

ORIENTATION TO CALLING SONG BY FEMALE CRICKETS, *SCAPSIPEDUS MARGINATUS* (GRYLLIDAE)

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INTRODUCTION

Regen (1913) has demonstrated that the calling song of a stridulating male cricket serves to attract conspecific females, and that this behaviour is independent of olfactory, tactile, and visual cues. Since Regen's classic experiments, however, no further details of sound-location behaviour have been reported. Autrum has postulated that among the Orthoptera having tibial tympanal organs orientation is accomplished by co-ordinating the movements of the prothoracic legs with the responses of the directionally sensitive tibial tympanic organs (Autrum, 1940, 1963): 'Let us suppose that the sound comes from a direction which makes the angle α with the longitudinal axis of the body; the grasshopper [i.e. *Tettigoniid*] begins by moving the leg situated on the side corresponding to the sound source, turning it in such a way that the intensity clearly decreases . . . the movement is stopped [when] the sound source penetrates the critical zone of the tympanic organ, where the intensity of the perceived tone diminishes suddenly. In turn, the symmetrical leg, further removed from the sound source, follows the direction of rotation forward. The combination of these two movements permits the animal to turn to the side whence the sound comes. The angle α is decreased with each step and, finally, the insect advances toward the sound source' (Autrum, 1963, p. 429).

More recently a number of physiologists have concerned themselves with the problem of location of a sound source in the course of their analyses of auditory interneurons (Suga & Katsuki, 1961; Suga, 1963; Rowell & McKay, 1969; McKay, 1970; Zaretsky, 1971). In spite of this abundance of interest in the control of orientation to sound, there is no quantitative description of the orientation behaviour of an orthopteran in response to conspecific song. The results presented here demonstrate the nature of the orientation behaviour of female crickets during their approach to a calling male.

The specific questions which motivated this series of experiments were the following. (1) What is the nature of the orientation behaviour and how accurately is a sound located? Can the observed patterns of orientation be correlated with previously described neurophysiological mechanisms for directional discrimination of acoustic signals? (2) Does sound location depend on the integration of the response of both

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tympanal organs, or is a single tympanal organ sufficient, as has been claimed by Regen (1926)? (3) Are there discernible patterns of leg movements involved in orientation to acoustic stimuli, and if so, are these patterns consistent with Autrum's (1963) hypothesis? (4) Does the cricket *S. marginatus* use directional information from an acoustical source when the legs and thus the tympanal organs are in motion with respect to the source, or is the decision to turn reached only on the basis of auditory input received before the cricket begins to move?

The results presented here demonstrate that female crickets can locate the position of the source of its species calling song and turn toward it, but when compared with similar behaviours in other arthropods (see Discussion) orientation is surprisingly crude. Female crickets generally distinguish only right from left; they do not possess the ability to determine the angle which the target makes with their midline. Successful location depends on the integrity of both tympanal organs; crickets having only one tympanal organ make circus movements and cannot locate the sound source.

METHODS

The female crickets used in these experiments were adults of the species *Scapsipedus marginatus* (Gryllidae) native to East Africa and grown in culture at Berkeley. The experimental animals were isolated from males for a period of at least 2 weeks before being tested. The age of the specimens varied from 3 weeks to 2 months beyond the adult stage.

All of the experiments were conducted in an anechoic room kept at a temperature of 23 °C. The calling song of isolated males was recorded in this room, at the same temperature, on a TEAC (model no. TCA 40) audio tape recorder at 7.5 in./sec tape speed, through a Sony ECM 22 microphone, and these recordings were played to the females through an Ionofane 601 high-frequency loudspeaker.

The arena consisted of a 4 × 4 ft sand-covered platform upon which animals were placed which had voluntarily entered the cardboard home tubes (Fig. 1). The song stimulus was played and the animal was allowed to respond. If an animal did not emerge from the tube after the song had been played to it for 10 min it was considered to have failed to respond and the experiment was terminated. Animals which did emerge from their tubes were allowed to walk freely until they either reached the speaker or walked off the arena, in which case the trial was a success or a failure, respectively.

In some experiments two identical Ionofane 601 loudspeakers were positioned as shown in Fig. 1. The speakers were used alternately as the sound source. When the cricket had located one speaker, the stimulus was then switched over to the second speaker. By switching between speakers at the appropriate moment, animals could be made to repeatedly orient first to one and then the other speaker, a procedure which allows for observations of the animals' orientation response when the angle between the sound source and the longitudinal body axis is large.

The movements of the animals were monitored using closed circuit television and recorded on a Shibaden model no. SV-700 video-tape recorder. The song stimulus being played to the animal was recorded simultaneously on the audio channel of this machine, allowing measurements of the latency between stimulus and response. The

monitoring and recording apparatus were located in a room adjacent to the anechoic chamber.

The video recordings were analysed by tracing the position of the speaker(s), and the successive positions of the orienting specimen. The occurrence of a chirp and the latency from the onset of the stimulus to the onset of movement were also noted.

