26 Phonotaxis in Crickets and Robots

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Over the past decade, we have built and tested several robot models to investigate a particular biological behavior, the sound localizing (phonotaxis) ability of the cricket. This work has had several purposes. One is to develop robotic technology, such as novel sensors and control systems, by copying biology. However, the primary motivation is the "reverse"—to use the technology to develop understanding of biological systems—in particular, how neural circuits control sensorimotor behavior. This is effectively a new methodology for biological modeling, discussed in Webb (to appear). In this chapter, the aim is to provide a summary of the problems addressed and the key results to date. (More-detailed presentations of the biological background and the implementations can be found in Lund, Webb, and Hallam, 1997, 1998; Webb and Scutt, 2000; and Webb and Harrison, 2000.)

BACKGROUND

Crickets are probably best known for their communication systems, which form an important part of their reproductive behavior and are thus critical to their species survival. We hear male crickets singing; what we usually do not see is the female approaching—able (if necessary) to locate a potential mate by this signal alone. She needs to identify the sound as one produced by a conspecific and not by another species or some other environmental sound source. She needs to determine the direction of the sound despite the noisy environmental conditions and the spatial and temporal limits of resolution of her sensory system. She needs to travel—by flying or walking —over a substantial distance with possibly interfering obstacles and predation risks, without losing track of the target signal. Typically, she is also faced with a choice—several potential mates calling within earshot—that must not result in irresolution but in direct approach to one or another.

Much behavioral, anatomical, and neurophysiological investigation of this phonotaxis (sound approaching) behavior has been done (e.g., reviewed in Huber and Thorson, 1985; Schildberger, 1988; Weber and

Thorson, 1989; Huber, 1992; Pollack, 1998). It has been established that some of the critical "recognition" cues for the female are the carrier frequency (typically around 4–5 kHz) and temporal pattern (regularly repeated bursts) of the song. The sound is produced by the male moving one wing against the other, which rubs a "file" across a "comb," the sound amplified by a resonant area of the wing. In the model described below, the main focus is to explain the female cricket's apparent preference for a particular repetition rate in the signal (typically 20–40 Hz), as established in a number of studies (e.g., Popov and Shuvalov, 1977; Thorson, Weber, and Huber, 1982; Doherty, 1985b; Wendler, 1990). As will be shown, the obvious task division—into first recognizing and then locating the sound—is not the only efficient and effective explanation of the female cricket's behavior.

In addition, recent work with the robot has studied how the basic sound-localizing behavior might be combined with other sensorimotor tasks. Although the cricket can locate sound in complete darkness, it can also use visual information if it is available. Studies of female cricket tracking have shown apparent improvement in tracking speed and angular accuracy under lit conditions (Thorson, Weber, and Huber, 1982; Atkins et al., 1987; Weber et al., 1987). One explanation might be that in these conditions, the cricket is able to use its optomotor response to maintain a more stable path direction. Evidence for the interaction of optomotor and phonotaxis responses has been provided by Bohm, Schildberger, and Huber (1991), who suggest that these two sensorimotor responses are simply additively combined in the animal's walking direction. We report some initial experiments on the robot model to examine this idea.

Description of the Model

The "robot cricket" is based on the miniature Khepera robot base.[1] It has an electronic sound-processing circuit, which has been designed to mimic the unique auditory system of the cricket. Crickets have tympanal organs on their legs, connected by tracheal tubes to each other and to other openings on their body (spiracles). Consequently, vibration at the eardrum represents a "pressure difference" between the sound waves incident on the external and internal sides. Because sounds from different directions will travel different path lengths to reach the inside and the outside, the phase cancellation of the signals and resulting amplitude of tympanal vibration will represent the sound direction (Michelsen, Popov, and Lewis, 1994).[2] Thus the cricket has strongly directional hearing (albeit confounded by signal wavelength), despite the relatively small separation of its auditory receptors. The same mechanism is implemented in the robot using programmable electronic delays and subtractions of the signal detected by two microphones placed a

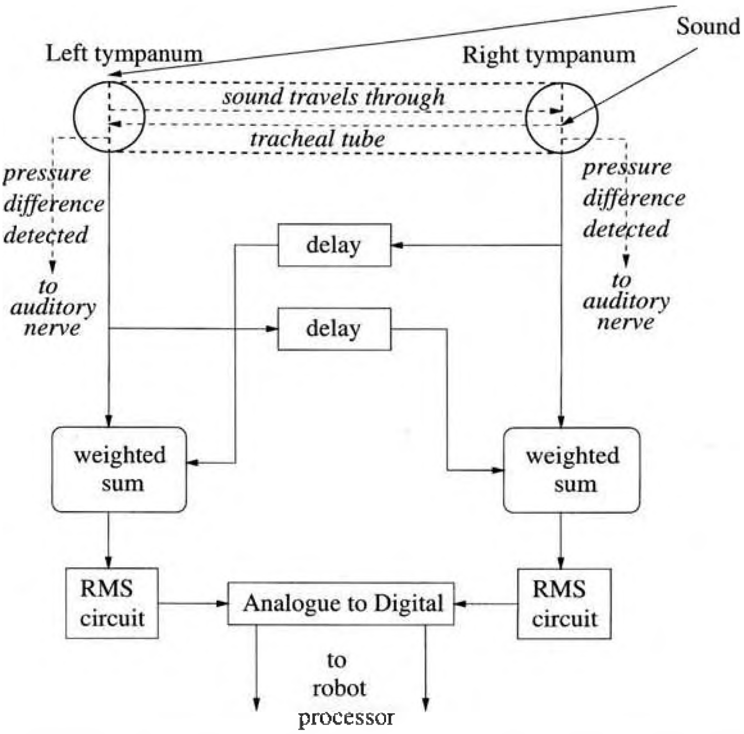


Figure 26.1 Cricket/robot ears: sound at each eardrum/microphone is combined with delayed sound from the other side. In the cricket (italics and dashed lines) this is via a tracheal tube connecting the tympani; in the robot (solid lines) an electronic circuit serves the same function. The amplitude thus depends on relative phase, which depends on direction and frequency of the sound source. For the robot, the sound was 4.7 kHz, the ear separation 18 mm and the delay 53 msec (i.e., corresponding to 1/4 the wavelength).

small distance apart (figure 26.1). One consequence of tuning the separation between the ears and the internal delay to match the carrier frequency of the cricket's calling song is that localization ability is worse for sounds of the wrong frequency (Lund, Webb, and Hallam, 1997). This side-effect is in fact a bonus, as it may help the cricket's selectivity for carrier frequency (e.g., Popov and Shuvalov, 1977; Stout, De Haan, and McGhee, 1983), which is somewhat more sharply tuned than can be explained purely by the frequency tuning in receptors.

