

A Robot Attracted to the Cricket Species *Gryllus bimaculatus*

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Abstract

Unlike most Artificial Life studies, we use biological data to verify a hypothesis about control mechanisms. We recorded male cricket *Gryllus bimaculatus* calling song, built a robot with the hypothesised control mechanism for phonotaxis behaviour and verified that it could account for the behaviour by observing the robot doing phonotaxis to the *real* cricket song. Further, we present a set of robot experiments that show how frequency dependence of the ear directionality in crickets can account for frequency selectivity in phonotaxis. Further, the results suggest that this mechanism also might account for part of the female choice behaviour.

1 Introduction

In the last decade or so, most Artificial Life experiments have been used to study behaviours, ecosystem dynamics, evolutionary processes, etc. A principal goal has been to use these experiments to underline the new paradigm that states that we have to study both “life as we know it” and “life as it could be” in order to obtain a general theory about life [5]. However, the distinction between “life as we know it” and “life as it could be” has resulted in nearly all Artificial Life researchers studying the latter, because this is what distinguishes the new paradigm from more traditional approaches toward the understanding of life. It seems quite peculiar that, where possible, the mainstream Artificial Life research has not tried to verify its hypotheses on natural life. This fact raises the serious

⁰The first author made the experiments and analysis described in the paper and wrote sections 1, 4, 6, and parts of 3. The second author provided the hypotheses tested and wrote sections 2 and 5. The third author designed the auditory circuit and wrote section 3.

question of whether many Artificial Life experiments are more than mere thought experiments or computer games.

There have been some Artificial Life studies that make use of biological data (for a recent review, see [15]), and recently, a few groups have started to use artificial agents or robots to verify hypotheses about control mechanisms of specific living animals.

Saito and Fukuda [12] made a robot of the same structure and size as a 7-8 years old female siamang ape in order to study brachiation. Grasso et al. [3] have made a robot lobster in order to test chemical orientation strategies that real lobsters might use to locate odour sources. We [8] used the Khepera robot in an experimental setup equal to the rats open field box experiment setup to show that one cannot conclude the construction of Euclidean cognitive maps in rats solely based on evidence from open field box experiments. Lambrinos et al. [4] built a robot with polarized light sensors in order to study how insect (desert ant, honey bee, cricket) nervous systems might extract compass information and do dead reckoning, which is unclear in neurophysiology/biology. It is significant, that these experiments were performed in the same environments as where biological experiments were performed, so the collected data is directly comparable with biological data.

Most modelling studies need to impose some artificial constraints to get a simulator or robot to work at all. But these constraints should not be such as to severely limit the potential for verifying the hypothesis against biological data, else the model tells us little. In this paper, our artificial organism (a robot) can be put under the same conditions as the living animal it models. Thus we can examine how the hypothesised control mechanism, implemented on the robot, can account for the animal’s behaviour.

Previously, we used a LEGO robot to show how a simple control mechanism could account for phonotaxis behaviour in crickets [17]. That is, the ability of a female cricket to locate the calling song of a male was reproduced. In particular the robot showed "preference" for certain songs in a manner that matched the female cricket, but using a much simpler decision mechanism than had previously been thought necessary.

However there were a number of limitations on that model that prevented a full evaluation against cricket behavioural data:

- It had a limited auditory processing speed that meant that the songs used were 10-20 times slower than real crickets (eg. *Gryllus bimaculatus* song consists of chirps with three syllables, each about 20ms long and separated by 20ms, with 200ms pauses between chirps; the robot song was 300ms syllables with 300ms gaps, and no chirp structure).

- a lower carrier frequency was used (2kHz vs. 4.7kHz) and it was not possible with that circuit to look at the effects of varying the carrier frequency although this is known to be an important factor in phonotaxis preferences (see below).

- the size of the robot restricted the experiments to be performed in an arena of size 200:1 with respect to the robot, where cricket experiments are normally performed in arenas of size 1000:1 relative to the animal.

In the current experiments we have re-implemented the circuitry and control mechanism on a Khepera robot. This has a faster processing speed so we can now use real cricket songs in testing the behaviour. We also have an arena that is almost 2500:1 the size of the robot. And the characteristics of the ear circuit allow us to test the previously unexplored assumption that characteristics of the *directionality* of peripheral auditory system of the cricket might be sufficient to explain some of the apparent preference for certain frequencies of song.

2 Cricket Phonotaxis and Frequency Selectivity

2.1 Calling song

Calling songs (CS) of most cricket species have a small bandwidth carrier frequency. The actual frequency varies with species from about 2 to 8 kHz. The most commonly studied species for phonotaxis experiments have carrier frequencies between 4.5kHz and 5.5kHz; *Gryllus bimaculatus* has a typical carrier of 4.7-4.8kHz. Individuals may vary by +/- 100Hz. However as Popov and Shuvalov [11] noted "it cannot be used as a basic [i.e. single] cue for recognition [of conspecifics] ...because, in most cases studied, the spectra of the CSs of sympatric species of crickets often overlap to a degree that cannot be resolved by their auditory system" (p. 114).

Sound is produced by the movement of a 'plectrum'

over a 'file' as the cricket closes its wings. The rate of tripping of the teeth of the file is determined by the resonant properties of the harp, a specialised area on the wing that radiates the sound. This produces a pure and fairly constant carrier frequency [1].

