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ACOUSTIC INTERNEURONS OF FIDDLER AND GHOST CRABS[1]

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The properties of acoustic interneurons in fiddler (*Uca pugilator* and *U. minax*) and ghost (*Ocypode quadrata*) crabs are described, as revealed by tests with pure tones. Three types of interneurons were present in all species: tonic, which fired for the duration of the stimulus; phasic, which fired briefly at the onset of stimulation; and inhibited, in which ongoing spontaneous activity was suppressed during stimulation. Spectral sensitivities of the cells differed among the species and were "matched" to the energy composition of the sounds. The combined properties of the cells were suited to resolve the most likely temporal differences between the sounds of each species: pulse repetition rate, sound duration, and interval between successive sounds. None of the cells coded tone frequency. The responses of all cells were suppressed during locomotion (walking) by the preparations. Finally, all interneurons were "nonhabituating" and in this respect resembled their functional analogues in cricket and grasshopper nervous systems.

It is now well established that acoustic signals are produced during agonistic and sexual behavior by fiddler (*Uca*) and ghost (*Ocypode*) crabs. We have specified the mechanisms of sound production, described the signals, and calculated the effective range over which they are transmitted in several species. The crabs also respond acoustically to one another and to playbacks of their own sounds (Horch and Salmon 1972; Salmon and Horch 1972; Horch 1975).

The acoustic system of these crabs resembles those shown by many orthopteran insects. For example, the crab sounds consist of species-typical patterns of pulses. Also, "spontaneous" sound production, when it occurs, is a prerogative of the male. Unlike the insects, however, significant signal energy is confined to the lower frequencies, is transmitted primarily through the substrate, and is detected as vibration. The receptor (Barth's organ) is located in the merus of each leg. While vibration-borne energies are the appropriate stimuli, the receptor can also respond to airborne sound (Horch 1971, 1975; Salmon and Horch, forthcoming). The organ contains two types of cells (Clarac 1968), and recordings from the leg nerves of fiddler crabs revealed two types of neurons: slowly and rapidly adapting cells (Salmon and Horch 1973).

We now describe three types of interneurons found in both genera which also process acoustic information. These cells are distinct in their properties from the sensory units and suggest which acoustic cues can be potentially important to the animals in species-specific discrimination and detection. Of particular interest is the similarity between these cells in crabs and their functional analogues among the insects.

METHODS

The experiments were done during the spring and summer at the Duke Marine

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Laboratory in Beaufort, North Carolina, and at the Mote Marine Laboratory in Sarasota, Florida. We used sexually mature representatives of three species: *Ocypode quadrata*, 2.5–4.0 cm in carapace width; *Uca minax*, 2.0–2.5 cm; and *U. pugilator*, 1.5–2.0 cm.

Uca were collected during the day from masses of crabs moving in "herds" at low tide. *Ocypode* were collected by digging animals out of their burrows (day) or catching them with nets at the water's edge (night). *Uca* were housed *en masse* in tanks provided with a shallow pool of fresh, running seawater. They were fed raw fish and shrimp daily. The crabs were used within a week of capture. *Ocypode* were housed separately in small plastic containers provided with a shallow layer of seawater and were used within two days of capture.

ANIMAL PREPARATION

Crabs were induced to autotomize both chela, then anesthetized by brief cooling in a refrigerator. They were placed in a specially contoured clamp which held the carapace firmly and allowed the legs to move freely below the body. A small hole was made in the exoskeleton just ventral to the rostrum exposing the brain (= supraesophageal ganglion). A small silver wire hook placed around one connective was used to pull the connective and brain forward and away from the esophagus. This eliminated movement of the nervous system caused by peristalsis of the esophagus and expedited locating cells in the brain. No attempt was made to open or remove the connective tissue ensheathing the nervous system. Soon after the operation was completed, the animals were fully recovered from the cold-induced anesthesia. Only data collected from animals which remained vigorous throughout the duration of the experiment have been included.

In some pilot tests, the clamped preparations were rotated upside down, and a small hole was made in the sternum. This permitted a search for acoustic cells in the thoracic ganglion and the circumesophageal connectives. None of these cells, however, was used for more detailed tests or for threshold determinations.

ACOUSTIC STIMULATION

The sinusoidal signal from a Heath audio oscillator was used to drive a General Radio Co. (G.R.C.) 1369-B tone-burst generator. The output from the generator was led directly to a stereo amplifier which drove one of two vertically mounted Wilcoxon Research (FI) shakers. Mounted above each shaker was an accelerometer topped with a small aluminum platform. Each shaker-accelerometer-platform system was shock mounted and positioned under one side of the animal, so that the crab's legs rested on the platform in a position resembling normal posture. It could also be positioned so as to contact only single legs. The output of the accelerometers was monitored by a G.R.C. sound-level meter and a G.R.C. 1556-B impact-noise analyzer, which provided a measure of the amplitude of vibrational stimuli in dB re: 10^{-3} cm/s^2. The system had a uniform response of 0.02–9.5 kHz.

Airborne sounds were presented in a similar fashion through a Nagra DH speaker-amplifier placed about 1 m away from the animals. Sound pressure levels were measured with the sound-level meter (SLM) either next to the animal or substituted for it at the end of the experiment. Appropriate controls were made for both substrate and airborne acoustic stimulation to insure that alternate paths or sources of excitation were not present (see Horch 1971).

NEURAL RECORDING

Glass micropipettes (1–3 Mohm impedance) filled with 3M NaCl saturated with fast green dye were used to record single-unit activity in the brain. The dye was used only to mark the locations of recording sites, and no attempts were made to trace neural connections. Most of the recordings were made from the ventral part of the ganglion, just medial to the entry of the connectives, since this was found to be the locus in which acoustically active cells were most abundant. The preparation was grounded with a chloridized silver wire inserted in the stump of one of the autotomized claws.

Conventional amplification and oscilloscope display techniques were used. Analogue tape recordings were made for later analysis of both the stimulus, as monitored by the SLM; and the neural response.

FIELD RECORDING OF ACOUSTIC SIGNALS

Field recordings of either induced or spontaneously produced sounds of each species were analyzed in order to guide in the selection of appropriate patterns of tonal stimuli. The sounds were monitored with Endevco accelerometers placed on the substrate near the animals or their burrows. Signal amplitudes were measured with a SLM, and the signals were recorded on a Uher 4000L tape recorder. Spectral analysis was done with a G.R.C. 1558 octave band analyzer and the impact-noise analyzer. Temporal patterning of the calls was measured from oscillographs.

DATA ANALYSIS

Visual observation of the microelectrode recordings on a storage oscilloscope was used to confirm that only single units were active. