1 indicates that it has not changed during transmission. A positive gain in the spiracles corresponds to a negative gain for the tympanal acoustic input, since sound arrives at the other side of the membrane.

intensity difference (IID) is also too low. In the absence of ITD or IID information, the cricket uses phase to determine direction. This is possible because the male cricket produces an almost pure tone, at around 4–5 kHz, for its calling song.

The physics of this system is well understood (Michelsen et al., 1994); the mechanism (see Fig. 1) is a pair of sound receivers with effectively four acoustic inputs, one on each foreleg, which are the external surfaces of the tympana, and two on the body, the prothoracic or acoustic spiracles (Michelsen, 1998). Connecting tracheal tubes between these four inputs mean that phase cancellation occurs as sounds travel inside the cricket, producing a directional response at the tympana to frequencies near to that of the calling song. The amplitude of vibration of the tympana, and hence the firing rate of the auditory afferent neurons attached to them, vary as a sound source is moved around the cricket and the sounds from the different inputs move in and out of phase. The outputs of the two tympana match when the sound is straight ahead, and the inputs are bilaterally symmetric with respect to the sound source. However, when sound at the calling song frequency is off-centre the phase of signals on the closer side comes better into alignment, and the signal increases on that side, and conversely decreases on the other. Consequently the cricket can turn towards the sound source by turning to the side with the higher tympanal vibration amplitude. Field crickets also show a directional response to the high frequency echolocation calls of bats (Miller and Surlykke, 2001), though bush crickets do not despite their auditory systems being sensitive to those frequencies. The cricket has separate

auditory receptor fibres for different frequencies, broadly divided into three different groups (Imaizumi and Pollack, 1999), two of which cover these bat and calling song frequencies. This allows the signals to be carried to separate control networks.

A simplified version of the auditory system using only two acoustic inputs was implemented in hardware (Lund et al., 1997), and a simple eight-neuron network was all that was required to then direct a robot to carry out phonotaxis towards a species-specific calling song (Reeve and Webb, 2003). This paper details an investigation into extending this system to include the high frequency (bat echolocation) response as well as the low frequency (calling song), and to include all four acoustic inputs. Data from Michelsen et al. (1994) is used first to construct a simulation, and an aVLSI hardware im-

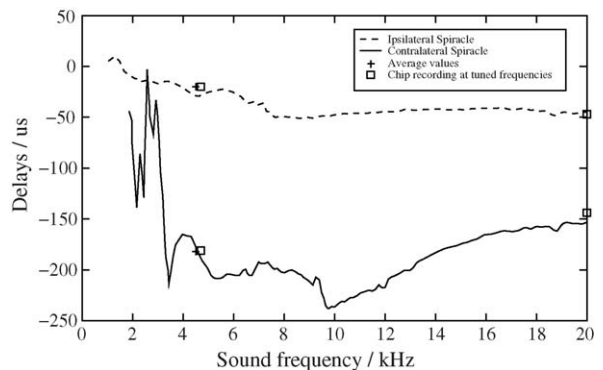


Fig. 3. Relative delays of sounds entering through spiracles when they arrive at the tympanum in a single field cricket (along with average values) from (Michelsen et al., 1994) with points showing corresponding values on the aVLSI chip (modulo period of sound).