It has been argued that these relatively low frequencies are advantageous for the propagation of sound over long distances, especially through vegetation which acts as a low-pass filter. However low frequency sounds pose difficulties for receptor directionality, particularly for small animals such as crickets. Michelsen (pers. comm.) suggests that the evolutionary discovery of the unique auditory apparatus of the cricket was a critical breakthrough in enabling these animals to use pure low frequencies for communication.

2.2 Auditory Apparatus

The cricket's auditory equipment comprises a pair of tympani, one on each front foreleg, a pair of auditory spiracles on either side of the front part of the body, and a set of tracheal tubes connecting these organs. Sound reaches each tympanum directly through the air, but also from the other auditory ports after delay and filtering in the tracheal tubes.

The vibrations of the tympani, which are transduced by auditory receptors, are thus determined by a combination of filtered delayed and direct sounds. The effect of the combination is as follows. Consider a sound impinging on the right tympanum from a source directly to the cricket's left. Sound also arrives via the right tympanum and spiracles after a certain delay. If the sound is of the correct frequency, the delayed version of the sound will arrive in phase with the direct sound and, since they affect opposite sides of the tympanum they will interact to cancel each other out. If this situation obtains, the delayed sound arriving at the left tympanum via the tracheal tubes will be in anti-phase to the directly arriving sound, and will reinforce the vibrations of that tympanum. In other words, provided the sound frequency matches the properties of the delay and filtering system implemented by the positioning of the acoustic ports and the structure of the internal tubes, the effect of the auditory morphology is to enhance the difference in perceived amplitude between the two tympani.

The simplest form of this model is when we assume that the internal delay between the tympani is equal to the time taken for sound to travel through the air between them. In that case, the two sound paths to the tympanum directly opposite the sound source always contribute in phase, and the response at that tympanum is minimal independent of frequency. For a maximal response from the tympanum closest to the source, the delay must then equal one quarter of the period of the incoming sound¹.

¹Plus any number of whole periods, of course.

Arriving sounds will then produce a tympanal response that depends strongly on the direction to the source, even though the amplitudes of the sounds arriving at each tympanum by the direct path will differ relatively little for a distant source.

2.3 Effects of varying the carrier frequency

A number of studies have shown frequency selectivity in the approach of female crickets to otherwise identical songs. Most commonly reported is the threshold intensity required to drive a phonotaxis response. Thus Popov and Shuvalov [11] reported that *G. bimaculatus* tested in a Y-maze reacted to 4.5kHz songs at 10dB lower intensity than 3 or 7kHz tones and no positive taxis occurred above 12kHz. Segejeva and Popov [13] testing flight reactions found signals of 5kHz had 15-20dB lower thresholds than those of 4 or 6 kHz. Moiseff et al. [9] showed for *Teleogryllus* a similarly shaped threshold curve centred on 5-5.5kHz. Stout et al. [14] report sharp tuning to 4-5kHz in arena tests of *Acheta domestica*.

Many of these studies assume the frequency selectivity in behaviour reflects frequency-dependent differences in sensitivity in auditory receptors, and this undoubtedly forms part of the explanation. However as Stout et al. [14] point out, the behavioural curves appear more sharply tuned than the acoustic inter-neuron response curves. An additional factor could be the observation that most crickets show negative phonotaxis to high frequency sounds (escaping from bats): perhaps the decreased response at frequencies higher than 6 kHz represents a conflict between positive and negative taxis?

A third factor may be that the *directionality* of the cricket’s ears is highly frequency dependent (see below for an explanation of why this is so). If the cricket cannot detect a difference between its ears it may not respond phonotactically even though the sound is ‘audible’. For example Boyd and Lewis [2] report that “an appreciable L-R difference was usually evident between about 4-6kHz but differences of more than 10dB were restricted to frequencies within a band of some 300Hz either side of the best frequency” (p.530). Michelsen et al. [7] showed that at different frequencies of sound (1-20kHz), the direction of the sound had a great or lesser effect on amplitude at the tympanum, with the biggest directional effect occurring at the calling song frequency.

Two behavioural studies emphasise this possibility. Oldfield [10] considered the accuracy of turns made during taxis to signals varying in frequency and found that (i) for 2.5 or 12kHz only chance levels of turns were made in the right direction (ii) the angle relative to the midline at which significantly more turns were made in the correct direction increased as the frequency increased, from 13 degrees for 4.5 kHz to 30 degrees for 5.5kHz, and 50 degrees for 6.5kHz or 9kHz.

Thorson et al. [16] note that in earlier arena stud-

ies crickets responding to songs of abnormal carrier frequencies “display behaviour similar to scanning without responding phonotactically” (Hill (1972) quoted in [16], op cit). They suggest this may be related to the effect they demonstrate on the treadmill whereby high intensity sound of abnormal carrier frequency causes “tracking phonotactically ...in systematically wrong directions” with angular error increasing with the frequency of carrier used. This systematic bias was also revealed in some arena experiments.

In the experiments described below we are investigating to what extent the frequency dependence of the ear directionality *alone* can contribute to frequency selectivity in phonotactic behaviour.

