

## SPATIAL ACUITY OF ULTRASOUND HEARING IN FLYING CRICKETS

ROBERT A. WYTENBACH\* AND RONALD R. HOY

*Neurobiology and Behavior, Seeley G. Mudd Hall, Cornell University, Ithaca, NY 14853-2702, USA*

*Accepted 9 May 1997*

### Summary

The minimum audible angle is the smallest angular separation at which two sounds are perceived as coming from distinct sources. To determine the spatial acuity of hearing in crickets, we measured minimum audible angles at various locations in azimuth and elevation. Crickets (*Teleogryllus oceanicus*) were able to discriminate between sources separated by  $11.25^\circ$  (1/32 of a circle) in azimuth directly ahead of them; acuity declined to  $45^\circ$  in azimuth for sound sources  $90^\circ$  to the side and then improved to  $33.75^\circ$  at the rear. Crickets were also able to discriminate between sources separated in elevation, although acuity was much poorer, ranging from  $45^\circ$  at the front and rear of the animal to  $90^\circ$  below the animal.

A habituation–dishabituation test was used to test

discrimination. This involved presenting a train of ultrasound pulses from one location, habituating the cricket's escape response. This train was followed by a test pulse of ultrasound from another location, after which a final pulse was presented from the original source. If the test pulse was discriminated from the habituating pulses, then the response to the final pulse was dishabituated. To determine the minimum audible angle, we repeated such tests while moving the two sound sources closer together until dishabituation no longer occurred.

Key words: dishabituation, minimum audible angle, discrimination, localization, phonotaxis, cricket, *Teleogryllus oceanicus*, hearing.

### Introduction

#### *Cricket phonotaxis*

The Polynesian field cricket *Teleogryllus oceanicus* has directionally sensitive tympanal ears on its front legs, which are held close to the body with the ears facing outwards during flight (Hill and Boyan, 1977). Like many other night-flying insects, these crickets steer away from the ultrasonic echolocation cries of bats. This negative phonotaxis can be elicited by a single brief pulse of sound with a carrier frequency above 15 kHz (Nolen and Hoy, 1986; Popov and Shuvalov, 1977). Steering in flight is manifested in a number of measurable body movements: forewing tilt, abdomen swing, head roll, antenna swing, and hindleg swing, all in the direction of the turn. Of these, wing tilt and hindleg swing are of proven aerodynamic significance (May and Hoy, 1990b). The fastest and briefest movement, hindleg swing, has a latency of 30–40 ms from onset of the sound pulse when the ultrasound is 10 dB or more above behavioral threshold (May and Hoy, 1990a).

#### *Minimum audible angle*

The minimum audible angle (MAA) is a standard measure of spatial auditory acuity (Fay, 1988). It is the smallest angular separation at which two sounds are perceived as coming from distinct sources. Spatial acuity varies with several factors, including the frequency of sound, the testing situation and,

most importantly, the location of the sound sources. For example, the MAA of humans ranges from  $1^\circ$  for sounds at 1 kHz directly in front to  $7.5^\circ$  at the side. At 2 kHz, however, MAA declines to  $3^\circ$  for sounds directly in front (Mills, 1958).

Although only one insect study has addressed MAA as such (Rheinlaender and Blätgen, 1982), sound localization in orthopterans has been investigated at several levels: the acoustic cues available, the directionality of the ears, the directional sensitivity of various auditory interneurons, and the phonotactic abilities of the animals themselves. So far, nearly all of this work has been restricted to attraction to calling song. Behavioral studies of sound localization have either measured an insect's responses to sounds from different directions (e.g. Pollack and Plourde, 1982) or tested its choices between sound sources separated by varying amounts (e.g. Rheinlaender and Blätgen, 1982). These approaches actually estimate the accuracy of phonotaxis (a combination of sensory, decision-making, and motor systems) rather than the acuity of perception as such, and are likely to underestimate spatial sensory acuity.

#### *Testing sensory discrimination*

Testing sensory discrimination in insects is problematic. With adult humans, discrimination tests involve some variation of asking whether pairs of stimuli are the same or different and relying on verbal responses. With non-verbal animals, the most

\*e-mail: rw12@cornell.edu.

effective way to test discrimination between two stimuli is to train subjects to respond in one way when two stimuli of a pair are the same and in another way when they differ. This approach has been successfully used with birds (Dooling and Brown, 1990), fish (Yan and Popper, 1993), and honeybees (Srinivasan *et al.* 1994). With animals that cannot be trained, or when unconditional responses to natural stimuli are of interest, testing discrimination becomes more difficult. Although some studies have attempted to infer discrimination from an animal's choice between two stimuli, this is questionable: the inference that two stimuli are discriminated if one is preferred to another may be valid, but the converse, that no preference means no discrimination, is not.

In research on human infants, habituation–dishabituation paradigms have been established to circumvent this problem (e.g. Miller and Morse, 1976); these have also been used to investigate auditory discrimination in monkeys (Morse and Snowdon, 1975) and birds (Nelson and Marler, 1989). As a stimulus is presented repeatedly, the response of the subject declines. That is, the subject becomes *habituated* to that stimulus. If a test stimulus is then presented, followed by one more repetition of the first stimulus, the response to the last repetition of the first stimulus may show release from habituation. That is, the subject may be *dishabituated*. Dishabituation occurs only if the test stimulus is perceived by the subject as novel relative to the habituating stimulus. Thus, dishabituation can be used as a measure of sensory discrimination, since dishabituation can occur only if the two stimuli are discriminated.

