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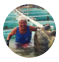

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REVIEW

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Acoustic detection and communication by decapod crustaceans

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Abstract This paper reviews behavioral, physiological, anatomical, and ecological aspects of sound and vibration detection by decapod crustaceans. Our intent is to demonstrate that despite very limited work in this area in the past 20 years, evidence suggests that at least some decapod crustaceans are able to detect and use sounds in ways that parallel detection and processing mechanisms in aquatic and terrestrial vertebrates. Some aquatic decapod crustaceans produce sounds, and many are able to detect substrate vibration at sensitivities sufficient to tell of the proximity of mates, competitors, or predators. Some semi-terrestrial crabs produce and use sounds for communication. These species detect acoustic stimuli as either air- or substrate-borne energies, socially interact in acoustic "choruses," and probably use "calls" to attract mates.

Key words Vibration · Invertebrate · Crab · Barth's organ · Chordotonal organ

Introduction

Decapod crustaceans have a variety of external and internal sensory receptors that are potentially responsive to sound (defined broadly to include near- and far-field stimuli) and vibration. A number of these receptors resemble (but are not homologous to) vertebrate receptors that respond to hydrodynamic stimulation, particle motion, and, possibly, pressure (e.g., Cohen and Dijkgraaf 1961; Breithaupt and Tautz 1990; Budelmann 1992). However, little work has been done to examine whether decapod crustaceans are capable of detecting underwater sounds or hydrodynamic stimulation.

At the same time, decapod crustaceans are known to produce acoustic signals (see reviews by: Cohen and Dijkgraaf 1961; Hazlett and Winn 1962; Schöne 1968; Hawkins and Myrberg 1983; Dunham and Gilcrest 1988; Budelmann 1992). Interestingly, while many decapods have specialized sound-producing structures (Dumortier 1963; Weygoldt 1977; Hawkins and Myrberg 1983), little is known about their sensitivity to either sound or vibration and, with the exception of certain semi-terrestrial crabs, even less is known about the use of these stimuli for communication.

This lack of information may stem from an old belief that these animals have a limited ability to detect acoustic stimuli (e.g., Breithaupt and Tautz 1990; Budelmann 1992). Such a view is plausible since, aside from the exoskeleton, most decapod crustaceans are basically of the same density as water and do not have any air-filled spaces such as those associated with pressure detection in fish (Hawkins and Myrberg 1983; Breithaupt and Tautz 1990; Popper and Fay 1999).

Based upon current knowledge, the sensitivity of aquatic decapods to particle displacement and hydrodynamic stimulation is poor compared to fishes (e.g., Breithaupt and Tautz 1990; Goodall et al. 1990). At the same time, many decapods have an extensive array of hair-like receptors both within (Cohen and Dijkgraaf 1961) and upon (Dumortier 1963) the body surface that could potentially or actually respond to water- or substrate-borne displacements (e.g., Breithaupt and Tautz 1990). They are also equipped with an abundance of proprioceptive organs that could serve secondarily to perceive vibrations (Burke 1954).

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Our purpose in this review is to describe the sensory structures used by aquatic and semi-terrestrial decapod crustaceans to detect acoustic (sound and vibration) stimuli and to review what is known about decapod acoustic communication. We show that, by virtue of their body plan and the constraints it imposes upon sensory structure, aquatic decapods are specialized to respond to particle displacement components of an impinging sound field and not to the pressures (as are the terrestrial vertebrates). The latter part of the review focuses on mechanisms and behavior associated with vibrational communication among semi-terrestrial crabs. These studies are important as they serve as the only known example of how the crustacean receptor systems are organized to promote complex communication through this channel.

Sensory systems

Decapod mechanoreceptors include setae (hair-like) cells on the surface of the body, chordotonal organs associated with joints of antenna, legs, or other body appendages, and internal statocyst receptor systems (Bush and Laverack 1982).

Surface receptors include sensory hairs (Breithaupt and Tautz 1990; Budelmann 1992). Sensory hairs cover the external surface of the cuticle and range in size from 20 μm to 2000 μm. Some may be both chemoreceptive and mechanoreceptive, while others are strictly mechanoreceptive (Derby 1982). Each mechanoreceptor consists of one or more hairs that are associated with sensory cells. Mechanical disturbances, such as acceleration, velocity and hydrodynamic flow, can result in stimulation of the sensory cells (Vedel and Clarac 1976; Wiese 1976). Hair fans, so far only described for a macruran decapod, are sensitive to both water flow and vibrational stimuli (Breithaupt and Tautz 1990). They respond to frequencies up to about 100 Hz with a single spike per cycle and are functionally analogous to the teleost lateral line. A similar receptor system is found in some cephalopods (octopus and squid; Budelmann 1989). Hairs may be tuned by virtue of their length to different frequencies (Tautz 1979). Other hairs are located in pits on the chelae of crayfish, and these respond to the acceleration component of water vibrations up to more than 150 Hz.