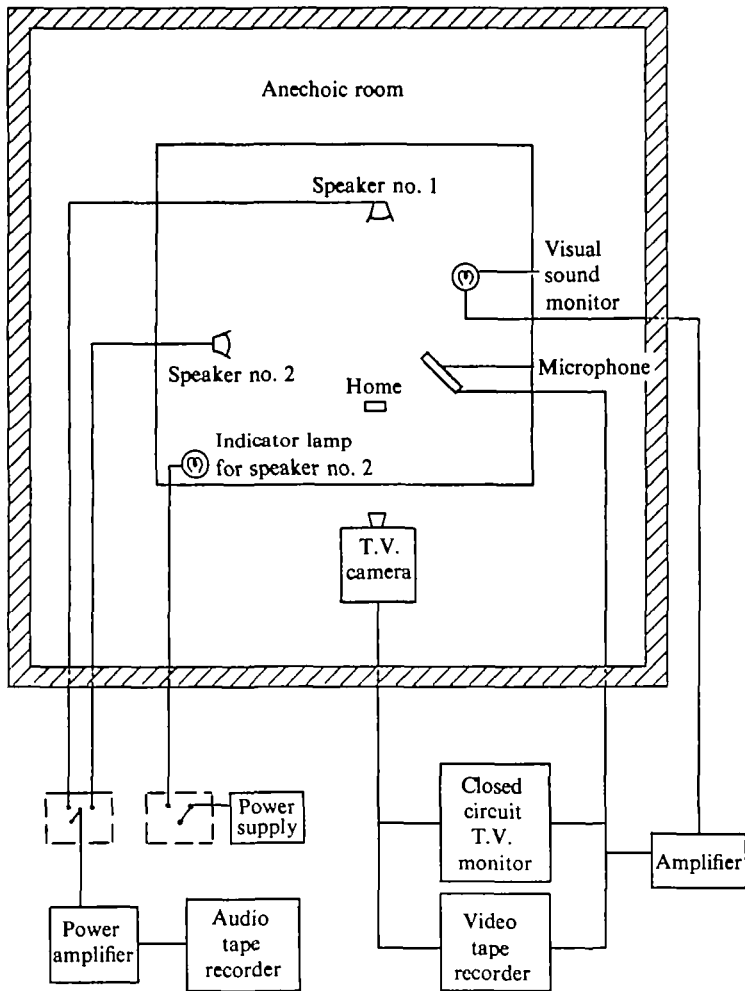


Fig. 1. The arrangement of recording and stimulating apparatus used in all experiments.

During the analysis the recorder was advanced a single frame at a time (the time between successive frames is $\frac{1}{25}$ sec). The target deviations and the angles through which animals turned in response to the sound stimulus were measured from these tracings.

RESULTS

*The orientation of normal specimens**Activation of sound location behaviour*

All animals do not respond immediately when the calling song is first presented. Specimens were given up to 10 min to respond to the continuously presented stimulus; the tape-recorded song elicited some response in 80% of trials, and in 75% of these specimens successfully located the speaker. Most animals which responded did

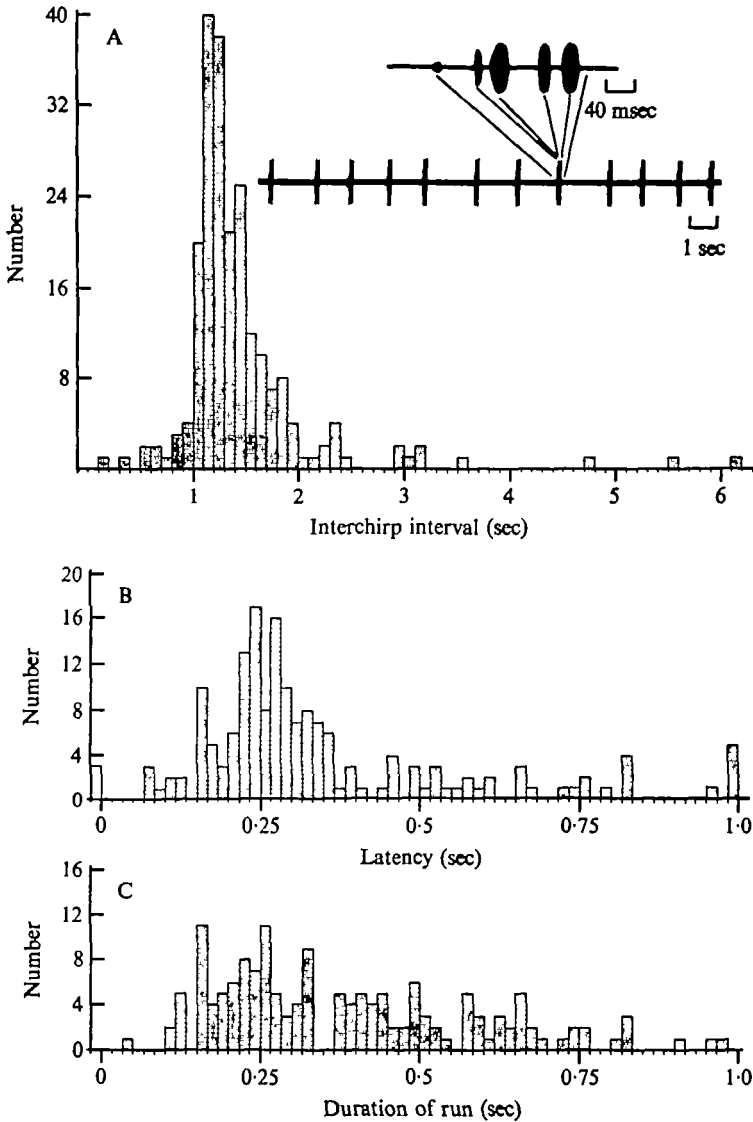


Fig. 2. The latency relationship between the stimulus and the motor response. A, Interchirp interval of the calling song of the male of the species. Inset, recordings of the song used in these experiments. B, Latency of the motor response measured from the beginning of the chirp to the first detectable movement. C, Duration of the motor response.

so within 5 min and some responded immediately. Often animals emerged part way from their home tube and withdrew back into it several times before attempting to locate the sound source. Complete emergence from the home tube is followed by a behaviour which is characteristic of all animals and which we call *scanning*. The animal turns first to one side, then to the other, varying numbers of times. It accomplishes these movements by means of the prothoracic and mesothoracic legs, pivoting on the metathoracic legs. Often false starts occur where the animal walks

