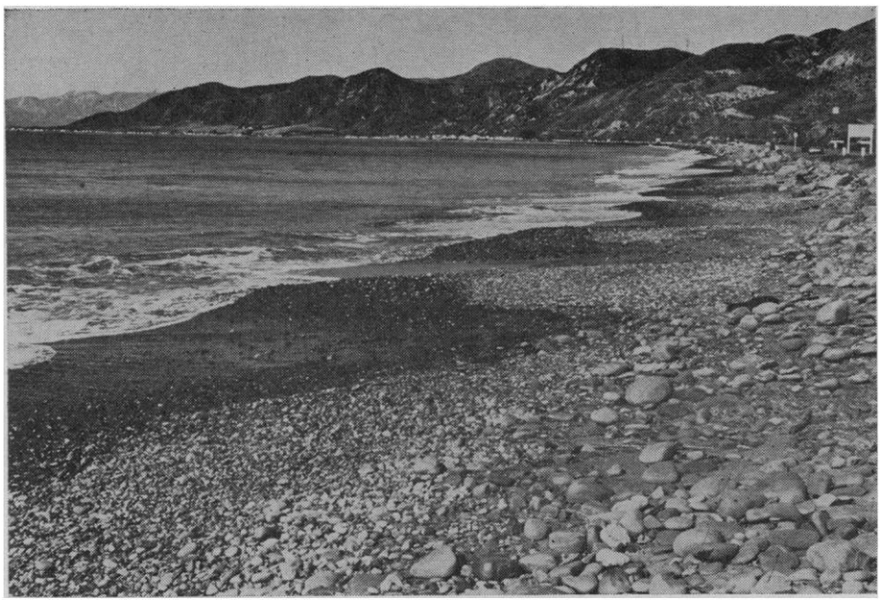

Fig. 1. Westward view of beach cusps on Emma Wood State Beach, 5 km west of Ventura, Calif., 28 November 1965. The cusps have an average spacing of about 24 m; the waves that made them were estimated to have been 1.2 to 1.5 m high.

onto the beach, so as not to produce longshore drift and erosion, such more or less straight-on action commonly results in an array of beach cusps that persist until destruction by a change of regimen, such as a rise in the tide, an increase in the height of waves, or development of longshore currents.

In bodies of water that are free from tidal effects, the cuspate structure may last longer and show a clearer relation to beach ridge or berm than it does on the usual marine beach. Where cusps form, they develop rapidly; and formation of a new set of cusps quickly obliterates an older one.

From many probable sources I have sought measurements that could be used to check the supposition that beach cusps may be a function of the segmentation of the cylindrical wave form against the beach according to some ratio consistent with Plateau's rule. Many measurements of cusp spacing are available, but few are accompanied by measurements (or even estimates) of the height of the waves that produced the cusps. Many examples have also been given of the variation in distance between cusps along the same beach (*5*); the variation may be considerable, yet the spacing between cusps tends to hover around a mean for any given beach and time.

A few examples in which wave height and mean spacing between cusps were known or could be estimated (*5, 6*) seemed to indicate a cusp-length: wave-height ratio of about 16 to 20. Longuet-Higgins and Parkin (*7*), however, have plotted nine measurements that suggest a ratio of only about 10—but with increase for the lowest waves. They find a closer relation between cusp spacing and swash length, but then swash length is related to the volume and velocities of water surging up the beach and thus also to segmentation of the cylindrical wave form. Russell and McIntire (*8*) have observed that occasional large waves may be more important than waves of prevailing height in shaping beach cusps; deviation from a straight-line relation between cusp-spacing and the observed height of waves may partly relate to this fact.

These all-too-few observations are consistent with but do not prove the hypothesis that beach cusps form in response to the nearly regular segmentation of the cylindrical wave form against the beach, as predicted from Plateau's rule, but with local complications due to hydrodynamic variations and beach regimen. If this hypothesis were true, the average spacing of beach cusps would reflect the height of the waves that produced (or is producing) them—a relation that, if it could be expressed more precisely, would contribute to the synoptic study of coastal conditions.

I hope that this suggestion will bring out, or lead to the making of, more and better measurements of the ratio of the spacing of beach cusps to the height of waves responsible for them, and of other, possibly related, variables that may indicate whether there is or is not a clustering of points along a curve corresponding to some function of Plateau's rule.

