HEARING AND STRIDULATION IN SPIDERS

BY

Fr. CHRYSANTHUS, O.F.M. Cap.

Voorschoten

The question whether spiders can hear or not, is answered hesitantly and vaguely by several authors and their answers are summarized by GERHARDT & KÄSTNER in the following sentence: "Gehörs-Empfindungen sind bisher nicht bei Spinnen nachgewiesen worden" (1937, p. 432). These authors, however, are of opinion that MEYER'S observations (1928) upon the stridulation of some species of spiders (see p. 63 of this paper) suggest that at least some kinds of them have the faculty of hearing. MILLOT has even a still more negative opinion when he writes: "on a quelques raisons de croire que les araignées n'entendent pas au sens propre du mot" (1949, p. 611) and further on: "Les recherches récentes amènent cependant à douter fortement que ces Arthropodes entendent, au sens véritable du terme" (Ibid. p. 631).

The presence or absence of hearing in invertebrates, and even in fishes is, as we know, a much discussed problem. Yet it would seem that if one combines the random observations and takes into account the results of some recent researches on various insects about this question, we may form a conclusion which is somewhat less vague and somewhat more decisive than that posed by GERHARDT & KÄSTNER, and MILLOT.

Our argumentation will proceed along the following lines: first after having explained what we mean by "hearing" we wish to put the question whether spiders react upon sounds; next we will discuss the stridulation in ants and spiders, the nature of the stridulatory sound and the problem whether congeners perceive the stridulation. According to our notion of "hearing" we will then try to find out whether air-borne sounds are perceived directly by them and in which way. After that we will try to solve the problem in which part of the body hearing is localized and finally give some remarks upon the biological significance of sounds to spiders.

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THE NOTION OF "HEARING"

There is much dissension — largely as a consequence of the different meanings attached to the word — about the question whether the lower animals possess the faculty of hearing. We shall not attempt to give a solution of theoretical questions, but following AUTRUM, HASKINS & ENZMANN, PUMPHREY and others we simply intend to make clear which meaning we wish to put on the term.

When we speak about "our" sensation of hearing, i.e. about human hearing, we have a well-defined idea of what we mean by that word, however difficult it may be to formulate it. The question whether animals enjoy the same sense of hearing as we ourselves, in other words, whether their sensations of hearing are of the same nature, is useless because we cannot enter into animal sensations at all. Consequently the problem whether some animals have the faculty of hearing can have but one meaning: can these animals perceive sounds or not ? — You might prefer for "hearing" the more general word "phonoreception" because it has not such an anthropomorphical sound. — The reaction of an animal upon a particular sound is the only indication which may make us conclude whether the animal has perceived this particular sound or not.

Sound waves are propagations of periodic vibrations in gaseous, liquid or solid objects. As spiders — save *Argyroneta aquatica* (Cl.) — are distinctly terrestrial animals, and as hardly anything is known about the perception of vibrations in liquids, by insects least of all, we drop this matter. According to the general usage and in imitation of most authors we do not call "hearing" the perception of vibrations in solid objects, but we attribute these perceptions to the sense of touch, especially the sense of vibrations (1). Finally we leave out of account the vibrations which are propagated through the air, but which the animal (also) perceives or at least could perceive because they set into co-vibration the substrate upon which the animal has settled (e.g. soil, web); for in this case we are not able to decide wich sense is the origin of any reaction.

With HASKINS & ENZMANN we should like to define hearing as "the power to perceive sound vibrations aerially transmitted" (1938, p. 98) or "the perception of and reaction to aerial vibrations" (ibid. p. 100). For clearness' sake it would be useful to add to the first definition "...perceive *directly*..." and to the second "... vibrations which affect *directly* any part of the body".

Some authors restrict the notion of hearing further by requiring the presence of a tympanum or tympanal organ (e.g. v. BUDDENBROCK 1937) or a cochlea (v. FRISCH & STETTER 1932). In the first case fish and in the second locusts, crickets etc. would be deaf by definition. At present, however, it is rather commonly assumed that these animals have the faculty of hearing. When speaking about these and similar animals it will be of use to give up all anthropomorphical ideas, to meet the facts objectively and not to hinder research by "a priori" demands (2).

DO SPIDERS REACT UPON SOUNDS ?

It is beyond all doubt that spiders sometimes react upon sounds. There are several credible stories of spiders emerging from their webs when there is music in the room and of their trying to approach as near as possible the source of the sound. Then they either remain on the ceiling and move when the source of the sounds moves or they drop at the end of a thread over it. We know observations of such behaviour at the sounds of a harp (WALCKENAER, entomologist, 1771—1852), a bagpipe (PELLISSON, literary man, 1624—1693), a harpsichord

(Grétry, musician, 1741—1813), a lute, a violin, and of singing (3). In an interesting book, suggesting us to take spiders as weather prophets, Quatremere-Disjonval (1795) recounts some similar stories with regard to a violin and a harp. Baglivus informs us in his study on the *Tarantula* (1699) that the peasants in the environment of Tarentum lure this spider out of its underground dwelling by imitating the humming of a bumble bee by means of a little reed pipe. Hudson (1892) says that several times he saw spiders walking in the direction of the sound of a guitar. Reclam (1859) recounts that at a concert in Leipzig he saw a spider descend from a lustre while a fiddler played a solo, but rapidly going back to the lustre as soon as the orchestra joined in. During the winter of 1948—1949 I myself observed the following case. While sitting near the fire with some colleagues to enjoy an hour of recreation I noticed on several successive evenings that a small spider came down from the ceiling at the end of a thread and stayed there between us, its legs spred; a closer inquiry revealed that it was a very small (3 mm !) adult male of *Theridium tepidariorum* C. Koch. Of course we were not singing, but talking: so I am inclined to infer that in the other cases, too, the spiders had been attracted not so much by the music, as by the sound as such. This is confirmed by the statement of O. Pickard Cambridge (1881), who saw some orb web spiders react upon shouting, and by an information of the French sculptor Maillol to Berland : whenever Maillol was cutting a statue in his studio, a spider came near him hanging on a thread (Berland 1932, p. 175). If we were not so careful in removing spiders out of our homes, and if we should pay more attention to them, observations of this kind would probably be much more numerous.

The cases just mentioned are but occasional observations ; in order to answer the problem in question exactly scientific researches are of course of much more value.

Boys (1881) first tested the behaviour of orb web spiders by putting a vibrating tuning fork on some point of the web : they reacted promptly by running quickly to the vibrating point ; their sense of vibrations may have been the origin of these reactions either exclusively or at least partly. Next he lured the spider to the tuning fork in the same way, then removed the fork from the web and after that he kept it still vibrating near the spider, but not upon the web : in this case he describes the reactions of the spider as follows : "The spider is aware of its presence and of its direction and reaches out as far as possible in the direction of the fork" (p. 150). When, however, he approached the vibrating tuning fork near the spider in the centre of its web without these preparations, the spider would drop at the end of a security thread.

The Peckham's (1887) first observed that spiders at rest in their webs did not react upon shouting, clapping and whistling in their immediate neighbourhood ; only "*Astia vittata* Hentz, when standing on a finger, jumped to one side when 'bang' was shouted in a loud voice, with the head turned away ; and when we whistled, it stood on the tip of its abdomen with its head held high" (p. 390). Imitating Boys, they used tuning forks in their further experiments in order to have a more "adapted" noise. Two of these forks were small (high-pitched) and one large (low-pitched). When they took one of these forks, not in vibration, near a spider standing in its web, they did not observe the slightest reaction. Large females of *Epeira strix* Hentz (= *Araneus cornutus* Cl.) standing in the centre of their webs did not notice the small vibrating tuning forks, "but when the large one was sounded, she raised her first legs almost vertically, holding them as though ready to ward off an attack" (p. 390). When the fork was sounded and taken to one side of her, she also moved the leg of the second pair on that side toward the fork. A small female of *Epeira labyrinthea* Hentz (= *Metepeira labyrinthea* (Hentz)) responded to all three forks ; five small individuals of *Epeira strix* got particularly excited at the sounds of the small forks. When they held the big fork in vibration over a large male of *Epeira insularis* Hentz (= *Araneus marmoreus* Cl.), an inch and a half up, "he threw up his first legs, making frantic efforts to reach it" (p. 391). A female of this species acted as the male had done, but seemed less exited by the vibrations. When they held the tuning fork near a female of *Epeira infumata* Hentz (= *Wixia ectypa* (Wlk.)) standing quietly on a wire screen, the spider did not move. "She was then placed in the web of another spider and the large fork was brought near her as she stood there. She appeared frightened and at once threw up the first and second pairs of legs. The fork was next held behind and to one side ... she turned toward the fork and almost fell backward in her efforts to reach it" (p. 391). A female of *Argiope riparia* Hentz (= *Argiope aurantia* (Lucas)) reacted in a similar manner. A young *Phillyra mammeata* Hentz (= *Uloborus mammeatus* (Hentz)), a cribellate spider, lifted the forelegs in response to a small fork. Several other spiders, e.g. some females of *Epeira labyrinthea,* dropped at the end of a security thread, whenever one of the forks was sounded near them. After having reacted in this manner several times they remained on their webs and merely raised their first legs. *Cyclosa conica* Pallas, too, reacted in the same way but ordinarily it did not raise its front legs. All these experiments were repeated many times and continually alternated with check experiments. After that the PECKHAM's tried their tuning forks upon spiders without a web (wolf spiders e.g.): they never reacted.