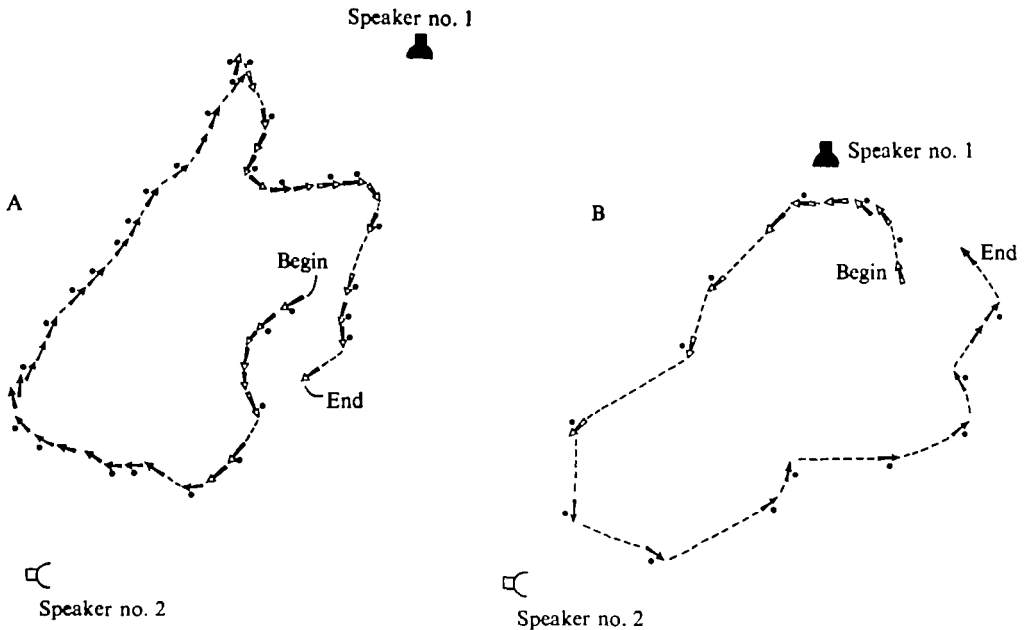


Fig. 3. Paths of normal females orientating to the calling song of a male. The song could be played through either of two speakers; the speaker functioning at a given position in the path is indicated by the open and solid arrows. Solid and open arrows indicate the sound was coming from the darkened and open speaker respectively. Two different animals are represented in *a* and *b*. The open circles indicate the positions at which a sound pulse occurred.

short distances in the wrong direction. Scanning also often occurs when the sound source is switched from a speaker which is in front of the animal, and toward which it has been moving, to one which is behind the animal (Fig. 3A uppermost turn). In most cases scanning lasts for 5–10 sec, and is followed by movements which are more highly directed toward the sound source. The distance covered during each movement between chirps gradually increases until a maximum is reached. This is clearly illustrated by comparing the paths of an animal just after leaving the home tube, and therefore before it is completely 'activated' (Fig. 6A) and of an animal performing at maximum speed (Fig. 3A, B) 1–2 min after leaving the home tube. Thus it appears that animals are activated to maximum responsiveness over a long interval even after they have begun to move toward a sound source.

Temporal relationships between stimulus and response

The chirp of the calling song of the male cricket *S. marginatus* consists of 2–3 pairs of sound pulses (Fig. 2 inset). Successive chirps are separated by a mean interval

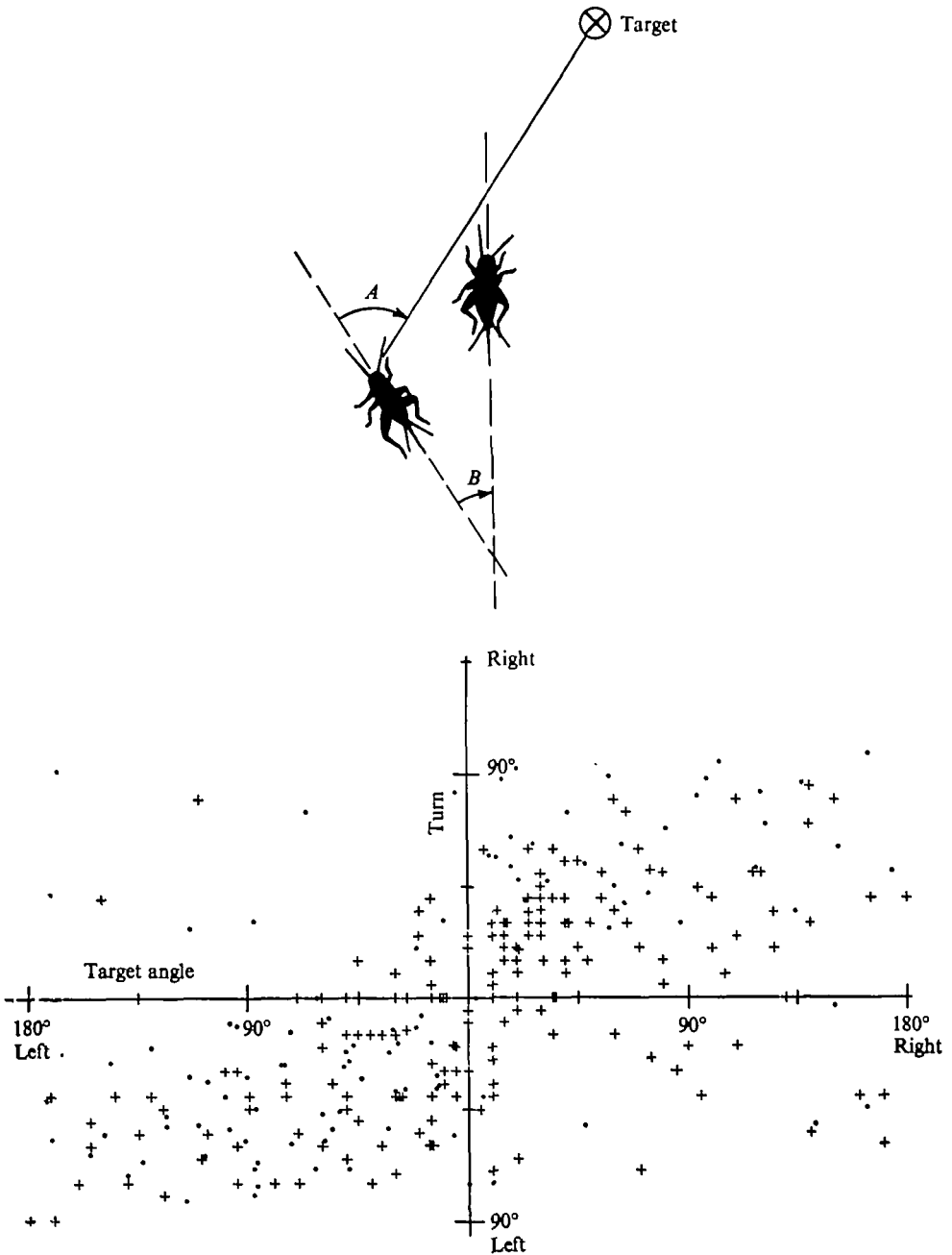


Fig. 4. The relationship between target position and the turn elicited. All points represent turns which were preceded by stimulus pulses. Turns which could not have been elicited by a chirp were omitted. A sample of the run for each animal represented here is given in Fig. 3. The crosses are the results for animal 3A, the dots for animal 3B. The inset indicates the angles plotted; angle *A* is the target deviation in angular degrees. Angle *B* is the turn elicited in angular degrees.

of 1.6 sec (Fig. 2A). Motor movements of orienting females are initiated with a mean latency of 350 ± 200 msec with respect to the onset of the chirp (Fig. 2B). The paths taken in response to calling song consist of distinct short runs of 395 ± 200 msec duration (Fig. 2C). The sum of the means of the latency and the duration of the runs, 745 msec, is less than half the mean interchirp interval. Locomotion therefore appears to be elicited by a single chirp. We will refer to those motor movements which begin less than one second after the onset of a chirp as *latency-locked*.

A run will sometimes occur after a latency-locked movement and before the next chirp. Runs which are not latency-locked usually occur when there is an abnormally long interchirp interval or when an animal is especially active. The proportion of these runs which occur in the absence of a stimulus chirp ranged from 2% in a slow-moving animal to 50% in a fast-moving animal. The movements which are not latency-locked are of short duration and usually do not involve changes in orientation. On the rare occasions when a chirp occurred during a movement, the animal did not alter its course.

Orientation in response to the sound stimulus

The locomotion of a female cricket which is attempting to locate a sound source is made up of a series of brief movements each followed by a pause. Typically, a movement consists of a turn followed by a short straight run. While the initial portion of a

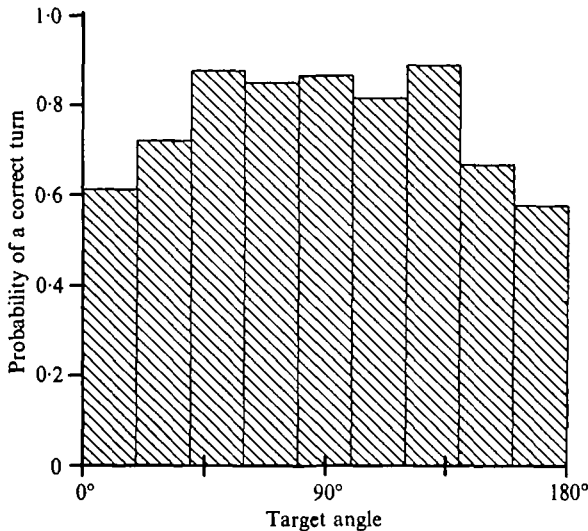


Fig. 5. Probability of turning toward the target as a function of target deviation. The lowered probability of a correct turn when the target is near the body axis has two sources. When the target is in front (0–40°) the turns are small and approximately 40% are incorrect. When the target is behind the specimen the turns are large and approximately 40% are incorrect.

movement is not always a turn, when a turn does occur it is within the first 1 or 2 cycles of leg movements, and succeeding leg movement cycles carry the animal along a straight path. There is no discontinuity in the movement between the turn and the subsequent straight portion of the run. Thus each segment of the paths shown in Fig. 3 consists of a continuous series of leg movements separated from the next series by a

brief pause in the movement. The paths of the animals which are shown in Fig. 3 (A, B) are representative of a slow-moving and fast-moving animal respectively.

The accuracy of sound location was measured by plotting the target deviation (angle *A*, inset Fig. 4) against the size of the turn elicited by the chirp (angle *B*, inset

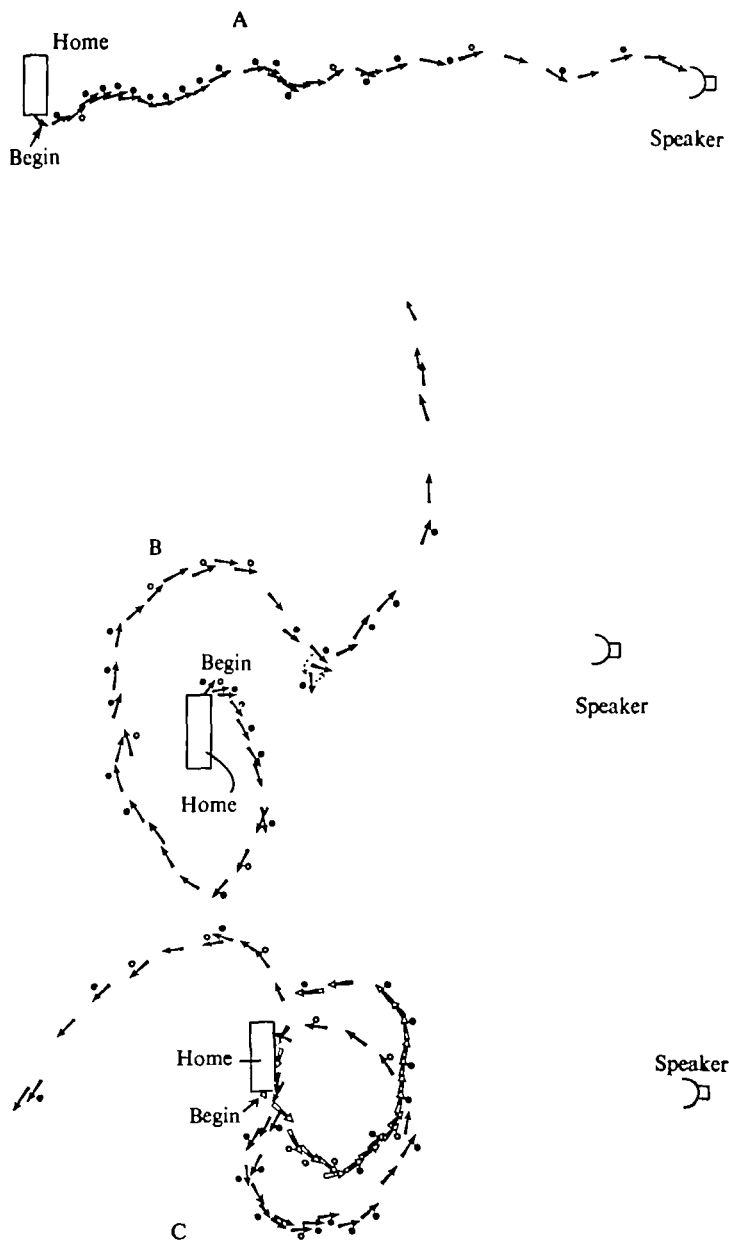


Fig. 6. The effect of the destruction of one tympanal organ. A, Path taken by intact animal no. 15 from home tube to speaker. B, Path taken by the same animal after destruction of the left tympanal organ. C, Path taken by animal no. 5 after destruction of the right tympanal organ. Two successive circus movements are shown in this figure. The initial circus movement is indicated by open arrows.