The sound signal is processed on the robot using a model neural network that is derived in part from identified neurons in the cricket. A pair of identified ascending interneurons (AN1) in the prothoracic ganglion appear to be critical in controlling phonotaxis (Schildberger and Horner, 1988). They receive direct input from the auditory receptors. Their firing response copies the pattern in normal song, and their firing rate and latency both encode the amplitude. These characteristics are replicated in the robot using a simple state-based "integrate-and-fire"

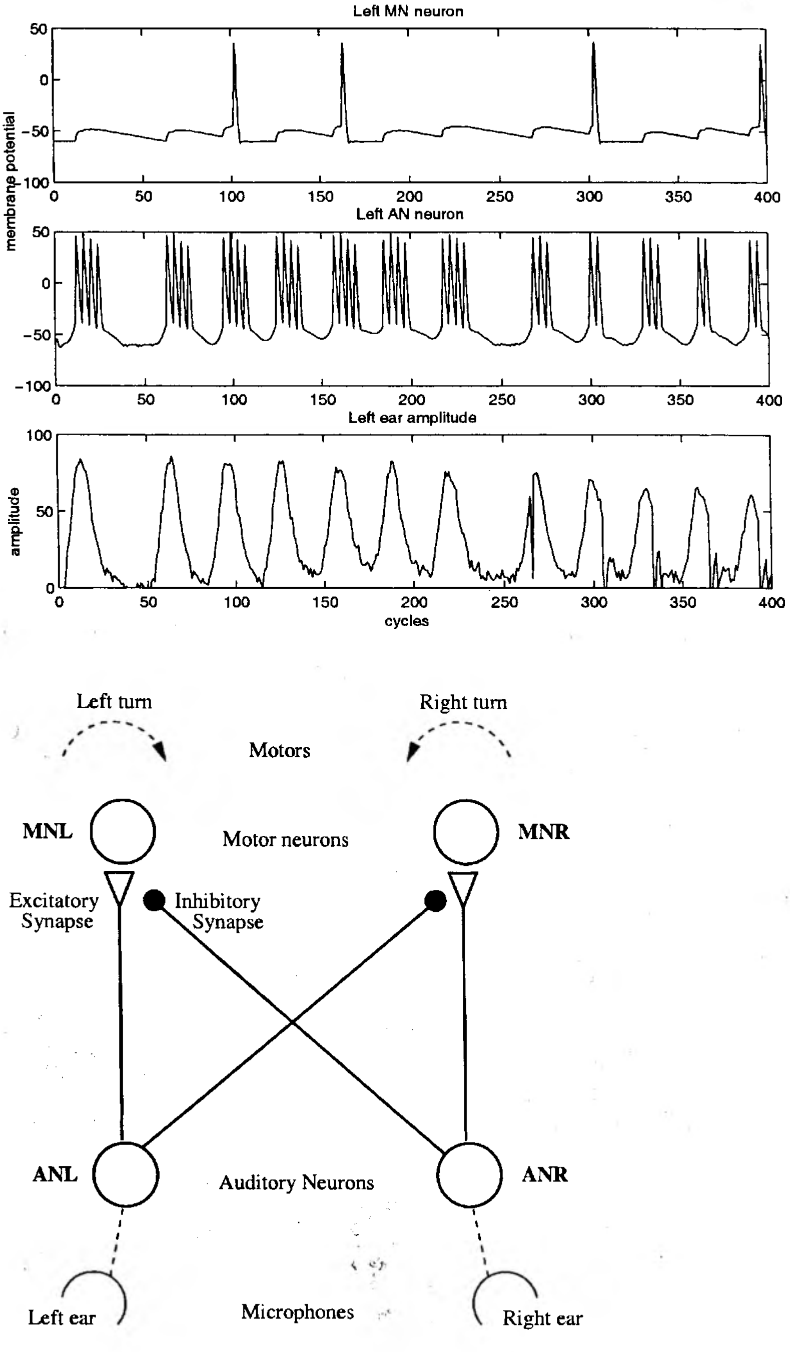


Figure 26.2 The four-neuron network used to control behavior. The AN receive sound and the MN control the motor response. Responses of the ears and neurons to a typical input pattern are shown.

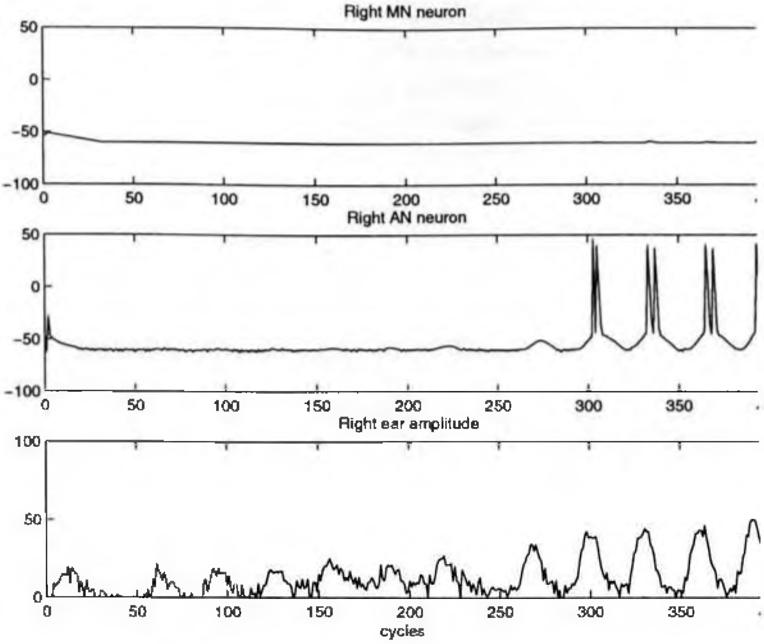


Figure 26.2 (continued)

model of membrane potential in single-compartment neurons (Webb and Scutt, 2000). In the model, the two auditory input neurons (AN) are connected to two output or motor neurons (MN) as illustrated in figure 26.2. Each AN makes an excitatory connection to the MN on the same side, and an inhibitory cross connection to the opposite AN-MN synapse. The synapse connections are represented by a single "weight" value, but the weight changes dynamically with the activity of the neuron. Thus the synapses show suppression (the weight is decreased) if a rapid series of spikes arrive at it and require a gap in input to recover. Synapse-on-synapse inhibition similarly decreases the weight at the target synapse.