VAN HASSELT (1893) mentions the following : "When one takes a blue bottle by its legs and makes it buzz in the immediate neighbourhood of the funnel-shaped enlargement of the web, one succeeds frequently in luring the spiders out even from their remote hiding places especially in the case of several species of the Agelenidae" (1893, p. XLV).

PRITCHETT (1904) tested two wolf spiders : she placed the animals into well isolated small cages with a bottom of mosquito netting. Then she brought several tuning forks of different pitch (128, 256, 320, 512 c/sec.) to the bottom of the cages : no reaction. Neither the beating of a hammer on a piece of steel (± 2300 c/sec.) nor of an iron bar on a trowel could induce the spiders to reaction.

FABRE (1905) observed that *Epeira angulata* Cl. (= *Araneus angulatus* Cl.) imperturbably continued the making of its web although a large crowd of people in festive mood passed at a distance of a few feet with fanfare, squibs and fireworks.

MC INDOO (1911) repeatedly put some crickets near a wolf spider (*Lycosa* spec.) and a jumping spider (*Phidippus* spec.): the spiders, however, reacted neither to the high tone of the young crickets, nor to the low tone of the old ones. In the open air, too, he made a similar observation.

GRÜNBAUM (1927) first observed the reactions of *Epeira diademata* (L.) (= *Araneus diadematus* Cl.) on vibrating tuning forks, placed *on* the web ; next he tried the effect of vibrating forks at some distance from the spider. When he advanced a fork (48 c/sec.) from some distance to 1 or 2 cm from the spider standing in the centre of its web, the animal put itself and the web into vehement vibrations. When he used another fork (128 c/sec.) the spider only convulsively stretched its palps, and the longer the tone continued the higher the palps were lifted ; the reactions were the same when the spider had settled on a single thread or on a solid substrate. A fork with a very high pitch (2048 c/sec.) did not cause a distinct reaction ; only when it was advanced silently near the spider and then suddenly struck, the spider reacted.

MEYER (1928) struck a tuning fork at a distance of 3 cm behind a *Dolomedes fimbriatus* (Cl.): the animal directly turned round. When he attached a fly to the fork, the spider pounced upon it after turning round. Most probably the fork did not touch the substrate on which the spider was sitting, for the author says : "Sie hatte auf jedem Fall die *Luft*erschütterung der Stimmgabel wahrgenommen" (p. 60). What he means a little further by : "Der vibratorische Reiz wirkt auf Entfernungen von 1 m und noch mehr" (p. 61), is not clear.

STRIDULATION

Before investigating the above mentioned data a little more closely we should first consider the problem of stridulation in spiders. By stridulation is understood, as we know, the causation of sound by the movement of one or more spines or of a rasp over a fine-ribbed plate (PROCHNOW 1928, calls it the "Schrillplatten-typus") or of two crossing rasps ("Schrillkamm-typus") (p. 63). These stridulatory organs are found in several groups of insects. As stridulation in ants shows much resemblance to that in spiders, and several investigations with ants in this department are of interest in spiders too, we are dwelling on this subject a little longer ; afterwards we shall also have to return to it occasionally.

Two subfamilies of ants, the Myrmicinae and the Ponerinae, possess a stridulatory organ of the "Schrillplatten-typus": the fine-ribbed plate (the mutual distance of the ridges varies from 0,5 to 3 micron) is in the middle of the front side of the third tergite, whereas the comb is on the second tergite (4). If an ant moves its abdomen alternately up and down, the comb is rubbed along the plate : this makes the stridulating movement.

After LANDOIS had discovered this organ in a Ponerin ant in the year 1874 (p. 133), there was for a considerable time a fierce argument in the camp of the myrmecologists about the question, whether is was really a stridulatory organ, i.e., a sound producing organ. LUBBOCK (1882) believes that *Lasius flavus* Fabr. possesses a stridulatory organ; but as no sounds have been perceived in this animal, he thinks that ants — at least some of them — produce sounds, which, however, are not audible to us (p. 229—233). Although several observers had heard the sound clearly, the received opinion was that, if ants made noises, they would be above the humanly audible range (above ± 20.000 c/sec.).

RAIGNIER, partly in conjunction with WIERSMA (1932, 1933) succeeded in making visible the stridulation of several ants by means of an oscillograph; he proved that the sound varies between 200 and 2500 c/sec., i.e. distinctly within the compass of the human ear. HASKINS & ENZMANN (1938), who used a quite different method, concluded that the stridulation of four species of ants, thoroughly investigated for this purpose, varied between 500 and 7400 c/sec. They give as their opinion: "... that the inaudibility of the stridulatory note of small ants is due, not to its very high pitch, but purely to lack of sufficient volume to induce oscillations in the human tympanum" (p. 123). RAIGNIER held the same opinion, and both investigators think that the stridulation is meant to alarm congeners. To HASKINS & ENZMANN it seems most probable that the vibration is transmitted by the ground, not by air waves (p. 142). The origin of LUBBOCK's error is the fact that these experiments are made with a kind of ant, *Lasius*, which possesses no stridulatory organ at all !

In the year 1936 AUTRUM published the result of his research in this field; it is a pity that he had not seen the publications of RAIGNIER and WIERSMA: this is not so surprising because they were written partly in Dutch, partly in French, and moreover the French publication appeared in a Portuguese periodical. He takes a different view of the question but does not refute the preceding opinion. He holds that the human ear is so sensitive to sounds from 800 up to 2000 c/sec. — exactly the field of the stridulatory sounds of ants — that a still greater sensitiveness would be intolerable. Between these limits therefore the production of sounds too feeble for our ears seems highly improbable to him. Even if ants could make such feeble sounds their power of penetrating would be extremely small and it would be hardly possible that they had a biological importance.

Stridulation occurs in spiders too. In the year 1843 WESTRING published his discovery of a stridulatory organ in a male of *Asagena serratipes* Schrk. (= *Asagena phalerata* (Panz.)), a member of the family of Theridiidae (1861, p. 175). It shows much resemblance to that of ants: the ribbed plate is on the back of the cephalothorax, a chitinous collar set with fine teeth is on the front of the abdomen. Gradually similar organs were discovered in several males of Theridiidae (*Steatoda bipunctata* (L.), *Teutana castanea* (Oliv.), *Lithyphantes albomaculatus* (de Geer), and several *Theridium* spec.; all these species — with the exception of *Teutana* — occur in the North-West European countries. Already in the year 1875 VAN HASSELT showed some mounts of stridulatory organs of Theridiidae at the Winter meeting of the Netherlands Entomological Society (5). In *Steatoda bipunctata* the ribbed plate measures 0,7 mm; at the beginning of the plate (the back of the cephalothorax) the distance of the ridges is more than twice as large as at the end; their average distance is 11 micron.

Quite another type of stridulatory organs occurs in the males of several Linyphiidae e.g. *Leptyphantes* spec.: here the ribbed plate is on the side of the chelicerae and a chitinous thorn is on the inner side of the femur of the palpi. The same type occurs in several tropical bird-catching spiders (Aviculariidae) too, but in these kinds also the female possesses a stridulatory organ. In the course of years eight or nine different types of stridulatory organs have been discovered in divergent families of spiders; among these there is but one case of the "Schrillkamm-typus", all the others are of the "Schrillplatten-typus" (6).

Many of the discovered stridulatory organs are described from animals in museum collections; on a small scale stridulating movements are observed in the living animal: the abdomen is moved alternately up and down, and this movement makes the comb strike along the ribbed plate, so that what happens is the opposite of what takes place in ants. In a few species only stridulatory sounds have been really heard.

THE NATURE OF THE STRIDULATORY SOUND

According to RAIGNIER the fast succession of the small plops caused by pushing the comb over a ridge brings about a small chirping "which can be compared... with that of a cricket but much smaller" (1950, p. 79). This chirping continually varies in pitch and intensity. Sometimes a pure tone (sine curve) turns out to be superposed above the usual curve of the plops; this tone however is very feeble (7).