Fig. 4). Movements which were not latency-locked were excluded from the analysis. The scattergram of the results for two animals which ran for long periods between two speakers (as explained in the methods section) is presented in Fig. 4. The animals clearly distinguish which side of the midline the sound is coming from, turning toward the target in 80% of the trials. However, the correlation coefficient between the

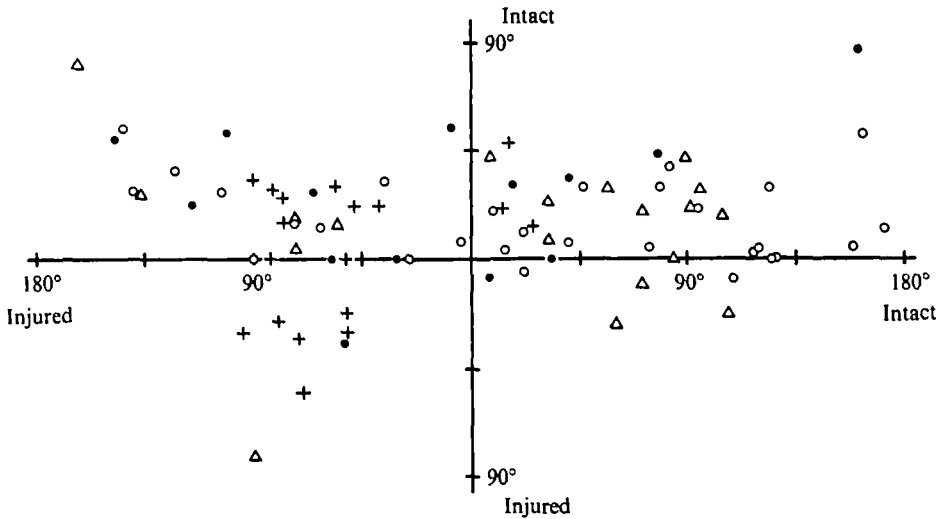


Fig. 7. The relationship between target position and turn for animals possessing only one intact tympanal organ. With the exception of the specimen indicated by crosses, none of the animals was able to reach the speaker.

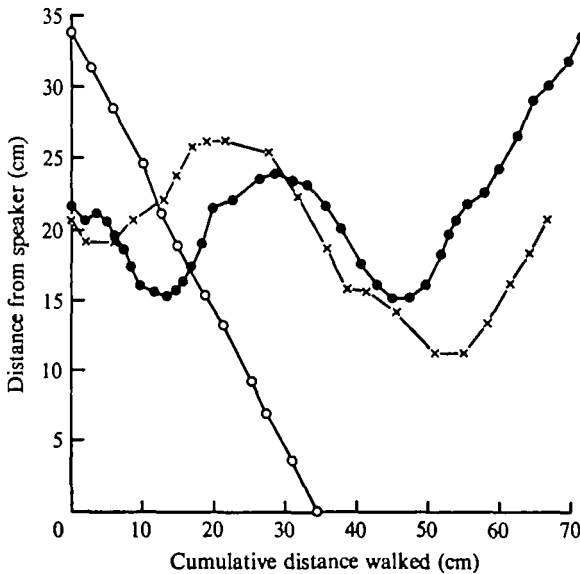


Fig. 8. The difference in the ability of animals with both tympanal organs intact and with only one intact tympanal organ to approach a sound source. The graphs are those of animal no. 15 with both tympanal organs intact (O), the same animal with the left tympanal organ destroyed (x), and of animal no. 5 having the right tympanal organ destroyed (●). The data used in these graphs were taken from the paths shown in Fig. 6.

size of the turn and the target deviation is small, 0.3. In spite of this small correlation between target deviation and turn produced there is some evidence which indicates that the female cricket can determine whether the target is ahead of her or behind her in addition to the determination of position with respect to the midline. The amplitude of turns, irrespective of sign, in response to posterior target positions (120–180° target deviations) is larger ($54 \pm 22^\circ$) than the amplitude of turns to anteriorly situated targets ($33 \pm 22^\circ$). A comparison of the results for posterior and anterior target positions by means of the t-test reveals them to be significantly different with a probability greater than 99%. Apparently sound location depends on two simple distinctions: (1) whether the target is to the right or left of the midline, and (2) whether it lies anterior or posterior to the animal.

The overall probability of a turn occurring in the correct direction – toward the target – has already been given as 0.8. The probability of a correct turn is distributed as a function of target deviation (Fig. 5). The distribution is symmetric about a target deviation of 90°, with minima near the midline (0–45° and 135–180°). These results were grouped according to whether the target deviation was near the midline (0–45°, 135–180°) or lateral (45–135°). A normal approximation to Fisher's two-by-two test was used to compare the frequency of errors (turns away from the target) in the two groups. The differences between the two groups are significant at the 99% level.

Orientation behaviour after destruction of one ear

In contrast with the well-directed path taken by an intact animal in response to conspecific calling song (Fig. 6A), animals which have had one tympanal organ destroyed are unable to locate the sound source (Figs. 6B, C, 7). Their movements are nearly always directed toward the side of the intact ear, regardless of the direction of the sound source (Fig. 7). Although two-eared animals often turn away from the sound source, their paths are such as to give monotonic decrease in their distance from the sound source. As often as not, one-eared animals walk so as to increase their distance from the sound source (Fig. 8).

We have tested animals in which both ears were destroyed and found no behavioural response to the species calling song, although these animals had responded well when their tympanal organs were intact.

Single tympanum lesions

The tibial tympanic organs of *S. marginatus*, as well as of most other gryllids and of all tettigoniids, are constructed each with two tympana. In the case of *S. marginatus* these are placed on opposite sides of the tibia and are of unequal size. It is not clear just how the excitation of both these membranes is coupled to the primary auditory sense cells. The sensory cells themselves are not attached to the tympanic membranes as they are in the acridid abdominal tympanal organs (Gray, 1960), but lie in a row in a separate hemolymph canal (Schwabe, 1906; Autrum, 1963).

In order to test whether both these tympana are required for a functional tympanal organ, one tympanum of each ear was destroyed. None of the five animals in which this operation was performed showed any response to conspecific calling song, although they had behaved in a normal phonotactic manner before this operation. One

animal in which a single tympanum was destroyed unilaterally behaved as did animals in which both tympana of one tympanal organ had been injured (Fig. 9). This animal with a lesion to a single tympanum walked in circus-like paths, and was unable to orient to the sound source. Two intact tympanal membranes are apparently necessary for the functional integrity of the tympanal organ in this species.

