# Modeling Biological Behaviour or
# 'Dumb Animals and Stupid Robots'

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## Abstract

This paper discusses some of the essential determinants of successful sensory-motor mechanisms in biological systems that are seriously under-represented in most Artificial Life models. These include specificity, non-centralised processes, and exploitation of the physical sensory and motor interface of the agent and environment. The ideas are illustrated in the interpretation of biological evidence, and the building of a robot model, for a hypothesised mechanism of cricket phonotaxis (the ability to track a conspecific auditory signal). The robot's behaviour confirms that the specificity of the task and effects of the environmental interface can be utilised to obtain a simple but effective location device.

# Modeling Biological Behaviour

In a previous paper [Webb & Smithers, 1992], the process of building models as a means of exploring the mechanisms that produce successful sensory-motor behaviour was discussed, and some of the problems inherent in drawing valid conclusions from the results of such modeling were presented. In particular, the importance of appropriate representation of the problem, and the need for support for the assumptions that underly the representation, were stressed (similar concerns are discussed in [Chan & Tidwell, 1992]). 'Animat' simulations, such as those discussed in [Meyer & Guillot, 1991], were criticised because they tend to involve assumptions about the nature of the problem for which there is little support when real examples of systems engaged in sensory-motor behaviour, such as animals and robots, are considered closely.

This paper uses cricket phonotaxis as an example to draw out some important characteristics of sensory-motor mechanisms in systems such as lower animals and simple but successful robots. It is not possible here to widely review the biological and robotics research supporting these ideas, but the approach is influenced by authors who have provided fuller discussion: including in robotics [Brooks, 1986], [Brooks, 1991], in biology [Varela *et al*, 1991], in psychology [Gibson, 1979] and in philosophy [Clark, 1989]. All these stress that the source of intelligent behaviour is *"not limited to just the computational engine. It also comes from the situation in the world, the signal transformations within the sensors and the physical coupling of the robot with the world"*[Brooks, 1991] and that understanding perception requires us *"to determine the common principles or lawful linkages between sensory and motor systems that explain how action can be perceptually guided in a perceiver dependent world"* [Varela *et al*, 1991]

# A Dumb Animal

Most work in Artificial Life (AL) claims to be inspired by the behaviour of animals low on the evolutionary scale, in contrast to the cognitive processes of humans that inspire traditional AI. But looking at the neuroethological evidence of behavioural mechanisms in insects or simpler creatures [Guthrie, 1987], [Hoyle, 1984] reveals little resemblance to typical AL 'bugs'. Most striking is the fact that such animal systems are vastly more complicated and less understood than seems to be generally supposed. This is certainly true of the cricket.

Cricket phonotaxis involves females moving towards the calling song of a potential mate. The song consists, typically, of rapidly repeated syllables of almost pure tone, produced by the male rubbing one wing against the other. Females can find the male by this cue alone over distances of twenty metres or more through rough vegetation. Despite extensive behavioural and neurological investigation over the last twenty years the mechanism is not well understood (see reviews in [Huber & Thorson, 1985], [Schildberger, 1988]).

*No central representation*

Taxis towards a sensory souce is both a common animal behaviour and a useful behaviour for mobile robots. It can be achieved by direct and reactive

links between sensors and motors; rather than requiring the sensors to construct a central represention of the situation, from which the location of the source is extracted and a path towards it planned. (The simplest example is the Braitenburg vehicle (2b) that, with a sensor and a wheel on each side, feeds the level of sensor response to the speed of the opposite wheel [Braitenberg, 1984]). In the cricket there are perhaps as few as four links between the auditory organs and the motor neurons, and excluding the receptor and motor neurons themselves, around ten neurons involved in the connection. It is not viable to treat this as a system where the sensory input results in a central representation of the current situation that can be used to drive the motor response. Rather, phonotaxis is the result of specialised linkages from sensors to actuators, which, combined with parallel links for other behaviours such as negotiating obstacles, results in the overall behaviour of the animal. Such a conception of behaviour (analogous to Brooks 'horizontal' division) needs to be adopted to appreciate the functioning of sensory-motor mechanisms at this level.