The ultrasound-induced escape response of crickets decrements with repetition in a manner consistent with standard criteria for habituation (May and Hoy, 1991). It declines nearly exponentially, recovers spontaneously, declines more rapidly with higher repetition rate or lower amplitude, and dishabituates following the presentation of a novel stimulus. In particular, a habituated response to ultrasound pulses from one side of a cricket is dishabituated by the presentation of another ultrasound pulse from the opposite side. Thus, dishabituation of the escape response can be used as a same–different test for crickets just as it has been used with human infants and other animals (Wytttenbach *et al.* 1996). In this study, we used dishabituation to determine the minimum angular separation required between habituating and test pulses for dishabituation to occur, the MAA.

## Materials and methods

### Subjects

We used adult Polynesian field crickets *Teleogryllus oceanicus* Le Guillou obtained from Hawaii and maintained in laboratory culture. Crickets were kept at high population density on a shifted light:dark cycle and used just after dark to increase the probability of flight. Crickets were tethered, using dental wax, to a thin wire at the dorsal intersection of the thorax and abdomen. The hindwings were clipped to stubs to make it possible to monitor steering movements. (In

tethered flight, crickets usually kept their hindwings folded, extending and vibrating only the forewings.) Crickets were flown upright in the minimum wind stream required to sustain flight (always less than  $3\text{ m s}^{-1}$ , the normal flight speed). Crickets were pre-tested for negative phonotaxis to ultrasound from each side.

### Procedure

Experimental procedures for determining MAA vary. To determine the MAA at the midline, one speaker could be fixed at the midline ( $0^\circ$ ) and another speaker moved closer to the midline until the two are no longer discriminated (e.g. Mills, 1958). This has the advantage that there is always a fixed reference point. Another approach is to bring two speakers symmetrically towards the midline until they are no longer discriminated. This has the advantage of truly measuring the MAA *around* the midline. It also avoids complications when testing MAAs at locations other than the midline. In measuring the MAA at  $90^\circ$  from the midline, for example, the first approach could give different results depending on whether the movable speaker were brought towards  $90^\circ$  from the front or from the rear. The two approaches are unlikely to give different results when MAAs are relatively small, as they are in humans. Since larger MAAs were expected for crickets, we chose the symmetrical approach to avoid this problem.

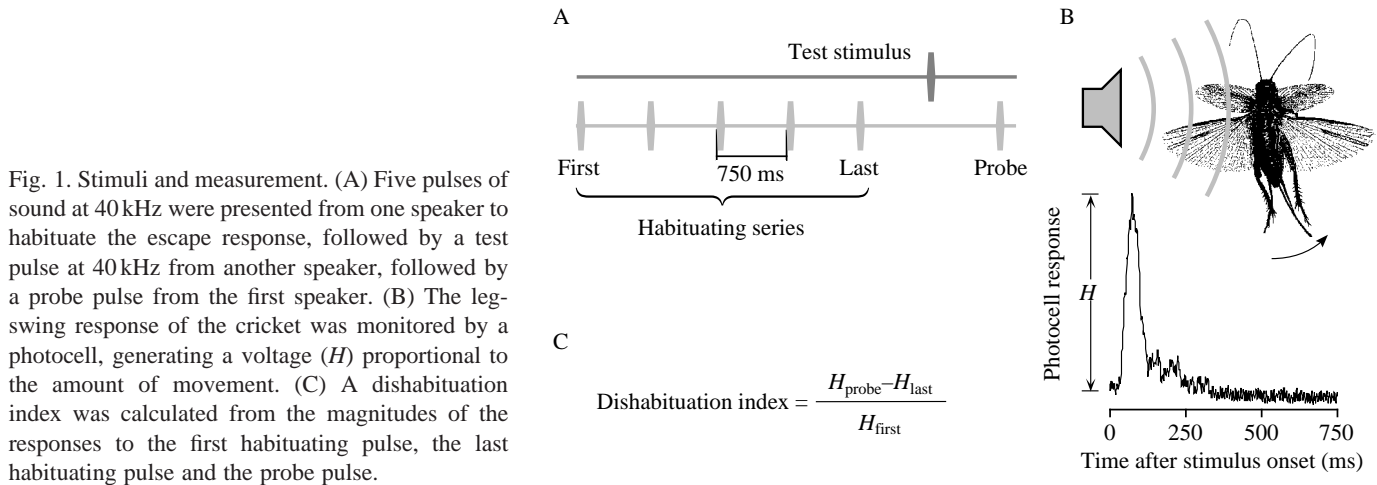
To test the discriminability of an angular separation  $\phi$  around an angular location  $\theta$ , speakers at  $\theta+\phi/2$  and  $\theta-\phi/2$  were used. Thus, to test a  $45^\circ$  separation around  $0^\circ$ , speakers at  $+22.5^\circ$  and  $-22.5^\circ$  were used. To test a  $45^\circ$  separation around  $45^\circ$ , speakers at  $22.5^\circ$  and  $67.5^\circ$  were used. The speaker closest to  $90^\circ$  was used for the habituating train and probe pulse; the other speaker was used for the test pulse.

A cricket was tested for as long as it continued to fly and give consistent responses. Thus, the number of angular separations tested per cricket varied widely, and any one cricket might be tested at only a few of the angular separations around a particular location. Experiments were continued until at least five crickets had been tested at each angular separation around each location.