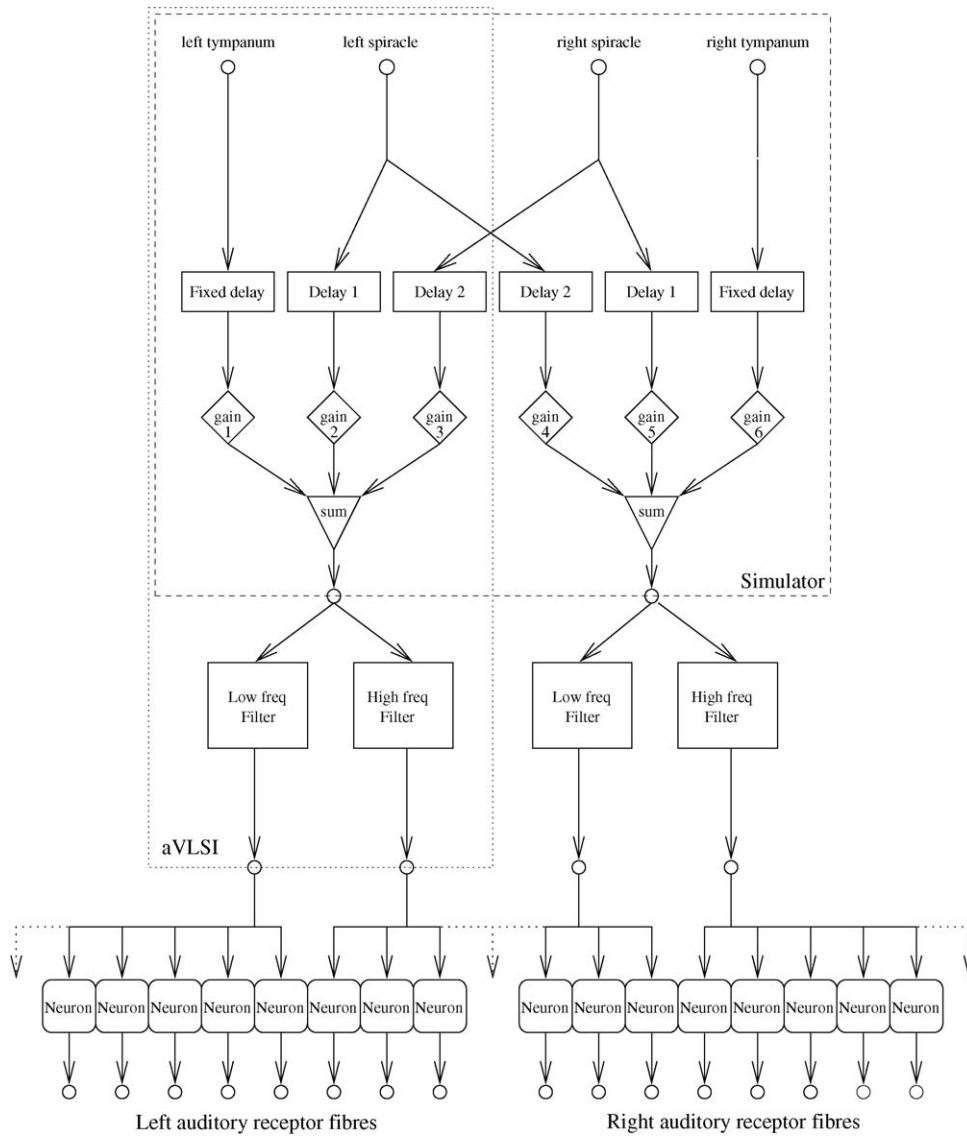


Fig. 4. A model of the auditory system of the cricket, used to build the simulator and the aVLSI implementation (shown in boxes).

78 plementation was then designed and built. These were  
79 tested with calling song and bat echolocation frequencies,  
80 and also investigated for any effects on sound direction-  
81 ality that might be caused by the tympana being on the  
82 forelegs during walking.

## 83 2. Methods

84 Data from Michelsen et al. (1994), Figs. 5 and 6 was digi-  
85 tised, and used together with average and “typical” values from  
86 the paper to choose gains and delays for the simulation. Note  
87 that the typical and average values are taken at 4.5 kHz for  
88 historical reasons, which is not the carrier frequency of the

89 cricket song (4.7 kHz). For clarity since the data was not pre-  
90 sented in the form we require in the original paper, and for  
91 later comparisons, we have replotted this data in Figs. 2 and  
92 3. Fig. 4 shows the model of the internal auditory system of  
93 the cricket, from sound arriving at the acoustic inputs through  
94 transmission down to auditory receptor fibres. The simulator  
95 implements this model up to the summing of the delayed in-  
96 puts, as well as modelling the external sound transmission, i.e.  
97 it models pure tones of a given frequency coming from a sound  
98 source at a specific distance and location to a cricket, entering  
99 the acoustic inputs, and being transmitted through the tracheal  
100 tubes to be summed at the tympana. All the parameters of the  
101 transmission process (gains and delays) can be controlled. The  
102 simulator interface is shown in Fig. 5.