*Specific tasks*

Like many other insects, the cricket has a simple and distinctive cue to find a mate, and consequently can have a sensory-motor mechanism that works for this cue and nothing else: there is no need to process sounds in general, provided this specific sound has the right motor effects. Indeed, it may be advantageous to have such specificity built in, because it implicitly provides 'recognition' of the correct signal through the failure of the system with any other signal. Hypotheses about phonotaxis (see [Weber & Thorson, 1988] for example) seem to be guided by the assumption that recognition of the song is a separate process from determining the direction to move by comparison of the intensity of the sound on each side. However, intensity is encoded both as firing rate and firing latency by the auditory neurons, and a comparison mechanism that utilizes the latter (i.e. the difference in time of onset of neural firing) will fail to work in the absence of the temporal patterning which is the distinguishing feature of the song. This idea is the basis of the mechanism implemented in the robot described below. Getting successful behaviour by having hardware dedicated to a specific task seems to be a common feature of animal sensory-motor mechanisms.

*Exploiting physical constraints*

Crickets are too small (1-2cm) relative to the wavelength of the song (5-6cm) for there to be much intensity difference between the ears (on their front legs), and phase differences are in the order of microseconds, which requires large scale neural processing (such as found in the owl [Konishi, 1993]) to detect. However, the ears are connected one to the other by a tracheal tube, so that vibration outside one tympanum is transfered through to the inside of the opposite tympanum. The resulting movement of the tympanum is a cancellation of the directly arriving sound, and the sound arriving indirectly via the trachea, the relative phase of which will depend on the orientation of the cricket to the sound source. Thus the intensity of the response is altered substantially by the direction of the sound. Note that such a system fails if the sound is of the wrong wavelength (as the trachea length is constant), an example of the principle discussed above. [Wehner, 1987] reviews

other biological examples of 'matched filters': sensory mechanisms that exploit the specificity of the task and the physics of their environment so as to greatly simplify the processing required to produce the right behaviour. In other words, the functioning of such sensors is a significant determinant of the subsequent neural processes that control the response: these control processes can't be properly understood in isolation from the physical mechanisms of sensing.

*Fixed mechanisms*

The initial neural connections in the cricket have been well studied. One pair of ascending neurons (AN1) has been particularly associated with phonotaxis, as it shows the best response to the calling song frequency, copying the syllable pattern provided it is not faster than the time constant of the cell, and coding the intensity at the tympanum in both the rate of firing and the latency before firing starts [Wohlers & Huber, 1982]. [Schildberger & Horner, 1988] have shown that hyperpolarization of this neuron will eliminate the phonotactic response. AN1 connects to brain neurons that apparently respond only to syllable rates that fall within the same range as those that elicit phonotactic behaviour, possibly by a summation mechanism [Schildberger, 1984]. These response properties are hardwired in the cricket, subject to modification by the level of hormones [Henley *et al*, 1992]: they do not develop from random connections of an arbitrary collection of neurons.

Such a fixed, specific neural structure is typical of lower animals, and learning (permanent alteration of function due to experience, as opposed to temporary adaption) may not play an important role for many such systems. There seems to be an assumption in AL that 'adaptability' in the sense of coping with environmental diversity requires alterations in the internal mechanisms that support it, [Kaebling, 1992] [Pfeifer & Verschure, 1992], but this is not always so in biology. Rather, efficient and effective fixed mechanisms exist that can perform the required function under a wide range of conditions.

It is often argued that, as evolution produced these mechanisms, using evolutionary processes may be the way to reproduce them [Koza, 1992] [de Garis, 1992]. But it is fair to suppose that mechanisms of comparable complexity will require comparable complexity of conditions to evolve in (rather than the sparse environment of a typical simulation), *and* will take a comparable time to evolve. Furthermore, having evolved, they will be as hard to understand as biological ones. While such research may contribute to understanding of the mechanisms of evolution, it is hard to see how it will improve understanding of sensory-motor control.