3 Auditory circuit

The hypothesised effect of the cricket’s auditory morphology is modelled using the programmable electronic circuitry whose block structure is shown in figure 1. Microphones 1 and 4 model the two tympani, while 2 and 3 model the auditory spiracles. Wideband (3–18kHz) pre-amplifiers buffer the microphone outputs, which are then fed to a set of delay lines that synthesise the two relative delays (τ_1 and τ_2) shown in solid lines² in the figure. The delayed spiracle signals are weighted and summed with each tympanal signal to generate the composite response to the sound field at each tympanum, then the amplitude of the latter is made available to the control software.

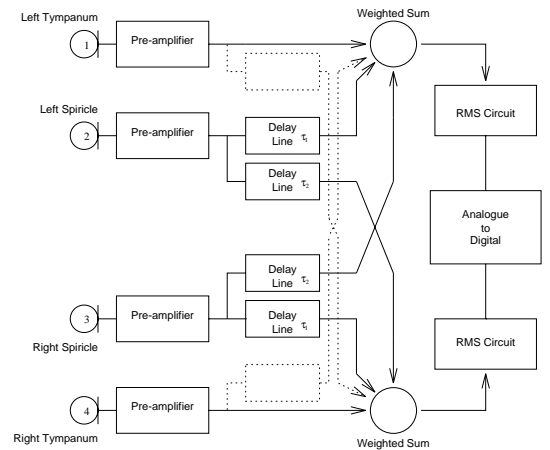


Figure 1: Block Diagram of the Peripheral Auditory Model. (©The authors, 1997.)

²Research [7] shows that the main contributions to the tympanal signal in the cricket are due to the tympanum itself and the two auditory spiracles — the contralateral tympanum makes only a small contribution to the signal. The dotted lines in the figure show the extra circuitry necessary to model a contralateral tympanal contribution. The system described here implements a simplified version of Michelsen and colleagues’ findings [7], in that the tracheal tubes are modelled by wideband channels and lateral symmetry is assumed.

The electronic circuitry allows a number of parameters to be adjusted in order to model known properties of the cricket auditory morphology. The gains of the pre-amplifiers are individually controllable over the range 6-120; the two relative delays are programmable up to $160\mu\text{s}$ (1 bit corresponds to 625ns , in which time sound at room temperature propagates about 0.2mm); and the contribution of each component of the weighted sum is programmable in the range ± 1 . All of these can be set within their respective ranges with 8 bit precision.

The electronics comprises two types of custom printed circuit board — *channel boards* which perform the signal processing, and a *clock board* which comprises the programming interface, delay synthesis circuitry, and bus decoding logic for connection to the Khepera robot. The latter board is round and plugs into the Khepera, while two channel boards are 55mm square and stand vertically above the clock board (see figure 2). Each channel board handles the signals from two microphones.

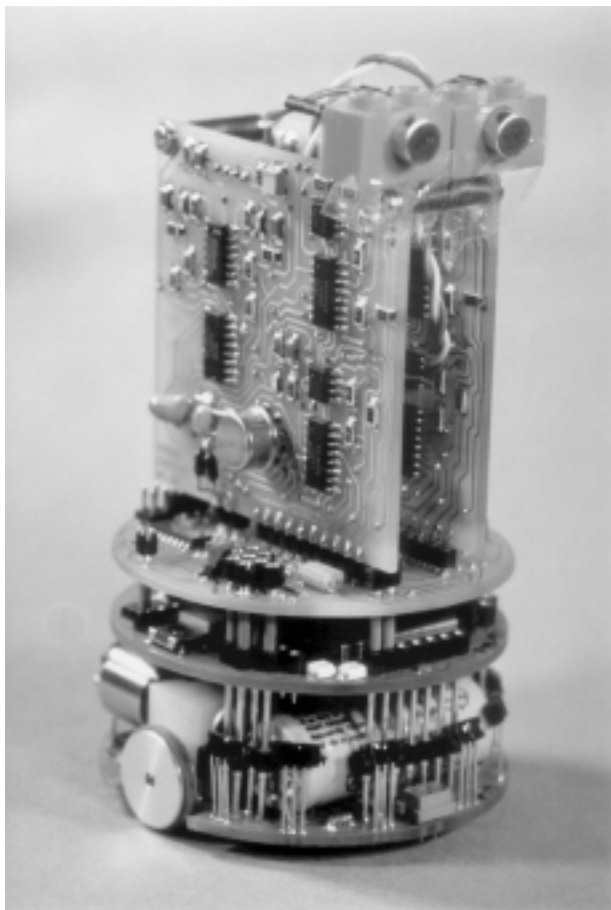


Figure 2: The Khepera robot with the auditory circuit. (©The authors, 1997.)

For the experiments described here, the circuitry is used in a somewhat simpler mode of operation. Spiricle contributions are neglected, and the model implemented

assumes that only the tympani contribute — as noted above, this is not strictly accurate, but in fact is a reasonable and simple approximation for our purposes here. To operate the circuitry in this mode, microphones 1 and 4 are omitted and the τ_2 delay is used to model the effect of the inter-aural tracheal tube. Note in particular that there are no narrow band filtering steps in the signal processing: frequency dependence and directional response both arise from the composition of multiple signal paths.

