

ACOUSTIC ORIENTATION IN THE CRICKET *TELEOGRYLLUS OCEANICUS* (LE GUILLOU)

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SUMMARY

New information is presented on acoustic orientation in crickets following a comparison between a species with a discontinuous song pattern, *Scap-sepidus marginatus* (Murphey & Zaretsky, 1972) and one with a continuous song pattern, *Teleogryllus oceanicus*. The females acuity for side discrimination is $\pm 10^\circ$ from the body axis whereas the total phonokinetic response shows a greater degree of error. Females can scan their turn angle to target angles beneath 60° . Error is expressed in terms of information loss through the total behavioural sequence. The cricket does not orient while moving, requires no fixed leg position during the stop for effective orientation and can establish source direction on the basis of at least two syllables. Evidence of differential anterior and posterior tympanic membrane function is suggested.

INTRODUCTION

Orientation in the Tettigonioidea and Grylloidea (Orthoptera) has been the subject of recent debate. Murphey & Zaretsky (1972) clearly established an alternative hypothesis to that given by Autrum (1940, 1963). Autrum suggested that the tympanal organ situated on the foreleg of the tettigoniid scanned the sound field for directional information. Their alternative hypothesis, based on a study of *Scap-sepidus marginatus* (Grylloidea), states that information on directionality is stored on an 'open-loop' system while the animal is stationary and is then used to orient the next forward movement. This was clearly paralleled by orientation in the water-strider (Murphey, 1971). Lewis (1974), basing his ideas on theoretical considerations derived from studies on the function of the auditory spiracle, repeated Autrum's assumption that the leg must scan the sound field in order to find the null position and hence directionality. Both Lewis (1974) and Nocke (1974, 1975), working on the physical aspects of sound reception in the Tettigonioidea, implicated the auditory spiracle and tympanic trachea running from the prothorax to the tympanic membrane in the forelegs.

Problems can arise from too close an analogy between two super-families of insects particularly when there are distinctive structural differences within their generally similar pattern. The study described in this paper arose from a critical examination of the hypothesis of Murphey & Zaretsky (1972) using a cricket with a consistent

long trill song pattern as opposed to an interrupted chirp call of the cricket used by these authors. Thus in *S. marginatus* there is a relatively long silent phase following the orientation cue (the chirp) and hence an opportunity for an open-loop system to operate before the next signal. When the information for orientation is continuous, as in *Teleogryllus oceanicus* (le Guillou), there must be some phase in the orientation response where the input is 'switched-off' before the next turn is elicited. The converse to this would be that the insect is using the continuous signal whilst scanning, thus supporting the original Autrum hypothesis. This was a question raised by Murphey & Zaretsky and is answered in this paper.

Other questions posed by both Murphey & Zaretsky (1972) and Lewis (1974) can be summarized as follows:

(1) Is the auditory acuity strengthened by a continuous stimulus (i.e. can the cricket identify the position of the male more efficiently with such a song)?

(2) Is there a differential function between the two tympana of the foreleg as expressed in the behaviour of the cricket? Murphey & Zaretsky performed some ablation experiments on one tympanum, we have demonstrated that there is a possible differential function between anterior and posterior membranes thus agreeing with postulates made by Johnstone, Saunders & Johnstone (1970) and Nocke (1972).

(3) Is the position of the foreleg important in orientation (i.e. limb posture during orientation must bear some relationship to the direction or accuracy of the turn)? Evidence presented here is added to that derived from the studies on *Scapsepidus marginatus*.

(4) What is the minimum information required for successful orientation? By analysis of orientation patterns during interrupted song stimuli it has been possible to make some statement on the number of syllables needed by the female to complete orientation.

METHODS

The pattern of the experiments described in this paper is centred on the elegant experiments using video analysis of Murphey (1971) and Murphey & Zaretsky (1972).

Adult virgin female *Teleogryllus oceanicus* with a post-imaginal period of more than 14 days were used throughout the experiments. Insects were acclimatized to the 'home-tube' situation by placing numerous rolled cardboard tubes in the holding tank before experimentation. This meant that the insects could be picked up from the holding tank in these tubes and placed in the experimental arena with the minimum of mechanical disturbance. The sound stimulus was produced through a pair of 57 mm 'Peerless' tweeters placed vertically on the floor of the arena. The arena itself was a cardboard disc 90 cm diam. and marked in 25 mm squares, it was surrounded by material with low sound reflectance.

The video camera was arranged to produce a dorsal view of the insect (i.e. vertical to the squared background of the arena). This allowed an accurate measurement of the relative position of the insect on the video screen as well as its position relative to the sound source. Measurement of posture and angular movements were made directly from the screen using the recorder's 'stop' facility. This allowed scan-by-

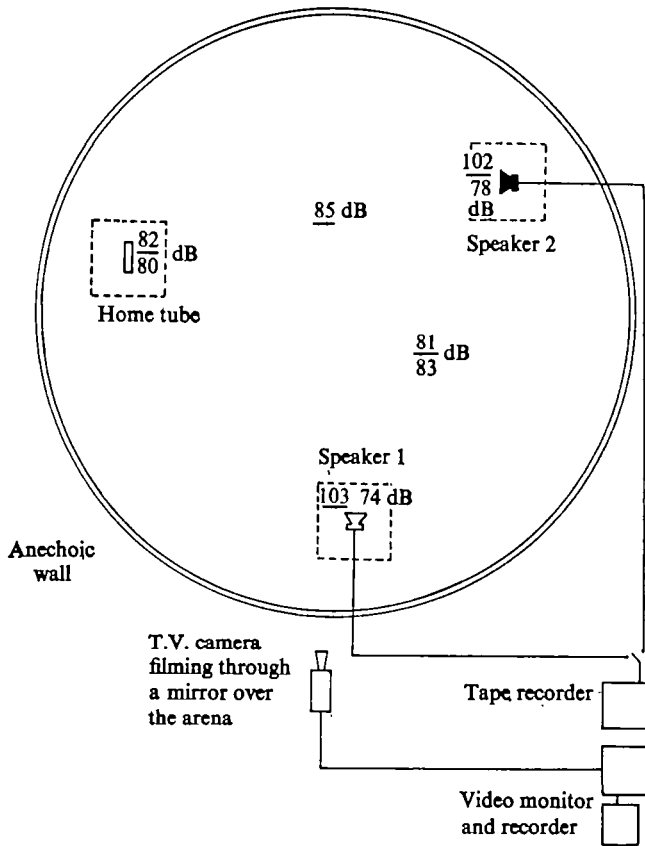


Fig. 1. Plan of the arena showing positions of stimulating and recording apparatus. Movements within the dashed boundaries were excluded from the analysis. Sound intensities are shown, those underlined refer to speaker 2.

scan analysis with an interscan time of 40 ms. Care was taken to avoid errors through spherical aberration.

Females were placed in the arena in their home tubes (Fig. 1) and left in this position for 3 min after which the sound stimulus was played from one of the two loudspeakers. If the female did not emerge within 10 min the insect was removed. The sound stimulus was a looped tape of a section of the calling song (Fig. 2). Frequency analysis of the song from the speaker gave a reasonable facsimile of the original song. The sound level at the centre of the arena was between 81 and 85 dB.

The tympana in the operated individuals were either dampened with an application of a rapid-drying paint or smeared with petroleum jelly. Experiments were always preceded by a filmed control orientation routine, thus if there was no clear orientation in the unoperated individual they were not used for experimentation.

Description of the song of T. oceanicus

The song of *T. oceanicus* has been described in the context of its function in pre-mating isolation (Hill, Loftus-Hills & Gartside, 1972) and its genetic control by Bentley (1971). The essential feature relevant to these experiments is summarized

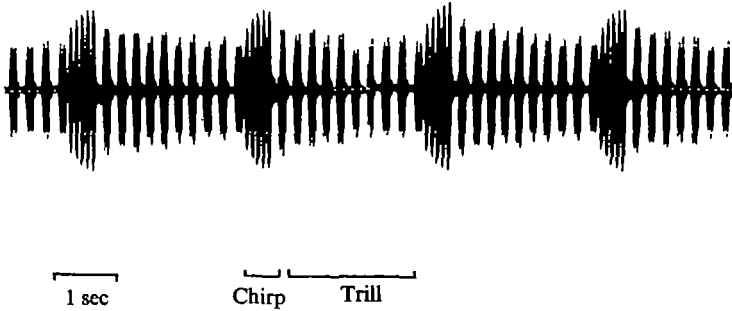


Fig. 2. Oscillogram of loop of song used as the stimulus. The naturally produced song is continuous and is illustrated in this experiment by a phrase of a five-pulsed chirp followed by 10 double-pulse trills.

in Fig. 2. The song has a carrier frequency of 4.5 kHz which is modulated by a series of syllables forming (a), the trill of a variable length with 8–10 double syllables, and (b) a chirp of 5–7 syllables in rapid succession. The total effect is a continuous stimulus of trill syllables interrupted periodically by chirp-sequence syllables. The song used for this recorded loop was a three-chirp sequence with eight double syllable trills.

Both playback recorder and speakers were capable of reproducing with reasonable accuracy the 4.5 kHz carrier frequency.

RESULTS

(1) *Orientation responses*

Of the 160 trials attempted in the course of these experiments more than 80 trials were started with the female emerging from the home tube and responding with positive orientation behaviour within a few minutes. Of the remaining trials the female could usually be coaxed out of the tube by gentle shaking and would then proceed to the orientation behaviour. These trials were used for observational experiments but were not filmed. Following normal emergence the female scanned by complete body movements the sound field, the antennae were moved in a slow but positive movement typical of orientation behaviour. Females varied in the length of time they would spend in this initial scanning. The movements are similar to those described by Murphey & Zaretsky (1972) for *S. marginatus*. After this scanning sequence the female made discrete movements towards the calling loudspeaker (target); these movements usually consisted of a turn followed by a short straight run. Occasionally there was a change in direction during the run but these changes appeared to be merely random deviations from a straight path and not directed to the target. Turns following a stop were completed in almost all cases within several cycles of leg movements (steps). As Murphey & Zaretsky discovered, the distance covered between each stop gradually increased until a maximum was reached. A typical path is shown in Fig. 3. Some females moved faster than others and these were usually associated with greater distances between stops.

Two series of televised trials were run with slightly differing filming techniques involving a total of 17 females. Both trials mutually confirmed the general conclusions

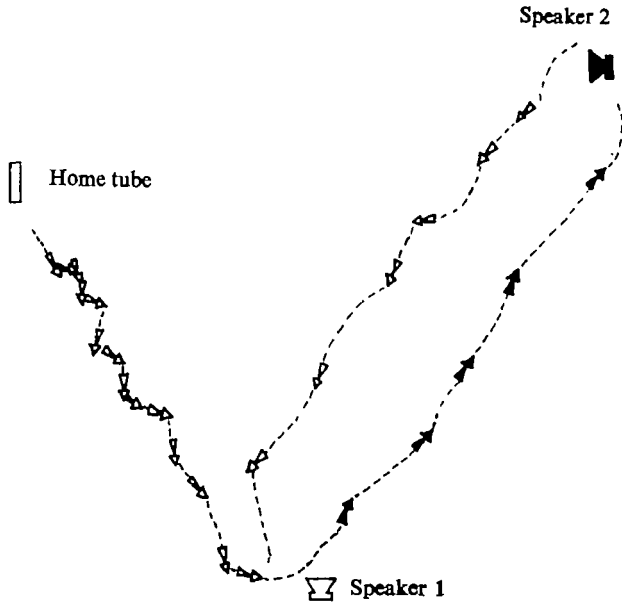


Fig. 3. Path of one female orientating to the male call song. Each arrow indicates one step of varying length, the respective speaker calling is shown by open (speaker 1) and solid (speaker 2) arrows.

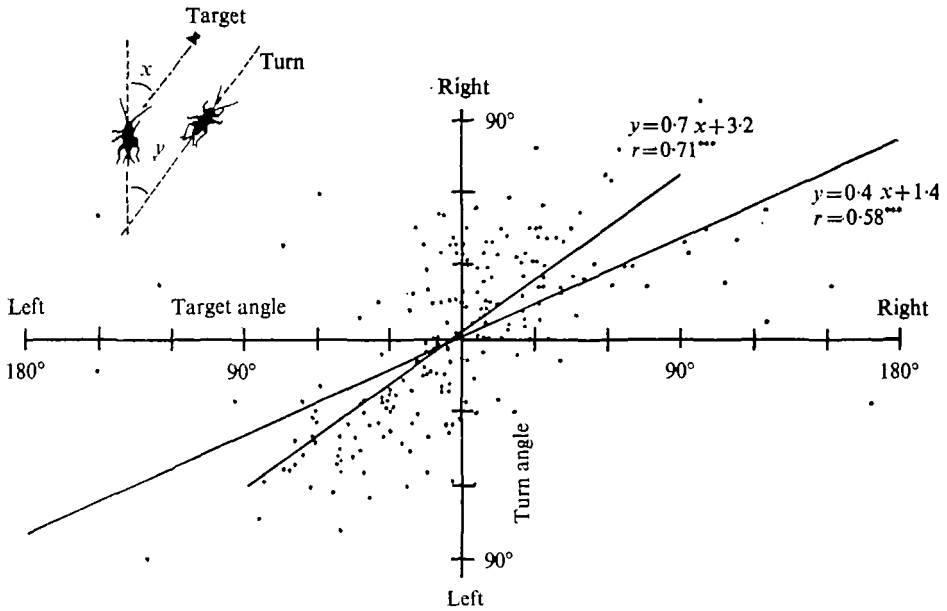


Fig. 4. The relationship between target position (angle) and turn angle. Grouped data for 6 females.