# A Stupid Robot

The previous section has made some suggestions for important characteristics of biological sensory-motor mechanisms in general, and shown how these ideas apply to cricket phonotaxis in particular. Similar points often arise in building robots (see for example [Flynn & Brooks, 1989] or [Horswill, 1992]): those who have tried to build real-world sensory motor devices often mention the necessity of eliminating central representations in favour of multiple direct connections, of concentrating on solving a specific task, and of having the right kind of sensors

and actuators, and it is also arguably true to say that more advanced behaviours have been shown by robots with designed behaviour than by those that learn from scratch. These similarities suggest that hypotheses about biological mechanisms may be usefully examined by building robotic models of those mechanisms.

The neuroethological investigation of cricket phonotaxis is noticably sparse in hypotheses, possibly reflecting the ethologist's bias towards observation over theorising. This makes interpretation and integration of the results quite difficult. The comments made above, however, point to a plausible mechanism for phonotaxis that is somewhat different, and somewhat simpler, than those that have guided researchers so far. The hypothesis is that the prior onset of firing for the side with higher intensity is the critical cue used to determine turning tendency, and that given certain sensory and motor response properties, such a mechanism is sufficient to explain why crickets only approach the 'right' kind of sound, without additional recognition mechanisms. The following sections describe the construction and testing of a phonotaxis-performing robot to evaluate this hypothesis. I have tried to make explicit the assumptions and limitations involved in representing the cricket by this model.

## Methods

### Hardware

The robot used is based on a Lego technic vehicle [Donnett & Smithers, 1990]. It is roughly 27cm long, 21cm wide and 19cm high, and propelled by two motors that drive tyred wheels ('full speed forward', 'backward', and 'stop' were the only states used), with a ball-bearing castor at the front. It can move up to 50cm/s, but the speed and evenness of the motors varies with battery power; the wheel rates are additionally affected by the stiffness of the gears, and the movement by irregularities in the friction and slope of the floor surface (linoleum); thus control of movement is fairly inaccurate. The robot has two bump and two infrared sensors to detect obstacles in its path, each returning binary data. It is controlled by a 68000 clone processor programmed in C.

Although the cricket is likely to have more complex and more accurate mobility than this robot (unfortunately it wasn't possible to use a six-legged robot), it is worth noting that given the complexity of its habitat, a comparable inability to get places by setting a fixed course is likely to ensue. In other words, both need to constantly readjust their direction of movement according to current cues in order to safely reach a target.

The auditory mechanism consists of two miniature microphones, which are positioned about 4cm above the main body and about 4.5cm apart from each other (roughly 1/4 the wavelength of the 2kHz signal used), connected to a circuit that mimicks the function of the tracheal tube in the cricket. That is, it compares the input at the left 'ear' with a delayed signal from the right 'ear', and determines a response value based on the amplitudes ($l_{amp}$ and $r_{amp}$), and relative phase ($l_{ph}$) of the waves:

$$response_L = \sqrt{l_{amp}^2 + r_{amp}^2 + 2l_{amp}r_{amp}cos(l_{ph})}$$

The same occurs for the right ear (i.e. the left ear signal is delayed and compared with the right ear input, and the relative phase $r_{ph}$ used in the equation above to determine $response_R$). This is the simplest model of the physics of the auditory system in the cricket [Hill & Boyan, 1977]; more complex models have been attempted [Fletcher & Thwaites, 1979] but the unreliability of most of the measurements required led to highly inaccurate results.

The sound was produced by an 2kHz oscillator, gated by a programmable processor to produce temporal patterns and fed to a 8 watt speaker. There was no special sound proofing, so the sound field was far from 'ideal', but this is true of natural cricket habitats also.

*Software*

The implementation of the hypothesis of latency comparison here intentionally involves a minimum of processing between the auditory input and motor output, and instead of central mediation is controlled by variables whose response represents hypothesised neural connections in the cricket. Excluding the MAIN task that forks and resets the others, there are five processes run in pseudo-parallel (4 ms time-slicing):

LISTEN controls the auditory circuit, initiating a reading every 35ms. The current (time $t$) response for each ear is combined with the previous response in the variables $an_L$ and $an_R$, where for each:

$$an_t = \frac{an_{t-1} * 7}{8} + response_t.$$

This approximates the intensity-dependent latency, the maintained firing and the relatively slow time-constant of the AN1 neuron in the cricket: over an intensity range of 2—16, a difference of 2 or more in the phase will cause a difference between the time for $an_l$ and $an_r$ to reach the 'onset of firing' threshold.