### Stimuli

Stimuli consisted of single 10 ms pulses at 40 kHz with 1 ms rise and fall times. A single pulse of 40 kHz was repeated five times from one speaker with a 750 ms interval to habituate the escape response. After another interval of 750 ms, a single test pulse from another speaker was presented, followed after another interval of 750 ms by a final pulse (the probe pulse) from the original speaker (Fig. 1A). All pulses, including the test pulse, were presented at an intensity 5–15 dB above the escape response threshold, which was determined for each cricket. An intensity was chosen that gave significant habituation; this ranged from 60 to 80 dB SPL. To prevent long-term habituation, a period of silence of at least 45 s was left between trials.

Stimuli were synthesized by a Macintosh computer with a GW Instruments MacAdiosII A/D board and custom-designed



software (Vrieslander *et al.* 1991), attenuated (Tucker Davis PA4), amplified (Crown D150) and delivered through Panasonic 40 kHz ultrasound transducers (EFR-OTB40K2) arranged in a circle around the cricket. For this purpose, 24 speakers were placed on a ring, with all speakers 27 cm from the cricket. Speakers were placed at  $0, \pm 5.625, \pm 11.25, \pm 22.5, \pm 45, \pm 67.5, \pm 78.75, \pm 90, \pm 101.25, \pm 135, \pm 157.5, \pm 168.75,$  and  $180^\circ$ , where  $0^\circ$  is directly in front of the cricket and positive angles are clockwise. (Decimal values correspond to the division of a circle into sixty-fourths.) This ring could be rotated to obtain angular separations of 5.625, 16.875 and  $33.75^\circ$ . The inside of the ring, the arms supporting it and the  $1\text{ m}^3$  box surrounding the apparatus were lined with acoustic foam to minimize reflections.

Stimulus intensities were calibrated using a Brüel & Kjær sound level meter (type 2209) with a 1/8 inch microphone (type 4138). The output of all speakers was then equalized by the stimulus synthesis software. The Panasonic transducers are very sharply tuned to 40 kHz, and there was very little energy ( $>50\text{ dB}$  attenuation) below 38 kHz or above 45 kHz, as measured by a Nicolet 444A spectrum analyzer. Echoes were minimal and did not overlap the pulse itself; no additive or destructive interference was seen.

#### Measurements

We measured the fast swing of the metathoracic leg as an indicator of steering, using a photoresistor device described by May and Hoy (1991). This consisted of a cadmium sulfide photocell masked to expose a triangular area. The photocell was one resistor of a voltage divider circuit. When the cricket moved its metathoracic leg to the side, it cast a shadow over the photocell, producing a deflection in the signal from the voltage divider (Fig. 1B). This signal is proportional to the amount of leg swing (May and Hoy, 1991). Photocell traces were digitized by the computer for measurement. After a habituation trial, all responses were normalized to the first response, and a dishabituation index was calculated as in Fig. 1C. A positive index indicates dishabituation; a negative index indicates continued habituation.

#### Results

The magnitude of the leg-swing response did not depend on the location of the sound source. This is consistent with earlier work showing that the magnitude of negative phonotaxis depends on the intensity rather than the location of the stimulus (May *et al.* 1988). The degree of habituation after five pulses at 40 kHz varied from trial to trial and between individuals, but the response to the fifth habituating pulse was reduced to 10–50% of the response to the initial pulse (Fig. 2). Habituation sometimes did not occur cleanly, so dishabituation was analyzed only for those trials in which there was a clear decrement of response during the habituating series.

The extent to which the response to the final probe pulse dishabituated depended on the separation between speakers. If the test pulse was replaced with silence, the probe pulse response recovered by only  $0.00 \pm 0.01$  units (mean dishabituation index  $\pm 95\%$  confidence interval, 17 crickets tested at all locations of the habituating speaker), showing that the absence of a 40 kHz pulse in that position was not sufficient to cause dishabituation or recovery of the response. Increasing the amplitude of the test pulse by 5–10 dB over the habituating pulses caused no dishabituation.

In the azimuth plane, MAA was determined at seven locations around the cricket,  $0, 11.25, 22.5, 45, 90, 135,$  and  $180^\circ$ . As shown in Fig. 3A, separations of  $90^\circ$  and greater resulted in dishabituation indices of 0.10–0.15 for all locations. As angular separation decreased, the amount of dishabituation decreased. When habituating and test stimuli came from the same speaker, the response continued to habituate, giving rise to indices of  $-0.05$  to  $-0.10$ . In the elevation plane, MAA was tested for four locations around the cricket,  $0$  (ahead),  $90$  (above),  $180$  (behind) and  $-90^\circ$  (below). As with the azimuth tests, dishabituation decreased with decreasing angular separation (Fig. 3B).