The sound observed with spiders is described rather differently. *Sicarius*, a species from East-Africa, allied to *Scytodes*, possesses an organ that shows much resemblance to that of the *Leptyphantes* spec.; the sound is produced both by females and males and resembles the buzzing of a bee. With several bird-catching spiders it is rather loud and according to WOOD MASON (1877) it resembles the noise obtained when one strikes the back of a knife across a strong comb; according to SPENCER (1895) the stridulation of an Australian bird-catching spider constitutes a sort of hissing. MEYER describes the sound of another bird-catching spider as "ein schnarrendes Geräusch" (1928, p. 7). He was the first to succeed in making audible — in natural circumstances (8) — the stridulation of *Steatoda bipunctata* and *Teutana castanea*, two Theridiidae. After it had appeared to him that the males of these species never used their stridulatory organ when by themselves, he placed a male near a female, which had made a small web in a tube of glass, 13.5 cm high and 5 cm in diameter. As soon as the male touched the threads of her web he made stridulating movements; during the introductory part of the copulation the movements were very intense but during copulation itself there was no stridulation at all. In both species the sound could clearly be heard, according to the investigator, owing to the strengthening by means of the glass tube. In *Steatoda* the sound was already heard at a distance of 10 cm, in *Teutana* at a distance of 20 cm. In the first species the tone had a metallic sound such as is obtained by plucking a steel string and it was identified as e' (325—345 c/sec.); in the second species the tone was dull and it was identified as a' (435 c/sec.). The experiments were repeated several times and the identification of the pitch was made by the experimentator and several "musikverständige Personen" independently of each other; their judgement was unanimous; so it seems that a pure tone is produced (7).

These considerations and facts lead us to the certain conclusion that stridulation both in ants and in spiders — at least in some cases — causes a sound audible to man. As to the origin of this sound we might put the following question: does stridulation immediately produce sound waves which are transmitted through the air (AUTRUM calls this "Luftschall"), or is the stridulation only the cause that the substrate whereupon the stridulating animal has settled gets into vibration and the substrate sends out sound waves in the air ("Körperschall") ?

AUTRUM (1936) holds that stridulating ants do not cause "Luftschall" either within the compass of the human ear (up to some 10.000 c/sec.) or beyond this range (from ± 10000 up to ± 100000 c/sec. „supersonic sounds") but only "Körperschall". When he held a stridulating ant at a distance of 1—2 mm from the membrane of a very sensitive condensor microphone which was coupled to a loudspeaker via an amplifier, no sound was perceived nor any supersonic sound could be demonstrated. When he did the same with two kinds of beetles *Necrophorus vespillo* L., a burying-beetle, and *Geotrupes stercorarius* L., a dung-beetle, supersonic sounds could indeed be demonstrated. As soon as one of the stridulating ants touched the membrane, even with one foot only, a sound very much resembling the chirping of a capricorn-beetle was clearly heard in the loudspeaker. From this he concludes that the body of the ant transmits to the substrate the vibrations produced by the stridulation; according to him the stridulatory sound is not radiated immediately into the air because the radiating surface is too small and the intensity of the vibrations is too poor. "Wenn man sich vorstellt, die Membran eines Lautsprechers habe die Grösze eines Ameisenabdomens: ein solcher Lautsprecher wird keine nennenswerten Energien (Lautstärken) an die Luft abgeben können" (p. 340).

BAIER (1930) maintains that the wingshells of beetles amplify the stridulatory sound: having cut part of the wings of *Crioceris* spec. the stridulatory sound became much weaker. Regarding the stridulation of ants he says: "PROCHNOW (1907—09) believes that the stridulation of ants is generally not heard because of the lack of suitable resonators. From the fact that the corporal dimensions of *Crioceris* are not significantly greater than those of ants, it would seem to follow that it is not the smallness of ants which is the major hindrance" (p. 182).

In their experiments RAIGNIER & WIERSMA always stuck the ants by means of plasticine to a condensor microphone; it is therefore impossible to decide whether there is "Luftschall" or "Körperschall". In his last publication, however, RAIGNIER says that he hopes to speak elsewhere more fully about AUTRUM's theory with reference to his experiments upon stridulation. "I only want to say that the stridulation of ants is audible to the human ear *without well-founded probability that this happens through the co-vibration of solid objects*" (9). And as to the sine curve he says: "Check experiments proved that our sine curve *was not produced by the apparatus but by the ant.*" (10).

MEYER has not put this question; he himself and several others clearly perceived the sound. The noise he heard, however, could not have been brought about by a co-vibrating substrate, for the total surface of the webthreads is certainly much smaller than the spider's abdomen and the energy is too poor surely to cause the glass to co-vibrate. From this it appears that in spite of AUTRUM's theory the small abdomen of the spider really immediately causes the sound. The concentration of the sound waves in the narrow tube probably explains why MEYER perceived the sound, whereas others before him did not perceive it because they observed the animal in larger spaces. He himself says that he chose a narrow tube for his experiments "um durch die Zylinderform den Ton zu verstärken" (1928, p. 10).

DO CONGENERS PERCEIVE THE STRIDULATION ?

Several investigators have stated that different species of ants react upon the stridulation of congeners (11). AUTRUM (1936) concluded, however, that they do not react to a stridulating congener, even when they touch it with their feelers, nor when the common substrate — on account of intensification — co-vibrates so heavily that the chirping is audible at one meter's distance. As he experimented with species different from the others we might perhaps draw the conclusion that in this respect not all kinds of ants behave in the same way. HASKINS & ENZMANN (1938) observed, too, that in different groups of ants the sensitiveness to sounds differed much. PUMPHREY (1940) warns: "... until it can be demonstrated that (stridulatory organs) serve some biological function other than communication, it is necessary to regard experiments purporting to show that the sounds produced are not perceived by other individuals of the same species with great reserve" (p. 130).

According to MEYER the female of his spiders hung motionless in her web during the preliminary stages of copulation while the male just below her stridulated intensively on his "Werbenetz". As soon as the stridulating male plucks the threads of her web she descends for the copulation. Has she perceived the stridulatory sound ? Is perhaps her motionless attitude the reaction upon it ? It may be ; a similar lethargic position as a preliminary to copulation occurs in different kinds of spiders and the male ordinarily causes it by stroking the female with his forelegs, so by tactile stimuli. But I do not know whether this explanation is right. MEYER thinks he is justified in concluding that the stridulatory sound plays a part in courtship. "Es ist wohl kaum anzunehmen, dasz die Natur hier etwas geschaffen hat, ohne einen Zweck damit zu verfolgen" (p. 11). GERHARDT & KÄSTNER, too, are of opinion that "irgendeine Wirkung dieser nur bei der Werbung hervorgebrachten Geräusche auf die Weibchen vorhanden sein musz" (1938, p. 526). But do they prove their views ?

According to observations bird-catching spiders stridulate when they are attacked, and while stridulating they rise high on their forelegs; they behave in the same way when they pounce upon their prey. I have found no indications that they perceive the stridulation of congeners. BERLAND concisely states: "On n'a aucune preuve que les araignées perçoivent les sons émis par elles" (1932, p. 180). As to spiders we probably can only make conjectures regarding this question. The fact that some species produce sounds is in itself no proof that these species are able to perceive sounds, no more may we draw an a priori conclusion that most species cannot perceive sounds because they themselves produce none (12).

ARE AIR-BORNE SOUNDS PERCEIVED DIRECTLY ?

The fact that many arthropods sometimes react upon sounds is proved by many investigators and is generally accepted (13). In the foregoing pages we have seen that spiders, too, sometimes react upon sounds. Before we can conclude to a faculty of hearing in these animals we must try to solve the above question (14).

AUTRUM (1936) draws attention to the fact that on closer inspection as regards investigations about ants it clearly appeared that the substrate co-vibrated ; in some observations it is not so clear but the possibility of co-vibration is at least not ruled out. However, apart from AUTRUM's experiments there are a few more by others, e.g. COLLART (1925), BAIER (1930), HASKINS & ENZMANN (1938), which prove a real "hearing" in ants.

With spiders, too, it is clear that in many reactions to sounds which are perceived, the sound vibrations are transmitted to the animal through the substrate or at least, that they may have been transmitted in this manner. This is, of course, the case in all those experiments where vibrating tuning forks were put into contact with the web upon which the spider had settled ; therefore we only incidentally mentioned these experiments in the foregoing pages.