The microphones are placed on the front of the robot pointing forward (see figure 2). We set them so that there is a spacing of approximately 18mm in between them, since 18mm corresponds to approximately $1/4$ wavelength of a 4.7kHz sound (the carrier frequency of male *Gryllus bimaculatus* song). Dependent on the microphones, we empirically set the pre-amplifiers to get an equal response as output from the pre-amplifiers when giving equal input to the two microphones. The microphones might be more or less responsive, so this empirical setting of the pre-amplifiers is necessary. We place the robot with the microphones directly toward one loud speaker at a distance of 100cm . By emitting sound from the loud speaker and looking at the output from the two pre-amplifiers, we can then adjust the gain to get an equal response on both sides. The two relative delays (τ_2) are set to the time sound propagates the length of $1/4$ wavelength of 4.7kHz . This corresponds to $53\mu\text{s}$ or approximately 85 bits as one bit corresponds to 625ns . On each side, the direct signal from the pre-amplifier and the delayed signal from the opposite side are fed into the mixer that, in our case, performs $1.0*\tau_1 - 1.0*\tau_2$. Each side's mixed signal is then sent through an RMS and an A/D converter to one of the Khepera's input channels.

As is shown on figure 3, this hardware processing of the auditory signal results in phase cancellation, when the input signal is of right carrier frequency (4.7kHz). When the robot faces 90 degrees away from the loud speaker and the left microphone is nearest to the sound source, there will be an increased output from the left channel and very low output from the right channel (figure 3 (1)). The opposite happens if the robot is turned another 180 degrees, so that the right microphone is closer to the sound source (figure 3 (3)).

In our hypothesised control mechanism, the output from the circuit is fed into a comparator mechanism similar to that described in [17]. That is, for each side the output is fed into a leaky integrator, and whichever side reaches threshold first causes a small turn to be made in that direction. The default movement of the robot is a forward movement.

4 Robot phonotaxis and frequency selectivity

4.1 Taxis to Real Sound

We made recordings of male *Gryllus bimaculatus* calling song at Life Science Department, University of Nottingham. The adult male cricket was sitting in a sand-floored arena and was recorded using a Maplin uni-directional dynamic microphone (YU-34) on a Marantz Stereo cassette recorder (CP230) from a distance of about 20cm. A 30s part of these recordings is played through a host Pentium computer with SB AWE32 sound card and was repeated twice for each experiment. The sound was fed through an amplifier to a loud speaker that was placed on a 240*240cm arena in our robot lab. It should be noted that we did nothing to control echos from the surrounding environment.

For each experiment, we placed the Khepera robot in the arena 150 cm away from the loud speaker. We alternated between two starting positions with the robot facing approximately 45 degrees away from the loud speaker either to the left or to the right.

In order to record the movements of the robot, we have built a simple video-tracking system [6]. We place a CCD camera approximately 2m above the arena, put a LED on top of the robot, and then use a Matrox Meteor frame-grabber with our software to collect data.

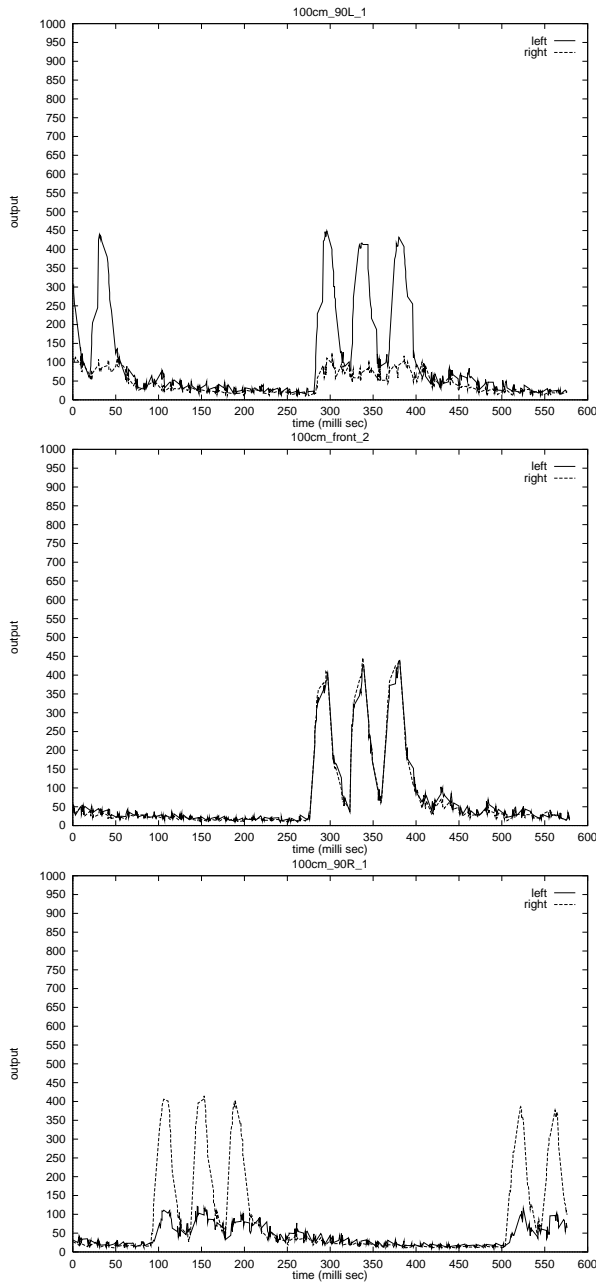


Figure 3: The output of the ears circuit's left and right channel when the robot is 100 cm away from the loud speaker that emits recordings of male cricket *Gryllus bimaculatus* song. The three figures show the output when the robot has the speaker at (1) 90 degrees left; (2) front; (3) 90 degrees right. (©The authors, 1997.)