In the dishabituation test, the MAA is defined as the smallest angular separation between the habituating and test stimuli at which dishabituation occurs. However, the dishabituation index (Figs 1C, 3) is graded rather than all-or-none, so there must be a criterion for whether dishabituation has occurred

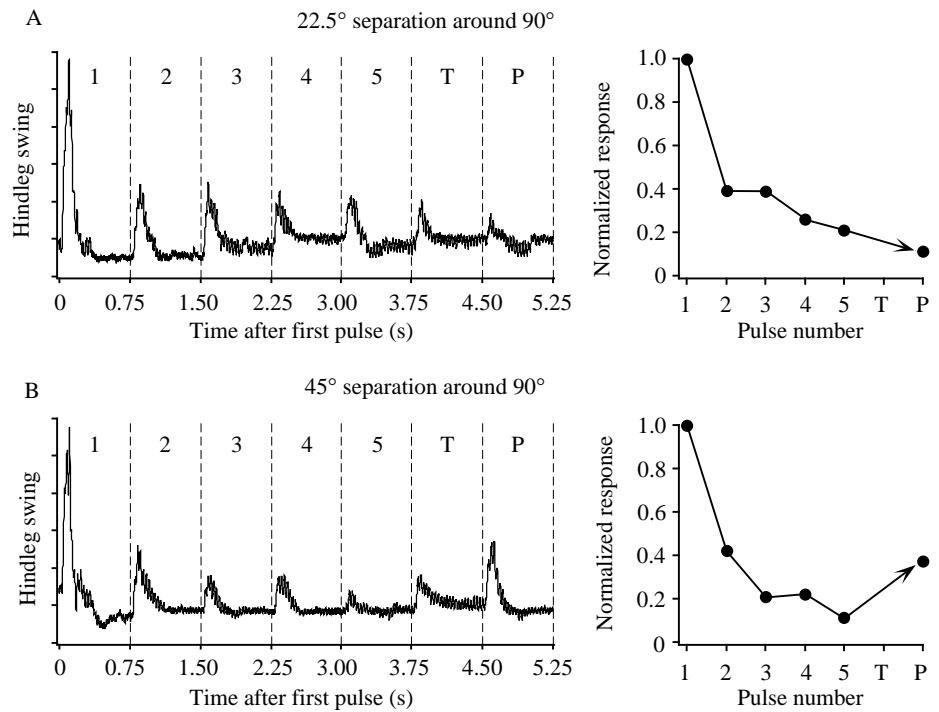


Fig. 2. Habituation and dishabituation. The left-hand panels show photocell traces from a single trial of one cricket; these are measured and normalized in the right-hand panels. (A) With habituating and test pulses from  $78.75^\circ$  and  $101.25^\circ$  ( $22.5^\circ$  separation around  $90^\circ$ ), there was no dishabituation. (B) With habituating and test pulses from  $67.5^\circ$  and  $112.5^\circ$  ( $45^\circ$  separation around  $90^\circ$ ), there was dishabituation. T, test stimulus; P, probe.

given a certain dishabituation index. Fig. 3 shows the MAAs resulting from two reasonable criteria for dishabituation. First, MAA could be defined as the smallest angular separation that evoked a dishabituation index significantly greater than that evoked when the habituating and test stimuli came from the same speaker (marked  $\times$  in Fig. 3). Second, MAA could be more conservatively defined as the smallest angular separation that evoked a dishabituation index significantly greater than that resulting from omission of the test pulse (marked  $\circ$  in Fig. 3). Both criteria were tested using a one-tailed *t*-test,  $\alpha$  set to 0.05 and *P* values multiplied by the number of tests (to correct for multiple tests). With either criterion, a truly *minimum* audible angle is not revealed by the statistical test: the actual MAA lies between the smallest angle that meets the criterion and the next smallest angle tested.

Fig. 4 shows the MAAs resulting from the second, more conservative, of these two criteria. In azimuth, MAA varied considerably, with the best acuity ( $11.25^\circ$ ) at the front and the worst acuity ( $45^\circ$ ) at the side (Fig. 4A). The first, less conservative, criterion would decrease each of these MAAs by one step without altering their pattern. In elevation, MAA varied from  $45^\circ$  to  $90^\circ$ , with the best acuity at the front and rear (Fig. 4B). The first, less conservative, criterion would decrease the MAA at  $-90^\circ$  by one step and leave the others unchanged.

When the stimulating speakers were near the midline ( $0^\circ$  in azimuth), many crickets made turns that were not always away from the speaker. For example, with the habituating speaker at  $11.25^\circ$  and the test speaker at  $-11.25^\circ$ , a cricket might make a right turn in response to each pulse, but the response to the final pulse would still show dishabituation, indicating that the

$22.5^\circ$  separation was discriminated. This regularly occurred when discrimination was tested in elevation, since all of those stimuli were near the midline of the cricket.

## Discussion

### Dishabituation

The dishabituation paradigm was originally developed for studies of perception in human infants because they could not give verbal judgments of same or different when presented with pairs of stimuli (e.g. Miller and Morse, 1976). These experiments on spatial discrimination and others on frequency discrimination (Wytenbach *et al.* 1996) illustrate that this technique can also be useful with crickets. There are several advantages of this method. First, only the stimulus used in the habituating series must elicit a measurable behavior. The test stimulus itself need not elicit a behavior, because its effects are seen in the response to the final probe pulse. Second, it is possible to show that two stimuli are discriminated even though both may cause the same magnitude and orientation of behavior. For example, ultrasound stimuli from  $45^\circ$  and  $135^\circ$  both caused left turns of approximately the same magnitude, but a test pulse from  $135^\circ$  dishabituated a habituated response to stimuli from  $45^\circ$ .