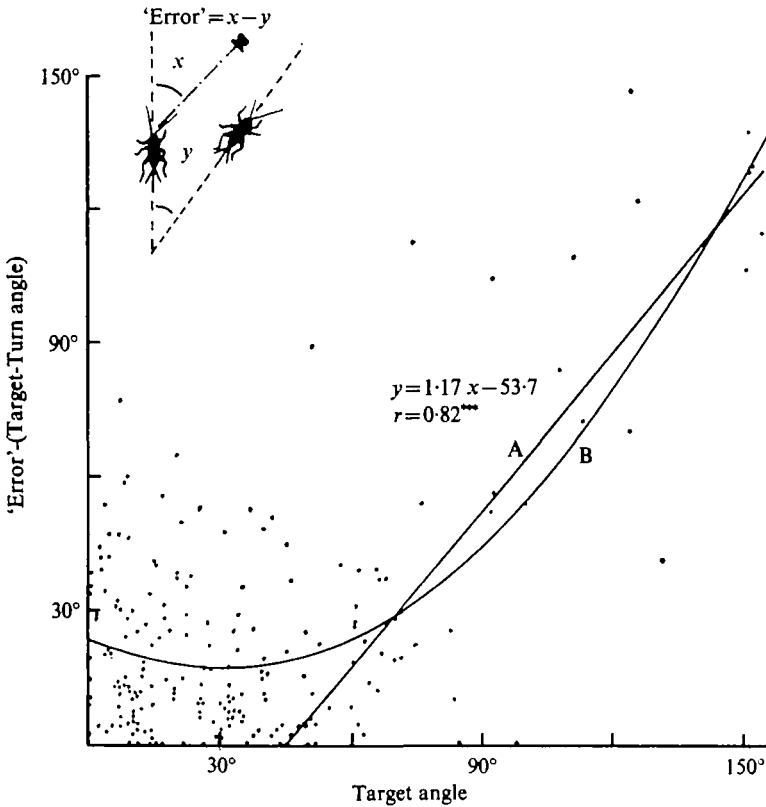


Fig. 5. Plot of the difference between the target and turn angle ('Error') against target angle. Line A is a linear regression for target angles greater than 60° , and B is a quadratic regression for all target angles.

although the second, involving 6 females, was considered to be more effectively controlled in terms of filming technique. The data from this second series of trials is presented in this work, and that from the first is occasionally used to substantiate data from the second.

The relationship between the angle turned by the insect and the target angle before the turn (i.e. the angular direction of the sound stimulus) is shown in Fig. 4 and illustrates data derived from 6 animals. Females can clearly distinguish from which side of the midline the sound is coming, 79% of turns were made to the correct side which is a figure remarkably close to the figure of 80% obtained by Murphey & Zaretsky with *S. marginatus*. The first provisional trial with 11 females produce a similar figure of 82.5%. The relevance of this ability to differentiate the side from which the sound is coming will be discussed in relation to the insect's general auditory acuity.

Murphey & Zaretsky (1972) found no evidence for the scaling of turns with target angles for *S. marginatus*; analysis of the various classes of target angles in *T. oceanicus*, however, indicate that beneath a critical angle the female is able to scale its turn (Table 1). It is evident that the female can detect angular deviation below 60° and although not statistically significant there would appear to be a

Table 1. *Turn angles elicited by various target angles in the orientating female T. oceanicus*

Target angle (°)	No. of turns	Mean angle turned (°)	S.D.	t diff.
0-30	119	23.18	16.43	3.86***
31-60	55	33.73	17.48	
61-90	23	47.74	18.82	3.16**
91-120	8	40.50	25.76	
61-90	23	47.74	18.82	0.97 n.s.
> 90	17	38.71	25.43	
0-60	174	26.51	17.42	1.73 n.s.
120-180	9	37.11	26.59	

Table 2. *Average number of pulses of song heard by different females during pauses in orientation*

♀ No.	No. of stops	Mean no. pulses heard
29	37	3.49
1	14	3.21
16	27	5.37
32	28	3.29
Total	106	3.89 (S.D. = 1.76)

greater mean angle for posterior target positions, 120-180°, than for anterior target positions. The argument in favour of scaling is taken further by analysing the error of the turn (Fig. 5), that is the difference between the target angle and the angle turned by the insect (target minus turn, signs ignored). The quadratic regression illustrates that below 30° the insect tends to scale its turn and that above this angle the errors increase with the increase in target angle until the errors approach direct proportionality over 60° (line A, $r = 0.82$, d.f. 43; slope, 1.17). Thus in terms of acuity (the ability of the insect to recognize the angular deviation of the target from its previous course), the evidence suggests that the female is able both to recognize the incident angle of the sound to the body axis and to scale its turn accordingly, albeit below a critical value. The effect of such an analysis in terms of the total phonokinetic behaviour is discussed.

Analysis of the accuracy of the turn angle against the distance from the loudspeaker showed no correlation. Hence within the range of sound intensities experienced in these experiments it is unlikely that the female is able to improve her acuity with an increase in sound intensity (i.e. as she approaches the sound source).