Chordotonal organs are associated with joints of flexible body appendages (reviewed in Budelmann 1992). The organs involve tonic and phasic receptor cells that are embedded in muscle, apodeme (internal projections of the exoskeleton), or connective tissue, and connect to the central nervous system of the animal. Depending upon organ structure, these receptors can signal joint position, movement, and stress (tension). They also respond to low-frequency waterborne vibrations (Taylor 1968) and, in some semi-terrestrial crabs (*Uca* and *Ocypode*), to vibration transmitted through the exoskeleton from the substrate and the air (Horch 1971; Salmon et al. 1977).

Statocysts are internal receptors located in the basal segment of each antennule in crabs (and in the head region or other body regions in other crustaceans; Cohen and Dijkgraaf 1961). The statocyst is a fluid-filled chamber that contains a mass, the statolith (or lith; Fig. 1). The statolith in decapods consists of sand grains embedded in a gelatinous matrix, which lies in contact with some of the sensory hairs that line part of the chamber walls (e.g., Cohen and Dijkgraaf 1961). Statocysts are primarily involved in maintaining equilibrium by triggering righting movements (Budelmann 1992; Cate and Roye 1997). These responses include compensatory eye movements that enable the animal to track the horizon (or nearby objects), even as the animal moves and changes position, and control of the antennules themselves. Since the statocysts are typically mass loaded (by the statolith), they could potentially detect particle motion, much as this type of stimulus is detected by the otolith-loaded inner ear hair cells in vertebrates (reviewed in Popper and Fay 1999). However, there is little or no evidence that the statocysts function in this capacity in decapods.

The statocyst of crabs has horizontal and vertical canals with three types of receptor hairs (Janse 1980; Cate and Roye 1997). Thread hairs and free-hook hairs

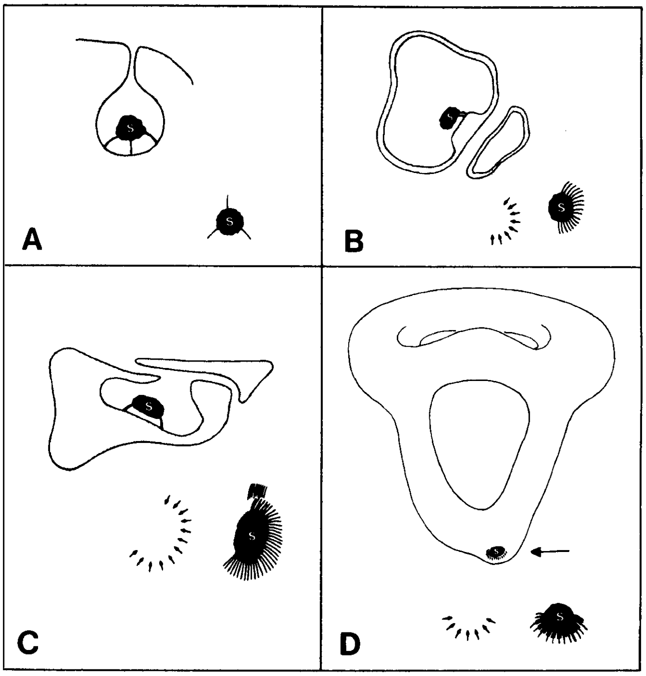

Fig. 1 Schematic illustrations to show the diversity of gravity receptor systems in Crustacea. **A–C** show transverse sections, while **D** shows a lateral view of the statocysts not drawn to scale. The small inserts show the dorsal views of the statoliths (*S*) along with the arrangement of the cuticular hairs and their directions of polarization (*arrows*). **A** Telson statocyst from *Cyathura polita*, an isopod. **B** Right uropod statocyst from the mysid shrimp *Praunus flexuosus*. **C** Crayfish and lobster statocyst from the basal segment of the right antennule. **D** Statolith organ (*large arrow*) in the vertical canal of the crab statocyst. All from Budelmann (1988), as reprinted in Budelmann (1992)

are not mass loaded and respond to fluid motion (e.g., Cohen and Dijkgraaf 1961). In contrast, statolith sensilla (hairs) are associated with the statolith (Cohen and Dijkgraaf 1961; Cate and Roye 1997). Presumably, this receptor type responds to displacement or acceleration of the statolith or to its vibration (Janse 1980; Cate and Roye 1997). In *Scylla* there are two rows of statocyst sensilla, one containing 40 sensilla and the other 15, while there are approximately 100 free-hook hairs (Janse 1980). According to Janse (1980), far fewer hairs are associated with the statocyst in *Scylla* (and presumably all crabs) than are associated with the statocyst in crayfish, suggesting that the functional role of these hairs is less significant in crabs than crayfish.