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26 September 1966

Ultrasonic Sensitivity: A Tympanal Receptor in the Green Lace Wing Chrysopa carnea

Abstract. Chrysopa carnea *can perceive ultrasonic frequencies up to at least 100 kilohertz modulated at pulse repetition rates as rapid as 150 per second. The receptor sites are a bilateral pair of small swellings in a vein of the fore wings.*

In conjunction with his studies on behavioral reactions of flying moths to simulated ultrasound of bats, Roeder (*1*) observed that green lacewings also responded to ultrasonic pulses. Previous anatomical studies on *Chrysopa carnea* Stephens (*C. vulgaris* Schneider) (*2, 3*) have revealed a swelling at the base of the fused radial and anterior-median veins in each fore wing. The dorsal wall of this enlargement is composed of a thick cuticle, while its ventral surface is membranous. Associated with

this structure are two chordotonal organs, each composed of numerous sensilla. Our histological and electrophysiological studies suggest that this small organ comprises a tympanal receptor sensitive to ultrasonic frequencies whose properties account for Roeder's observations on free-flying chrysopids.

The small swelling, or bulla (Fig. 1, *TO*), is located approximately 0.5 mm from the articulation of the fore wing with the mesothoracic axillary sclerites. We used a method of vital staining with methylene blue (*4*) to investigate the nerve supply and chordotonal organs of the wing base. Our results confirm the distribution of nerves and chordotonal organs reported by Zachwilichowski (*3*), except that only a single chordotonal organ, rather than two, could be reliably differentiated at the proximal base of the bulla. Cross sections (*5*) of the bulla show that the asymmetrically swollen dorsal portion is strongly arched away from the ventral tympanic membrane (Fig. 2, *TM*), creating an enlarged blood space within the wing vein. A small trachea (Fig. 2, *Tr*) lies just internal to the dorsal cuticle, and cells (Fig. 2, *SC*), presumably representing the chordotonal organ, are suspended between this trachea and the tympanic membrane. On the tracheal side of the cell body, these cells give rise to single, elongate processes which follow the ventral surface of the trachea for some distance. Although we have not traced out their final terminations, it seems likely that these processes provide the axonic connections with the trunk nerve of the vein.

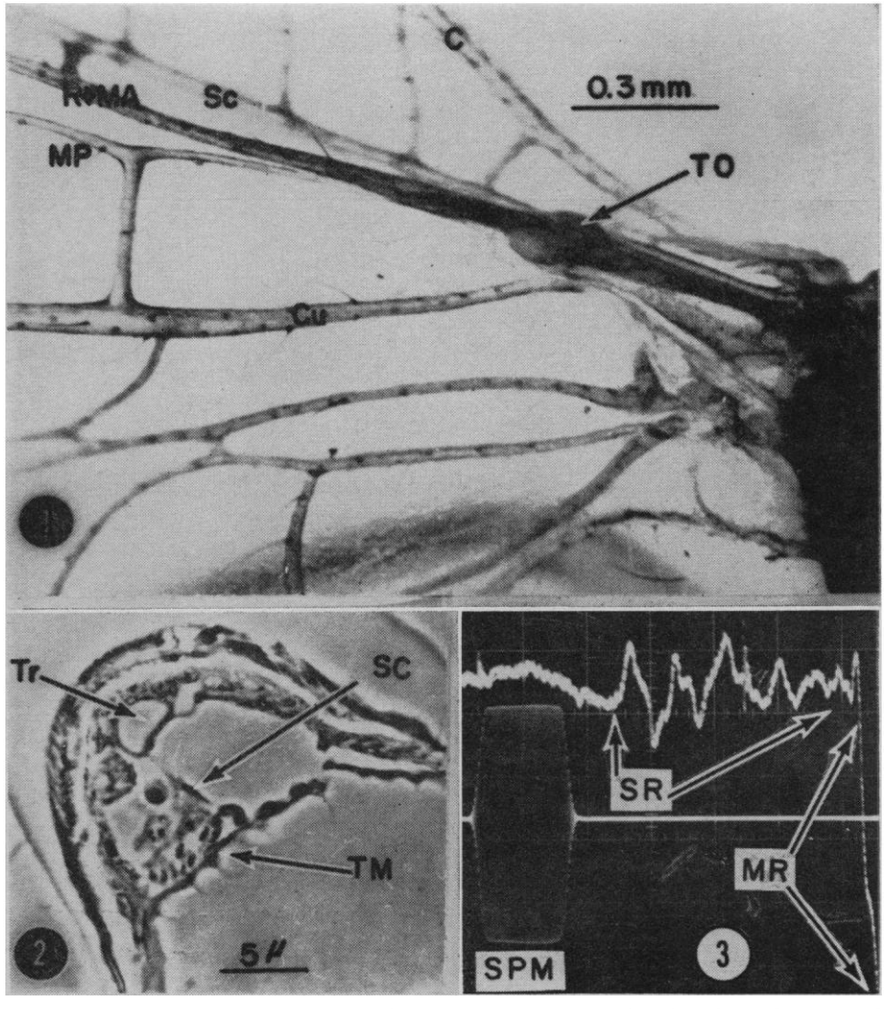

Fig. 1. Proximal base of left fore wing of *C. carnea*, showing location of tympanal organ: *C*, costa; *Cu*, cubitus; *MP*, posterior median; *R+MA*, fused radius and anterior-median veins; *Sc*, subcosta; *TO*, bulba of tympanal organ (approximately × 66). Fig. 2. Cross section through tympanal organ: *SC*, sense cell; *TM*, tympanic membrane; *Tr*, trachea (× 2375). Fig. 3. Electrical response of radial nerve proximal to tympanal organ: *MR*, motor response of wing-flexing muscle; *SPM*, monitor of ultrasonic pulse on same time base as electrical responses of insect; *SR*, sensory response of chordotonal cells. Stimulus for 3 msec at 26 khz. (Scale of large divisions: horizontal division equal to 2 msec; vertical division equal to 0.1 mv.)

Roeder's initial observations (*1*) and our own studies on *C. carnea* (*6*) have shown that the visible response of a flying chrysopid to an ultrasonic stimulus is to fold the wings and drop. This folding is accomplished by the contraction of the wing-flexing muscles inserted on the third axillary sclerites of the wing bases. When the wings are restrained in an outstretched position, attempts to close the wings result in a visible movement of the third axillary sclerite as the wing-flexing muscle contracts. This response, which has been observed only when the insect is stimulated by an ultrasonic pulse, provides a simple behavioral assay for the perception of acoustic stimuli by the insect.

To verify the inferred localization of the ultrasonic reception to the tympanal organs of the fore wings, we placed specimens in a dish of paraffin under a low-power stereoscopic microscope and pinned the fore wings away from the body. We then stimulated these specimens with pulses of ultrasound (*7*) and watched for movements of the third axillary sclerite while various portions of the insect were destroyed or removed. We found that only if both tympanal organs were ablated did the responsive contractions of the wing-flexing muscles cease. Ablations of other areas of the wings, or of only one tympanal organ, failed to prevent the muscle response on either side of the body. In the latter case the response is more pronounced ipsilaterally. These experiments also suggest that the site of ultrasonic reception is the tympanal organs of the fore wings.

We have also studied the afferent electrical responses of the radial nerve proximal to the tympanal organ (*8*). An insect was pinned out in a paraffin dish, as described above, 1 meter from an ionic loudspeaker. A small incision was made in the vein about halfway between the bulla and the wing base, and an electrolytically sharpened tungsten recording electrode (*9*) was placed in the vein cavity. A reference electrode of lower impedance either was placed in a pool of insect Ringer solution (*4*) overlying several cut wing veins distal to the recording electrode or was inserted into the abdomen.

Figure 3 shows a typical complex nerve response. We believe that the train of small spikes, the onset of which has a latency of 4 to 6 msec, comprises the sensory response (*SR*) of the

tympanal organ since these spikes closely follow the parameters of the stimulating pulses: that is, the spike amplitude of the sensory response is directly proportional to the intensity of the stimulus, indicating the recruitment of additional neurons; and the sensory discharge follows the pulse-repetition rate (PRR) of the stimulating sound very closely over a wide range. In addition, a long stimulus (500 msec) elicits a slightly longer response caused by an afterdischarge. If the reference electrode is placed in the abdomen, large spikes (Fig. 3, *MR*) of 4 to 8 mv amplitude (off scale in Fig. 3), each lasting 1 to 3 msec, are recorded immediately after the sensory response. These are not recorded when the reference electrode is on the wing. The onset of these spikes has a latency of about 13 msec and follows the PRR only up to three per second, above which they disappear after the initial pulse of the stimulus. We interpret these large potential changes to result from the depolarization of the nearby wing-flexing muscle after the arrival of an efferent stimulus in the muscle from the central nervous system. This conclusion follows both from the longer latency of this spike and from visual observations of the movement of the third axillary sclerite; this movement, like the large spikes, disappears when the PRR exceeds three per second.