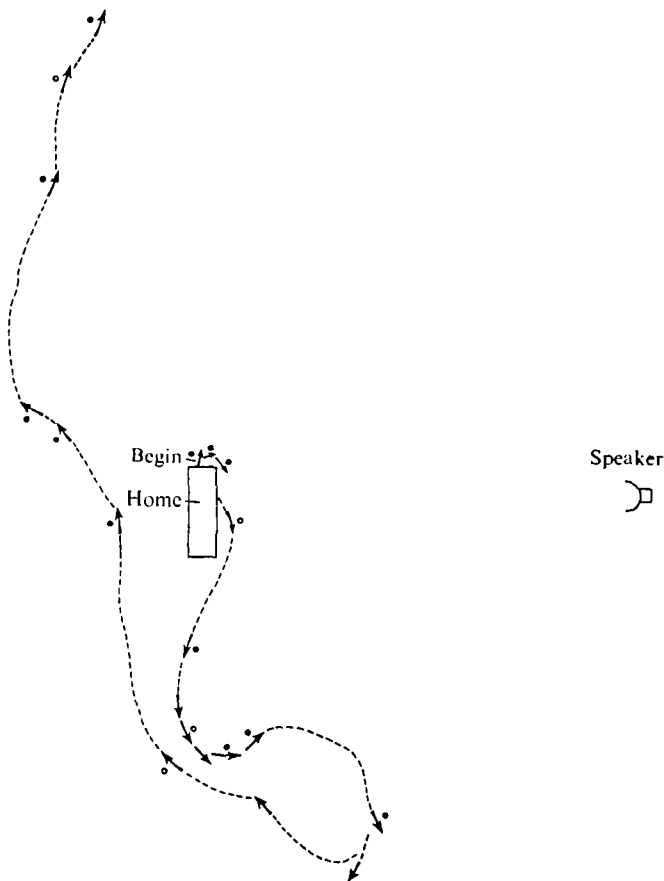


Fig. 9. The effect of destroying a single tympanum of one of the ears. In this case the larger of the two tympana of the left ear was destroyed.

The pattern of leg movements during orientation

The leg movements during three turns in response to calling song were examined using video close-ups. A turn is produced by movements of the prothoracic and mesothoracic legs (Fig. 10). The turn shown in Fig. 10 consists of two cycles of leg movements which occur over frames 9–16 and 18–23 inclusive. In both instances the prothoracic leg ipsilateral to the target (right leg) is promoted and the contralateral (left) leg is remoted. The ipsilateral mesothoracic leg pulls the animal's body sideways and the contralateral mesothoracic leg is pulled under the body. There is much variability in the pattern of leg movements during these small increments, as an examination of the changes in leg position between frames 20 and 21 and between frames 21 and 22 reveals. We were not able to draw any general conclusion regarding

the pattern of leg movements which produce turns, except that they are not as Autrum predicted. In the Discussion we will return to this point with reference to Autrum's hypothesis.

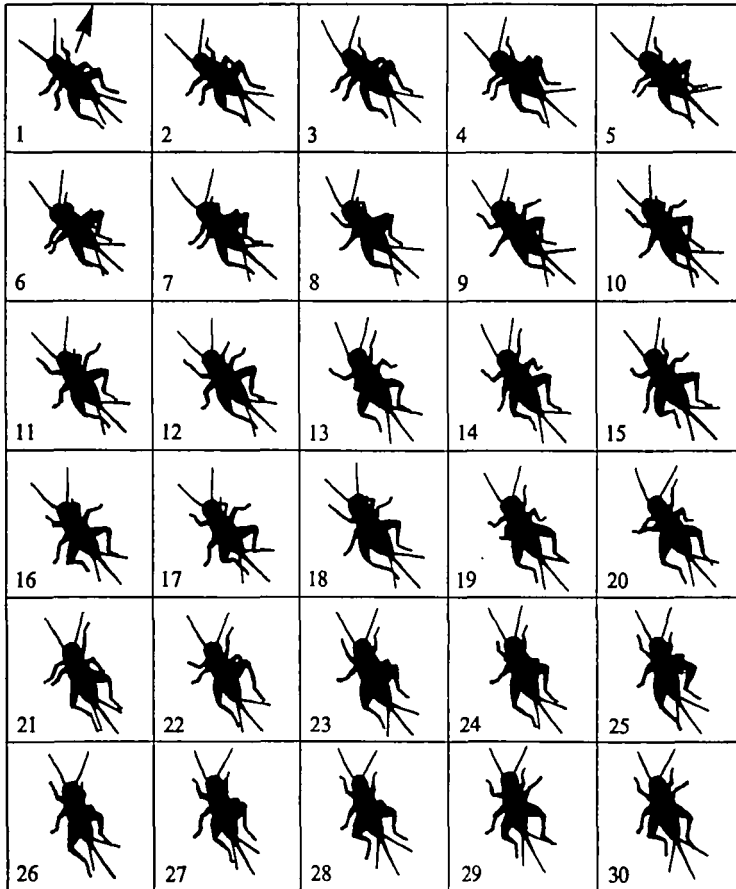


Fig. 10. Leg movements during turning. Tracings of frame-by-frame photographs taken from a video-taped close-up of a single turn. Note the movements of the prothoracic legs especially in frames 11-15 and 18-21. The arrow in frame 1 points to the loudspeaker.

DISCUSSION

Orientation by intact animals

We suggest that the control system underlying orientation to sound in the cricket is an open-loop system, i.e. that locomotion toward a target is determined by input received before a movement is begun and is independent of input during movement. There are two lines of evidence to support this suggestion: (1) locomotor responses are latency-locked to the stimulus and the stimulus is over before the movement begins; feedback from the sound source is therefore not available during the turn; (2) when the animal is moving and a sound pulse occurs, course corrections do not occur.

The song of *S. marginatus* is somewhat unusual in that the interchirp intervals are of long duration, 1.6 sec. The control system may therefore of necessity be functioning

as an open loop. It would be very interesting to know whether females of species with calling songs having shorter interchirp intervals orient in a distinctly different manner. We think that other species will orient in a similar discontinuous manner, although the discrete latencies and the open-loop nature of the system may be less obvious.

The ability of crickets to locate a stimulus source can be compared with the comparable ability of other arthropods in which an open-loop system controls orientation. Water striders (Gerridae) locate prey by responding to surface ripples produced by prey objects trapped in the surface film. These animals very accurately determine the direction of the source of a surface disturbance. The size of the turn is highly correlated with the target deviation (Murphey, 1971*a, b*). However, part of this increase in accuracy may be attributed to the utilization of six points of reference – there are receptors in each of the six legs – in contrast with the two tympanal organs of the cricket. Similarly, jumping spiders (Salticidae) locate prey and mates visually, and they are capable of producing turns such that the change in body angle is highly correlated with the angular deviation of the target from the longitudinal body axis (Land, 1969, 1970). By contrast, the sound-location ability of the cricket *S. marginatus* is relatively unsophisticated. Female crickets apparently distinguish only whether potential mates are to the left or right. The size of turn is not scaled to the target deviation. Furthermore, it is not clear that a more accurate sound-location apparatus would actually facilitate pairing. In the natural state many obstacles are present which could produce echoes and change the apparent direction of a sound source.