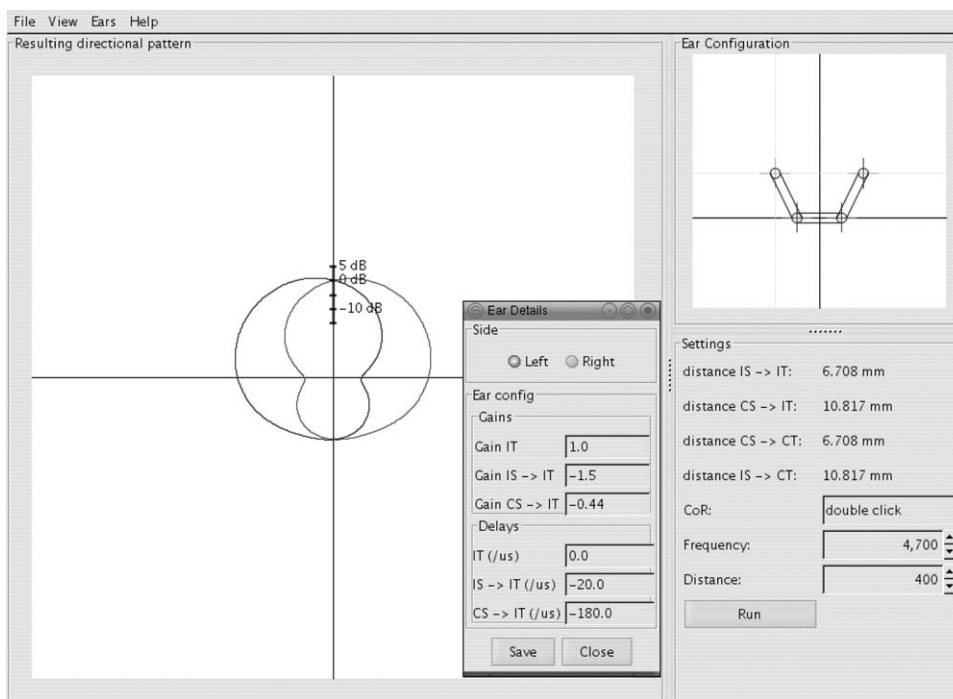


Fig. 5. The cricket auditory simulator. The top right pane allows the physical positioning of the spiracles and tympana, as well as the centre of rotation of the sound source. The bottom right selection is used to choose the sound frequency and the distance of the sound source from the centre of rotation. The dialog box is for setting the gains and delays inside the tracheal tubes. The left hand pane shows the amplitude of vibration at the left and right tympana of sound as the sound source rotates round the animal.

103 Results from the simulator were used to check the directionality of the system at different frequencies, and to gain a better understanding of its response. It was impractical to check the effect of leg movements or of complex sounds in the simulator due to the necessity of simulating the sound production and transmission. The aVLSI chip was designed to implement the same model, both allowing more complex experiments to be run, and experiments to be run in the real world.

111 The chip comprises two delay filters, three gain circuits, a second order narrow band bandpass filter, a first order wide band bandpass filter, a first order highpass filter, as well as supporting circuitry (including reference voltages, currents, etc.). The low frequency filter shown in Fig. 4 is divided into two parts on the chip since the filter's response (Imaizumi and Pollack, 1999; Fig. 3) separates well into a narrow and a wide bandpass; these filters are then added back together to reproduce the biological filter. Thus, a single aVLSI chip includes half the necessary circuitry to model the complete auditory system of a cricket (see Fig. 4). The complete model of the auditory system can be obtained by using two appropriately connected chips. The chip was fabricated using the MOSIS AMI 1.6  $\mu\text{m}$  technology and designed using the Cadence Custom IC Design Tools (5.0.33).

126 The chip was tested using Matlab. Fig. 6 shows the set-up used. Given that the output from the chip and the gain circuits is a current, a current-sense circuit was used to enable the output to be probed by either an oscilloscope or soundcard.