In this circuit, the spikes in the MNs are used to generate turns by the robot. A sound signal on the left will excite the left AN, which excites the left MN, and also suppresses the excitation of the right MN by the right AN. Effectively, this means that whichever AN fires first will control the response. Thus it is the latency coding of the amplitude that is used, rather than the firing rate. Also, because of the synaptic suppression, only the onset of AN activity contributes significant excitation to MN. Thus the MN response usually requires several onsets, with gaps in between, to reach threshold and fire, signaling a turn. This use of temporal properties of the neural signal to determine turning to the sound inherently makes the neural circuit selective to the pattern in the signal. A continuous or rapidly repeated sound will cause continuous firing in AN, which, due to exhaustion of the synaptic connection, will cease to contribute to MN. A slowly repeating sound will not allow successive activations of MN to summate above threshold and cause a turn. The ideal signal for generating turns will fall within a specific band of repetition rates. Thus in the process of locating the sound, the signal is also "recognized," in that incorrect signals will fail to generate appropriate movements toward the sound.

Results

Although this four-neuron network appears very simple, it is in fact able to account for a wide range of observed behaviors in the cricket, including behaviors usually taken as evidence for separate recognition and choice circuits (Webb and Scutt, 2000). We were able to test the robot using stimulus and behavior paradigms comparable to the cricket. For example, constraining the robot to turn only on the spot and not move closer to the sound mimics the behavior of a cricket on a Kramer treadmill (Weber, Thorson, and Huber, 1981). Playing recorded cricket songs from a speaker under these conditions leads the robot to oscillate about the sound direction, reliably following a switch in speaker direction (cf. the criteria for phonotaxis suggested by Thorson, Weber, and Huber, 1982). This behavior can then be used as an assay for the preference shown for simulated signals with varying characteristics.

First the robot was tested with simulated songs of different syllable repetition intervals (SRI). As noted above, the SRI appears to be a critical recognition cue for the cricket. The robot was tested with a 4.7 kHz tone repeated at intervals of 18, 26, 34, 42, 50, 58, 66, 74, and 82 milliseconds, with the duty cycle held constant at 50%. As illustrated in figure 26.3, it showed no tracking to the fastest rate or slowest rates and did track between 26 and 58 msec SRI, with the best (closest) tracking between 34 and 50 msec SRI. Thus this network successfully tracks only the correct syllable repetition rates and effectively ignores other signals. The preference closely resembles that shown for crickets (Thorson, Weber, and Huber, 1982).

It would be fair to argue that this behavior is not "true" recognition: But what is the evidence that the cricket actively recognizes correct signals rather than, like the robot, merely fails to track incorrect ones? One paradigm that has been taken to indicate an independent "recognizer" uses a song played from a speaker directly above the animal, which provides no consistent directional cue (Weber, Thorson, and Huber, 1981; Schmitz, Scharstein, and Wendler, 1982). Crickets nevertheless show "phonotaxis-like" behavior—that is, they modify their walking speeds and make turns in a manner that is not normally seen when not trying to track sound. Moreover, when a continuous signal is then

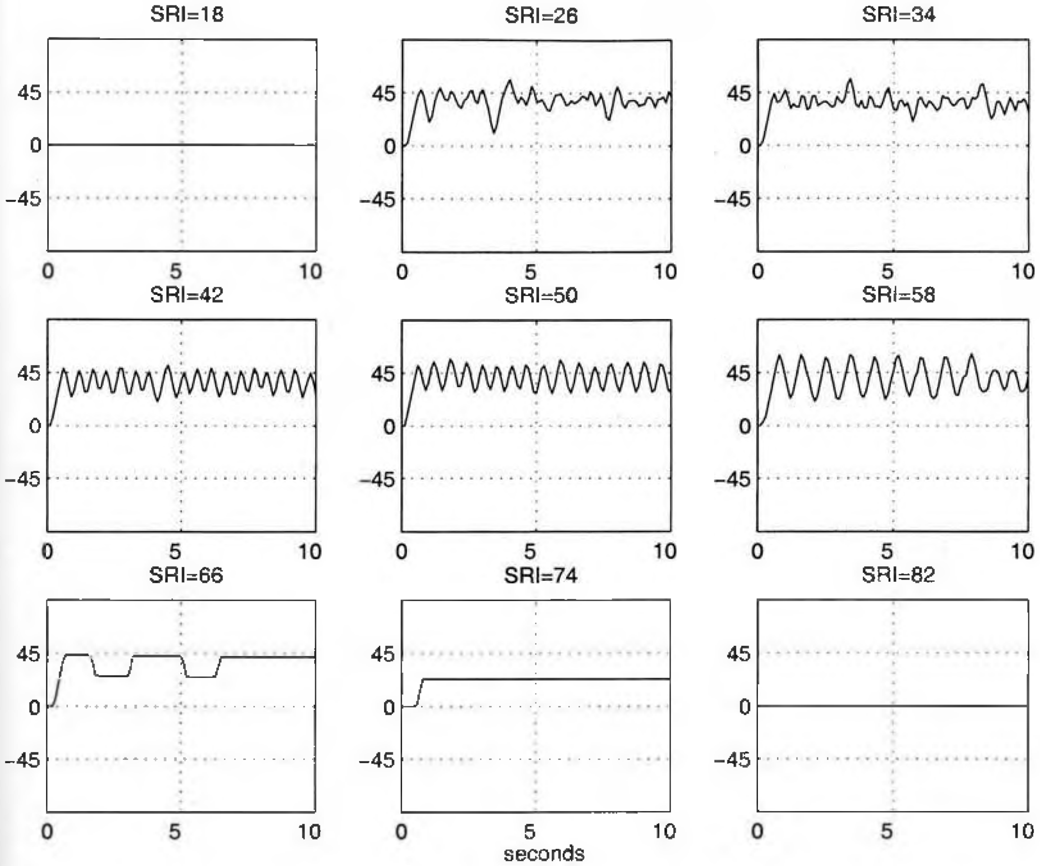
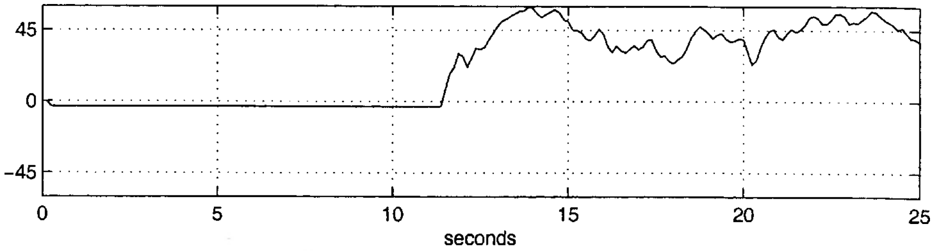


Figure 26.3 The robot tracking songs with differing syllable rates. The speaker is at 45°, and the robot's heading over time is plotted; it only tracks syllable repetition intervals between 26 and 58 msec. (Reprinted from Webb and Scutt 2000.)

added from one side of the animal (Stabel, Wendler, and Scharstein, 1989), it attempts to turn *away* from this sound—that is, toward the side that has a clearer song signal rather than the side that has a higher amplitude response. This has lead to the suggestion that "the signals ... are filtered individually on each side with respect to the syllable and/or chirp frequency before the right/left comparison occurs" (Stabel, Wendler, and Scharstein, 1989, p. 175).