Although widely used as a discrimination test, dishabituation is not well understood and its use involves several assumptions. First, it is assumed that the decline in response during habituation is not merely due to sensory or motor adaptation. The fact that dishabituation can occur supports this assumption. Second, we assume that dishabituation in these experiments occurred because of a

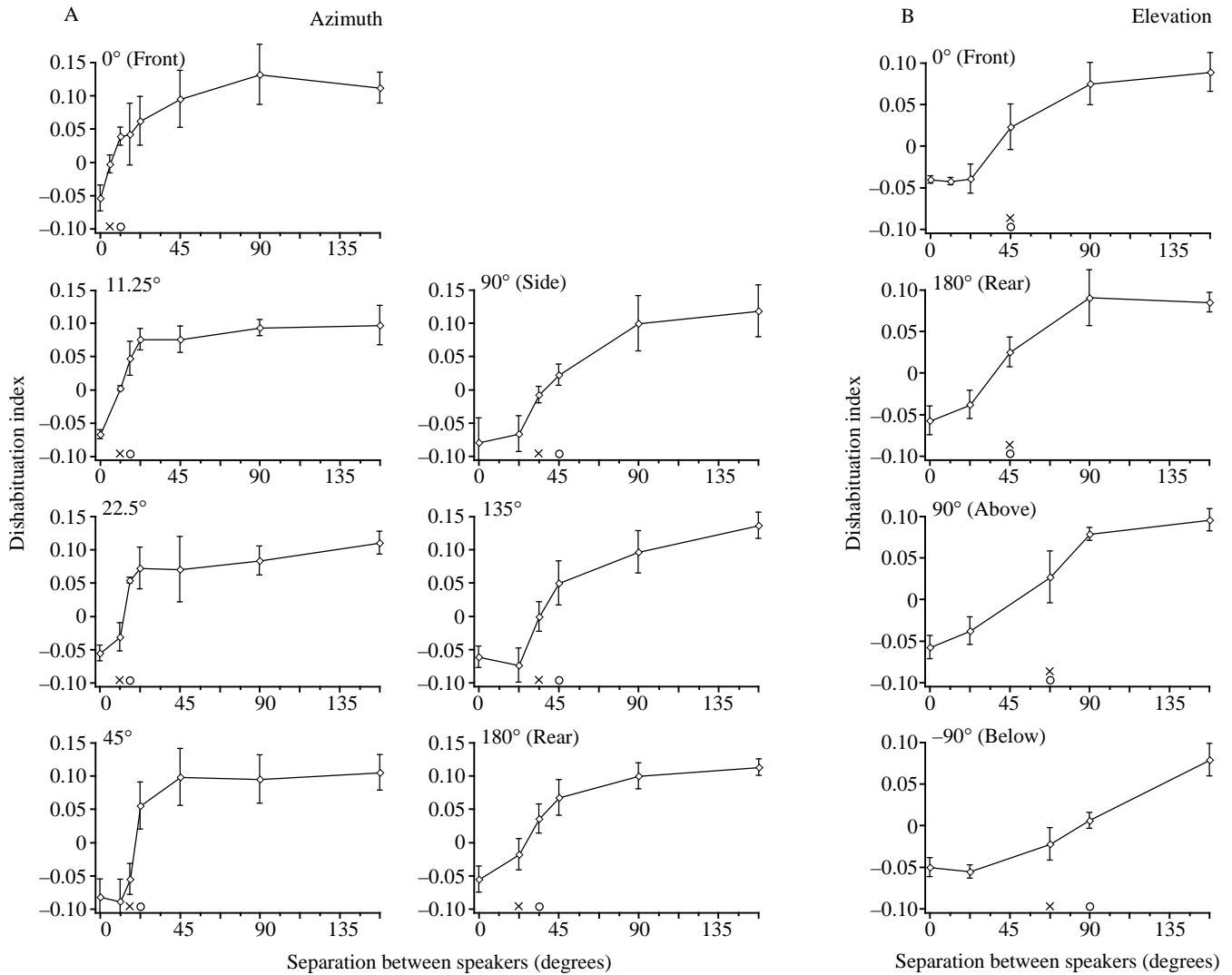


Fig. 3. Dishabituation tests. Graphs show dishabituation indices when habituating and test speakers were separated by the angles indicated on the  $x$ -axes. The smallest separation evoking dishabituation is shown on each graph:  $\times$  marks the smallest separation with a dishabituation index significantly greater than that at  $0^\circ$  separation;  $\circ$  marks the smallest separation with a dishabituation index significantly greater than that when the test pulse was omitted. (A) These separations were tested around  $0, 11.25, 22.5, 45, 90, 135,$  and  $180^\circ$  in azimuth. (B) These separations were tested around  $0, 180, 90,$  and  $-90^\circ$  in elevation. Mean  $\pm 95\%$  confidence interval, five crickets per point, at least three trials per angular separation per cricket; see text for details of significance testing.

change in the location of the test pulse relative to the habituating pulses rather than because of some other difference in the stimuli. The only likely difference other than location is intensity. Because neither omitting the test pulse nor increasing its intensity caused dishabituation, intensity differences cannot account for our results. Finally, the dishabituation test assumes that a lack of dishabituation implies a lack of discrimination. This is difficult to prove, but we have shown that the lack of dishabituation at small angular separations in our experiments was not due to either the test pulse or the probe pulse being inaudible to the cricket. Thus, test pulses that did not dishabituate could still cause leg-swing (e.g. Fig. 2A), and a probe pulse that could cause a small response when preceded by a test pulse at a small separation could cause a larger,

dishabituated, response when preceded by a test pulse at a larger separation.