129 The first experiments on the chip were to tune the parameters. After that, recordings were taken of the directional responses to high and low frequency sounds.

132 Movement of the forelegs was then simulated by generating appropriate sounds for each input (a simpler solution for testing than trying to attach moving microphones), and the angle at which the sound was equal on each tympanum (the null direction) was measured relative to the forward direction of the

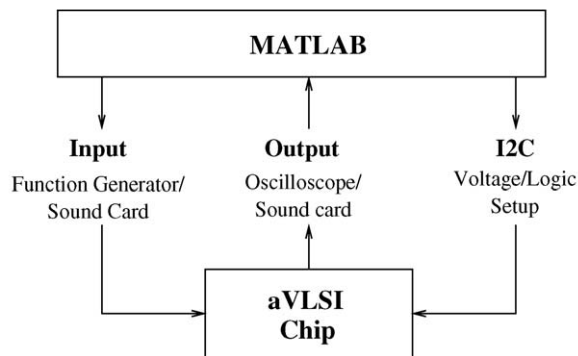


Fig. 6. The experimental setup for the aVLSI chip. Sound was generated on the computer and played through a sound card to the chip. Responses from the chip were recorded by an oscilloscope, and uploaded back to the computer on completion. Parameter setting on the chip and associated circuitry was achieved via an I<sup>2</sup>C interface.

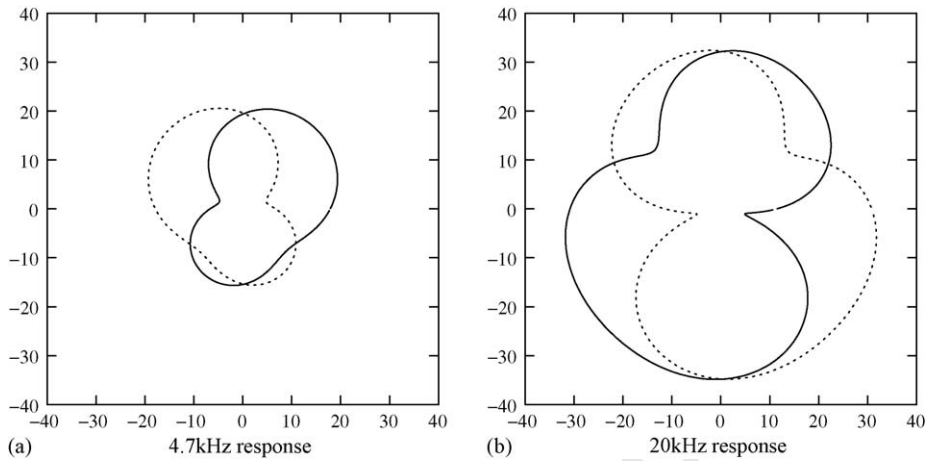


Fig. 7. Vibration amplitude of the left (dotted) and right (solid) virtual tympana measured in decibels in response to 4.7 and 20 kHz tones calculated by simulation of the tones coming through the spiracles and onto the tympana. The plot shows the amplitude of the tympanal responses as the sound source is rotated around the cricket: (a) 4.7 kHz response, (b) 20 kHz response.

137 system. In a two input pressure difference receiver such as that  
138 used in the experiments of Lund et al. (1997) and Reeve and  
139 Webb (2003), the null direction will be offset by exactly the  
140 angular offset between the two inputs during walking, and we  
141 use this as one of our comparisons for the four-input system.  
142 The other comparison we make is with the angular offset of  
143 the legs themselves as this is the angle between the tympanum  
144 and the acoustic spiracle. If the four-input system is particu-  
145 larly well suited to removing leg-movement-related error, we  
146 should see the null direction closer to zero for it than for these  
147 comparators; however, if the four-input system solves some  
148 other problem, for instance simply that the body lengths are  
149 wrong for phase cancellation on a two-input system, then we  
150 should expect to see a response between the comparators. Two  
151 different body widths and leg lengths were also chosen to see  
152 if the effects were consistent across them.