(2) *Song heard during a pause in orientation*

(a) *Continuous normal song*

Females varied in the length of pause between runs in any orientation programme, however, pauses were of the order of 400 ms. The number of pulses of the trill section of the song would indicate the quantity of acoustic input required for orientation. Table 2 shows the analysis of the number of double pulses heard during

Table 3. *Number of stops made by orientating females during which certain segments of song were heard (results from 4 animals)*

No. of stops	Song segment	
	Chirp only	Trill only
Observed	11	75
Expected	16	70

$$\chi^2_{(1)} = 0.74 \text{ n.s.}$$

each stop. The unit referred to is demonstrated in Fig. 2 and is part of the trill. There was no correlation between correct and incorrect turns when a comparison was made between stops during which two or less double pulses were heard and those with more than two. Further, there is no correlation between the total number of pulses heard during a stop and the accuracy of turn (target minus turn angle) ($r = 0.081$, d.f. 104).

Stops coincided periodically with the chirp part of the song rather than the trill section. The percentage of the calling song with the chirp is 18.7%, giving 81.3% for the trill section. The expected proportion of stops during which these two sequences may be heard can be calculated assuming random stopping. The expected and observed data are shown in Table 3 indicating that stopping is random and that orientation is not likely to require specifically one or the other.

(b) *Experimental disruption of the song*

Observations were made with 5 females where gaps were made intermittently in the taped song stimulus. After a stop where no sound occurred the female tended to move straight ahead; if a turn was made its direction was random with respect to the target. Stops tended to be longer where there was no sound stimulus and when the sound was recommenced during a stop the female made a correct turn to the sound source. If a female was moving away from the sound source during a quiet section and the sound was recommenced whilst it was moving, the female did not change direction until the next stop. Several stops were noted where there was an absence of song in the latter half of the stop; the female still made a correct turn. Evidence of this nature strongly supports the view that there is no information used in orientation during movement.

(3) *Orientation after tympanal disruption*

In all of the 6 females tested, disruption of the anterior tympana had no effect on side discrimination and all females located the speaker. However, in all but one case (female 24) disruption of the larger posterior membrane led to a significant rise in the number of errors, and no female was able to locate the speaker. This exactly confirms the reports of Murphey & Zaretsky (1972) for *S. marginatus*. In the one example cited, female 24, side discrimination was not significantly worse though less than normal, but its accuracy in turning was significantly below that of its control sequences.

Circular movement patterns similar for those reported for *S. marginatus* are shown in Fig. 6. The grouped data for 6 females with posterior membrane disruption are

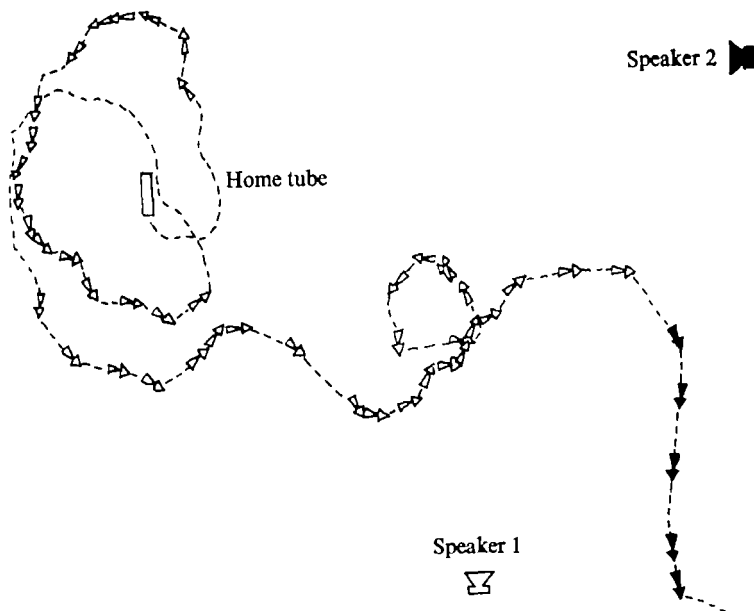


Fig. 6. Path of female with the right posterior tympanal membrane blocked. Note anti-clockwise turns to the intact side.

