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INVERTEBRATE BIO-ACOUSTICS

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New Instances of Known or Suspected Sound Production

Evans (38) described well-defined tegminal stridulatory surfaces in a new, upper Triassic cercopoid homopteran, *Eoscartoides bryani* (Eoscartellidae). If, as he thinks, they were scraped by a femoral device, then this represents an extinct device as well as an extinct bug. Rosin and Shulov (117) described drumming sounds produced by the males of two Israeli scorpions, *Scorpio maurus fuscus* H. & E. and *S.m. palmatus* H. & E., produced by rapidly striking the mesosoma (thick part of the abdomen) against the substrate. They observed drumming (a) after fights with other males, (b) after escape of a pursued female, (c) after escape of a pursued locust, and (d) as a result of artificial "irritating stimuli". A rate difference of unknown significance exists between the two subspecies. Such descriptions of new methods of sound production in arthropods will probably continue indefinitely, but a very unusual example is Cloudsley-Thompson's (25) description of a 40-second, distracting stridulation by an automotized anal leg of the Ghanan scolopendromorph centipede, *Rhysida nuda togoensis* Kräp -- carried on while the startled former owner was darting to cover! The mechanism is uncertain, but the sound may have been caused by the inner end of an unusually large pre-femoral apodeme rubbing against the inner side of the integument.

Studies on Hearing

Roeder and Treat (115) (116) have added more to their fascinating story of the moth's ear and the bat's cry. Now they have shown that bats can be detected more than 100 feet away through amplification of the response of sensitive noctuid tympana to echo-location cries. Differences in intensity and direction could be determined, the latter more clearly when a preparation of two tympana was used. Using a stereophonic tape recorder and a preparation of two tympana in the field, they concluded that the "moth's nervous system receives information that would enable it to determine whether a distant bat was to the right or left, but if the bat was at close quarters this information would not be available." Photographs of moths and other insects show looping, twisting flight when they were subjected to simulated bat cries as they moved across a flood-lighted area. Such sounds as rustling leaves, cricket chirps, and ultrasonic components in the wingbeat sounds of other moths also initiated pulses in the tympanic nerve fibers. We are still held in suspense as to whether or not moths *really do evade bats* as a result of hearing their cries through the tympana.

In the migratory locusts, *Locusta migratoria* and *Schistocerca gregaria* (Acrididae), Horridge (55) (56) found that the 70-80 sensory axons of the tympanic nerve do not all respond identically to different frequencies. Further, differences among the inputs of sensory neurons are reflected in recordings made from connectives, for example, between thoracic ganglia -- in such ways as to indicate that the metathoracic ganglion discriminates among them. Horridge concluded that while the brain may receive rudimentary information related to the pitch of an irregular noise, pitch differences are probably of no great significance to locusts. Busnel and Loher (24) showed that in the acridid *Chorthippus brunneus* (Thbg.), stridulatory reactions to artificial sounds resembling those of the species are elicited with a consistency directly relative to the transiency or suddenness of onset of the sound. To test the effect of direction, Authrum *et al* (8) recorded electric potentials in the auditory nerves of individuals of *Locusta migratoria* subjected to directional sounds while fastened to a special rotating table. The tympanic nerve reacted more quickly and more strongly to more intense sounds, and it was estimated that the animal may be able to detect intensity differences of about 20 db. on its two sides. A directional function in the third thoracic ganglion was postulated. Suga and Katsuki (131) found that in the katydid, *Gampsocleis burgeri* (Tettigoniidae), the tympana respond to sounds ranging from 0.6 to 75 KC, with a sensitivity peak at 10 KC; and the cerci respond between 30 and 2000 cps, with peaks between 400 and 500 cps. Tympanic nerve fibers transmit information to the prothoracic ganglion, and then -- after a delay of about 12 msec. -- simultaneously to the brain and the metathoracic ganglion. Cercal fibers transmit eventually to the mesothoracic ganglion. Most interesting was their finding (later confirmed pharmacologically (132))of inhibitory interaction between the tympanic nerves on the two sides of the animal, suggesting a central nervous system role in sharpening information relating to intensity differences on the two sides of the animals, and thus accenting the already considerable directionality of the tibial tympanic receptor system. This mechanism did not seem to be present in the cercal system. They also found that the number of impulses transmitted from the side nearer the sound source is greater, and the difference is most marked at the frequencies dominant in the species' stridulation: "This difference is due to the mutual inhibitory interaction of neurones which modifies the number of impulses without changing the threshold of the tympanic large fiber." By its nature, the tettigonioid system has a greater evolutionary potential to directionality than that of acridids or cicadas, and one wonders how much this has influenced the directions of elaboration of acoustical communication in these different animals.

Meske (96) found that four centipedes, *Glomeris marginata*, *Polydesmus angustus*, *Cylindroiulus tentoricus*, and *Schizophyllum subulosum* all give disturbance reactions (pausing and moving the antennae, curling the head and first body segment) to tones between 100 and 2000 cps, the first three species invariably at 500 and 1000 cps, and the fourth invariably at 1000 and 2000 cps. A similar reaction previously demonstrated in *Lithobius forficatus* was greatly reduced with destruction of a specialized organ on the head. No difference between species were observed, and no sound production is known in these species.

In the area bordering that of "hearing" in the narrow sense, Liesenfeld (73) calculated the amplitude threshold of the vibration response in the metatarsal lyriform organ in the spiders, Zygiella x-notata (Cl.) and Tegenaria sp., to be from 10^{-3} to 2 x 10^{-3} cm. between 10 and 100 cps, to decrease between 100 and 600 cps in Tegenaria to about 10^{-7} cm., and hold this value between 600 and 4000 cps. In Zygiella the threshold decreases continuously above 600 cps to about 10 A. at 5000 cps.

In a physiological study related to acoustical behavior, Voskresenskaya and Svidersky (152) found that in Cicada ornia the timbal rhythm of 180 vibrations per second can be produced with only 45 stimulations per second of the timbal or sympathetic nerves. But because the rapid response can be measured in the mesothoracic ganglion, timbal nerve, and sympathetic nerve as well as in the timbal muscle, and because it could be eliminated by eliminating participation of the sympathetic nerve, Voskresenskaya and Svidersky conclude that it is neurogenic rather than myogenic.

Signal Analysis

Moore (105) illustrated by audiospectrograms and described in detail sounds of 11 species of Hempitera and 13 species of Homoptera, and he went into the technical details of recording soft sounds of tiny insects. Six stridulatory structures are listed for hemipterans: prosterno-labial in Phymatidae and Reduviidae; tergo-alary in Cydnidae and Piesmatidae; and tibio- or femoro-tergal, -pleural, or -cephalic in Corixidae and Aradidae. All homopteran sounds mentioned are produced by tergal abdominal timbals (Cercopidae, Cicadellidae, Membracidae, Fulgoridae). Hemip-homop sounds are grouped as (a) common, (b) courtship, and (c) disturbance signals. Although all are fairly simple sounds they are definitely specialized. But Moore added that no acoustical function has been demonstrated in any of the above groups; no auditory organs are known; and it is not even possible to speculate confidently as to whether principal reception might be through air, water, or substrate, when alternative possibilities exist. Species differences occur, and water boatmen, froghoppers, leafhoppers, and treehoppers were recorded sonifying in the absence of external disturbance.

Esch (37) analyzed the sound made during the straight run of the honeybee waggle dance and found it to be a 250-cps signal lasting about 15 msec. It was made up of pulses and intervals of equal length delivered at a rate between 35 and 40 per second. He could not directly correlate sound and distance of feeding place.

Communicative Interactions

Alexander (2) emphasized acoustical behavior in a study of aggressiveness, territoriality, and sexual behavior in field crickets, showing that there is more chirping in intensely aggressive encounters, that aggressive chirps alone can elicit the entire repertoire of aggressive actions in a hyper-aggressive male, and that aggressive sounds reinforce the subordination of a male which has just lost a severe fight. Playbacks of aggressive chirps coupled with artificial antennal lashing could be used to reverse repeatedly the dominance status of two males by continually eliciting aggression in the dominant and then defeating him with the articial stimuli. Three "basic" sound signals (calling, courting, aggressive) are illustrated by audiospectrograms for eight field crickets representing six genera and two sub-families (Brachytrupinae, Gryllinae). Calling songs show more differences than courtship songs among sympatric, synchronic species. According to Alexander this is because they represent an earlier operating mechanism in the mating sequence and therefore are more efficient as reproductive isolating mechanisms.

Books and Reviews

Cohen and Dijkgraaf (26) briefly summarized what is known of hearing and sound production in Crustacea. Defining hearing as special sensitivity to air- or water-borne successions of waves conducted at characteristic velocities, and excluding solid substrate transmission, they noted that "hearing" has not been demonstrated in any crustacean, though "sound reception" has been observed with some probability in a few instances. "Vibration perception" seems to be rather common (in general evoking only "flight reactions or reflex-like jumps directed away from the source of vibration"), and three types of of sound production are known: (a) "snapping" closures of enlarged claws in shrimp upon disturbance; (b) creaking, filing, and scraping sounds (produced by rubbing a specialized antennal pad across the rostrum) in palinurids that are disturbed or struggling with one another; and (c) stridulation in various crabs by structures that are sometimes better developed in the male or absent in the female, the sounds seeming to be higher-pitched and louder if the animals stridulate while in their holes and (perhaps) to "serve to warn trespassers that a burrow is occupied."

Haskell's book (54) is the third dealing with insect acoustics. It is more general than Pierce's (1947) book and the 1955 orthopteran acoustics symposium volume edited by Busnel, and it follows both by a sufficient interval to allow it to bring together a considerable amount of new information. Seven chapters are included: recording and analysis; sound-producing mechanisms; hearing; song patterns; behavior associated with sound; "some physiological aspects of acoustic behavior"; and "sound in the insect world". There are some awkward passages, and some of the illustrations could have been improved.

Thus, fig. 8 does not resemble Pterophylla camellifolia, and fig. 78 is the sketchiest sort of representation of meadow grasshopper wings. On pp. 167-168, Haskell renews his old "argument" with Busnel and co-workers as to whether or not transients or pulse rates are the significant characteristics of insect songs. In fact, a minimal transiency seems necessary to cause sound to be significant to orthopterans, or even to produce a pulse rate, for that matter. This does not deny that either pulse rate or transiency is important. On the contrary, it emphasizes the significance of both. Further, it seems clear that species differences in response are likely to be considerable, for example, in an insect which trills continually at a rate of 75 pulses per second versus one which produces a single pulse at irregular intervals of several seconds, or in an insect in which timing between male and female sound units is most significant. Haskell and Busnel have in some cases used as examples insects in different families, and insects which produce sounds differing in precisely the respects mentioned here. But these are minor criticisms. Haskell has brought together a great deal of material in a clear fashion, and this is a very worthwhile book. Together with Frings and Frings (1958: Ann. Rev. Ent.), Alexander (1960: AIBS Publ. 7), and DuMortier, Huber, and others (in press: In Busnel, Animal Acoustics), it will bring reviews of insect acoustics approximately to the beginning of the present review.

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