The characteristics of the delay and filter circuits were then  
tested using Golay codes to construct the impulse response.  
Golay codes have the property that their autocorrelation func-  
tions cancel in all places except at the origin. To construct an  
impulse response, two Golay codes are used. Each one is used  
as the input to the filter and they are then added to give the im-  
pulse response. Once the impulse response is obtained simple  
mathematical operations are used to obtain the frequency re-  
sponse or group delay of the filter under test. More information  
on Golay codes and their use in determining impulse response  
is given by Foster (1986).

### 3. Results

Simulation of the auditory system produced clear di-  
rectionality both at the calling song frequency from the

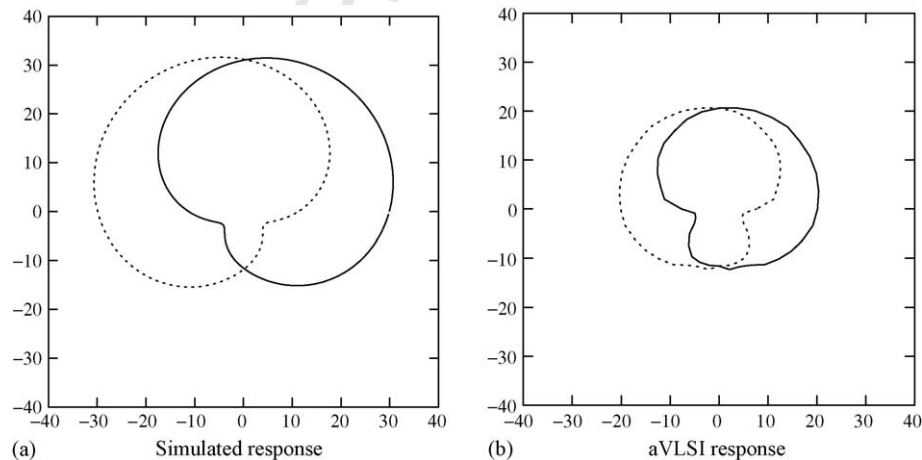


Fig. 8. Vibration amplitude of the left (dotted) and right (solid) virtual tympana measured in decibels in response to a 4 kHz tone in simulation and on the aVLSI chip. The plot shows the amplitude of the tympanal responses as the sound source is rotated around the cricket: (a) simulated response and (b) aVLSI response.

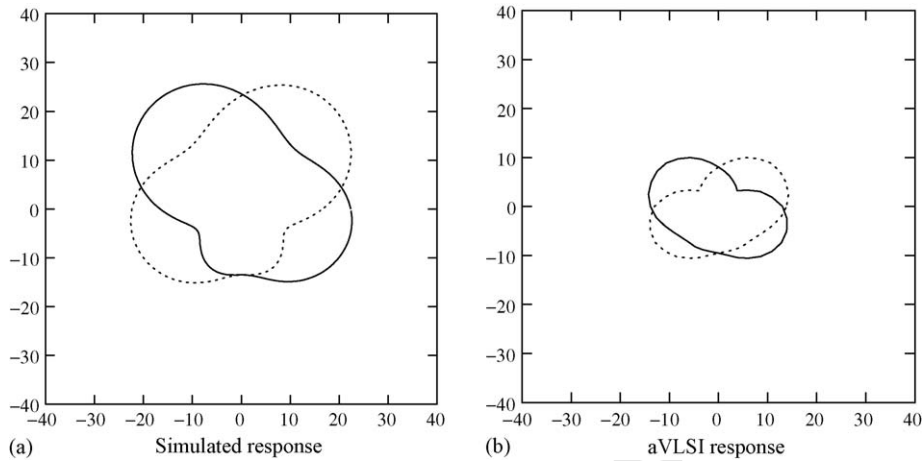


Fig. 9. Vibration amplitude of the left (dotted) and right (solid) virtual tympana measured in decibels in response to a 20 kHz tone in simulation (with parameters adjusted to account for chip error) and on the aVLSI chip. The plot shows the amplitude of the tympanal responses as the sound source is rotated around the cricket: (a) simulated response and (b) aVLSI response.

front, and at the chosen echolocation frequency (20 kHz) from the rear (Fig. 7). The former result agrees with those found by Michelsen recording directly from the tympana of crickets in the same paper.

The aVLSI chip was then tested to measure its gains and delays, which have been indicated against the plots for the cricket in Figs. 2 and 3, respectively. Due to an error in the specification for the chip, the 20 kHz response has a gain inverted; however, the plot only shows the absolute value. The gain on the ipsilateral spiracle is also too low, but simulation results show that this has very little effect on directionality. The chip was then compared with the simulation to check that it was faithfully modelling the system. Data was recorded in 1 kHz intervals from 1 to 20 kHz. Results are shown at 4 and 20 kHz in Figs. 8 and 9, respectively. The drop in amplitude of the signal was expected and is due to noise in the (non-simulated) circuit. This noise was not simulated, but is known to be present in any physical system including both the cricket and the chip, and so the drop in amplitude is not a cause for concern.

Simulated leg movements were then fed into the chip to test the movement of its null direction for sound during walking. This will move since two of the acoustic inputs are situated on the legs. This movement was compared with the angles between the tympana and with the change in angle between a tympanum and the ipsilateral acoustic spiracle as the legs moved, to see whether the null direction of the four-input system moved less than those of two-input systems consisting of just those inputs. The results from two typical body configurations in Fig. 10 show that the four-input system fits in between the two comparators, as one would expect considering

the positioning of the inputs. There is no special property of the configuration which makes the system more robust to leg movements, such as would be expected if only the spiracles were being used for directionality (the latter is not possible because the gap between the spiracles is too small to get phase cancellation).

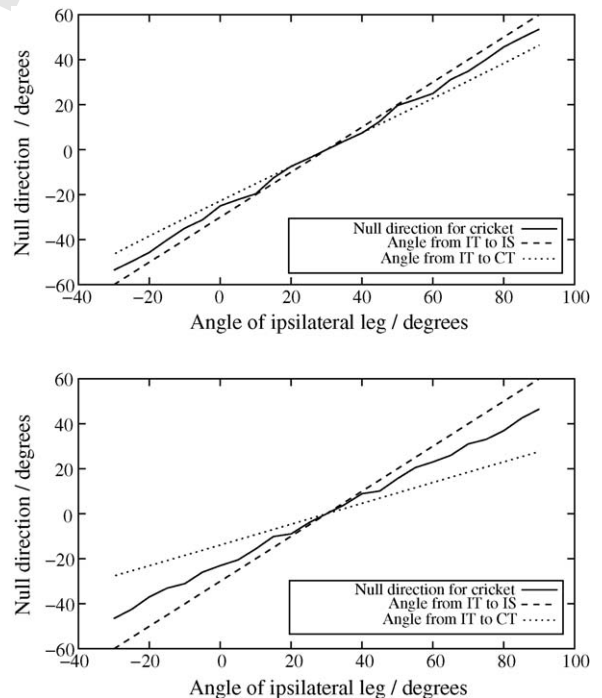


Fig. 10. Comparison of the effect of leg movements on the null sound direction with the actual layout of spiracles and tympana against two simpler layouts of acoustic inputs. The two graphs represent the results from two different plausible cricket body shapes.

#### 4. Discussion

The aVLSI auditory sensor in this research models the hearing of the field cricket *Gryllus bimaculatus*. It is a more faithful model of the cricket auditory system than was previously built by Lund et al. (1997), reproducing all the acoustic inputs, as well as the responses to frequencies of both the conspecific calling song and bat echolocation chirps. It also generates outputs corresponding to the two sets of behaviourally relevant auditory receptor fibres. Results showed that it matched the biological data well, though there were some inconsistencies due to an error in the specification that will be addressed in a future iteration of the design. A more complete implementation across all frequencies was impractical because of complexity and size issues as well as serving no clear behavioural purpose.

The physical auditory system of the cricket, as we see in the simulation and its hardware implementation, is directional at the behaviourally relevant frequencies. It does sufficient information processing at the level of the tympana and tracheal tubes to leave little processing required by the neural circuitry in the cricket. The response to echolocation chirps is even reversed compared to calling songs, matching behaviour. It is not possible to draw conclusions about how this high frequency response relates to cricket behaviour, as the high frequency sound may be shadowed by the body resulting in the contralateral inputs receiving smaller signals, a factor which is not modelled here and needs to be studied in greater detail.