It would seem to me that the stridulation of *Steatoda bipunctata* and *Teutana castanea* also belongs to this category ; for the web upon which the male is stridulating communicates by means of threads with that of the female : the vibration of his body may therefore reach the female through these threads, too. Perhaps she also perceives the vibration of the air as such, but how can we prove it ? MEYER takes it for granted on the ground of some considerations without any evidence. The conclusion of GERHARDT & KÄSTNER, therefore, does not seem to me quite reasonable : "(die) Beobachtungen Meyers legen aber nahe, dasz wenigstens einige Arten Hör-Sinn besitzen" (1937, p. 432).

One might be inclined to attribute the appearance of spiders when there is music in the room, exclusively to reactions of their sense of vibrations. The vibrations caused by music, singing, speaking and sculpturing may have been transferred along the ground, the walls and the ceiling, and in this way may have set the web into vibration. The vibrations of the air caused by the music etc., too, may have set the threads of the web into co-vibration. It seems to me, however, that the behaviour of the spiders argues against this interpretation. For, if an insect settles upon a web and puts it into vibration on the particular spot, the spider directly rushes up to the origin of the vibrations. When by means of a tuning fork, a trembling blade, etc. vibrations are applied to the web, the spider often promptly reacts by running to it (15). Unlike some other investigators RABAUD obtained manifest reactions with house spiders (*Tegenaria* spec.) and also with other Agelenidae; the above mentioned observations refer in all likelihood exclusively to this family of spiders — with exception of *Theridium tepidariorum*. These spiders always make for that point of their web from which the vibrations originate; their sense of direction is very fine in this respect. In all the above mentioned cases, however, they leave their web and settle either on the ceiling straight over the origin of the sounds or they descend there at the end of a thread to approach this origin as near as possible: so they do not take their bearings towards a point of their web from which the vibrations may have reached their body, but towards the point of the space from which the vibrations originate. It seems to me that this behaviour cannot be explained unless they are able to perceive and localize immediately the sound vibrations of the air.

The observation of RECLAM is very instructive : the spider descended at the end of a thread during the solo of the violin, but no sooner had the orchestra started than the whole hall vibrated as well as the web, and the spider climbed up in a hurry to this new and strong source of vibrations.

It seems to me that the case of the *Tarantula*, too, can hardly be interpreted in another way: these animals live underground in a small gallery, which they excavate themselves, the covering of the gallery is entirely interwoven with particles of the soil and will therefore hardly get into vibration; conduction of vibrations through the body of the whistling peasant and the ground is scarcely imaginable. In the case I observed in a male of *Theridium tepidariorum* it has to be remembered that mature males of web spiders do not live upon a web but freely wander about in search of a female: here the possibility of co-vibrating threads is excluded too.

As to the experiments we may remark as follows. The behaviour of *Astia vittata* seems to indicate real hearing, but not without a shade of doubt: the possibility that a different "vibration" of the experimentator in each case causes the different behaviour of the spider, is not obvious but cannot be absolutely excluded. The other experiments of the PECKHAMS and those of BOYS and GRÜNBAUM, too, refer to spiders of the garden-spider-type sitting (mostly) in the centre of their webs; here we observe two wholly different reactions. Small species and young specimens of larger species drop at the end of a thread when low tones are produced; larger animals behave altogether differently with respect to the large tuning fork which is held at a small distance — the smaller animals do the same with respect to the small forks —: the vibrating tuning fork appears to have a strong attraction. Their reaction much resembles that which they show when their web is set into vibration by a buzzing and struggling insect entangled in the viscid threads or by a vibrating tuning fork, blade etc. put upon the web. For in this case these spiders too directly make for the origin of the vibrations, exactly as the Agelenidae do, and try to get hold of it; they even attempt to entangle the end of the fork, as they do with a buzzing fly (16). To a vibrating fork that does not touch the web, however, they react by stretching their forelegs to it, and when the fork is sounding next to them or from behind, they stretch their legs in this direction and sometimes try to catch the fork. This behaviour, too, cannot be accounted for if we admit that they are excited by web threads put into co-vibration by the sound of the fork, for, if so, they would hurry to those threads and try to catch the origin of vibrations. Now they clearly react into the direction of the sound vibrations, which approach them through the air.

From the preceding data we may draw the following conclusion: spiders sometimes clearly show that they perceive directly vibrations of the air, and therefore they possess a real faculty of hearing.

HOW ARE SOUND VIBRATIONS OF THE AIR PERCEIVED ?

Since we ourselves perceive sound waves by means of the tympanic membrane we are more easily led to believe that animals possessing tympana can hear, even though they are insects. It appears, however, e.g. from experiments by VON FRISCH and co-operators (1932), that tympana are not indispensable for real hearing, because they have demonstrated that fishes which are without tympanic membranes possess the faculty of hearing and even a fairly well developed one. In spite of the most exact anatomical research either in ants or in spiders tympana or tympanal organs have never been discovered.

Before we can answer the question how these animals can hear, we should try to realize some important notions regarding acoustics which are of great importance in this question (17).

Sounds (in the air) originate from vibrations of the air molecules; these vibrations propagate as longitudinal waves and cause periodical condensations and dilutions of the air, periodical pressure changes (AUTRUM calls this "Schalldruck" — sound pressure). Now, upon these changes the tympanic membrane of man and mammals reacts: AUTRUM therefore calls it "Druck-Empfänger" — pressure receiver. If, however, we do not pay attention to the result of the vibrations of the molecules — the periodical condensations and dilutions of the air on a particular spot — but to the movements of the molecules themselves, it appears that they possess a definite velocity at a definite moment; AUTRUM calls this "Schallschnelle" — sound velocity. This "velocity" varies periodically and is greatest when the vibrating particle passes the position of equilibrium (18). This "velocity" is not to be confused with "velocity of sound propagation" (19). PUMPHREY objects to the use of the word "Schallschnelle" (velocity) and prefers "displacement of the air molecules"; we will follow him and use the word "displacement".

A priori it does not seem impossible that some animals should not be sensitive to pressure changes while sensible to displacement; the reverse might be the case as well. In order to examine this point the two components have to be separated. In moving waves they are not separated but in standing waves they are. These waves originate when a moving wave perpendicularly pushes against a wall and is thrown back by it: the wave which falls in and the wave which is thrown back form together a standing wave. At the reflecting wall a maximum of pressure change originates but in consequence of the strong resistance of the wall the movement of the molecules is strongly braked and a minimum of displacement is the result. At a distance of $\frac{1}{4}\lambda$ from the wall ($\lambda =$ wave length) pressure change is minimal (pressure minimum), but the displacement of the molecules maximal (displacement maximum).

All this can be very clearly observed in a "Tube of Kundt" (20), which also shows that the human ear perceives the sound only in those spots where the pressure changes are strongest (pressure maximum), so at distances of $\frac{1}{2}\lambda$, 1λ, $1\frac{1}{2}\lambda$, 2λ, etc. from the stationary wall.

Feelers or hairs of insects (and spiders) never can react on pressure changes, because these changes equally affect them on all sides, but it seems possible that they are moved by the fastly moving air molecules. In standing waves it will occur at distances of $\frac{1}{4}\lambda$, $\frac{3}{4}\lambda$, $1\frac{1}{4}\lambda$, $1\frac{3}{4}\lambda$, etc. from the stationary wall, when we and animals with similar tympana hear nothing (pressure minimum).

In order to find out whether this abstract possibility is concrete reality too, AUTRUM (1936) experimented with ants: his results are briefly as follows. The ants were in a space where standing waves only could originate on a gauze which could not co-vibrate and which was at a distance of ± 1 cm from the reflecting wall. Using strong sounds with frequencies from 50 up to 10.000 c/sec., never did he perceive reactions of the ants; ants do not react upon sound pressure.

Experiments which consisted in a kind of training in order to detect sensibility to sound pressure in ants, appeared to be impossible: which forces us to draw the same conclusion. When AUTRUM placed the reflecting wall below the animals at a distance of 10—10.4 cm they did not react on frequencies of 750 c/sec. and lower, nor on frequencies of 900 c/sec, and higher. When he, however, used frequencies between 790 and 840 c/sec., the ants reacted as soon as the sound rang: suddenly they stopped, then altered their direction, ran away terrified and were permanently disturbed. The wave length of these frequencies is between 40 and 41.5 cm: $\frac{1}{4}\lambda$, therefore, between 10 and 10.4 cm ! A feeler of a recently killed ant was adjusted to a small bar which could not co-vibrate, after this it was placed in the instrument on the same level, and a microscope, which magnified 180 times, was focussed on it: as soon as a tone of 810 c/sec. sounded, the feeler lost its sharp contours; as soon as the tone stopped, they again became sharp. AUTRUM considered this a proof that at this frequency the feeler was taken away by the „Schallschnelle" (velocity). When he used a tone of 1320 c/sec. he observed reactions of the ants at a proper distance from the reflecting wall.