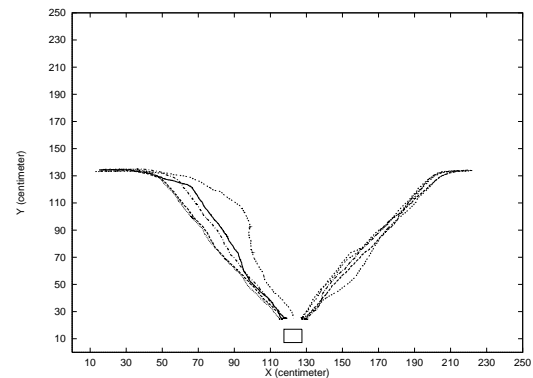


Figure 4: The robot's behaviour when recorded song of a male *Gryllus bimaculatus* is emitted from the loud speaker. (©The authors, 1997.)

Figure 4 shows the trajectories of the robot when the male *Gryllus bimaculatus* calling song was emitted from the loud speaker at the bottom. The experiment was repeated ten times. It is evident that the robot successfully responded to the real cricket song, and navigated toward it. Initially, the robot moved forward a small amount of time before it reacted to the cricket calling song that was emitted from the loud speaker. Then, it turned toward the sound and navigated very directly toward the sound. At the scale of this figure, it is difficult to notice

all the small turns that the robot performed in response to the calling song. In fact, in a distance of approximately 1m away from the sound source, the robot responded to most of the syllables (of a length of approximately 20 ms). On average, the robot made 7 turns/second, but most of them were around the midline toward the speaker and the trajectories appear very straight on the scale of figure 4. This result shows that the robot with the simple control mechanism based on comparison of signals on each side does phonotaxis very well when put under exactly the same condition as crickets in arena experiments. Hence, the simple control mechanism is enough to account for the female cricket's behaviour under these conditions.

4.2 Taxis to Different Frequencies

To test whether the frequency dependence of the ear directionality might contribute to frequency selectivity in crickets, we made another set of experiments, in which we played song with different carrier frequencies, namely of 2.35kHz, 4.7kHz, and 9.4kHz. 4.7kHz is the carrier frequency of the *Gryllus bimaculatus* calling song (wavelength λ_1), while 2.35kHz has a wavelength (λ_2) twice the size of 4.7kHz, and 9.4kHz has a wavelength (λ_3) of half the size of 4.7kHz. For 4.7kHz, sound at the near ear arrives in antiphase (it is delayed by $\lambda_1/2$) and gives a net amplitude of 2 at that ear, roughly. For 9.4kHz it is delayed by λ_3 and arrives in phase, giving a low amplitude; and for 2.35kHz it arrives delayed $\lambda_2/4$ and gives a 1.4 amplitude. Therefore, we would expect the robot to be less responsive to 2.35kHz, and not to respond to 9.4kHz at all (if the signals were perfect, which they are not).

As in biological experiments with varying carrier frequency (see section 2.3), we did not use recordings of cricket song in this case. Instead, we generated artificial songs ourselves with chirps of three syllables with 200ms in between chirps. The syllables were of 20ms, and pauses in between syllables were 20ms. That is, the pattern of sound was as in the real cricket calling song.

Because the individual microphones might be more or less responsive to different frequencies, we once again calibrated the sound input via the programmable pre-amplifiers so that the output of the pre-amplifiers were at equal levels for sound of the different frequencies. This means that we cancel out any frequency-dependent differences in auditory receptors, and effectively can test whether frequency dependence of ear directionality alone can account for frequency selectivity in phonotaxis.

Figure 5, 6, and 7 show the results of the experiments with the songs with three different carrier frequencies. We allowed the robot to move ten times for 60 seconds with starting positions alternating between facing approximately 45 degrees left or right away from the loud speaker at a distance of 150cm. This was done for all three carrier frequencies.

As hypothesised, the robot would not respond to song of 9.4kHz, but just move in a straight line, since forward movement was the default movement (see figure 7). On the other hand, the robot performed phonotaxis to both 4.7kHz (see figure 5) and 2.35kHz (see figure

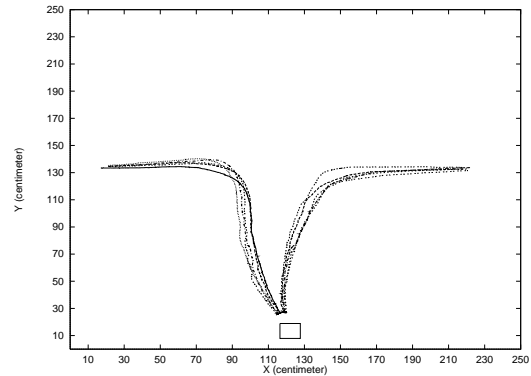


Figure 5: The robot's behaviour when computer generated song of 2.35 kHz is emitted from the loud speaker. (©The authors, 1997.)

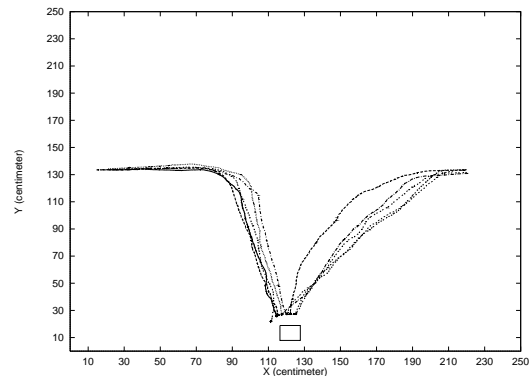


Figure 6: The robot's behaviour when computer generated song of 4.7 kHz is emitted from the loud speaker. (©The authors, 1997.)