While the anatomy of the free-hook hairs and statolith sensilla is basically similar (Cohen and Dijkgraaf 1961), there is evidence that they have different responses, with the free-hook hairs responding phasically to the velocity of flow of a jet of saline, while the statolith sensilla respond tonically (Janse 1980).

A variety of studies (e.g., Sandeman and Okajima 1972; Janse 1980) demonstrate that the statolith and free-hook hairs are directionally sensitive, i.e., they give their strongest responses to stimulation from particular directions. Since the rows of hairs curve somewhat, this suggests the possibility that the statolith sensilla, as a group, could resolve directional components of different stimuli relative to the animal.

Janse (1980) investigated the response of the free-hook hairs and concluded that they respond to fluid movements in the statocyst organ over a wide range of frequencies and are deflected as a result of body pitch movements (Cohen and Dijkgraaf 1961). Keeping in mind that these hairs are not loaded, they are unlikely to respond to any external acoustic stimulation. Other studies of the thread receptors indicate that they respond to changes in animal position relative to gravity (Janse and Sandeman 1979a, 1979b).

Janse (1980) describes the statolith sensilla as being stimulated by lateral movements of the statolith, and to a lesser degree by movements in other directions. Apparently low frequency statolith displacements result in suppression of the resting activity of the receptors, while higher frequency oscillations (e.g., 25 Hz) activate the receptors. Janse concluded that the statolith sensilla provide information about the amplitude and direction of body movements, but not about absolute position of the body. This system functions to provide slow eye compensatory movements (Cohen and Dijkgraaf 1961) and is probably much more extensive in crayfish and lobsters where many more sensilla attach to the statolith (Takahata and Hisada 1979). In crabs, statocyst receptors also appear to be involved in antennal withdrawal (Cate and Roye 1997).

Acoustic detection by crayfishes and lobsters

Without doubt, the most extensive studies of hearing by aquatic decapod crustaceans have involved various species of crayfish and lobsters. There is evidence that these animals use a variety of different receptors to detect water-borne sound and vibration (reviews: Cohen and Dijkgraaf 1961; Breithaupt and Tautz 1990). Many of these investigations have involved direct studies of the physiological responses of the various receptors, done by placing recording electrodes into the receptors or innervating neurons (reviewed in Breithaupt and Tautz 1990; Goodall et al. 1990). Fewer studies have involved investigation of behavioral responses.

On the other hand, the finding that lobsters and crayfish primarily respond to hydrodynamic stimulation has been confirmed through behavioral studies. The Norway lobster (*Nephrops norvegicus*) showed a specific set of postural responses to sound frequencies of 20–180 Hz in a laboratory experiment (Goodall et al. 1990). In a field experiment, they showed that the response was to particle displacement and not pressure. Thresholds were near 0.9 μm over a range of 20–200 Hz. Responses could not be elicited when the stimulus (produced by a US Navy J9 transducer) was much more than 0.9 cm from the animal. These sensitivities were comparable to those for the crayfish *Procambrus clarkii*, as measured physiologically (e.g., Tautz and Sandeman 1980).

Such sensitivity levels are substantially poorer than those shown by fishes over the same range of frequencies (Hawkins and Myrberg 1983; Lu et al. 1996; Popper and Fay 1999). Goodall et al. (1990) suggest that since sensitivity in crayfish is so poor, it is unlikely that any naturally occurring stimulus would elicit a behavioral response from these animals if the signal was at any reasonable distance from the animal. At the same time, they point out that the sensitivity of *Nephrops* is within the range of the fish lateral line for detection of very close-by particle motion (also Kalmijn 1988, 1989; Coombs and Montgomery 1999). The receptors were probably hairs on the chelae (e.g., Tautz and Sandeman 1980). Responses may be analogous to the free neuromasts of the fish lateral line, which primarily respond to water motions produced within a fish-length of the detecting animal (e.g., Kalmijn 1988, 1989; Coombs et al. 1992; Coombs and Montgomery 1999).