The directionality of the system during walking is not shown to be helped by the positioning of the spiracles and tympana on the body. However, recent experiments by Hedwig (2004) indicate that *G. bimaculatus* can turn towards a target as little as 5° to one side of the direction of travel. The amplitude difference of sounds at the tympana at this small an angle can be only 1.5 dB, which would be very hard to detect. However, with the legs moving, the direction of the target will vary over a large range centred on that angle; the amplitude difference rises to over 10 dB in this range, which is much more easily detected. More time will be spent in this high-amplitude-difference area on the side away from the sound source than on the reverse, thus potentially changing the problem to one of simply averaging over the time each side can clearly detect a signal. This oscillation in its detection patterns may therefore aid the cricket in target localisation. As yet no simultaneous recordings of cricket auditory neurons and leg movements have been made to test this hypothesis.

The long-term aim of this work is to better understand simple sensorimotor control loops in crickets and other insects. The next step is to mount this circuitry

on a robot to carry out behavioural experiments, which we will compare with existing and new behavioural data (such as that by Hedwig and Poulet, 2004). This will allow us to refine our models of the neural circuitry involved. Modelling the sensory afferent neurons in hardware is necessary in order to reduce processor load on our robot, so the next revision will include these either onboard, or on a companion chip as we have done before (Reeve et al., 2005). We will also move both sides of the auditory system onto a single chip to conserve space on the robot.

It is our belief and experience that, as a result of this intelligent preprocessing carried out at the sensor level, the neural circuits necessary to accurately model the behaviour will remain simple.

#### Acknowledgements

The authors thank the Institute of Neuromorphic Engineering and the UK Biotechnology and Biological Sciences Research Council for funding.

#### References

- Foster, S., 1986. Impulse response measurement using golay codes. Proceedings of IEEE International Conference on Acoustics, Speech, and Signal Processing '86.
- Hedwig, B., 2004. Personal communication.
- Hedwig, B., Poulet, J.F., 2004. Complex auditory behaviour emerges from simple reactive steering. *Nature* 430, 781–785.
- Huber, F., Thorson, J., 1985. Cricket auditory communication. *Sci. Am.* 253, 60–68.
- Imazumi, K., Pollack, G.S., 1999. Neural coding of sound frequency by cricket auditory receptors. *J. Neurosci.* 19 (4), 1508–1516.
- Krapp, H., Hengstenberg, R., 1996. Estimation of self-motion by optic flow processing in single visual interneurons. *Nature* 384, 463–466.
- Lund, H.H., Webb, B., Hallam, J., 1997. A robot attracted to the cricket species *Gryllus bimaculatus*. In: Husbands, P., Harvey, I. (Eds.), Proceedings of Fourth European Conference on Artificial Life. MIT Press/Bradford Books, MA, 246–255.
- Michelsen, A., 1998. The tuned cricket. *News Physiol. Sci.* 13, 32–38.
- Michelsen, A., Popov, A.V., Lewis, B., 1994. Physics of directional hearing in the cricket *Gryllus bimaculatus*. *J. Comp. Physiol. A* 175, 153–164.
- Miller, L.A., Surlykke, A., 2001. How some insects detect and avoid being eaten by bats: tactics and countertactics of prey and predator. *BioScience* 51 (7), 570–581.
- Nolen, T., Hoy, R., 1986. Phonotaxis in flying crickets. I. attraction to the calling song and avoidance of bat-like ultrasound are discrete behaviours. *J. Comp. Physiol. A* 159, 423–439.
- Reeve, R., Webb, B., August 2003. New neural circuits for robot phonotaxis. *Philos. Trans. R. Soc. London A* 361 (August), 2245–2266.
- Reeve, R., Webb, B., Horchler, A., Indiveri, G., Quinn, R., 2005. New technologies for testing a model of cricket phonotaxis on an outdoor robot platform. *Robot. Auton. Sys.*, in press.
- Wehner, R., 1987. Matched filters—neural models of the external world. *J. Comp. Physiol. A* 161, 511–531.