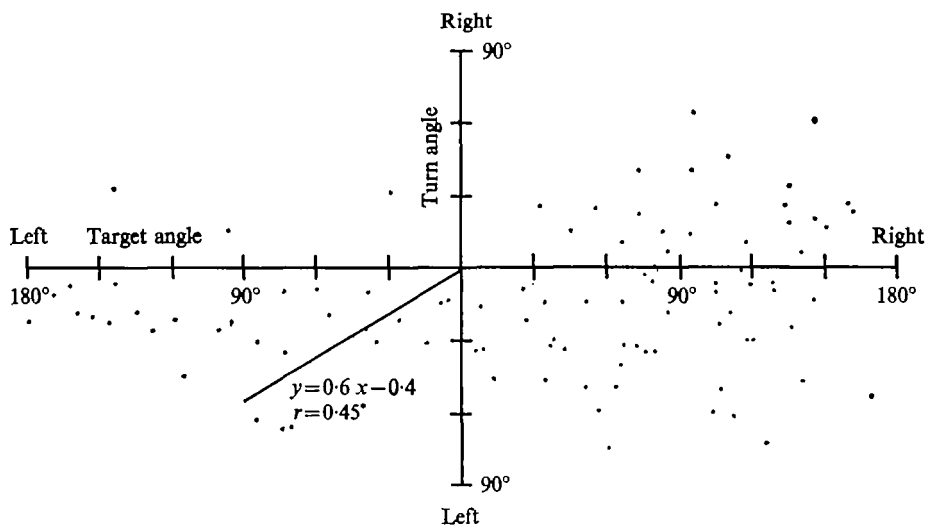


Fig. 7. Relationship between target position and turn for animals having the right posterior tympanal membrane blocked. (Grouped data for 6 females.)

shown in Fig. 7. From these data it is evident that significantly more turns were made to the intact side and the number of turns made to the operated side is biased towards target deviations on that side. This would strongly suggest that some factor other than the posterior membrane alone affects side discrimination. It is worth noting that in females with both posterior and anterior membrane disruption only

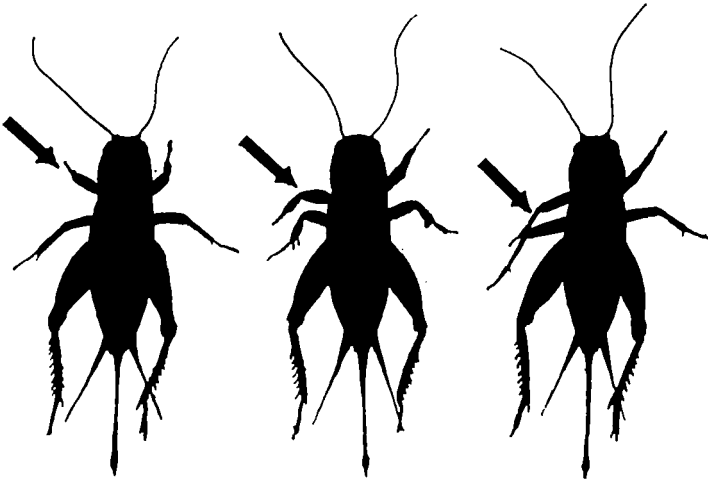


Fig. 8. The classes of femur position of the prothoracic leg. Forward, median and backward.

Table 4. Comparison of accuracy (as indicated by target, turn difference) of turns following stops during which the prothoracic legs were held in different positions (refer Fig. 8)

Leg position	No. of stops	Target minus turn ($^{\circ}$)		<i>t</i> diff.
		Mean	S.D.	
Forward	58	21.78	20.62	0.18 n.s. } 0.46 n.s.
Median	37	22.59	22.36	
Backward	4	27.00	38.45	

one turn was made in all the trials away from the intact side. This evidence might implicate the anterior membrane in side discrimination in the absence of the posterior membrane.

When the target is ipsilateral to the intact side in cases with females with only the posterior membrane disrupted, the turn elicited by the stimulus is correlated with the target angle for target angles less than 90° (left quadrant of Fig. 7). The correlation does not hold for all target angles, no doubt due to the larger proportion of target angles which are larger than 90° .

(4) Position of the prothoracic legs during pauses in orientation

Murphey & Zaretsky (1972) were not able to draw positive conclusions from their single video frame analysis of *S. marginatus* as to the relationship between leg position and turn accuracy. We have classified leg positions into three classes (Fig. 8) and data are derived from an analysis of 99 stops. Table 4 shows no correlation between accuracy, target minus turn angle (accuracy of turn) and leg position. A correlation was found at the 5% level between the angle at which the ipsilateral prothoracic femur is held and the turn angle. This correlation did not hold for females making turns in the absence of the sound stimulus, i.e. it is unlikely to be associated merely with the physical mechanism of turning.

Orientation of the tympanal membranes on the tibia with respect to the femur were observed to alter by rotation of the femur about its axis. There was thus the possibility that tibial angle, rather than femur angle, could be related to the target angle. The video technique was not sensitive enough to allow the measurement of the tibial angle, however, enough stops were examined to suggest that orientation of the ipsilateral prothoracic tibia with the target does not occur.

DISCUSSION

(1) *Side discrimination and auditor acuity*

The results of this work compliment those of Murphey & Zaretsky (1972) in that orientation is via an open-loop system where the female receives directional information while stationary and translates this into a phonokinetic response. They comment on the parallels between this behaviour and that found in both water-striders and salticid jumping spiders. Further comparison could be made with the optomotor memory described for crabs (Horridge, 1966) where there is retention of angular information before adjustment to a new stimulus. In crickets angular information is stored during the pause and rapidly translated into a motor pattern.