#### *Spatial acuity*

The spatial acuity of a cricket should be determined by three factors. (1) The sound field around the cricket, resulting from diffraction and reflection by the body, gives rise to interaural intensity differences (IIDs) at the ears that vary with the direction of the sound source. (2) The ears themselves have directional sensitivities resulting from the properties of the tympana and other sound inputs such as that from the acoustic trachea. This inherent directionality gives rise to differences in auditory responses of the two ears that vary with the direction of the sound source. (3) Whatever part of the central nervous

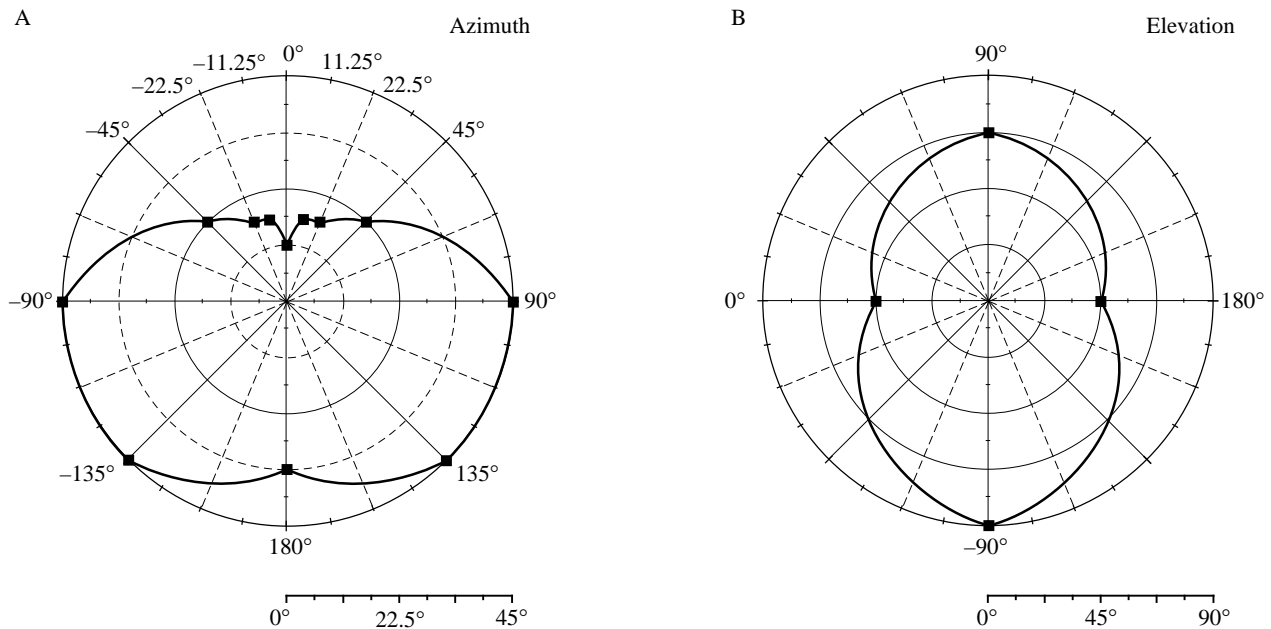


Fig. 4. Minimum audible angles. The minimum audible angle (MAA) for a position was defined as the smallest angular separation around that position that evoked dishabituation (according to the second criterion, marked  $\circ$  in Fig. 3). MAA is shown as the distance from the center. (A) In azimuth, acuity was best ( $11.25^\circ$ ) around  $0^\circ$  and worst ( $45^\circ$ ) at  $90^\circ$ . Data on the left and right sides of this graph are the same. (B) In elevation, acuity was best ( $45^\circ$ ) in the front and rear and worst ( $90^\circ$ ) below the cricket (MAA scale is double that in A). Points are connected by linear interpolation of MAA *versus* position.

system compares interaural differences in auditory responses must have a minimum resolvable difference. This is an absolute measure, independent of the locations of the sound sources.

These three factors can be experimentally investigated, but may be difficult to separate. (1) The sound field can be determined by placing an omnidirectional microphone at the position of an ear and measuring changes of intensity as a sound source is moved around the cricket. (2) The directional sensitivity of an ear independent of the sound field cannot be determined directly, simply because the ear cannot be removed intact from its sound field. Therefore, the combined effects of the sound field and the directionality of the ear are measured either physically, as the magnitude of tympanal displacement, or physiologically, as the response of auditory neurons, as a sound source is moved around the cricket. However, it should be possible to calculate the inherent directionality of the ear from this combined measure and measurements of the sound field. (3) The discriminability of interaural response differences cannot be measured directly, but might be calculated from behavioral MAAs and the directional sensitivity of the ears. Depending on how the directional sensitivity of the ears was determined, this calculation will show a threshold difference in spike number or rate or a threshold difference in tympanal movement.

Unfortunately, measurements of the sound field and directionality of cricket ears have concentrated on calling song to the neglect of ultrasound. The directionality of the ears is very dependent on frequency, especially around 4–5 kHz

(Michelsen *et al.* 1994; Boyd and Lewis, 1983). In general, at low frequencies, IIDs due to shadowing by the body are very small, but the ear is an inherently directional pressure-difference receiver, receiving input from both the tympana and the spiracles. At higher frequencies, however, the impedances of the trachea are such that the ear acts as a simple pressure receiver. The ear is not itself directional at these frequencies, but the body of the cricket is large enough relative to the wavelength of the sound for usable IIDs to occur (Michelsen and Larsen, 1985).