RESPONSE detects a time difference in onset of the *an* variables, increasing the value of $stime_L$ or $stime_R$ if $an_L$ or $an_R$ reaches threshold before the other. The relvant *an* response must fall below half value before another onset will be detected. In effect, this response constitutes low pass filtering, removing rapid alterations from the sound input. $stime_L$ or $stime_R$ are also increased if the infrared sensors indicate an obstacle. $stime_B$ is increased if the bumpers indicate a collision.

LEFT, RIGHT and BACKUP control the motors, based on the value of respective *stime* variables. For BACKUP, the wheels are put in reverse if $stime_B$ is greater than zero. For LEFT and RIGHT, when *stime* exceeds the current time, the corresponding wheel is stopped for a short time (causing a turn if the other wheel is going forward) then both wheels stopped until the excess time has elapsed. If the *stime* is increased again during this pause, the turn is resumed until the excess time has elapsed. The parameters are set so that a single turn and pause is quite small, but increases of *stime* with sufficient frequency will lead to continuous, hence larger, turns. In effect it is a high pass filter for the frequency of onsets, comparable to the function of some brain neurons in the cricket.

Thus, provided with a sound signal patterned into regular syllables, the ideal rate is determined by the low-pass filtering in RESPONSE (requiring infrequent

syllables to detect onsets) and the high-pass filtering in LEFT and RIGHT (requiring sufficiently frequent syllables to facilitate turning). In fact, the noise in the auditory processing sets a limit on the fastest syllable rates for the readings to lead to detectable syllable responses, and the relative speeds at which the vehicle moves forward and turns sets a limit on the slowest syllable rates for effective course alteration. Nearly all of the parameters within the program are determined by these two physical considerations.

*Measurement*

Modeling a specific animal system provides a clear basis for evaluating the behaviour of a robot (which can often be difficult) and furthermore suggests some methods for measurement. The results below were based on the 'arena' paradigm, where the cricket is allowed to move towards a sound-producing speaker within a limited area, and the track is recorded and analysed. For the robot, an overhead camera and tracking system follows a bright light placed on the robot, generating position estimates at video frame rate (25hz). The arena used was 3x4metres which was the limit of the camera's field of view. The video track was converted to polar floor coordinates centered on the speaker, and could be summarised as a series of vectors connecting the turns. The combined length of vectors in each direction relative to the sound can be used to indicate directional tendencies (see figure 1b); or the mean vector for the track can be calculated [Mardia, 1972], which points in the mean direction of the movement and has length (between 0 and 1) representing the variance, or degree of deviation, around that mean direction (figure 2b).
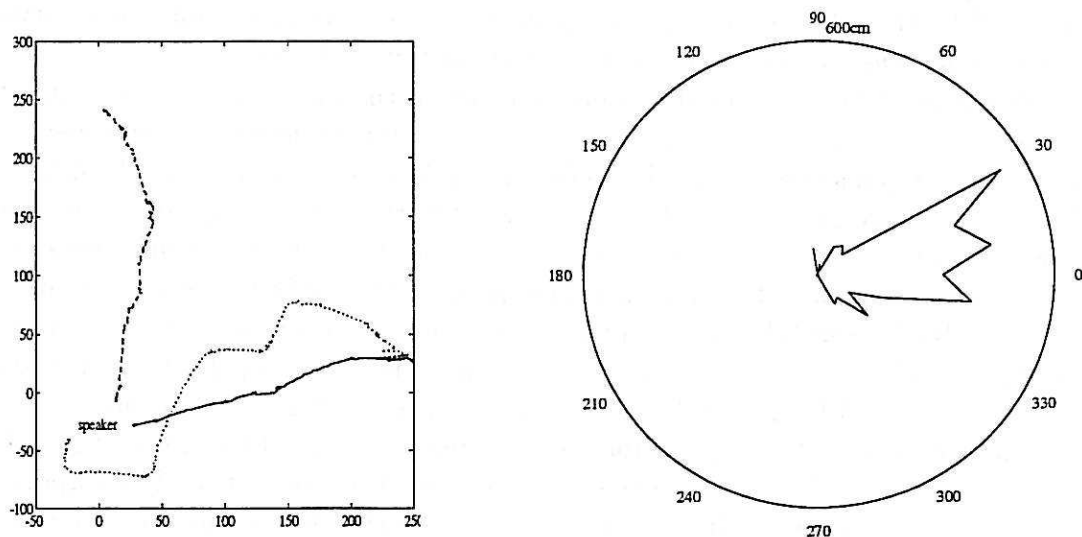