We tried testing the robot under the same conditions and the results are shown in figure 26.4. Sound from above, relative to no sound, clearly produces a change in the robot's behavior—in which it appears to be tracking, but not in any consistent direction. This response occurs because despite the equal amplitude of sound reaching the microphones, slight differences in the processing circuitry are enough to produce slight differences in the neural response and, consequently, turning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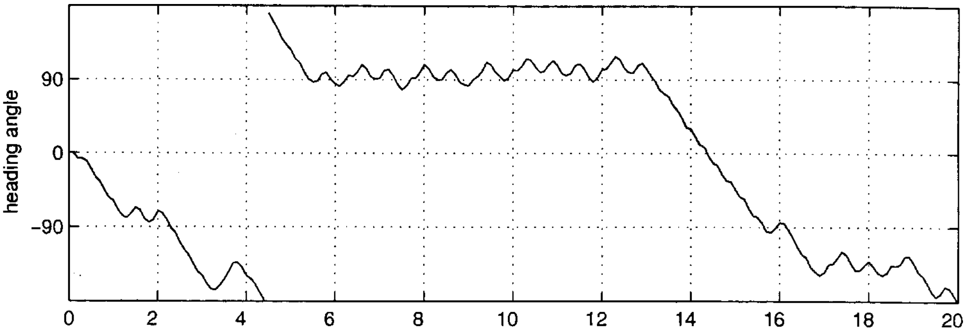
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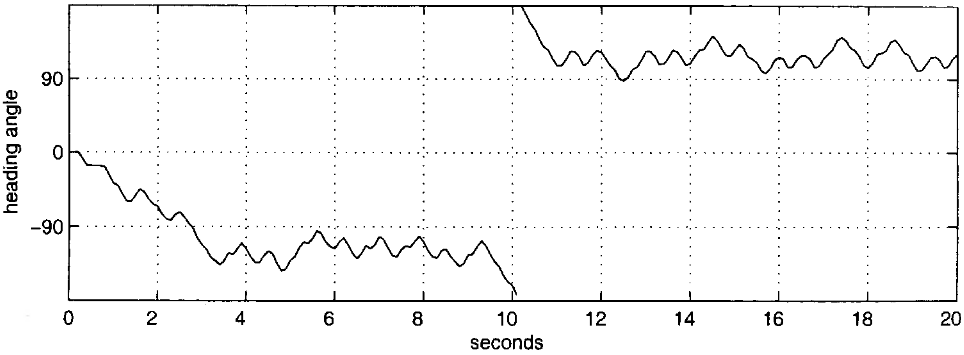
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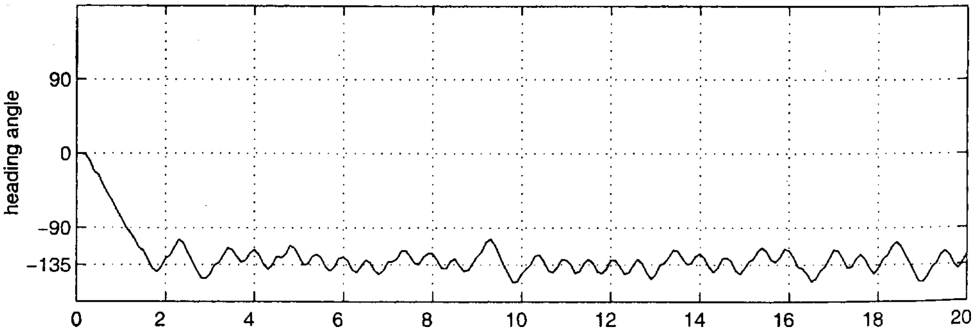
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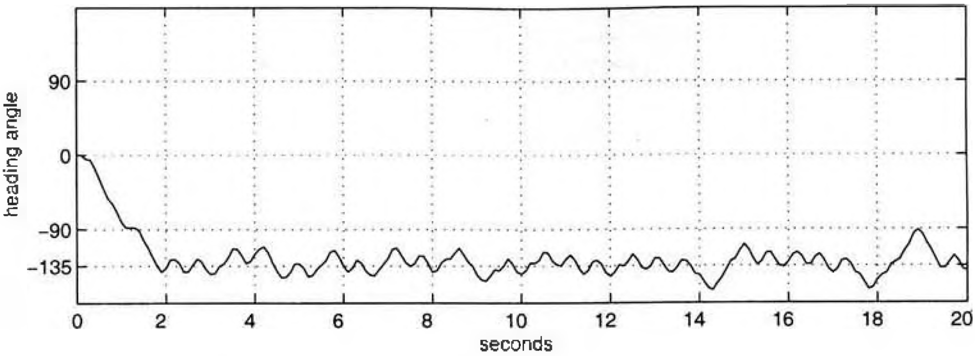
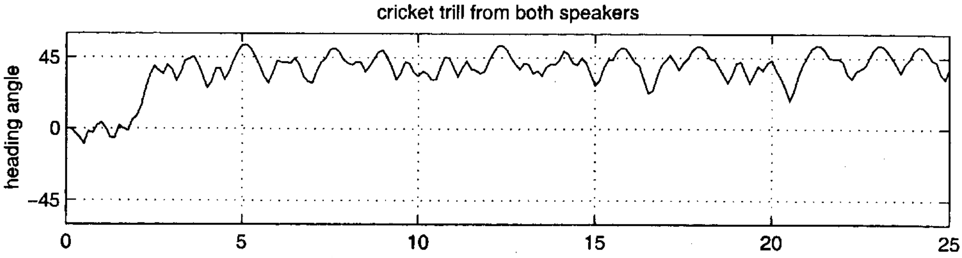


Figure 26.4 The robot "tracking" sound from directly above: (a) when a recorded song is switched on it starts to meander; (b–c) the tracking direction changes over time; (d–e) the robot tracks 180° away from a continuous sound source added at 45° (cf. Stabel, Wendler, and Scharstein, 1989; reprinted from Webb & Scutt 2000).

behavior. There seems no reason to suppose that the cricket's auditory and neural systems are more reliable than the robot's in this situation—that is, that a sound directly above the animal results in precisely equal activation of each side of the sound processing system. Moreover, adding the continuous signal from one side produces a response in the robot directly analogous to the cricket—it turns and tracks 180° away from the continuous sound source direction. This behavior can be explained in just the same way as for the cricket—the song pattern is better represented on the side away from the continuous signal, and as the pattern is necessary to produce a response in MN, the robot turns that way. But neither explicit filtering nor explicit comparison takes place in the robot.