Though PUMPHREY thinks it fairly sure that many insects perceive sounds by means of long, fine and extremely mobile hairs and though he admires AUTRUM's experiments, he does not see that the „Schallschnelle" (velocity) causes the reactions. According to him AUTRUM only proves that either the displacement or the velocity or the acceleration of the air molecules acts upon the animals. It seems impossible for him to discriminate by this method which of the three components — all optimal at $\frac{1}{4}\lambda$ — causes the reactions. Anyhow it is proved that not the pressure changes but the movement of the air molecules (or a function of it) acts as a stimulus. Further it seems equally probable to him that, in view of the great sound intensities which AUTRUM used, not the feelers only but the whole ant vibrated (1940, p. 128—129).

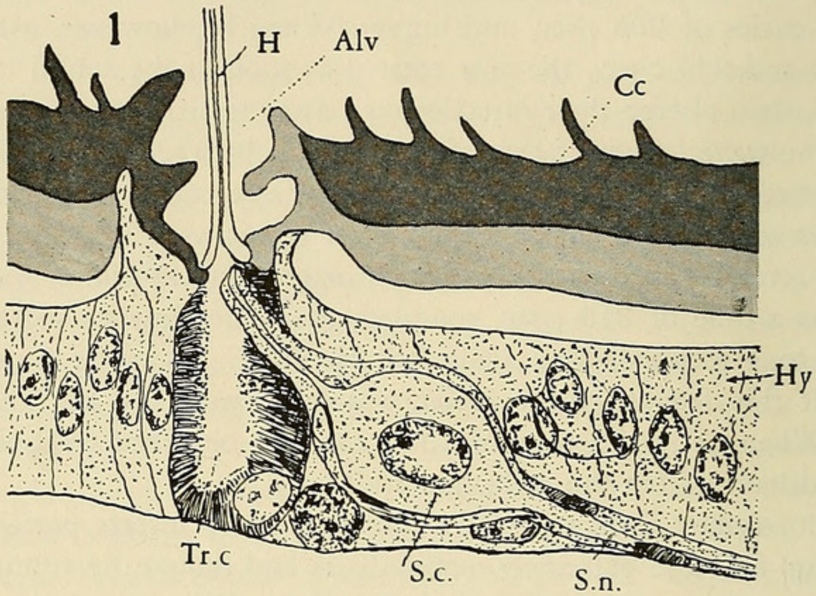
In natural circumstances small animals which have no tympanal organs and are on a solid substrate (e.g. the soil) will sometimes be hit by standing waves and consequently perceive no sound, because the displacement maximum, i.e. the spot where they are able to perceive the sound, will always be some cm above the substrate. They can perceive moving waves; here, however, they do not perceive the pressure maxima, as we do, but the displacement maxima. In natural circumstances moving waves occur much more than standing waves, but in the experiments just mentioned they could not be used, as has been said, because separation of sound pressure and displacement is impossible in these cases. Flying insects and spiders which have settled in their webs are mostly exposed to moving waves and are therefore always able to perceive sounds.

From several experiments it appears that similar "displacement receivers" must act a part in other insects too.

As early as the year 1874, MAYER was sure that the males of mosquitos can perceive sounds because the long hairs on their feelers are set into vibration by sounds as he clearly observed under his microscope. EGGERS (1924) fully agrees with him.

When MINNICH (1925, 1936) experimented with more or less hairy caterpillars, it appeared that those animals reacted to low tones (mainly from 200 to

500 c/sec.); when he, however, burnt off their hairs, clogged them with a water-spray or with flour or exposed the animals to a constant air stream, the response was greatly reduced or even abolished. ABBOTT (1927) and BAIER (1930) obtained almost identical results in their experiments.



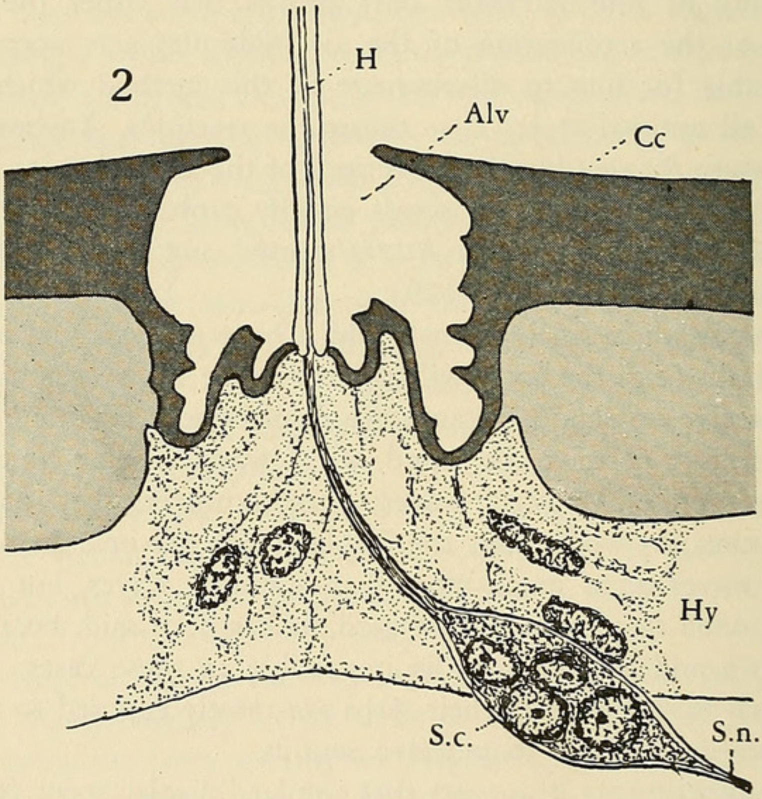


Fig. 1. Section through the base of a long hair sensillum from the anal cercus of *Gryllus campestris* L. (× 825); enlarged at the same scale the hair would be 1—2 meters in length. (After SIHLER 1924). Fig. 2. Section through the base of a trichobothrium from the tarsus of *Meta menardi* Latr. (× 990). (After GOSSEL 1935). H = hair ; Alv = alveolus ; Cc = cuticula ; Hy = hypodermis ; Tr. c. = trichogenous cell ; S.c. = sensory cell ; S.n. = sensory nerve.

With modern electro-physiological methods of research PUMPHREY & RAWDON-SMITH (1936) could demonstrate that hairs acted as sound receivers. The anal cerci, threadlike appendices on the abdomen of the house cricket (*Gryllus domesticus* L.) and the American cockroach (*Periplaneta americana* L.), are set underneath with thin, exceedingly mobile hairs, which under the binocular swing to and fro with the least sigh; at their feet is a sensorial cell (fig. 1). When sounds were produced, the nerves of those anal cerci gave clear action potentials, a proof that the nerves passed stimuli. "Its responsiveness to sound was discovered accidentally and the remarkable similarity of the oscillograms from the cercal nerve in response to pure tones to those obtained from the cochlear nerve of mammals excited immediate interest" (21). When the experimentators covered the hairs with dust or smeared them with vaseline no action potentials could be perceived in the nerves (22).

The auditory organ of locusts (crickets and butterflies ?), which undoubtedly possess tympana, is, according to PUMPHREY (1940) and AUTRUM (1941, 1942), not a pressure receiver like the ear of man and higher animals but fundamentally a displacement receiver; AUTRUM calls it a "Druckgradient-Empfänger" (pressure-gradient receiver). As these organs do not belong to the subject of this article we shall leave them alone; regarding the importance of displacement reception which occurs in the human ear beside pressure reception we refer to AUTRUM (1941).

Finally: the stimulation of the nerve-endings in the organ of Corti in the human ear is ultimately a tactile (i.e. vibration) stimulus; now, as long as it is a perfect problem to us how such a stimulus is "transformed" into a sound perception in our central nerve-system, it would be more prudent not to deny too apodictically — as some authors do — the possibility of real "hearing" in animals whose sound receiving organs are built wholly differently from ours.

The preceding considerations are able to throw some light on the behaviour of spiders with respect to sounds. The result of the experiments of BOYS and the PECKHAMS could be explained as follows. Web-spiders generally reacted to the sounds of vibrating tuning forks: they perceived the displacement in the moving waves; hunting spiders did not react. AUTRUM (1936) thinks it probable that the experimentators held their tuning forks over the animals so that standing waves were produced with only sound pressure on the soil, which they cannot perceive. It may be, however, that hunting spiders are more or less "deaf" because besides standing waves certainly moving waves too hit these animals; moreover in PRITCHETT's experiments they were exclusively exposed to moving waves and nevertheless they did not react. From other experiments it also appears that in these species the sense of touch, especially the sense of vibrations, is much less developed than in web-spiders. Another explanation is possible, too, about which we will speak on p. 78. We lack further details which might account for the different behaviour of the spider on the wire screen (see p. 60).