Two parameters emerge from the total behaviour of cricket orientation. One is the sensory input in terms of the direction of the sound stimulus and secondly the interpretation of this into locomotor output, presumably monitored by various levels of proprioceptive feedback. Side discrimination may be linked with auditory acuity; alternatively there could be a double system where the insect is able to discriminate from which side the stimulus is coming, but through various neural pathways the magnitude of the behavioural response to the angular information may contain degrees of errors. Hence, side discrimination in terms of measurable behaviour may rely on the insect's ability to swing its body through the midline axis, but the magnitude of the turn will be decided by the efficiency of interpreting that information into the correct turn angle. Errors in terms of angular deviation may therefore be cumulative, each level of sensory input and motor output would contribute its own degree of error, increasing the deviation around a mean. It is difficult to isolate these various levels of error. However, it is evident from the data presented (Fig. 5, Table 5) that side discrimination could influence target angles below 10° and the effectiveness of angular acuity expressed in terms of total behaviour could account for errors for target angles below 40° . *T. oceanicus* obviously has a preferred turn angle (Fig. 9) which could be the limit of its auditory acuity or the extent to which it can retain information while turning. Thus, once the target angle exceeds this limit ($30\text{--}40^\circ$) angular information could be progressively lost with the more complex turn manoeuvre, particularly as information affecting the turn appears to have little effect on directionality once the insect commences the locomotor phase.

If side discrimination was subject to angular limitations of the target position then one would expect a high proportion of error turns to be made around the midline. The width of that error margin would provide some indication of auditory acuity. Table 5 shows the accumulated data from the two series of experiments for each decade of target angles from 0 to 30° in the four quadrants illustrated by Fig. 4. χ^2 analysis shows that in both trials the difference between the incorrect and correct

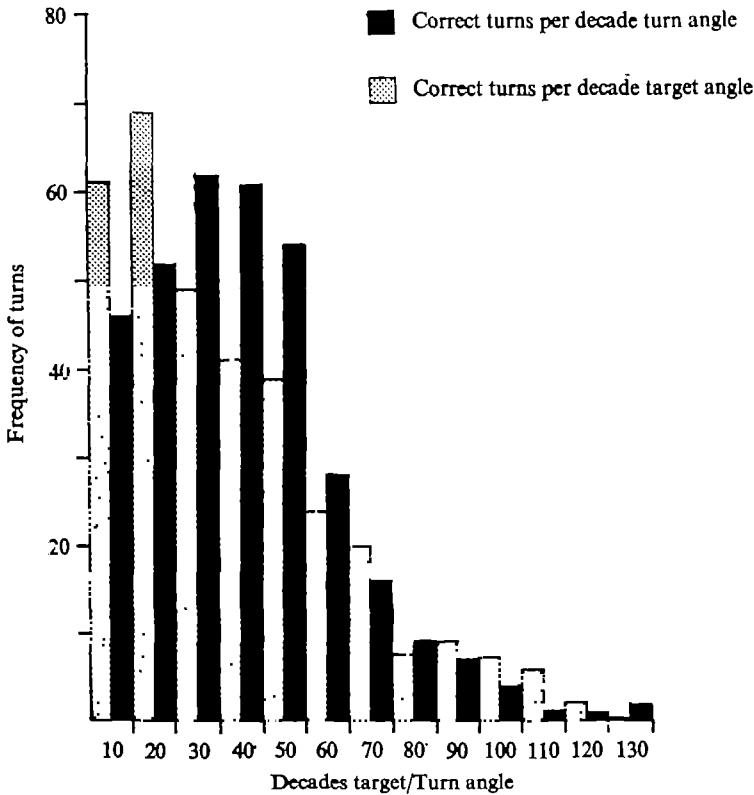


Fig. 9. Frequency of turns per decade of turn angle (solid) and frequency of turns per decade target angle (stippled) below 130° .

Table 5. Showing the number of turns to the correct and incorrect sides with varying decades of target angles below 30°

Target angle ($^\circ$) ...	Σ	(a) Incorrect left (b) Correct left				Correct right Incorrect right			
		< 30	20-30	10-20	0-10	0-10	10-20	20-30	Σ < 30
Trial I									
No. turns (a)	15	4	0	11	13	22	12	47	
(b)	42	14	18	10	5	0	0	5	
Trial II									
No. turns (a)	18	2	5	12	22	18	11	51	
(b)	39	12	11	16	5	1	2	8	

turns within 10° of the midline are not significant, whereas both trials show a marked difference in the decades 10-20° and 20-30°; a comparison between the total number of turns under 30° for correct and incorrect turns is highly significant. The same totals have been abstracted from the data on *S. marginatus* (Murphey & Zaretsky, 1972) where a similar difference was found.