A third set of experiments examined the ability of this simple circuit to re-create the choice capabilities exhibited by female crickets. The fact that crickets can track one from several simultaneous songs and apparently choose between attractive signals has also been cited as evidence for more-complex recognition processes than the simple circuit we have proposed (Doherty, 1985a; Weber and Thorson, 1988). Although it had not been designed with this issue in mind, it was simple to test what the robot would do when played similar or differing signals simultaneously. The results of several experiments are shown in figure 26.5. Faced with identical signals (recorded cricket song) from two speakers, the robot turns and reliably tracks one of them, rather than getting confused. The one chosen can be controlled by varying the amplitude; the louder sound is preferred. When two songs differing slightly in syllable-repetition interval (40 vs. 60 msec) are played, the robot tracks the faster song. The same behavior is observed in the cricket.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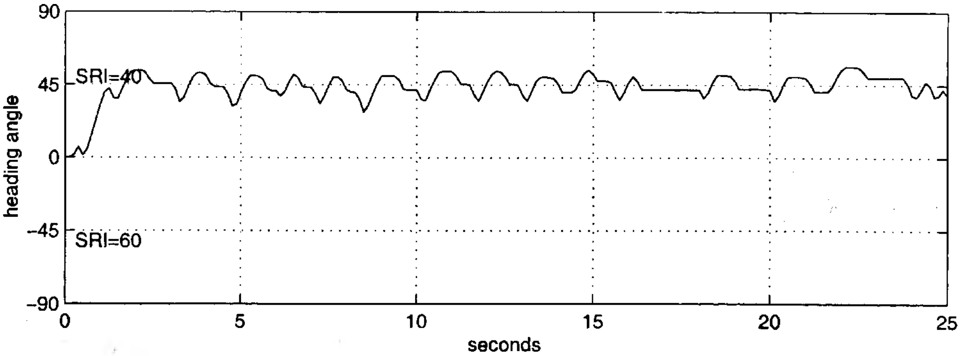
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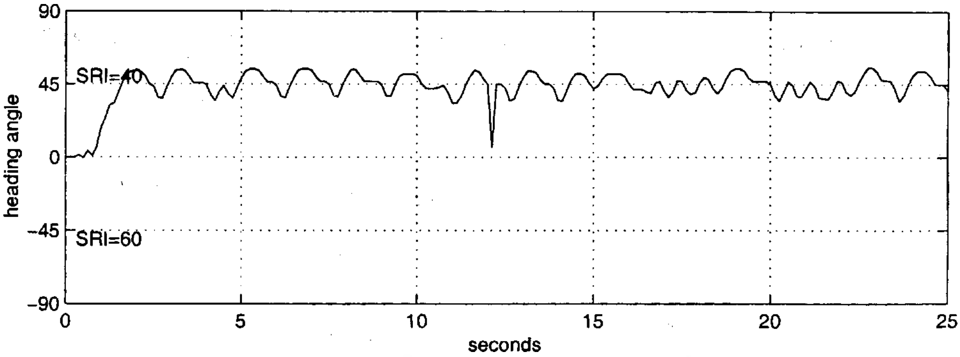
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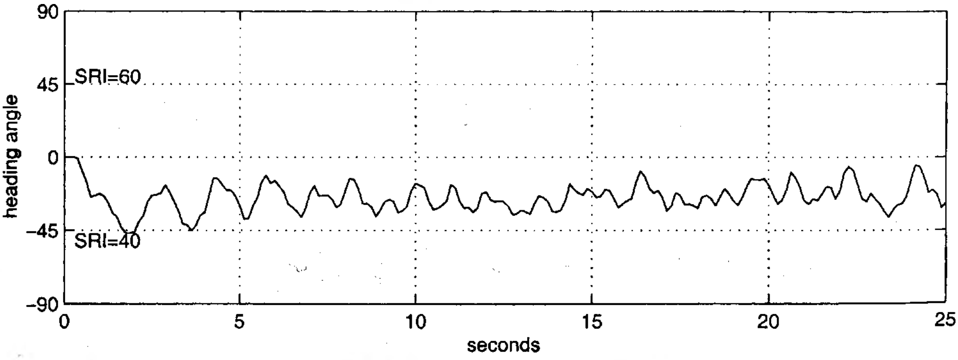
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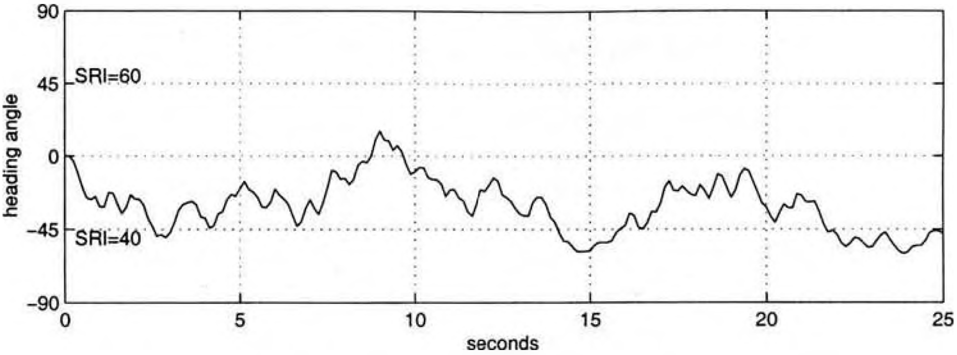

Figure 26.5 The robot "choosing" the louder of two identical sound sources, or the faster of two acceptable syllable rates. (Reprinted from Webb and Scutt, 2000.)

ADDING AN OPTOMOTOR RESPONSE

So far, we have shown that a simple four-neuron network appears to be sufficient to explain much of the cricket's phonotaxis behavior. The cricket actually has around 100,000 times more neurons than this—so it might be asked: Why? One obvious difference is that the motor control system of a two-wheeled robot is simpler than the cricket's six multi-jointed legs. Another is that the robot only does phonotaxis, while the cricket has a wide range of other behaviors and sensorimotor systems. Moreover, these must in some way be coordinated. As a starting point for investigating some of these issues, we have looked at integrating a visual response into the phonotaxis model. If a simple visual reflex such as the optomotor response is added to the robot, how can the behavioral controller best utilize both signals? Can the observed improvement in the cricket's tracking behavior under lit conditions (Weber, Thorson, and Huber, 1981; Weber et al., 1987) be replicated?

Description of the Model

The implementation of the optomotor response was achieved in collaboration with Reid Harrison, who has developed a neuromorphic analog VLSI (very-large scale integration) chip that processes light signals in a manner akin to the known neural circuitry in insect brains (described in chapter 2 of this volume). Briefly, the chip computes a local measurement of motion between adjacent pairs of photoreceptors using delay and correlation, implemented by inherent lag in low-pass filters and multiplier circuitry. The output is a summation across the circuit, which is further low-pass filtered (time-constant = 100 msec) to provide an analog signal that indicates the approximate velocity of the visual field. Using this signal to bias the speed of the robot's motors, with an appropriate gain, creates an optomotor reflex—that is, when a deviation from straight-ahead movement is signalled by a rotating visual field, the robot applies corrective compensation.