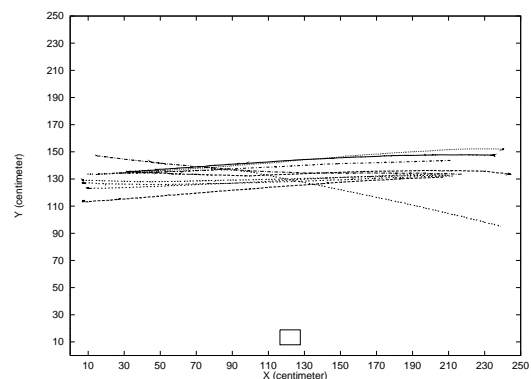


Figure 7: The robot's behaviour when computer generated song of 9.4 kHz is emitted from the loud speaker. (©The authors, 1997.)

6). However, the movements seemed more straight toward the loud speaker at 4.7kHz, especially at the right side of figure 5, while the robot seemed to move very close toward the middle of the arena before turning when presented with song of 2.35kHz. This suggests, that the

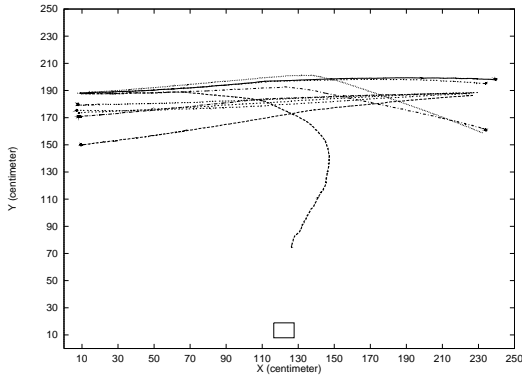


Figure 8: The robot's behaviour when starting further away as computer generated song of 2.35 kHz is emitted from the loud speaker. (©The authors, 1997.)

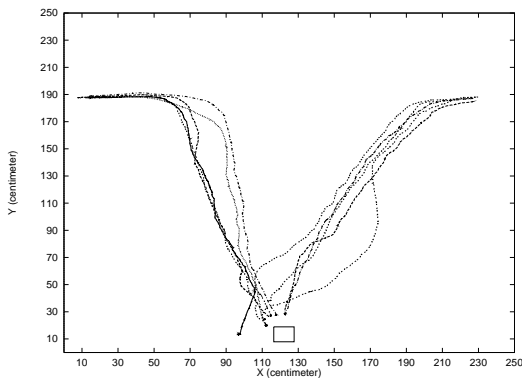


Figure 9: The robot's behaviour when starting further away as computer generated song of 4.7 kHz is emitted from the loud speaker. (©The authors, 1997.)

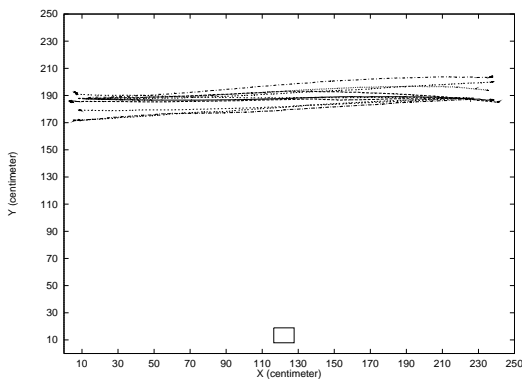


Figure 10: The robot's behaviour when starting further away as computer generated song of 9.4 kHz is emitted from the loud speaker. (©The authors, 1997.)

robot was more responsive to 4.7kHz, since it was able to turn at a smaller angle toward the speaker when presented with 4.7kHz — when moving straight toward the centre, the angle between loud speaker and microphones increases toward 90 degrees, at which point, an ideal signal would produce the highest output from the auditory circuit according to the hardware settings.

To further investigate whether selectivity of carrier frequency of 4.7kHz was the case, we did an additional set of experiments, in which the starting position of the robot was increased to 200cm away from the loud speaker. The robot was still able to perform quite successful phonotaxis to 4.7kHz, even though it seemed to make a slight miss once out of the ten runs³ (see figure 9). Not surprisingly, the robot still did not perform phonotaxis at 9.4kHz (see figure 10). However, the behaviour at 2.35kHz changed dramatically (see figure 8). Where the robot did phonotaxis when started closer to the sound source, it did not respond to the sound of 2.35kHz at this distance. Rather, it simply performed the default movement of moving forward. However, in one case out of the ten runs it responded to the sound, but made a very slow turn, so that it could not reach the sound source within the 60 seconds, and in a couple of other runs it responded once or twice which changed the movement only slightly. Hence, this distance seemed to be just above the maximum distance at which the robot could do phonotaxis to a song with carrier frequency of 2.35kHz.