Debate concerning the models of Lewis (1974) and Nocke (1974), both working with tettigoniids, is centred on directionality, the ability of the insect to gauge the target angle. Murphey & Zaretsky (1972) state that *S. marginatus* cannot scale its

turn to the target angle and that orientation in this insect is comparatively crude compared, for example, to water-striders (Murphey, 1971). We would contend that at least in *T. oceanicus*, with its very different song pattern, the female is able to scale its turn to the target angle. Fig. 5 shows a plot of target angle minus turn angle (error) against target angle and illustrates the degree to which the female is capable of scaling its turn. A quadratic function demonstrates that below 30° the female is capable of scaling its turn angle to the target. However, once this exceeds the optimum turn angle (mean target angle for all turns 25.8° s.d., 30.32 , also peak of histogram (Fig. 9) in the decade $20-29^\circ$) the insect becomes progressively worse until the error is directly proportional to the increase in target angle. The curve beyond a target angle of 60° tends to linearity with a slope approaching unity. (Line A is drawn as a linear regression for target angles over 60° - the slope of this line is 1.17.)

The optimum turn angle could be influenced by both the mechanics of the locomotor movement, and by a progressive loss of information from proprioceptors once movement had started. Phonokinesis is a highly directive behavioural activity and thus it is meaningless to compare random movements without sound to those while the insect is orientating; hence it is not possible to assert that the optimum turn angle is merely a factor of the general locomotor behaviour of the cricket. Indeed the discussion on 'errors' would indicate that this turn angle is linked to the optimum level of angular acuity.

Murphey & Zaretsky found that the number of correct side-discriminating turns was maximum with the target perpendicular to the body axis. The plot of the number of correct turns to target angle (Fig. 9) confirms this and more probably due to the higher number of observations in these experiments (330 turns) does show a slightly higher acuity than in *S. marginatus*. *T. oceanicus* could thus be used to support Nocke's (1975) hypothesis on the directionality of the hearing system. This model, however, is not sufficient to explain the high acuity to angles in front of the insect in terms of side discrimination and the behavioural explanation presented in this discussion would add to evidence from the neurophysiological work on tettigoniids. Similar work in crickets is obviously needed.

(2) *Leg position and movement*

It has been established in both this work and earlier work with *S. marginatus* (Murphey & Zaretsky, 1972) that leg-scanning movements in the Grylloidea do not directly influence orientation behaviour. Indeed, results from experiments with artificially interrupted song of *T. oceanicus* indicate that once the insect is moving there is no course correction until the following stop. Nocke (1974) suggested that orientation, if mediated by the auditory trachea through the laterally placed spiracles, would be independent of leg position and the following features of our own experiments support this hypothesis.

(a) The movement of the ipsilateral prothoracic foreleg just prior to a stop with acoustic input appears to be identical to stop positions when there is no acoustic input. Thus there is no prepositioning of the leg during a stop.

(b) The angle at which the ipsilateral femur is positioned during a stop bears no relationship to the target angle and the femur does not stop in line with the sound

source. If tibial angle is related to the femur angle, which is by no means certain, then this information would invalidate the hypothesis of Lewis (1974) at least as applied to the Grylloidea. The reason for the correlation between the femoral angle and the turn angle in the presence of the song is unclear. An explanation could be that the angle of the femur is related to the average position of the leg during orientation turns (i.e. related to the predominance of 30° turns during orientation (Fig. 9)).

(c) Most accurate turns were made when the stimulus was absent from the early and latter portion of the total stop period. Thus limb position and post-stimulus scanning (see Nocke, 1974) could not have occurred.

Preliminary observations on the orientation of the tettigoniid *Pachysagella maculata* (Hebard) indicate that the situation may not be the same in tettigoniids and that orientation could well take place while the limb is moving.

(3) Anterior membrane function

Histological studies of the tympanal organ of *Teleogryllus* (Young & Ball, 1974) clearly indicate that the anterior membrane is both small and highly damped by underlying tissue. Nocke (1972) indicated that there could be a differential function in forms of dual-frequency discrimination. We have found in females with one posterior membrane covered that there is a correlation between turn and target angle when the target is less than 90°. This can either be due to a directional property of one posterior membrane, and from general evidence this would seem unlikely, or by some input from the intact contralateral anterior membrane. From anatomical studies of this membrane this function would also appear unlikely. Further, because the turns to the intact side were less accurate than those turns made by the totally intact control of the same animal, one could assume that the cumulative effect of both anterior and posterior contralateral membrane in target angle could be envisaged. There was also a greater-than-expected number of ipsilateral turns towards the side where only the anterior membrane was present compared to fewer turns in animals with both membranes ablated. The role of these membranes require further experimentation both at the behavioural and neurophysiological level.

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