Mechanism of sound location

The circus movements toward the intact side, which result from unilateral ablation of one auditory receptor organ, argue strongly for classification of this behaviour as a tropotaxis, i.e. the auditory input received by the two ears is compared and turning occurs toward the side which is more highly excited (Fraenkel & Gunn, 1940). This result is contrary to the report that unilaterally deafened female crickets can locate a sound source (Regen, 1926). Of the six unilaterally deafened animals tested one did reach the speaker. When this animal was re-tested it did not respond at all. The remaining unilaterally deafened animals showed no ability to orient toward the sound source; rather, they turned toward the intact ear even when they were very near the sound source, a phenomenon which was never observed in animals which had both tympanal organs intact. We can only conclude that when one-eared animals come near to the sound source they do so only by chance and not because they are able to orient with one ear. The circular paths which one-eared animals take can result in a momentary near-encounter with the sound source, and this phenomenon might be the basis of Regen's claim.

The difference between the levels of excitation of the two tympanal organs could result from any one or all of the following: (1) the stimulus intensity at the ipsilateral ear is greater than that at the contralateral ear; (2) the time of arrival of the stimulus at the contralateral ear is delayed with respect to that at the ipsilateral ear; (3) there is a phase difference between the stimuli to the two ears. We will discuss each of these in turn.

The fundamental frequency of the calling song of *S. marginatus* is 5 kHz. Although frequency components up to 60 kHz are present in the calling song, the band width of

the audio tape recorder used in our experiments did not go above 12 kHz. Furthermore, there is no difference in the orientation behaviour of *S. marginatus* females when the stimulus consists of artificial song of pure 5 kHz pulses with interpulse and interchirp intervals identical to those of the calling song (Zaretsky, 1971). The discussion of the mechanism of orientation can therefore be limited to the case of a stimulus with the appropriate pulse and chirp parameters of the species calling song, but with a pure 5 kHz frequency spectrum.

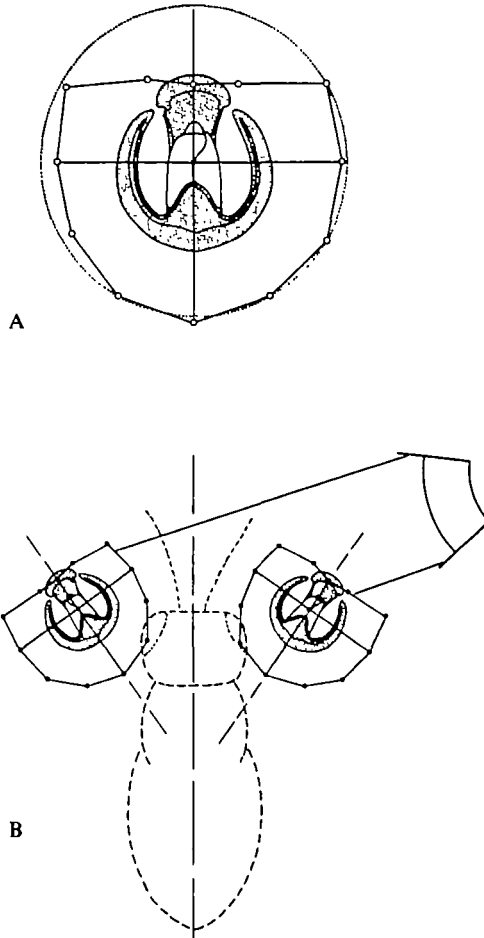


Fig. 11. Directional sensitivity of the tibial tympanal organ of a tettigoniid. The upper portion of the figure plots the sensitivity of the ear of *T. viridissima* in polar quadrants (from Autrum, 1940). The lower diagram is a schematic explanation of the implications of this result. When the sound source is in the position shown the animal would have to turn *away* from the tympanal organ which is most intensely stimulated. Our results for unilaterally deafened animals indicate that the animal turns toward the more intensely stimulated ear, implying that the directionality of the ear as demonstrated by Autrum (1940) is not important to sound location.

A difference in the intensity of sound incident at the two ears would have to result either from scattering or absorption of sound by the cricket's body. The wavelength of the fundamental frequency, 66 mm, far exceeds the dimensions of the body of *S. marginatus* (5 mm in diameter and 15 mm in length). Calculations for the scattering

of sound by elastic spheres and cylinders indicate that a sound wave will not be scattered by an object that is an order of magnitude smaller than the wavelength. The cricket's body is not, however, perfectly elastic, and absorption could account for differences in the sound intensity incident at the two tympanal organs (Morse & Ingard, 1968). In order to test for such a difference in intensity, pulses of pure 5 kHz frequency were played at a cricket oriented 90 degrees to the source, and the intensity of sound on both sides of the animal's body was measured with a calibrated non-directional Brüel and Kjøer 6 mm microphone. No difference between the intensities at the positions of the ipsilateral and contralateral tympanal organs could be detected by this method. It would be desirable to repeat these measurements using a smaller microphone, and to measure the difference in the response at the level of the tympanic nerve.

The individual tympanal organs could have directional properties which would produce differences in their response when the target does not lie along the cricket's longitudinal axis. Directional properties have been measured for the tympanal organ of Tettigoniidae (Autrum, 1940, fig. 11 A). These directional properties, however, do not appear to be the principal contributing factor to the differential response between the two tympanal organs. If this were the case, and Autrum's results are correct, the response of the contralateral tympanal organ would be greater than that of the ipsilateral tympanal organ (Fig. 11 B). Such an outcome would contradict the results reported in this paper as well as the results of physiological experiments on tettigoniids (Suga & Katsuki, 1961; Suga, 1963; McKay, 1970).

The delay between initial times of arrival of the signal at the two tympanal organs is at most 30 μ sec, varying with the orientation of the animal with respect to the sound direction and reaching a maximum when the target direction is perpendicular to the longitudinal body axis (see Appendix). It is possible that this delay coupled with inhibitory interactions at various levels could allow for directional discrimination. Inhibitory interactions in the auditory system of certain orthoptera have been shown to exist (Suga & Katsuki, 1961; Rowell & McKay, 1969; McKay, 1970).