Phonotaxis at 2.35kHz only occurs when the robot is close enough to the sound, and if we place the robot even closer to the sound source, phonotaxis at 9.4kHz can occur (data not shown here). These results can be interpreted as the robot being responsive to song of different carrier frequencies down to specific intensities. We have not measured the intensities of the song at different distances from the loud speaker, but obviously the intensity drops when further away from the loud speaker. The experiments show that frequency dependence of the ear directionality *alone* can contribute to frequency selectivity in phonotaxis, and the obtained results are comparable with the behavioural studies on crickets. Indeed, both behavioural studies with crickets [9, 11, 13, 14] and the present experiments with the robot show that the crickets react to songs with the ideal carrier frequency at lower intensity than to songs with carrier frequencies away from the ideal.

4.3 Taxis to Two Songs

To further investigate frequency selectivity, we did a number of experiments with two different sound sources.

³However, the reason for this miss seemed to be interference from the Khepera motors on the auditory circuit, so that the interaural delays changed. In the new circuit that we are producing there will be a 3.3V regulator that should isolate the auditory circuit from interference from the Khepera motors.

We placed two loud speakers in the arena and emitted computer generated song with carrier frequency of 4.7kHz from one loud speaker, and computer generated song with carrier frequency of 6.7kHz from the other loud speaker. The songs had the same pattern as the songs used in the previous experiments, and they were played in synchrony. With two different sound sources, it is difficult to calibrate the auditory system to ensure no frequency-dependent differences in sensitivity. Hence, the pre-amplifiers were set to an intermediate level. Regardless of this, the robot showed selectivity toward the song with the *Gryllus bimaculatus* carrier frequency of 4.7kHz, as shown on figure 11. Indeed, in nine out of the ten runs with different starting positions, the robot would navigate toward the 4.7kHz song, while it would move toward the 6.7kHz song only when placed very close to the loud speaker that emitted this song.

On the other hand, when the robot was placed at a starting position equidistant from the two sources, as shown on figure 12, the robot showed selectivity toward the song with 4.7kHz carrier frequency in all cases. It should be noted that we did not have a decibel meter or other equipment available to determine the output level from the two loud speakers. Hence, in order to obtain equal volume levels, we used the robot's auditory circuit to empirically set the outputs from the loud speakers' amplifier.

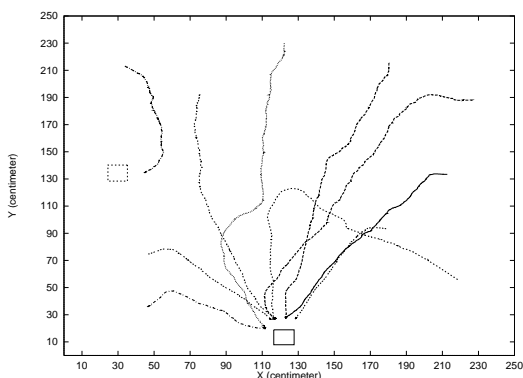


Figure 11: The robot's behaviour when computer generated song of 4.7 kHz is emitted from the loud speaker at the bottom and computer generated song of 6.7 kHz is emitted from the loud speaker to the left. The robot is placed at ten different starting positions. (©The authors, 1997.)

Where the previous results could be interpreted as interspecies choice/selectivity for the conspecific song, we made an extra set of experiments to test for intraspecies choice. Hence, we emitted the 4.7kHz song from two loud speakers in the arena. Again, the songs were played in synchrony. This would model two crickets sitting a bit more than 1m apart and singing (even though that they most often do not sing in synchrony). As is shown

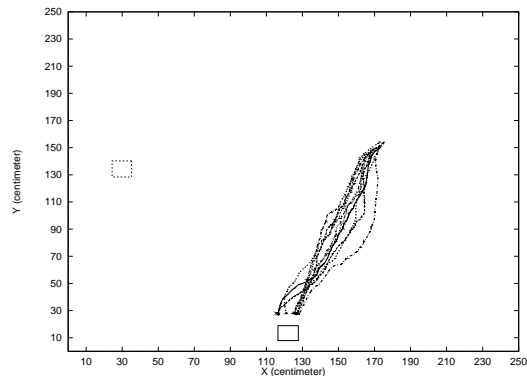


Figure 12: The robot's behaviour when computer generated song of 4.7 kHz is emitted from the loud speaker at the bottom and computer generated song of 6.7 kHz is emitted from the loud speaker to the left. The robot is placed at a starting position equidistant from the two sources in all ten runs. (©The authors, 1997.)

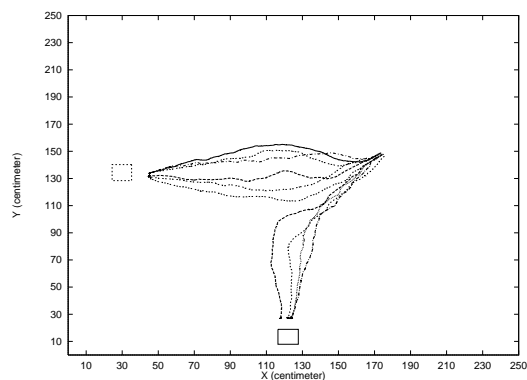


Figure 13: The robot's behaviour when computer generated song of 4.7 kHz is emitted from the two loud speakers in stereo. (©The authors, 1997.)

on figure 13, the robot would "choose" one of the sound sources and move fairly straight toward that one.