Figure 1: *Robot taxis in the arena.* **a:** *Longest, shortest and median tracks from ten trials.* **b:** *Combined vectors for all ten trials.*

# Results

*Taxis*

The first thing to test was whether the robot could find a sound reliably under these conditions. The physical constraints indicated an ideal syllable repetition interval of 600ms. Using equal syllable and gap lengths (300ms), in ten trials, starting five times on each side, the robot approached the speaker quite directly in each trial (fig 1 shows the shortest, longest, and median path and the combined length of vectors in each direction over ten trials). The paths also showed a feature
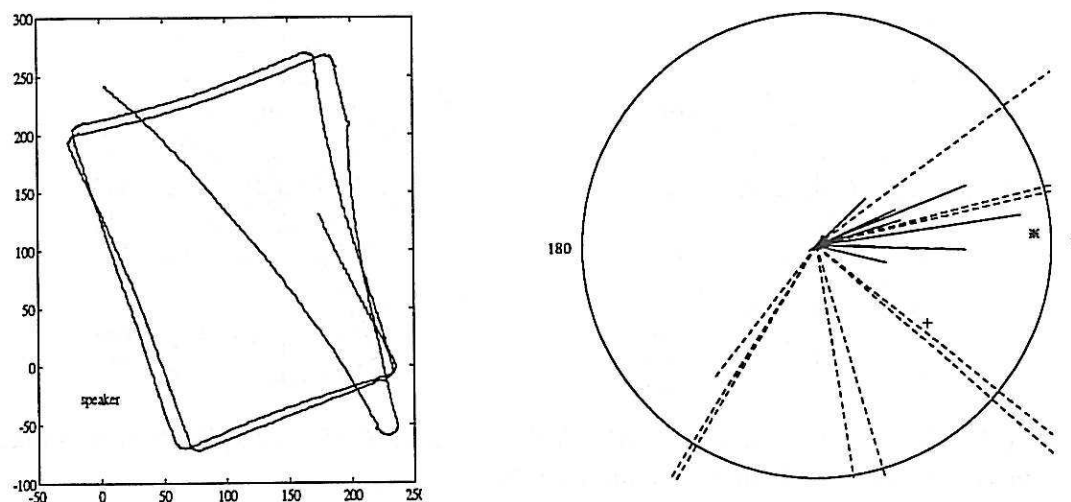


Figure 2: **a:** *Track with no sound.* **b:** *Vectors and vector mean of track with no sound (dashed lines, + symbol) and median track from Fig. 1 (solid lines, * symbol); note that for latter, vectors are concentrated around 0° direction, and mean is near (0,1)*

of cricket phonotaxis, which is a tendency to oscillate between heading slightly to the right, then slightly to the left of the speaker (producing a 'zig-zag' path). The robot was clearly finding the speaker far faster than by chance: without the sound it would generally circle the enclosure, heading equally in each direction (see fig 2; the difference is also evident in the vectors and vector mean of the tracks in each condition).

*'Recognition'*

The first demonstration that the robot is 'recognising' the temporal pattern of the signal is the fact that, with a continuos tone (i.e. no syllable pattern) the robot's response was almost identical to the no sound condition. The temporal pattern of the cricket song has several parameters, principally rate of repetition of syllables, length of syllables, typical number of consecutive syllables (groups of syllables separated by longer pauses are referred to as chirps) and rate of chirps. [Thorson *et al*, 1982] found that though the normal song of *Gryllus campestris L.* had a fixed syllable length and chirp pattern, altering these would not eliminate phonotaxis, whereas deviation from the syllable repetition rate of 30Hz would, the

response becoming gradually worse at higher or lower rates. They proposed the '30Hz hypothesis': that this feature of the signal is the criteria for the 'recognition mechanism' that subsequently switches on the location mechanism. However, as discussed above, the location mechanism based on onset comparison in the robot inherently requires a particular syllable rate. It should be possible to demonstrate a difference in the robot's performance of taxis to different syllable rates.

Ten trials were run at each of 6 repetition intervals from 200—1200ms. The results for 400, 600 and 1000 were compared statistically (see figure 3a). The mean
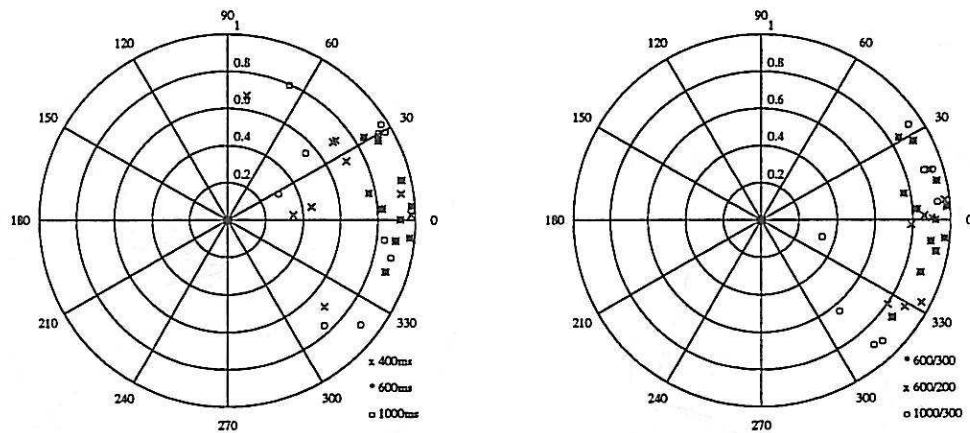


Figure 3: *Mean vectors* **a:** *Different syllable rates* **b:** *Different syllable rate/syllable length combinations. Compare distances from (0,1).*

vector of an ideal path (straight to the speaker) would have direction 0 and length 1, so the distance of the means from (0,1) can be used to rank them and thus obtain a non-parametric statistic for the difference between the conditions. Using the Mann-Witney test with $n_1 = n_2 = 10$, it appears that 600ms is significantly better than both 400ms ($U = 17, p < 0.0057$) and 1000ms ($U = 11, p < 0.0010$). The very fast and very slow rates (200ms and 1200ms) were fairly ineffective for taxis; at 800ms taxis was reasonably good but every small turn would be followed by a movement forward, resulting in a curved rather than zig-zag path.

The different rates compared above also had different syllable lengths (half their respective rate) so to check that this was not the cause of the observed difference two further sets of trials were run: at 600ms rate but with 200ms syllables; and at 1000ms rate but 300ms syllables. The same procedure was followed to produce mean vectors for each trial and these were compared with the original 600/300 condition (figure 3b). There was no significant difference between 600/300 and 600/200 ($U = 38, p > 0.2$) but 600/300 was significantly better than 1000/300 ($U = 19, p < .0093$). This indicates that the 600ms rate, rather than the 300ms syllable, is the critical parameter for the better performance.

The '30Hz hypothesis' has been challenged by [Stout & McGhee, 1988] who have demonstrated that syllables at the correct rate are not always sufficient, nor necessary, to elicit phonotaxis in a cricket; that is, some animals will not do it in the absence of chirps, and others will do it when only the chirp pattern is present. This disagreement is probably largely due to differences in experimental

procedure and what is classified as a phonotactic response. Nevertheless, the paths with slow syllable rates suggested a possible advantage of having this additional patterning in the natural calling song: moving forward between every turn can be quite efficient *if* heading in the right general direction, but is disadvantageous if heading the wrong way. By breaking a fast syllable rate into chirps the best of both behaviours is possible: within a chirp there are frequent onsets allowing a large adjustment, while between chirps there is uninterrupted movement in roughly the right direction. Some evidence for this could be shown in the robot (although it was limited by the small arena size): with chirps of three syllables followed by a gap of the same size, the robot performed phonotaxis quite effectively, often more quickly and with fewer turns than with continuous syllables, and the 'zig-zag' pattern was more evident.