Goodall et al. (1990) emphasized the importance of measuring these responses under appropriate acoustical conditions, and not in small tanks where boundaries result in reflections and distort relationships between sound pressure and particle velocity (Parvulescu 1964). To make a real determination of the nature of a response, the experiments must be conducted in the field, or under carefully controlled semi-natural laboratory conditions.

Sound production, detection and processing by ghost and fiddler crabs

In marked contrast to other crustacean species, two genera of semi-terrestrial crabs – *Ocypode* and *Uca* (Family Ocypodidae) – not only produce sounds, but also respond behaviorally to acoustic signals (Salmon and Atsaides 1968; Horch and Salmon 1969; Horch 1971; Salmon and Horch 1972). Thus, they serve as ideal model systems for investigating how signals are produced; the physical properties of the signals; how they are transmitted, detected, processed, and used in communication. Here, we review some highlights of that research.

General ecology

Both fiddler and ghost crabs live in burrows. Fiddler crabs are found primarily in sheltered (estuarine) habitats within the intertidal zone (reviews: Crane 1975; Dunham and Gilcrest 1988). They live in dense aggregations ("colonies"), but each crab maintains its own burrow where it remains hidden and inactive during high tide. At low tide, fiddler crabs open their burrows and are active on the surface where they feed, court and often fight with conspecifics. The burrow in all species serves as refuge from predators. In some species the burrow is also used to brood eggs, store food, dissipate heat, and replenish water lost by evaporation (from a pool at the bottom). All fiddler crabs are active during diurnal low tides but some species, especially those found in temperate regions, are also active at night (Salmon 1965).

Ghost crabs are more commonly found on oceanic (sandy) beaches (review: Wolcott 1988). Immature individuals may live in intertidal burrows, but adults are usually found much higher on the beach, well above high tide. Adults usually remain in their burrows during the day, perhaps to conserve water, though they may make brief diurnal forays to scavenge for food. Most ghost crabs are nocturnally active, and begin this activity with a migration to the surf zone to replenish their water supply (Wolcott 1988).

Signal characteristics and detection

"Spontaneous" sounds (those emitted in the absence of stimulation from other crabs) are produced by male fiddler and ghost crabs, either from within their burrows or at the burrow entrance (review: Salmon 1983). The sounds are emitted at night and for hours at a time, especially during phases of the tidal or lunar cycle when females are receptive. Since acoustically active males are stationary, their sounds are presumed to function as both an attractant to females and as a warning (territorial defense) to male competitors. However, because no one has done the appropriate experiments, there is no behavioral evidence to support either of these hypotheses.

While the sounds of each species are distinct in temporal pattern as well as spectral energy distribution, they are similar in temporal organization. Each sound consists of several (~3–10) closely-spaced "pulses," with consecutive sounds produced at intervals ranging from 2 s to 15 s (Salmon 1983). Undisturbed males produce sounds at relatively slow ("calling") rates but, when stimulated by sounds of other crabs or by the nearby movements of neighboring crabs, rates of sound production can more than double for brief periods. These faster, and typically louder, emissions are known as "courtship" sounds (Salmon 1965, 1967).

Most of the spectral energy in the calls is confined to frequencies between 300 Hz and 3 kHz, but there is variation depending upon how the signals are produced. Higher spectral energies are typical of "rapping" (striking the claw against the substrate) or stridulation (rubbing two body parts together), while a lower range of frequencies is generated by leg vibration ("honking") in fiddler crabs (Salmon 1967). But as the sounds are propagated through the substrate, the higher frequencies attenuate rapidly. Thus, at near-threshold distances, only the lower frequencies are present (Horch and Salmon 1972; Salmon and Horch 1972). Threshold sensitivity to vibration shown by *Uca* and *Ocypode* illustrate that the crabs are most sensitive at these lower frequencies. For *Uca*, greatest sensitivities are to frequencies between 300 Hz and 700 Hz (Salmon et al. 1977; Hall 1985a) while for *Ocypode*, best frequencies are from 1 Hz to 2 kHz (Horch 1971).

Sounds are detected by a receptor (Barth's myochordotonal organ) in the meral segment of each walking leg (Horch 1971; Salmon et al. 1977). Externally, this receptor is marked by a thin-walled exoskeletal "window." Internally, a small (accessory) muscle inserts by ligaments upon the exoskeleton at the window. Imbedded in the ligament and muscle are bipolar neurons that respond to mechanical vibrations of the window, regardless of how these are generated. Thus, sensory responses can be induced by sufficient intensities of either air- or substrate-borne energies. Sensitivity to these stimuli is drastically reduced (>20 dB) by making a small incision in (fiddler crabs) or around (ghost crabs) the window, or by severing the accessory muscle tendon (in ghost crabs; Horch 1971). Control operations (near the window) have no such effect.

Since Barth's organ and other chordotonal organs sensitive to vibration are present in many crab species, sensitivity to vibration is presumed to be widespread. But in the ghost and fiddler crabs, the window is thinner and, especially in ghost crabs, enlarged and distinct. Functionally, Barth's organ in fiddler and ghost crabs expands the crabs' sensitivity to a higher range of frequencies (above 300 Hz). By doing so, the receptor should allow the animals to detect frequencies above predominant background noise in their habitat (<200 Hz), but still below the higher frequencies that attenuate most rapidly with distance (Horch and Salmon 1972; Salmon 1983).

For a detailed analysis of the physics of fiddler crab signal transmission through the substrate and walking leg, see Aicher et al. (1983) and Aicher and Tautz (1984, 1990).

The "adequate" stimulus

Because the receptor responds to sufficient amplitudes of both air- and substrate-borne sound, it is important to determine which of these channels is actually used for communication. This has been done directly by behavioral (Salmon and Atsaides 1969; Horch and Salmon 1969) and physiological (Horch 1971) experiments, and indirectly by measuring transmission distances of the signals under natural conditions. On windy evenings, the relatively faint air-borne components of sounds produced by the crabs are overwhelmed by background noise, even close to the sound source. The fact that the crabs continue to spontaneously call on such evenings suggests that this interference is unimportant. Background noise levels in the substratum are hardly increased on windy evenings. These observations suggest that the substrate should be the primary channel for intraspecific communication. In the fiddler crabs, which produce fainter air-borne sounds and are markedly less sensitive to air-borne than to vibrational stimuli, this generalization probably applies. Physiologically, fiddler crabs can detect the vibrational signals produced by conspecifics at least one meter distant (Salmon and Horch 1972).

Field measurements of transmitted sounds, as well as thresholds of detection, suggest that the louder vibrations of ghost crabs can be detected at distances of 10 m (Horch and Salmon 1972), even on windy evenings when the air-borne component is masked by noise. But *Ocypode* are more sensitive to both air-borne sound and substrate vibration than *Uca*. It is therefore possible that under natural conditions these animals can detect biologically important stimuli as sounds, i.e., that they make use of a capacity to "hear" (Fig. 2).

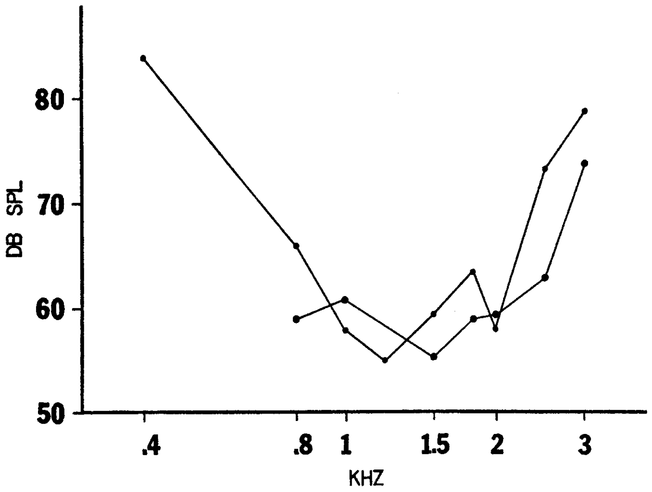

Fig. 2 Hearing thresholds from two *Ocypode ceratophthalmus*, supporting their own weight on a sand substrate. No measurable vibrations were detected in the sand. Sound pressure is given re: 0.0002 μbar (from Horch 1971)

Stimulus processing

Sensory impulses generated by Barth's organ are conducted to sensory interneurons (Salmon and Horch 1976) whose cell bodies in fiddler crabs are located in the thoracic ganglion (Hall 1985a, 1985b). The axons course anteriorly through each ispilateral hemi-ganglion (serving individual legs and the claw), then through the connectives to the brain (supraesophageal ganglion) where they cross the midline to terminate on the contralateral side. Hall could distinguish between five branching patterns among these cells. He also found five functional neuron categories (two types of phasic, two types of tonic, and one "inhibited" interneuron). Peak sensitivity of four cell types was broadly tuned to frequencies between 200 Hz and 400 Hz, corresponding to the peak spectral energies produced by calls of his subjects (*Uca minax*). Tonic II cells, however, showed a more complex response: excitation to frequencies between 100 Hz and 300 Hz, and inhibition at higher frequencies (350–1000 Hz); they thus act as low-pass filters. Tonic cells accurately responded to artificial sound pulses that were extended in duration or increased in repetition rate compared to natural sounds. Phasic units, however, responded only to the pulse onset, while inhibited units showed spontaneous activity that was inhibited for the duration of the entire sound. Taken together, then, these cells accurately code the temporal, as well as the gross spectral, properties of the calls. Units with similar properties were also found in other fiddler species (Hall 1985b).

All of the units projected to a previously undescribed, paired neuropil located in the dorso-medial area of the tritocerebrum (DMTN; Hall 1985b). The DMTN was uniquely developed among the semi-terrestrial crabs (*Uca*, *Ocypode*, and the grapsid wharf crab *Sesarma*), and was larger in size in fiddler and ghost crabs than in wharf crabs. These results suggest that the DMTN plays a major role in the processing of vibrational information.

There are interesting correlations between the structure of this detection system and its putative role in mediating vibrational information. For example, Horch (1971) found that removal of several ispilateral legs only slightly decreased sensitivity to vibration in ghost crabs (as measured from single cells in the brain), as long as at least one leg was left intact. This observation is consistent with interneuron morphology, as each cell projects to all of the ipsilateral thoracic hemiganglia (Hall 1985a). Such redundancy means that crabs can loose legs (by autotomy) with little loss in vibrational sensitivity. Anatomical organization also suggests that sound localization (if it occurs!) involves a comparison of arrival time between two sets of legs (those on each side of the body). Measurements of propagation through the substrate suggest that velocities are slow enough to be informative (Horch and Salmon 1972; Horch 1975; Aicher and Tautz 1990).

Behavioral interactions

While we know little about how female fiddler and ghost crabs respond to the calls of males, interactions between males result in behavioral changes that are obvious and can be duplicated in some instances through playback experiments (review: Salmon 1983). Presumably, these more tractable responses represent acoustic competition and/or threat (in a sexual context) between neighboring males. That, at least, seems like a reasonable hypothesis given the broad similarity between the acoustic calling systems of the crabs and other animals (such as birds, frogs, and a few fishes).

Male fiddler crabs, for instance, stimulate one another to intensify their courtship signaling. During the day, males "call" to females using visual signals (waving their enlarged claw). When one male sees his neighbors waving more vigorously (perhaps in response to an approaching female), he also increases his waving rate (Salmon 1965). Males that attract females by waving to their burrow continue to court by producing a rapid flurry of sounds from just inside their burrow entrance. Playback experiments demonstrate that these sounds stimulate neighboring males to wave more vigorously (Salmon 1965).

At night, when males produce acoustic calling signals, sound playbacks also influence male acoustic behavior. For example, playbacks of courtship (fast and loud) sounds will induce calling males to increase their rate of sound production. They will also induce silent males to become acoustically active (Salmon 1965). Thus, males "pay attention" to the acoustical activity of their competitors (males with nearby burrows) and can be induced to join acoustic "choruses."

Horch and Salmon (1972) and Horch (1975) have shown that neighboring ghost crabs also pay attention to one another's acoustic emissions. Playback experiments showed that neighboring males avoid call overlap, and that such avoidance occurs not only within single-species assemblages, but also between species that are calling at the same time and place. While the sounds of different ghost crab species are distinct in their temporal pattern, they overlap in frequency spectra. Thus, such a response presumably enables prospecting females to clearly discern (and perhaps, acoustically locate) conspecific males even if they call within a mixed-species chorus.

Summary

Aquatic decapod Crustacea are equipped with a number of receptor types potentially capable of responding to the displacement (particle motion) component of underwater sound, and some species have been shown to respond behaviorally to such stimuli. Most, if not all, decapods have sensory structures capable of responding to substrate borne vibrational stimuli, and at least two genera of semi-terrestrial crabs have been shown to use this sensory pathway for acoustic communication. While the potential for detection of air-borne sound exists, at least in *Ocypode*, direct evidence for behaviorally relevant sensitivity to such stimuli is lacking at present.

Compared to the wealth of knowledge about the visual, tactile and chemosensory systems in these animals, the acoustic sensory system of decapod crustaceans remains relatively unstudied and holds promise as a fertile area for future research.

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