The fact that many spiders reacted more intensely to low than to high tones (23) agrees with what is said: at decreasing frequency the displacement increases and hence, too, the intensity of the stimulus, as regards these animals. Why other (younger) specimens behaved just the other way round, is not clear.

The web-spiders, which appeared sensitive to music (see p. 58), could easily perceive the sounds because moving waves could freely reach them. Also the male of *Theridium tepidariorum* and the *Tarentula*'s mentioned on p. 59 were perhaps hit by a few standing waves but certainly by many moving waves, too.

WHERE ARE THE AUDITORY ORGANS SITUATED ?

In order to solve this question the PECKHAMS (1887) took several web-spiders and amputated the palps, the first pair of the first and second pairs of legs. When two or three days afterwards the animals had recovered from the operation, they reacted just as normal animals do; when missing the first pair of legs, they stretched out the second pair; when missing these too, they tried to stretch the third pair. In these animals the auditory organs are, therefore, not exclusively situated in the palps and the two first pairs of legs.

DAHL (1883) was the first who thought to have found the auditory organs of spiders in a particular kind of hairs, which occur in many species of spiders, generally on the three last leg-joints (tibia, metatarsus and tarsus) and on the palps only. These hairs are as a rule strikingly long and very thin, sometimes finely feathered at the top; they stand perpendicularly on the limbs. The root of each hair is planted in the bottom of a cup-shaped excavation and in this root are the spurs of a few adjacent nerve cells (fig. 2); these hairs are extremely mobile and the least sigh makes them swing to and fro (24). DAHL placed the leg of a freshly killed spider under the microscope — not in liquid — and observed the end of such a hair, which was magnified 600 times. When low tones of a violin were produced, the sharp contours of the hair disappeared and did not return before the tone had finished. DAHL is convinced that these hairs serve as sound receivers and therefore calls them "Hörhaare" (acoustic hairs). In his earlier systematical publications he paid much attention to these hairs and made much use of them in his keys. In his later publications he calls them trichobothria, which name is now practically common.

Since DAHL's discovery there has been a large controversy about these trichobothria (25). SAVORY (1928) summarized the discussions as follows: "... their true function is, to say the least, problematic" (p. 88).

MEYER (1928) observed that the trichobothria on a leg cut off from a wolf spider vibrated when at 5 meter's distance the strings of a mandolin were touched; they also reacted to tones of a piano and a tuning fork; the trichobothria of a garden spider reacted to a tuning fork, too. Those of a small living wolf spider reacted just as well to the buzzing of a fly, those of a water spider to tones of a mandolin. When, however, he enclosed the leg of a wolf spider or a small living wolf spider in a little plastiline box with glass bottom and upper side no reaction could be perceived either to the tuning fork or to the buzzing fly; when by means of a needle he made a little hole in the wall of plastiline the reaction to the tuning fork was clearly visible. He thinks, however, that the trichobothria do not serve as auditory organs because under a strong binocular he did not observe any movement of these hairs in a female of *Steatoda bipunctata* while the male was stridulating; when he put a leg of this female under the microscope and sounded a tuning fork to the same pitch as the stridulatory tone of the male, he could not perceive any vibration in the trichobothria even if he magnified the leg to the maximum.

With regard to this experience AUTRUM (1936, p. 360) remarks that in this case most probably standing waves had been produced — because the experimentator held his tuning fork perpendicularly over the cover-glass — and the trichobothria were most probably just in a displacement minimum. He silently passes the fact that there was no visible reaction of the trichobothria during the stridulation itself when the female had settled upon her web over the male. Though certainly standing waves were not exclusively operating in this case, the absence of visible reactions of the trichobothria does not seem to prove MEYER's thesis that trichobothria are not subservient to the perception of sounds. The trichobothria of *Steatoda bipunctata* are rather short and in short trichobothria DAHL could not observe reactions to low tones of a violin even when he magnified them 600 times. We may infer, therefore, that the shortness of the trichobothria, the small intensity of the stridulatory sound, together with the rather feeble magnifying (± 100 times) have been the causes why MEYER did not perceive reactions. The author himself says that these trichobothria did react upon the tones of a mouth-organ and of a mandolin, "die stärkere Lufterschütterungen hervorbrachten als die der Stimmgabel" (p. 64). This investigator is not always very clear when describing his experiments and views about strongly divergent subjects. Thus e.g. arguing with DAHL he says: "Ich bin gegenteiliger Meinung, dasz nicht die Töne, sondern die durch Töne hervorgerufene Erschütterungen mit Hilfe der Trichobothrien wahrgenommen werden" (1928, p. 62). When he tries to explain the fact that the trichobothria on a leg of a spider enclosed in a box of plastiline does not react to sounds, he again makes the same distinction between "Töne" (sounds) and "durch Töne hervorgerufene Erschütterungen" (vibrations caused by sounds) and the context shows that he speaks about vibrations of the air. Now we fail to see the difference between the two notions. With "Töne" he means perhaps sounds as we perceive them, emphasizing the human sensation of sounds and with „Erschütterungen" sounds as physical phenomena. It may be, of course, that this distinction is well-founded, but this seems to me a question which cannot be solved (see p. 58). Further on he speaks about "Erschütterungen aus der Entfernung", "durch Lufthauch, also durch Erschütterung...". All this makes it difficult to find out what he means exactly and to discuss his theories.

THOMAS (1929) observed under the binocular the trichobothria of several living spiders belonging to divergent families while the tones of a bracket clock or of a piano were sounding: the animals were always separately locked up in a glass tube with two perforated metal covers: the experimentator could not perceive any vibration of the trichobothria. Then he made different flies buzz near the cover, finally he placed a fly in a tube where a crab spider, *Xysticus audax* (Schrank), had settled motionless on its egg-sac: in these cases, too, no reaction of the trichobothria could be perceived. He concludes, therefore, that trichobothria — at least in living animals — do not react to sounds and that DAHL and MEYER came to a "wrong" conclusion because they used amputated legs. He forgets, however, that MEYER perceived vibrations of trichobothria in a living spider as well. Though his research certainly deserves attention and an explanation of his negative results is not directly at hand, they do not, in our opinion, refute conclusively the different positive observations of other investigators.

BERLAND (1932) remarks only in general that the trichobothria serve the perception of sounds "ou plus exactement la réception des vibrations" (p. 84 note).

PALMGREN (1936) made an extensive study about the part which trichobothria act in the life of the house spider, *Tegenaria derhami* (Scop.); he compared the behaviour of normal animals with that of specimens where he had taken away carefully all (± 200) trichobothria. His results are briefly as follows: 1) Where he took away the trichobothria, the sensitiveness of the spider towards small vibrations of the web diminished slightly; the sense of vibrations, however, had by no means disappeared (p. 10). 2) The sensitiveness of the spider towards feeble air currents diminished considerably (p. 19). The author is of opinion that the perception of air currents is not indeed the only function of the trichobothria although their principal one (p. 11). 3) Further he observed a less easy orientation of the spider in its web and a general weakening of the animal (p. 23 and 26). 4) He thinks, however, that the trichobothria do not play an important part in the life of a spider, because he found two specimens, which by nature lacked nearly all trichobothria and nevertheless behaved in a perfectly normal way (p. 26).

It is a pity that PALMGREN did not make investigations about the reactions of these animals to sounds. When he examined their sense of vibrations he always touched the web with his tuning fork as he explicitly declares (p. 8). When AUTRUM (1942) writes that from PALMGREN's experiments it appeared that the reactions of these animals "auf Stimmgabel-Töne" (to the sounds of a tuning fork) had diminished (p. 71), it seems to me a wrong interpretation. But on the other hand the results of PALMGREN's experiments do not, I think, exclude the possibility of trichobothria reacting directly to sound vibrations of the air. Indeed, these hairs swing tumultuously with the least sigh and slightly vibrate when the web upon which the spider has settled is set into vibration, but this fact does not exclude the possibility of their being so mobile that they vibrate — at least at the top — when they are hit by air molecules, put in motion by sound vibration (26). A priori it does not seem impossible that these divergent movements of the trichobothria — which even bend when they are touched — cause divergent stimulations of the nerve-endings in their feet, and that the animal can distinguish these different stimuli. Of course we do not know whether this is matter of fact but it does not seem reasonable a priori to reject the possibility.