*More complex conditions*

To test whether the simple mechanism in the robot could account for cricket behaviour under more complex conditions, some additional experiments were run. First, the environment was made more complex by adding obstacles between the starting point and the speaker. The tracks shown in Figure 4 are from 8 trials with five wooden boxes in the arena, and 5 trials with a wooden wall, blocking the direct route from corner to speaker. Although a variety of routes were taken, in every trial the robot successfully found the speaker, without significant back-tracking.
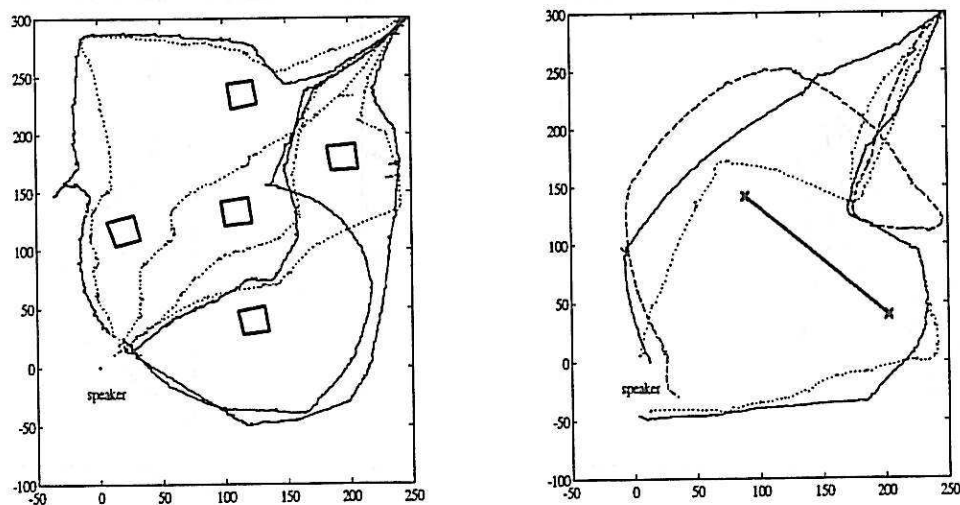


Figure 4: **a:** *Eight trials with five obstacles* **b:** *Five trials with a wall*

A second set of experiments examined the behaviour with two sound sources. This 'choice' situation has been studied with crickets and it is generally assumed that their ability to go fairly directly to one sound under these conditions indicates more complex internal processing of the signal than basic taxis. In figure 5, the tracks of the robot in ten trials with simultaneous songs from two speakers are shown: it goes quite directly to one or other speaker. [Weber & Thorson, 1988] found that if syllables came alternately from each speaker (instead of each having a normal song) then the cricket tended to walk between the sounds rather than
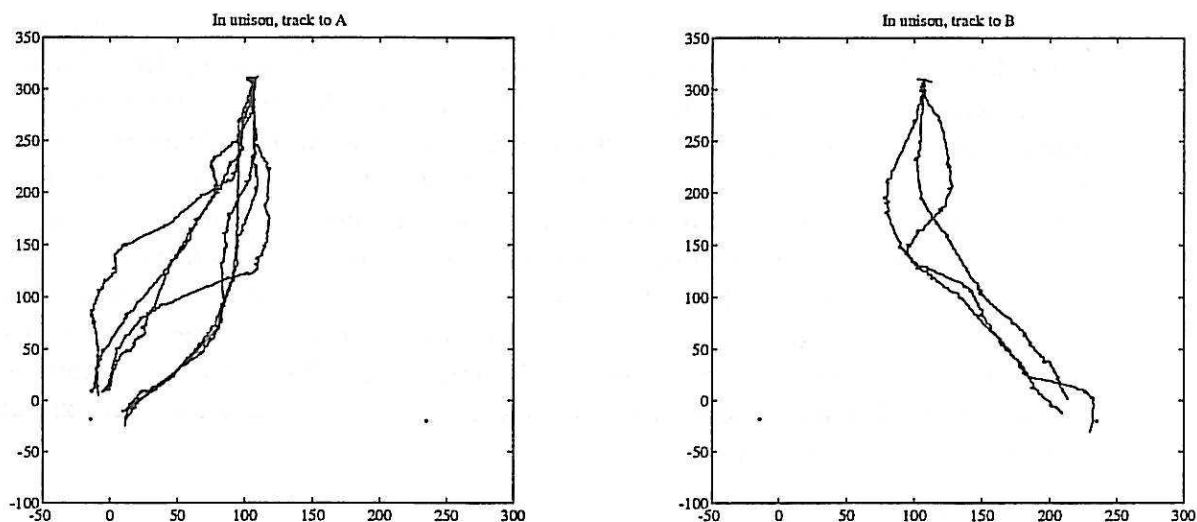
Figure 5: *Tracks with song simultaneously from two speakers. Robot goes directly to one or other*