Although this information does not allow quantitative predictions of MAAs at 40 kHz, some qualitative predictions can be made. To discriminate two sound sources, a cricket must, at minimum, compare the magnitude and sign of the IID of the first sound with those of the second sound. The extent to which these two IIDs differ determines the discriminability of the sounds. Assuming that the ears are omnidirectional at 40 kHz but that diffraction by the body is significant, this difference in IIDs would be greatest for pairs of sounds coming from opposite sides of the midline, and this is where the MAAs were smallest. For pairs of sounds coming from the same side, the difference in IIDs should be much smaller, and this is where MAAs were greatest.

Several behavioral studies have addressed the directionality of cricket phonotaxis in azimuth. Nolen and Hoy (1986) investigated lateralization (left–right steering) of the ultrasound response for stimuli presented from a number of angles around the cricket. For stimuli between  $20^\circ$  and  $160^\circ$  to the side, crickets turned away from the stimulated side. At

angles of 0–20° and 160–180°, all crickets made a left or right turn, not necessarily away from the speaker, but away from the ear that had previously been determined to have the lower threshold. In the current experiments, a left or right bias was often seen in response to stimuli near the midline (including elevation stimuli). However, this does not imply that the cricket cannot discriminate between such stimuli. For example, stimuli from +11.25° and –11.25° both caused left turns in some crickets, but this did not prevent a stimulus from –11.25° from dishabituating the response to the stimulus from +11.25° (Fig. 3A, 22.5° separation around 0°). This highlights a point that may not be immediately obvious: discrimination of two sound sources does not require that each source be accurately localized, but only that the difference in their IIDs be discriminable.

Of the experiments using positive phonotaxis, the work of Pollack and Plourde (1982) is most directly comparable with ours. They used tethered flying *T. oceanicus* and measured the magnitude of steering towards synthetic calling songs presented from different angles. (The magnitude of positive phonotactic steering varies with the location of the sound source, while that of negative phonotactic steering varies with stimulus amplitude.) Steering magnitude increased as the speaker was moved from 10 to 50° off midline, leveled off from 50 to 130°, and then declined again from 130 to 170°. There was rarely any steering response to speakers less than 10° from the midline. It may be possible to extract some MAA information from these results. The magnitude of steering was significantly different between 10 and 25°, 25 and 40°, and 130 and 155°. This suggests that separations of 15° were discriminated in the range 0–40° and that separations of 25–40° were discriminated in the range 90–155°. These results are consistent with our finding of MAAs of 11.25–22.5° between 0 and 45° and of 33.75–45° between 135 and 180°. However, Pollack and Plourde (1982) showed that responses to 40, 50, 90 and 130° were not significantly different, nor were responses to 10, 20, 155 and 170°. They interpreted this as evidence of non-discrimination within these two groups. That would imply an MAA of approximately 90° around 90°, as well as a strong front–rear ambiguity, with pairs such as 10 and 170° not being discriminated. In contrast, we found an MAA of 45° around 90° and no front–rear ambiguity, with pairs such as 45 and 135° being clearly discriminated (Fig. 3, 90° separation around 90°). However, the lack of statistically significant differences in responses cannot be taken as evidence for non-discrimination. The similarity of the responses in the 40–130° range may simply indicate that the steering response is saturated or that the accuracy of steering is less than the accuracy of localization.

Rheinlaender and Blätgen (1982) reported an MAA of 30° around the midline for the cricket *Gryllus bimaculatus*. They tested lateralization (right–left choice) in walking phonotaxis to calling song. Female crickets were placed in a Y-maze with an active speaker at the end of one branch and a variable angle between the branches of the Y. When the active speaker was less than 15° from the midline, crickets chose randomly

between the two maze branches. This implies an MAA of 30°, considerably greater than that (11.25°) found in our tests. That is probably because the dishabituation test is more sensitive than a choice test, but could also be due to the conditions of their tests: walking phonotaxis, calling song and the unclear sound field of a maze relative to that of a flight chamber.

Neural studies of localization have focused on the auditory interneurons of the prothorax and generally report lateral differences in activity as a function of calling song stimulus position (e.g. Boyd and Lewis, 1983). Such studies tend to show that IIDs measured at the ears are passed on to the brain by ascending interneurons. Boyan (1979) made bilateral extracellular recordings from two unidentified ascending auditory interneurons of *Teleogryllus commodus* and showed that a shift of 5–10° from the midline gave rise to significant differences in spiking rate between the left and right interneurons. Shifts of this amount around 45° and 90° did not reliably give rise to such coding differences. These results are consistent with the MAAs of our study, but do not themselves predict specific MAAs.

Pairs of sounds differing only in elevation at the midline should be very difficult to discriminate, since they should generate very similar IIDs. The relatively large MAAs in elevation tend to confirm this, although shortening the hindwings may have affected these results. (Payne *et al.* 1966 found that the sensitivity of moths to elevational ultrasound stimuli varied considerably with the position of the wings.) Other than the demonstration of May *et al.* (1988) that crickets pitch downwards in response to ultrasound from above and upwards in response to ultrasound from below, there has been no previous work in orthopterans on sound localization in the elevation plane. Our results confirm that crickets can distinguish stimuli on the basis of elevation, not only between above and below, but between pairs of stimuli from above and between pairs of stimuli from below. However, it is not clear what cues are used for localization in elevation, since none of the mechanical studies of ears, measurements of sound fields or neural studies have addressed this point.