Apart from the initial delay between arrival of the signal at the tympanal organs it is unlikely that phase differences between ipsilateral and contralateral stimulation could be of significance in directional discrimination. The response of an individual receptor is much too slow to enable it to phasically follow a signal which is at least an order of magnitude faster than the time constants of the receptor potentials themselves.

Leg movements during a turn

S. marginatus females listen to the entire chirp of the male before turning and walking. Chirps which do rarely occur during movement are not effective in changing the animal's course. Crickets listen with their legs in a stationary position, and therefore the tibial tympanic organs do not move when the stimulus occurs. During leg movement the stimulus is absent. Autrum (1940, 1963) has proposed a model for orientation toward acoustic stimuli by Tettigoniidae, which have tibial tympanal organs similar to those of Gryllidae. Our results on both the timing and the pattern of leg movements which occur during turning in response to sound directly contradict Autrum's model.

Autrum states that turns are accomplished through a differential movement of the

prothoracic legs, which bear the tibial tympanal organs. The legs are turned until the sound strikes the zone of the tympanal organ where its intensity suddenly diminishes, and in so doing the leg ipsilateral to the sound source is not moved as far forward as that which is contralateral. The result is a turn in the direction of the source. Examination of the movements of the prothoracic legs during turning reveals that such is not

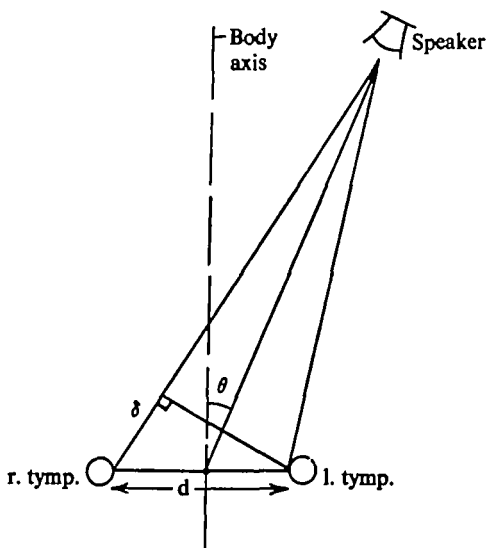


Fig. 12. The path travelled by sound waves emitted from a point source and incident at the tympanal organs of a cricket (details in Appendix).

the case. Frames 12 and 13, and 18 and 19 of Fig. 10 show the position of the legs as a small turn is made. The ipsilateral prothoracic leg extends in the direction of the turn and the contralateral prothoracic leg is retracted. But, more significantly, the legs do not scan to find the 'critical zone'; no turning occurs during the sound stimulus. Apart from these considerations Autrum's theory implies a more highly correlated relationship between target and turn than is indicated by the data of Fig. 4.

Physiological correlates

The directional properties of central auditory neurones of Orthoptera fall into two classes. The first consists of those which receive excitatory input from the ipsilateral tympanic nerve and inhibitory input from the contralateral tympanic nerve thereby enhancing the directional response. Examples are the T fibres of the tettigoniids *Gampsocleis buergeri*, *Homorocoryphus lineosus* and *Homorocoryphus nitidulus vicinus*, and the beta neurone of the acridid *Gastrimargus africanus* (Suga & Katsuki, 1961; Suga, 1963; McKay, 1970; Rowell & McKay, 1969). In the non-habituated state all of these neurones show directional discrimination in 100% of the cases when the direction of sound is 90° to the longitudinal axis of the animal. No central auditory neurones belonging to this class have been found in Gryllidae.

The second class consists of those interneurones which lack inhibitory input from the contralateral ear but receive excitatory input from both the ipsilateral and the

contralateral tympanic nerves, the ipsilateral input being stronger. Central neurones belonging to this class have been found in Gryllidae (Suga & Katsuki, 1961; Zaretsky, 1971). The alpha neurone of the acridid *Gastrimargus africanus*, a member of this class, can signal the direction correctly in 70% of the trials when the source is at 90° to the body axis if differences in both spike number and response latency between ipsilateral and contralateral units are taken into account (Rowell & McKay, 1969). Similar measurements have not been made on the gryllid interneurons of this class.

The behavioural results reported here do not exclude either mechanism, although the lack of reports of crossed inhibitory links among gryllids tends to implicate the second type of directional discrimination.

SUMMARY

1. Video-tape recordings of the orientation behaviour of female crickets *Scapsipedus marginatus* in response to the calling song of conspecific males demonstrate that turning and locomotion of the animal toward a target are determined by the sensory information received before the movement is initiated and are unaffected by auditory input received during movement, i.e. the control system is an open-loop type.

2. Sound location comes about through the animals' ability to turn toward the sound source. The probability of turning in the correct direction is maximal when the sound source lies in the lateral quadrant with respect to the longitudinal body axis, and it is symmetric about the perpendicular to the body axis.

3. The correlation between the angle of the turning response and that of the direction of the sound stimulus is very small. Animals tend to make smaller turns when the target angle is less than 60° than when it is greater than 60°. Sound which is incident from the posterior direction elicits larger turns than sound which is incident from the anterior direction. Thus, the cricket can tell whether sound is coming from the forward or backward direction and respond accordingly.

4. One-eared animals usually turn toward the intact ear in response to auditory stimulation. The orientation behaviour therefore depends on a comparison of stimuli incident at the two ears. This result contradicts the findings of Regen who claims that one-eared animals can locate a sound source.

5. The leg movements demonstrated by video close-ups of single turns show varying patterns. The pattern postulated by Autrum, however, is not among these.

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APPENDIX

The path travelled by sound emitted from a source located in the horizontal plane of the tympanal organs differs for the two tympanal organs by $\delta = d \sin \theta$, where d is the distance between tympanal organs and θ is the target angle (Fig. 12). It is assumed that $d/l \ll 1$, where l is the distance of the sound source from the cricket. This path difference gives rise to a delay $\Delta t = \delta/v$ between arrival of the signal at the two tibial tympanal organs, where v is the speed of sound in air, 330 m/sec. For most field crickets $d = 1$ cm, giving a delay of $\Delta t(\mu\text{sec}) = 30 \sin \theta$. The phase difference ($\Delta\phi$) between the signals arriving at the two tympanal organs is $\Delta\phi = f\Delta t$ where f is the frequency of the signal.

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