choose one or other. In figure 6, the tracks of the robot show a similar tendency when syllables were alternated.
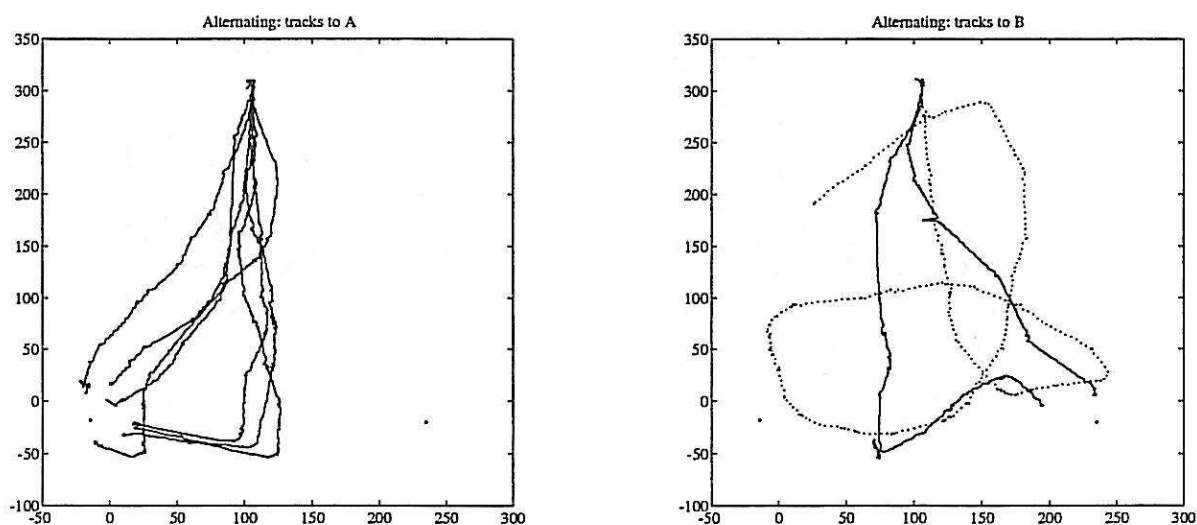


Figure 6: *Tracks with syllables alternating between speakers. Robot tends to go between speakers before turning to one or other.*

## Conclusions

This work has confirmed the hypothesis that a simple direction mechanism can be sufficient to account for 'recognition' and 'choice' aspects of cricket behaviour. It suggests some directions for future investigation for the cricket, in particular an examination of the response of the brain neurons to differences in the

response level between the ears to see whether, as suggested here, their response may indicate a comparison of onset latency.

This work has also shown that combining biology and robotics in the investigation of sensory-motor systems is viable and useful, and demonstrated the practical truth of the characterisation of such systems as specific devices dependent on physical conditions. This tends to point to the conclusion that there is no single 'principle' to be discovered that will be the key to producing successful behaviour. Rather, animals contain a huge range of complex, task-specific mechanisms, and to build robots we will need to design a comparable range of mechanisms for the tasks they perform. While this conclusion may be disappointing to those hoping to find the secret of intelligent behaviour in biological models, it doesn't necessarily imply that modeling biology is a hopeless undertaking, but rather that the methods are best used in the investigation of particular problems of sensory-motor control.

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