So, can this optomotor correction simply be added to the established phonotaxis response and produce improved behavior? To test this, it was necessary to reimplement the phonotaxis system on a larger robot that could also carry the lens and circuitry used with the VLSI chip. We used a Koala robot because it is designed to be closely compatible with the Khepera. The same electronic ear circuitry and spiking-neuron processing program was used for the phonotaxis as described above. Given the output of the phonotaxis controller—a fixed-length turning signal is produced each time an MN neuron spikes—the issue was how to modify this signal so as to integrate the visual response. Initially, this was done by simply adding the optomotor gain directly to the motor commands that had been produced by the sound (figure 26.6).

An immediately apparent problem was that any turn toward the sound generated by the phonotaxis system produced an excellent "visual rotation" signal, which the optomotor system would correct (i.e., turning the robot back away from the sound). This was a convincing empirical demonstration of what Robert and Rowell (1992) describe as an "old conundrum"—how does an animal operating with an optomotor response ever manage to make intentional turns? There are several "old" proposed solutions. Perhaps the best known is the principal of *reafference* (von Holst and Mittelstaedt, 1950)—that when making a turn, a predictive countersignal is sent to cancel out the anticipated optomotor signal. Another suggestion is that the intentional turns might be fast or slow enough to fall outside the range of movement normally detected by the optomotor system. However, having already chosen biologically justified ranges for turning speeds in our system, it seemed inappropriate to change these. A third solution is that the intentional movement simply suppresses or switches off the optomotor response.

Reafference is an attractive principal, but its practical application is more problematic. A perfect reafferent signal would consist of the inverse of the expected optomotor pattern—but how can the reafferent system precisely predict what it will see when the optomotor response depends not only on the animal's rotational velocity but also on the (unknowable) spatial patterning in the visual field? An approximate signal is easier to achieve, and could be sufficient, but would at minimum require tuning—not only in magnitude but also in timing. The command to turn and the visual feedback are not coincident, so it becomes important to supply the right "cancellation" signal at the right time.

A switching or suppression scheme has the advantage of simplicity over reafference. There is also biological evidence from several different systems that optomotor reaction might be simply switched off during intended turns; for example, in response to "escape" signals in the lo-

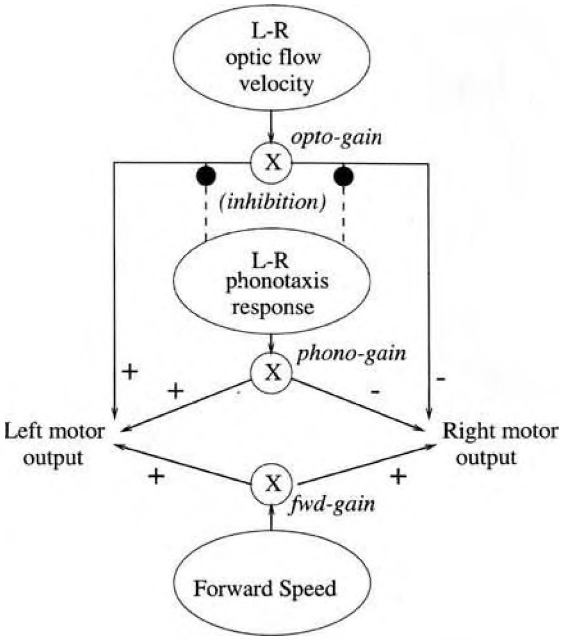

Figure 26.6 Controllers that combine phonotaxis with an optomotor repsonse using simple addition of the two turning tendencies, with the phonotaxis response inhibiting the optomotor response.

cust (Robert and Rowell, 1992), and during pursuit turns in the housefly (Srinivasan and Bernard, 1977). Heisenberg and Wolf (1988) suggest, for *Drosophila*, what could be called a "hybrid" reafferent-suppression scheme, in which visual motion in the expected direction is suppressed but in the opposite direction is still used. It should be noted that the data taken to support the "summation" of the phonotactic and optomotor responses in the cricket (Bohm, Schildberger, and Huber, 1991) is in fact consistent with switching because it is based on average direction of tracking. If the animal alternately responds to the visual and the auditory signal, on average it will steer a course between them.

Thus we decided to test the robot with a simple switching mechanism based on inhibition (figure 26.6). The motor signal is normally modified by the optomotor gain signal. When the phonotaxis gain signals a turn toward the sound, it also inhibits the optomotor response. The robot was first tested without the optomotor response to create a baseline for comparison and ensure that the mechanism that had worked on the smaller robot also worked on this one. We used an "arena" paradigm (cf. Atkins et al., 1987 for crickets) in which the robot was started from several points in the room and had to approach the sound source. One difficulty was that the larger robot was moving a larger distance (several meters) and consequently needed to be able to

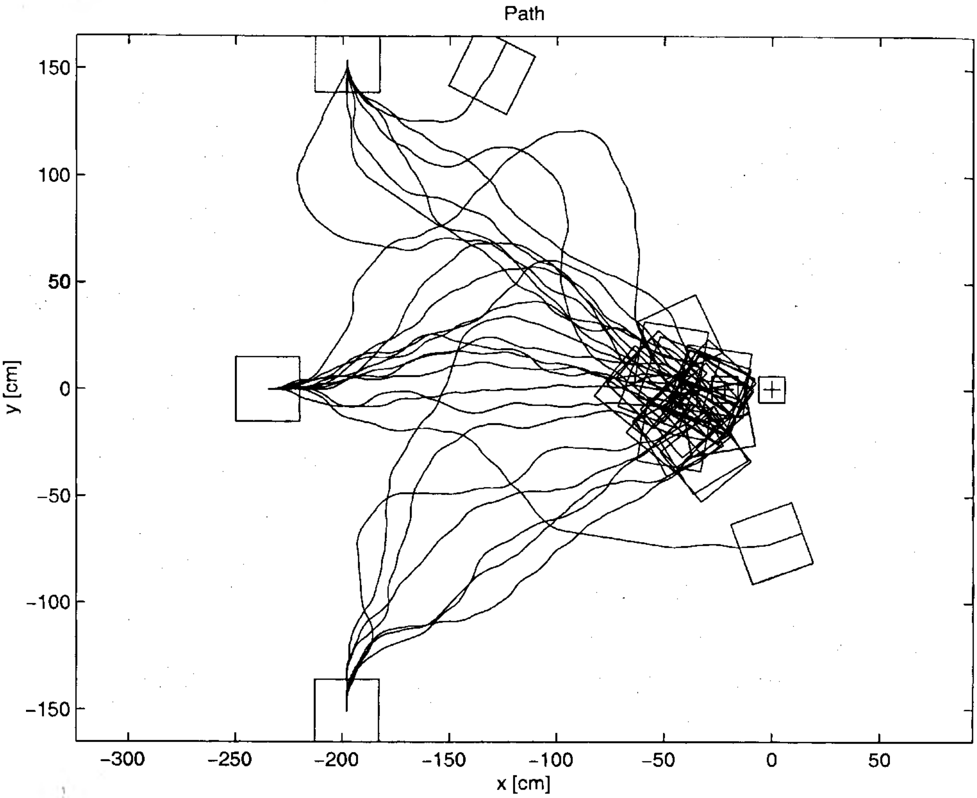

Figure 26.7 Tracks of the Koala robot toward the sound with no optomotor response. The robot is fairly successful in tracking the sound.