5 Discussion

These experiments show that at least a certain amount of frequency selectivity in phonotaxis behaviour can be derived from the properties of the directionality of the ears. That is, the robot, and presumably the cricket, have difficulty approaching songs of the wrong frequency simply because their ears cannot provide accurate directionality at those frequencies.

As discussed in section 2 this is probably not the whole explanation of frequency selectivity. Crickets do have a certain degree of frequency tuning in their auditory receptors and are most sensitive to the calling song frequency. Nevertheless the current results show that the directional effects are likely to play a significant additional role, even under complex conditions such as choos-

ing a song of one frequency over another.

6 Conclusion

With this work, we have shown that our hypothesised control mechanism can account for phonotaxis behaviour not only under artificial experimental settings, but also when tested under biologically true conditions: the robot with the newly developed auditory circuit does phonotaxis to *real* cricket song. Hence, we can conclude that the hypothesised control mechanism can account for the female cricket's phonotaxis behaviour, even though that these experiments cannot tell whether this is the cricket control mechanism — only neurophysiological evidence can tell that. However, this simple control mechanism has been verified to be a possibility.

In future experiments, we will use the Khepera with the newly developed auditory circuit to make syllable rate experiments, in which we want to determine at what range of syllable lengths and at what syllable repetition rates taxis is performed. Further, we will investigate the female choice behaviour more thoroughly, for example by playing syllables of an ideal song alternately in each speaker and by investigating what the minimum pitch difference is for statistical consistent choice of the ideal song.

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References

- [1] H. C. Bennet-Clark. Songs and the Physics of Sound Production. In F. Huber, T. E. Moore, and W. Loher, editors, *Cricket Behaviour and Neurobiology*, pages 227–261, Ithaca, New York, 1989. Cornell University Press.
- [2] P. Boyd and B. Lewis. Peripheral auditory directionality in the cricket (*Gryllus campestris* L., *Teleogryllus oceanicus* Le Guillou). *J. comp. physiol.*, 153:523–532, 1983.
- [3] F. Grasso, T. Consi, D. Mountain, and J. Atema. Locating Odor Sources in Turbulence with a Lobster Inspired Robot. In P. Maes, M. J. Mataric, J. Meyer, J. Pollack, and S. W. Wilson, editors, *From Animals to Animats 4: Proceedings of the Fourth International Conference on Simulation of Adaptive Behavior*, Cambridge, MA, 1996. MIT Press.
- [4] D. Lambrinos, M. Maris, H. Kobayashi, T. Labhart, R. Pfeifer, and R. Wehner. An autonomous agent navigating with a polarized light compass. Technical report, Computer Science Department, University of Zurich, 1997. Submitted to *Adaptive Behavior*.
- [5] C. G. Langton. Artificial life. In L. Nadel and D. Stein, editors, *Lectures in Complex Systems*, Reading, MA, 1992. Addison-Wesley.
- [6] H. H. Lund, E. d. V. Cuenca, and J. Hallam. A Simple Real-Time Mobile Robot Tracking System. Technical Paper 41, Department of Artificial Intelligence, University of Edinburgh, 1996.
- [7] A. Michelsen, A. V. Popov, and B. Lewis. Physics of directional hearing in the cricket *Gryllus bimaculatus*. *J. comp. physiol.*, 175:153–164, 1994.
- [8] O. Miglino and H. H. Lund. Open Field Box Experiments with Rats and Robots. Technical report, C.N.R., Rome, 1996.
- [9] A. Moiseff, G. S. Pollack, and R. R. Hoy. Steering responses of flying crickets to sound and ultrasound: Mate attraction and predator avoidance. *Proc. Natl. Acad. Sci. USA*, 75:4052–4056, 1978.
- [10] B. P. Oldfield. Accuracy of Orientation of Female Crickets, *Teleogryllus oceanicus* (Gryllidae): Dependence on song spectrum. *J. comp. physiol.*, 141:93–99, 1980.
- [11] A. V. Popov and V. F. Shuvalov. Phonotactic behaviour of crickets. *J. comp. physiol.*, 119:111–128, 1977.
- [12] F. Saito and T. Fukuda. A First Result of The Brachiator III — A New Brachiation Robot Modeled on a Siamang. In C. Langton and K. Shimohara, editors, *Proceedings of ALIFE V*, Cambridge, MA, 1996. MIT Press.
- [13] M. V. Segejeva and A. V. Popov. Ontogeny of positive phonotaxis in female crickets, *Gryllus bimaculatus* De Geer: dynamics of sensitivity, frequency-intensity domain and selectivity to the temporal pattern of male calling song. *J. comp. physiol. A*, 174:381–389, 1994.
- [14] J. F. Stout, C. H. De Haan, and R. W. McGhee. Attractiveness of the male *Acheta domesticus* calling song to females I. Dependence on each of the calling song features. *J. comp. physiol.*, 153:509–521, 1983.
- [15] C. E. Taylor and D. Jefferson. Artificial life as a tool for biological inquiry. *Artificial Life*, 1(1-2):1–13, 1994.
- [16] J. Thorson, T. Weber, and F. Huber. Auditory Behaviour of the Cricket II. Simplicity of Calling Song recognition in *Gryllus* and Anomalous Phonotaxis

at Abnormal Carrier Frequencies. *J. comp. physiol.*,
146:361-378, 1982.

- [17] B. Webb. Using robots to model animals: a cricket test. *Robotics and Autonomous Systems*, 16:117-134, 1995.