Though from the experiments of DAHL and partly from those of MEYER, too, it is now definitely certain that trichobothria on amputated legs — probably also those on living animals — can be set into vibration when noises are made in the neighbourhood, it seems to me not yet decisively made out that in these experiments they were set into vibration by air borne sounds only. The possibility —probably a very small possibility — remains that these sounds caused a co-vibration of the substrate upon which the spider had settled. In this way the leg or the whole animal may have slightly co-vibrated and this extremely small co-vibration may have been the origin of the vibration of the trichobothria.

If, however, we hold that spiders possess the faculty of hearing — and from the foregoing pages this seems at least very probable — these animals must have organs to perceive directly the sound vibrations of the air. Both from theoretical speculations and from comparison with other arthropods we may reasonably consider the trichobothria of spiders as auditory organs. No reaction to sounds has ever been perceived in any of the other organs sometimes mentioned as possible auditory organs, viz. the slit organs, the lyriform organs and the tarsal organs. The tarsal organ is certainly an organ of scent (BLUMENTHAL 1935); the significance of slit organs and lyriform organs is not yet clear: VOGEL (1921, 1923) thinks that they are organs to perceive tensions in the chitinous cuticle, KASTON (1935) regards them as organs of the chemical sense (organs of scent). According to TURNER & SCHWARZ (1914), chordotonal organs, which in insects are often considered as auditory organs, are wanting in all Arachnoidea: they are ruled out, therefore, in spiders. On the other hand we have repeatedly proved that the trichobothria do react to sounds. Consequently we may infer with great probability that the trichobothria are the auditory organ of spiders.

THE BIOLOGICAL SIGNIFICANCE OF SOUNDS TO SPIDERS

The question about the biological significance of sounds to particular animals leads us to a field fully open to all sorts of speculations. But it is extremely difficult to check and verify the possible hypotheses by means of observations and experiments. Hence we confine ourselves to some random remarks and reflections.

Since MEYER takes it for granted that the female perceives the stridulatory sound of the male, he thinks it to be pretty certain that this sound plays a part in alluring the female. Several authors before him felt inclined to this opinion, too, and at first sight this interpretation or a similar one is obvious. GERHARDT & KÄSTNER (see p. 65) are of the same opinion, though they hold that in this process tactile stimuli have greater importance. We know, however, that stridulatory organs occur sometimes in both sexes, e.g. in bird-catching spiders, and that these animals use this organ when they are attacked by enemies or attack a prey themselves. In order to solve this difficulty "a Solomon's judgement" (27) has been passed: if only the male stridulates, the stridulation serves to lure the female or bring her into the required mood and is of importance for sexual selection; if both male and female stridulate, the stridulation serves to intimidate enemies and prey and is of importance for natural selection. This distinction does not only seem very arbitrary but has strong arguments against it. For by far the most kinds of spiders — and among them many very common species — are without stridulatory organs and kinds which stridulate "deterrently" are no less caught by their enemies than the "mute" ones. Here, however, we touch the general problem of "warning"-colours etc.; which subject we do not intend to deal with.

AUTRUM (1936) suggests that stridulatory organs might have been evolved as a sump for surplus energy (1936, p. 7, note); both PUMPHREY (1940, p. 130) and RAIGNIER (1950, p. 96) reject his suggestion.

BERLAND finishes his reflections about stridulation in spiders (and insects) with the following sentence: "En réalité on ne connaît pas d'explication valable de l'émission de sons chez les arthropodes" (28).

It appears that some kinds of spiders make another sound besides stridulation. It is audible to man and they produce it by tapping with their palps, chelicerae, abdomen or legs on the soil or dry leaves : *Lycosa kochii* "the purring spider" (29), *Tarentula pulverulenta* (Cl.) (30), *Lycosa chelata* (O. F. Müller) (31), three wolf spiders and *Euophrys frontalis* (Wlk.) (30), a jumping spider. CHOPARD (1934) points to a remarkable resemblance of behaviour between these spiders and a wingless cricket, *Arachnocephalus*. In this species the male has no elytra and, therefore, he cannot stridulate; he taps, however, with his abdomen on the leaves. He acts in this way only in the adult stage and his tapping makes the females approach him, just as other species do towards a stridulating male. It seems, however, that in some spiders the females are the "inviting party" because CHOPARD saw and heard but tapping females.

PRELL (1917) observed this tapping, most probably with the abdomen, in *Pisaura mirabilis* (Cl.). He thinks that this tapping "die Annäherung der Geschlechter erleichtern soll. So konnte ich in mehreren Fällen beobachten, dasz beim aufsuchen eines trommelnden ♂ auch ein sich in seiner nächsten Nähe befindendes ♀ aufgeschreckt wurde.... Auf künstliches knarren" — to that end he used a file which he scratched with his nail — "reagierten die eingezwingerten Spinnen" — the context makes clear that he had only males in captivity — "gewöhnlich nur dann durch zusammenzucken, wenn die benutzte Feile mit dem Tische auf dem der Zwinger stand, in Berührung kam" (p. 63). Probably, the vibration of the substrate and not the sound caused the reactions. It seems to me that SAVORY does not give an accurate description of these experiments when he writes: "He (PRELL) has been able to imitate the sound or the vibration or both with a wet file, and has observed that the spiders upon which he was experimenting would only look for each other while his artificial notes were sounding" (1928, p. 98).

It does not require proof that sounds of tuning forks and musical instruments in themselves have no biological significance for spiders. When these animals, however, react to them, this must be because the sounds have a similar effect on their auditory organs as causes which do imply biological significance (32). Among them we may mention: possible prey, enemy or mate. From several observations above mentioned it appears that the sounds of prey and enemies alarm the spider, in the first case to an offensive, and in the second to a defensive attitude.

A buzzing insect which approaches a web will alarm the spider and when it comes close, the spider will try to catch it; only when the sounds are too strong or too low as compared with the size of the spider the latter will drop by means of a security thread; a spider acts in the same way when a prey which is too big gets entangled in the web. It is not clear whether the so-called "Schüttel-reflex" (see p. 61) is a protection against danger: some experts hold that the spider behaves in this way to make itself invisible to its enemies. It seems a plausible statement that very loud sounds have the same effect as the sudden approach of a big object: all at once the spider will be greatly alarmed.

About the possible significance of the stridulatory sounds we have already spoken.

Further it seems certain that spiders are able, to a certain extent, to determine the direction from which the sounds originate for they approach the origin of the sounds (see p. 58; cf. HENKING 1891) and stretch their legs in the right direction.

The question how they may perceive this direction by means of their trichobothria can be answered with the aid of the data given before. In moving waves the air molecules vibrate in a well-defined direction i.e. the direction in which the sound wave propagates itself. Hairs which lie precisely in the same direction are not affected by the moving air molecules; the farther these hairs deviate from this direction the stronger they are moved by the displacement and the stronger, therefore, is the stimulus. The latter will be maximal when the hairs stand perpendicularly upon the direction of the sound (33).

It may be that the perceived sound also informs the spider of the nature of the sound producing object. The different pitch of the stridulatory sound in *Steatoda bipunctata* and *Teutana castanea* and the different behaviour of the spiders as regards high pitched and low pitched tuning forks are perhaps indications for this view.

DAHL (1883) observed that the length of the trichobothria — they often form rows — generally decreased more or less regularly towards the basal end of each limb. He inferred, therefore, that this phenomenon might be related with the perception of different tones. He is not fully satisfied, however, with his experiments in this field: sometimes two or three hairs vibrated at the same tone or the same hair at different tones.

MEYER (1928) is of opinion that in spiders the "auditory organ" of each species is tuned to the stridulatory sound of the same species; he thinks it difficult to suppose that they are able to discriminate tones because "dann hätten sie Gehörorgane, die denjenigen höher entwickelten Tiere funktionell entsprächen" (p. 14).

MAYER (1874) agrees with DAHL as regards the hairs on the feelers of mosquito males, for he supposes that hairs of different length are set into vibration by different tones; his experiments seemed to prove this view. He holds, however, that these animals are unable to discriminate tones of different pitch because their nerve system is not sufficiently developed for such a task; but as the tone of he buzzing females continually changes these hairs must be able to react to different vibrations (34).

MINNICH (1925) sticks also to the theory of resonance as regards the hairs of caterpillars. He cannot explain, however, some results of his experiments. (p. 466, 467).

BAIER (1930) thinks that in all probability insects with stridulatory organs and auditory organs can discriminate "the specific sonification of the species" from that of other species or groups. He does not deal with the question how this may be done (p. 229).

AUTRUM (1936) only says that he has begun some experiments about the faculty of ants to discriminate tones, that the research, however, is difficult (p. 357).