deal with a greater range of sound amplitudes while still responding appropriately. We solved this problem by imposing an approximate logarithmic compression to the input amplitude before feeding it to the neural processor.

Results

With just the phonotaxis system operating, the robot was quite reliably able to find the sound source when started either directly opposite the speaker (10 trials) or at either side of the room (6 trials each). The tracks shown (figure 26.7) were reconstructed from the shaft encoders on the robot. The two failures to reach the sound seemed principally due to adverse echoes in the unsoundproofed environment.

Next, we added the optomotor response, and ran the same sequence of trials. In this case, the robot never failed to find the speaker, and the tracks, on visual inspection, look a little more direct (figure 26.8). However, we found no statistically significant difference in the mean lengths or heading errors of the paths, though there was a difference in the

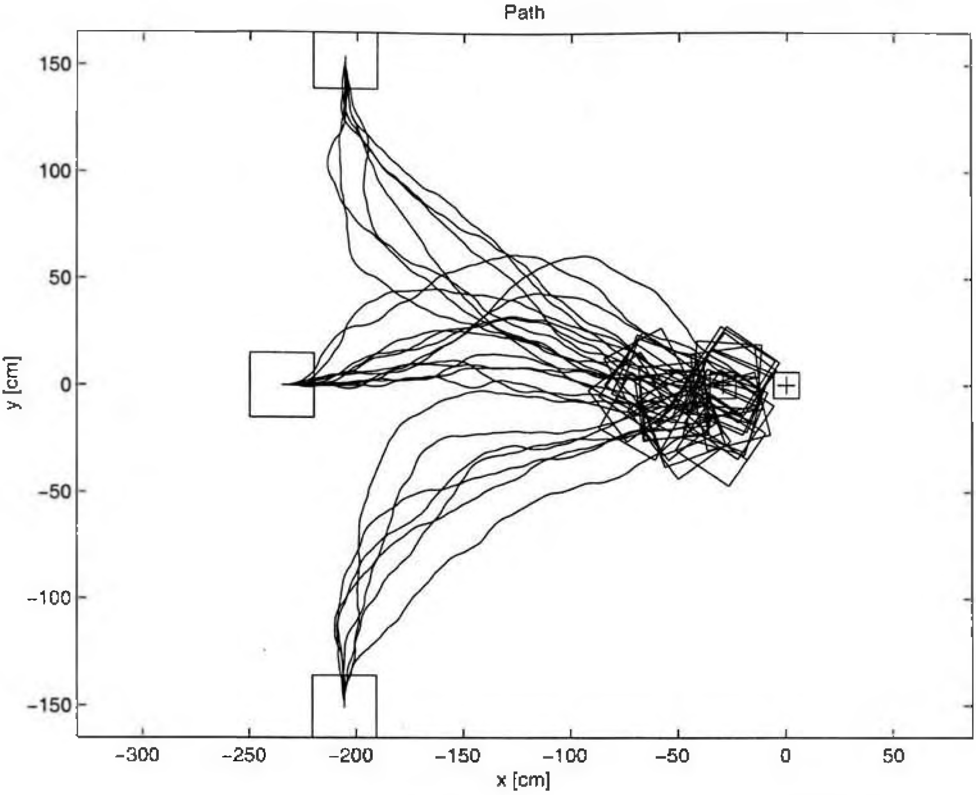

Figure 26.8 Tracks of the Koala robot toward the sound with an optomotor response. There appears to be a slight improvement, but not a substantial one.

variance of these measures—that is, without optomotor control, a wider range of paths (both more and less direct) were seen. The lack of obvious improvement can be largely attributed to the fact that phonotaxis control was already fairly good at getting the robot directly to the sound source, because there was little else to put it off course once it had turned to face the right direction. The main function of an optomotor response is to maintain a straight-line heading when subject to disturbance or drift. The Koala robot, when instructed to move in a straight line on a flat floor, has little difficulty maintaining a straight course and hence little to gain from an optomotor reflex.

Hence we decided to add a disturbance to the robot's normal behavior: a systematic bias in its normal motor speeds, such that the left motor would run 20% faster than the right. Most crickets walking on a treadmill show some systematic directional bias (Schul, 1998), and crickets in their natural environment often have motor asymmetries as well as environmentally caused deviations. With this bias, the robot without phonotactic or optomotor control would turn in a circle. With