The electrophysiological study indicates that the tympanal organ is sensitive to acoustic pulses of from 15 to 17 khz to at least 100 khz at pulse-repetition rates up to 150 per second. Below a PRR of three per second, the visual assay also indicates the ability of the insect to perceive sounds in this frequency spectrum.

A taxonomic survey by one of us (*10*) has disclosed that apparently similar tympanal organs are widely distributed among many species of the Chrysopidae, being absent from only a group of five genera which, on the basis of other structural and chromosomal characteristics, seems to be quite generalized. Adams (*11*) has recently grouped these less specialized forms together as the distinctive subfamily Nothochrysinae and has pointed out that all known fossil Chrysopidae of the Tertiary period are also referable to this subfamily. It is possible, then, that the evolution of the tympanal organ may have been a relatively recent event.

A possible function of this organ seems to be the reception of sounds generated by other chrysopids. Sound production has never been demonstrated for these insects, but, on the basis of the structure of the base of the abdomen and metathoracic femora, Adams (*12*) has suggested that males of *Meleoma schwarzi* probably stridulate, and he has speculated that such sound might play a role in courtship. Unspecified alary chordotonal organs (the tympanal organ was apparently not observed) or pedal chordotonal organs were mentioned as the possible receptors. Although stridulatory sound may have such a function in this case, as well as in other species of Chrysopidae, it seems improbable to us that the basically lower-frequency sound likely to be produced by stridulation is received by the tympanal organ of the wing. Possibly the pedal chordotonal organs, or perhaps the trichobothrial setae of the last abdominal segment (*13*), will be found to be the receptor for these sounds.

Hunting bats use ultrasonic pulses at low repetition rates to scan the environment, raising the PRR to as high as 200 per second when in pursuit of a specific target (*14*). In its sensitivity to a broad spectrum of ultrasonic frequencies and PRR's, the tympanal organ of *C. carnea* is well suited for the reception of these signals, and it seems likely that the principal adaptive role of the organ is to minimize predation by echolocating bats. Furthermore, it appears probable that a majority of the large group of species possessing a tympanal organ will be found to enjoy a similar advantage over bats, and that the apparent sudden rise to dominance of this night-flying group since the mid-Tertiary period is very likely the direct result of this advantage.

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5. The tissue was fixed with 3 percent glutaraldehyde in a phosphate buffer (*p*H 7.3 to 7.4), embedded in glycol methacrylate, sectioned at 1 to 3 μ on a glass knife, stained with 0.05 percent toluidine blue O in 0.02*M* benzoate buffer (*p*H 4.4), and photographed, in this case, with phase optics.
6. Culture procedures are given by E. G. MacLeod, *Nature*, in press.
7. Ultrasonic stimuli were generated in the following manner: the output of an audio oscillator was modulated into pulses by a Grason-Stadler electronic switch, with a variable rise-and-fall time, externally triggered by the stimulus pulse from a Grass stimulator. The switch output was led via an attenuator to a transducer driver [J. J. G. McCue, *Inst. Radio Eng. Int. Conv. Rec.* **6**, 310 (1961)], then to a Dukane Ionovac Duk-5 ionic loudspeaker, the sound pressure level of which was calibrated in decibels referred to 0.0002 μbar from 10 khz to 150 khz at 1 m with a 0.64-cm microphone (Brüel and Kjaer). The switch, transducer driver, and loudspeaker were modified by us. All experiments were carried out at a sound level of 78 to 88 db.
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Chlorinated Hydrocarbon Pesticides: Degradation by Microbes

Abstract. *In culture, most of the actinomycetes and filamentous fungi tested degraded PCNB; several actinomycetes dechlorinated DDT to DDD, but no microorganism degraded dieldrin.* Streptomyces aureofaciens *degraded PCNB to pentachloroaniline.*

Chlorinated hydrocarbon pesticides are very resistant to physical or microbial degradation, and remain unaltered in soil for many years after they are applied (*1*). The ecological hazards which these resistant chemicals present are well known (*2*). Reports of microbial degradation of chlorinated hydrocarbon pesticides are few. DDT [1,1,1-trichloro-2,2-bis(*p*-chlorophenyl)-ethane] is converted to DDD [1,1-dichloro-2,2-bis(*p*-chlorophenyl)ethane] by a yeast and a few bacteria (*3*). There are no reported instances of degradation of dieldrin or pentachloronitrobenzene (PCNB) by any microbe. Our investigations were undertaken to dis-