Unlike other behavioral studies of sound localization in insects, our study treated the accuracy of spatial discrimination separately from the accuracy of steering or turning. In experiments in which perceptual and motor systems are not separated, the results can only indicate the less accurate of the two, even though they are often interpreted as showing perceptual accuracy. This study raises several issues for future investigation. First, the acoustic and neural investigation of localization should be extended into the ultrasound. Second, MAA should be investigated at lower frequencies. Finally, the effects of elevation have been neglected in studies of directional hearing and remain open to investigation at the acoustic, neural and behavioral levels.

We thank members of the Hoy laboratory and two anonymous reviewers for helpful comments on the manuscript. This work was supported by NIDCD grant R01-CD00103 and

NIMH grant K05-MH1148 to R.R.H. and by a NSF graduate fellowship and NIMH graduate training grant T32-MN15793 to R.A.W.

### References

- BOYAN, G. S. (1979). Directional responses to sound in the central nervous system of the cricket *Teleogryllus commodus* (Orthoptera: Gryllidae). I. Ascending interneurons. *J. comp. Physiol.* **130**, 137–150.
- BOYD, P. AND LEWIS, B. (1983). Peripheral auditory directionality in the cricket (*Gryllus campestris* L., *Teleogryllus oceanicus* Le Guillou). *J. comp. Physiol.* **153**, 523–532.
- DOOLING, R. J. AND BROWN, S. D. (1990). Speech perception by budgerigars *Melopsittacus undulatus*: Spoken vowels. *Percept. Psychophys.* **47**, 568–574.
- FAY, R. R. (1988). *Hearing in Vertebrates: A Psychophysics Databook*. Winnetka, IL: Hill-Fay Assoc.
- HILL, K. G. AND BOYAN, G. S. (1977). Sensitivity to frequency and direction of sound in the auditory system of crickets (Gryllidae). *J. comp. Physiol.* **121**, 79–97.
- MAY, M. L., BRODFUEHRER, P. D. AND HOY, R. R. (1988). Kinematic and aerodynamic aspects of ultrasound-induced negative phonotaxis in flying Australian field crickets (*Teleogryllus oceanicus*). *J. comp. Physiol.* **164**, 243–249.
- MAY, M. L. AND HOY, R. R. (1990a). Leg-induced steering in flying crickets. *J. exp. Biol.* **151**, 485–488.
- MAY, M. L. AND HOY, R. R. (1990b). Ultrasound-induced yaw movements in the flying Australian field cricket (*Teleogryllus oceanicus*). *J. exp. Biol.* **149**, 177–189.
- MAY, M. L. AND HOY, R. R. (1991). Habituation of the ultrasound-induced acoustic startle response in flying crickets. *J. exp. Biol.* **159**, 489–499.
- MICHELSSEN, A. AND LARSEN, O. N. (1985). Hearing and sound. In *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, vol. 6 (ed. G. Kerkut and L. Gilbert), pp. 495–555. New York: Pergamon Press.
- MICHELSSEN, A., POPOV, A. V. AND LEWIS, B. (1994). Physics of directional hearing in the cricket *Gryllus bimaculatus*. *J. comp. Physiol.* **175**, 153–164.
- MILLER, C. L. AND MORSE, P. A. (1976). The “heart” of categorical speech discrimination in young infants. *J. Speech Hearing Res.* **19**, 578–589.
- MILLS, A. M. (1958). On the minimum audible angle. *J. acoust. Soc. Am.* **30**, 237–246.
- MORSE, P. A. AND SNOWDON, C. T. (1975). An investigation of categorical speech discrimination by rhesus monkeys. *Percept. Psychophys.* **17**, 9–16.
- NELSON, D. A. AND MARLER, P. (1989). Categorical perception of a natural stimulus continuum: Birdsong. *Science* **244**, 976–978.
- NOLEN, T. G. AND HOY, R. R. (1986). Phonotaxis in flying crickets. I. Attraction to the calling song and avoidance of bat-like ultrasound are discrete behaviors. *J. comp. Physiol.* **159**, 423–439.
- PAYNE, R. S., ROEDER, K. D. AND WALLMAN, J. (1966). Directional sensitivity of the ears of noctuid moths. *J. exp. Biol.* **44**, 17–31.
- POLLACK, G. S. AND PLOURDE, N. (1982). Directionality of acoustic orientation in flying crickets. *J. comp. Physiol.* **146**, 207–215.
- POPOV, A. V. AND SHUVALOV, V. F. (1977). Phonotactic behavior of crickets. *J. comp. Physiol.* **119**, 111–126.
- RHEINLAENDER, J. AND BLÄTGEN, G. (1982). The precision of auditory lateralization in the cricket, *Gryllus bimaculatus*. *Physiol. Ent.* **7**, 209–218.
- SRINIVASAN, M. V., ZHANG, S. W. AND WITNEY, K. (1994). Visual discrimination of pattern orientation by honeybees: performance and implications for ‘cortical’ processing. *Phil. Trans. R. Soc. Lond.* **343**, 199–210.
- VRIESLANDER, J. D., SKOVIRA, J. F. AND CAPRANICA, R. R. (1991). Modular expandable microcomputer workstation for synthesizing complex auditory stimuli and for recording and analyzing neurophysiological responses. *Soc. Neurosci. Abstr.* **17**, 1213.
- WYTENBACH, R. A., MAY, M. L. AND HOY, R. R. (1996). Categorical perception of sound frequency by crickets. *Science* **273**, 1542–1544.
- YAN, H. Y. AND POPPER, A. N. (1993). Acoustic intensity discrimination by the cichlid fish *Astronotus ocellatus* (Cuvier). *J. comp. Physiol.* **173**, 347–351.