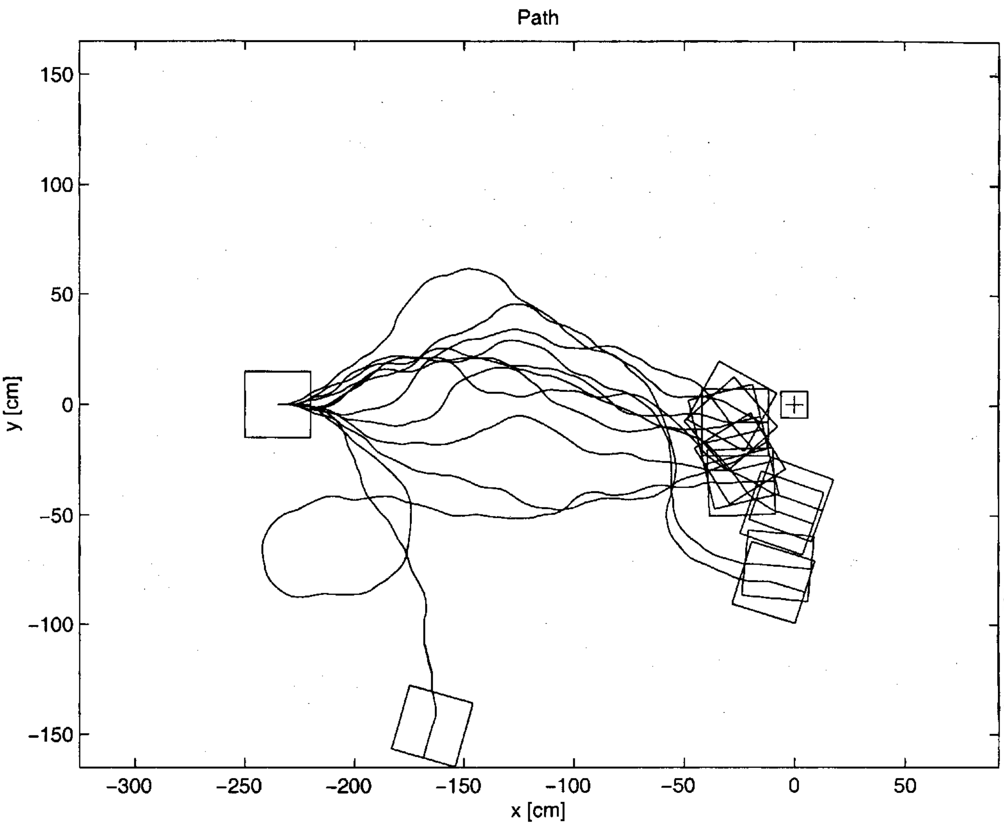

Figure 26.9 (Left) Tracks of the robot with a biased motor system and no optomotor response. The robot is less successful in tracking the sound. (Right) Tracks with a biased motor system and an optomotor reflex. The robot is able to track the sound.

optomotor control (and no sound), it was able to correct for the bias to make an approximately straight path (this replicated the experiments described in Harrison and Koch, 1999).

Figure 26.9 (left) illustrates 10 sound-tracking trials with the bias and without the optomotor reflex. The robot still reaches the sound in half the trials, but the tendency to head to the right of the speaker is clear. In one case, it loses the sound altogether; in another, it makes a complete circle in the bias direction before moving to the sound. When the optomotor response is added (figure 26.9, right) there is a clear improvement in the behavior. In fact, the tracks become comparable to those in the original, no-bias conditions (see figures 26.7 and 26.8).

CONCLUSIONS

Using robot technology, we are able to rigorously test hypotheses about biological sensorimotor control. We can determine, by testing the robot

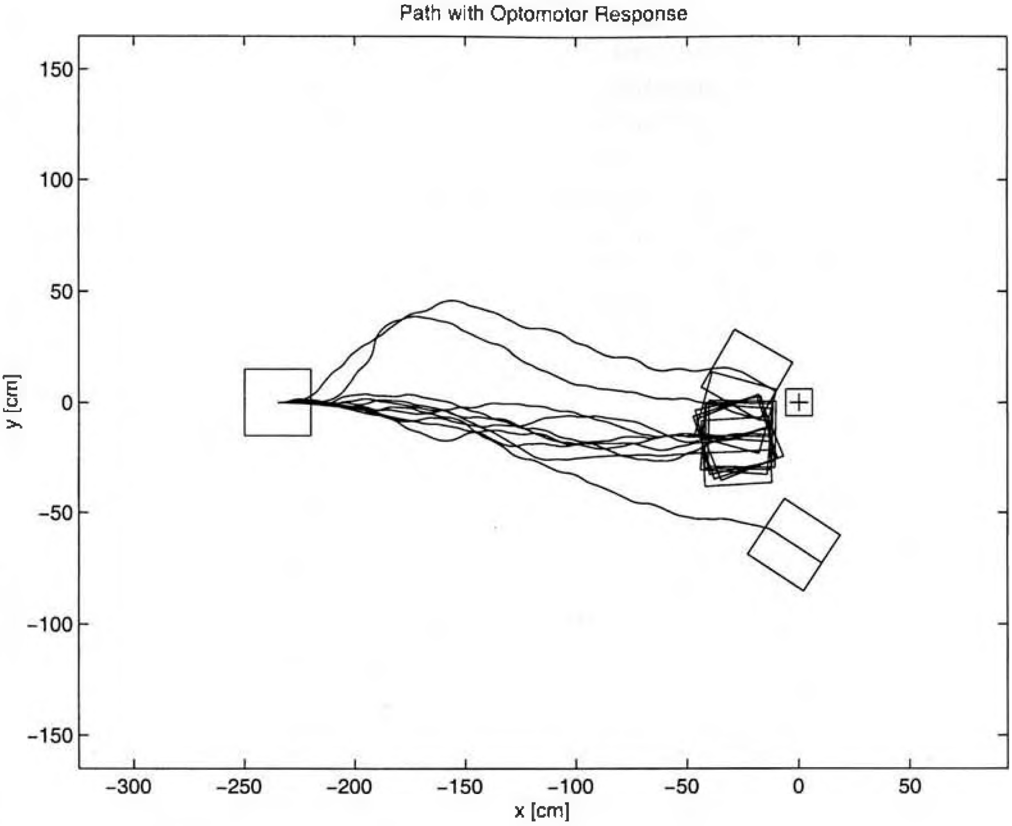

Figure 26.9 (continued)

in the same experimental paradigms as the animal, whether our understanding of the system is sufficient to replicate the behavior it displays. A robot has the advantage over simulation such that you do not have to simulate the environment in which it operates, which can not only be difficult but positively misleading if some real-world effects are inadvertently left out. From the robotics perspective, the animal provides a number of novel insights into ways of achieving efficient behavioral control.

In the work described here, we have shown that a relatively simple neural control system can suffice to reproduce a suprisingly wide variety of the female cricket's behavior in approaching sound. A key reason for this success is the tuning of sensory mechanisms and motor actions to the task environment. We used sensors that were closely based on the animal's sensors, and thus well matched to the task. Another is the explicit use of some of the temporal processing properties inherent in real neurons (which are often ignored under the traditional firing-rate interpretation of neural function). Because the circuit uses onset latencies, it is inherently sensitive to temporal patterns, and this can suffice to copy the cricket's apparent preferences for certain sounds. To say whether this is actually how the cricket does it requires further biological experimentation; we claim only that the evidence available so far does not require a more complex explanation than that embodied in the robot.

The extension to incorporate an optomotor response indicated that while simple summation may not suffice to successfully combine the behaviors, simple suppression is adequate and a reafferent signal is not needed. When the robot's motor task is made more difficult, the optomotor response significantly improves the phonotaxis behavior. We plan further investigations in this critical area of multimodal sensor fusion, using additional sensors such as antennae and more-realistic motor situations, including outdoor terrain and legged locomotion.

NOTES

1. While a legged robot would more accurately represent the cricket, nearly all available data on cricket behavior is at the level of whole-body trajectories (not individual leg movements), which a simple wheeled robot is able to replicate. A legged implementation is one of the intended outcomes of a current research project in collaboration with Quinn and Ritzmann (see chapter 20 of this volume).

2. In fact, the story is a little more complicated, involving membranes within the tracheal system that actively delay the internal signal.

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