PUMPHREY (1940) is sure that insects provided with hair sensilla as described on p. 70 are able, to certain extent, to discriminate tones, "... it is arguable a priori — and it has been so argued — that any discrimination of the quality of sound is impossible in animals which possess nothing remotely resembling a cochlea. But such an argument flies in the face of the facts." The discrimination, however, is not made by means of resonance : "(the hairs) can... be excited to visible movement by sounds of adequate intensity and show no special preference for a particular frequency i.e. they are not-resonant", but it is possible for these animals to make the discrimination because "the nervous response is synchronous at least initially, up to a frequency of 800 c/sec." From the reproduction of the "oscillograms", which are added, this appears abundantly clear. The result of MINNICH's experiments above mentioned has a plausible explanation in PUMPHREY's experiences (35).

The problem whether a particular sound has biological significance to the animal with which experiments are made, is of great importance in the researches about the faculty of hearing. For if an artificial sound has no resemblance to sounds which are of interest in the ordinary life of the animal, it is not surprising that the animal does not react upon it. In such cases we must not draw the conclusion that the animal has not perceived the sounds and therefore is "deaf" (36). As early as 1887 the PECKHAMs pointed it out when they observed that web spiders did not react upon shouting, clapping and whistling. "We felt, however, that this was not enough to warrant us in concluding that they were deaf, since there is nothing in the habits of these spiders that would lead them to make any active response to loud noises, even supposing they did hear them" (p. 390).

RAIGNIER (1933) puts the same idea in a nice comparison: "when I am walking quietly on the footpath and I do not at all react upon the brisk hooting and clattering of motor-cars, trams and bicycles it does not prove that I do not perceive that noise" (p. 15).

These reflections must caution us. The fact, e.g., that in several experiments wolf spiders did not react upon sounds, cannot be considered a sufficient argument to prove the view that these animals, as opposed to web spiders, are deaf. It was the PECKHAMS (1887) who drew attention to it : "(the fact that wolf spiders do not react to sounds) may, perhaps, be partially explained by the difference in the feeding habits of the two groups" (p. 97). Wolf spiders which possess a well developed sight hunt with the aid of this very faculty. From the information given by BAGLIVUS and from MEYER's experiments with *Dolomedes* we may conclude that in some circumstances, at least some kinds, appear to possess the faculty of hearing. When judging we should also take into account that the animals used for the experiments may be in different moods (satiety, moulting, this action is always preceded and followed by a short time of fasting, mating mood etc.).

On the other hand, if we put the question whether hearing will have much significance in the life of spiders, it would seem to me that the answer must be negative. As sounds act such an important part in our own lives (speech, music, sounds from the environment, which inform us aubout many things happening), we are easily inclined to suppose that sounds, and consequently hearing too, will have much importance in the lives of animals as well. Apart from some domestic animals, which we have trained, we should not generalize nor apply this to animals generally. Certainly, for some higher animals hearing has more or less importance in detecting their prey or in avoiding possible enemies, but the part which sounds and hearing play in the lives of by far most animals is very small (37).

PUMPHREY (1940) ends his very interesting review of hearing in insects with the following statement : "It is to be hoped that this review will be helpful in indicating some of the directions in which further experimental work is urgently necessary" (p. 129). At the end of this study I should like to repeat his words : because with regard to the hearing of spiders even much less is known to us.

To give a survey, we want accurate studies on the following subjects :

(1) the stridulatory sounds as observed with the aid of modern methods (cf. RAIGNIER & WIERSMA, PIERCE);

(2) the behaviour of the females of different kinds when the male stridulates (cf. MEYER, REGEN). (As the males have but a short life the stridulatory sounds might probably be fixed on records to be reproduced at will afterwards.)

(3) how spiders of those species of which both females and males stridulate react on stridulating congeners ;

(4) the reactions of different spiders towards artificial sounds. (These sounds must be exactly determined and the proofs be severely checked in order to avoid vibrations of the substrate (cf. HASKINS & ENZMANN, REGEN, BAIER). In this way the experiments of BOYS, the PECKHAMS and several others will have to be repeated).

(5) the reactions of the trichobothria, both on amputated legs and on the living animal — under the conditions just mentioned (cf. MEYER, THOMAS).

(6) Further we are in need of an electro-physiological reseach of the perceptive nerves which pass from palps and legs to the central nerve system, when tones of various frequencies are incident on these limbs (cf. PUMPHREY & RAWDON-SMITH, WEVER & BRAY).

(7) Lastly we should wish a research about the faculty of orientation and discrimination of tones with the aid of the trichobothria (cf. MAYER, PUMPHREY).

NOTES

(1) For a more theoretical explanation of the connection between the sense of touch, the sense of vibrations and hearing, see PUMPHREY 1940, p. 108—109.

(2) Cf. LUTZ 1924, p. 363—366 ; AUTRUM 1936, p. 332—333 ; PUMPHREY 1940, p. 107—110.

(3) Further details about the cases mentioned are to be found in MACCOOK 1890, p. 305—308 ; BERLAND 1932, p. 175—176. Cf. BONNET 1945, p. 698—699.

(4) Figs. see e.g. HASKINS & ENZMANN, RAIGNIER.

(5) Tijdschr. Ent., vol. 19, p. C—CI.

(6) For detailed descriptions and figures see e.g. SAVORY, MEYER and BERLAND. Cf. BONNET 1945, p. 699.

(7) By "pure tone" I mean any musical tone, eventually with overtones, that is the opposite of a "noise".

(8) WESTRING heard the stridulation of several Theridiidae when he slightly pressed the animals or held them between his fingers close in his ears (1861, p. 175, 185, 186).

(9) 1950, p. 96 ; italics are mine.

(10) Ibid. p. 88 ; italics are mine.

(11) Cf. e.g. RAIGNIER, HASKINS & ENZMANN.

(12) Thus, in general, KREIDL 1926, p. 756.

(13) Further details and more extensive literature is to be found e.g. in RAIGNIER, AUTRUM (1936), HASKINS & ENZMANN (ants); HANSSON (bees); REGEN, AUTRUM (1941) (locusts); EGGERS (moths); MAYER (mosquitos); MINNICH, ABBOTT, BAIER (caterpillars).

(14) Cf. our definition of hearing on p. 58.

(15)' Cf. e.g. RABAUD 1921.
(16) Cf. e.g. PETERS 1931 and RABAUD 1921.
(17) Cf. AUTRUM 1936, p. 350—351 ; 1942, p. 69—75 ; PUMPHREY 1940, p. 110—112.
(18) Cf. the movement of a pendulum.
(19) It seems to me that RAIGNIER 1950, p. 94 makes this mistake.
(20) Cf. various textbooks of physics.
(21) PUMPHREY 1940, p. 125.
(22) PUMPHREY gives a summary of those experiments 1940, p. 125—127.
(23) Cf. also GRÜNBAUM on p. 61 of this paper.
(24) Cf. the hairs on the anal cerci of crickets and cockroaches.
(25) Cf. e.g. WAGNER 1888, MACCOOK 1890, HANSEN 1917, DAHL 1911, 1920, BONNET 1945, p. 698.
(26) According to AUTRUM (1936, p. 356) the amplitude of these molecules will ordinarily be but a few microns ; PUMPHREY (1940, p. 127) has calculated that the lower limit of the sensitiveness of the hairs on the anal cerci of crickets was at an amplitude of ± 0,06 micron !
(27) BERLAND 1932, p. 180.
(28) 1932, p. 181 ; cf. LUTZ 1924, p. 337—338 ; 367—372.
(29) DAVIS 1904, LAHEE 1904, ALLARD 1936 ; most probably *Lycosa gulosa* Wlk. is meant : cf. CHAMBERLIN 1908, p. 263—268, ALLARD p. 68.
(30) BRISTOWE & LOCKET 1926.
(31) CHOPARD 1934.
(32) Cf. DAHL 1905 ; LÉCAILLON 1906.
(33) AUTRUM 1936, p. 361 ; cf. MAYER (1874, p. 586—587), who observed distinctly that the hairs on the feelers of male mosquitos behaved as we have said. The faculty of orientation in animals with tympanal organs is discussed in detail by PUMPHREY 1940 and AUTRUM 1941, 1942 ; we leave this matter alone.
(34) p. 582—588 ; cf. LUTZ (1924, p. 335—336), who summarizes MAYER's experiments.
(35) p. 125—127. The question whether animals with tympanal organs can discriminate different tones and to which extent, is discussed by AUTRUM, WOLVEKAMP and PUMPHREY ; we shall leave it alone.
(36) Cf. DAHL 1905 ; DEMOLL 1917, p. 68 ; LUTZ 1924, p. 364 ; KREIDL 1926, p. 756.
(37) Cf. KREIDL 1926, p. 754—756.

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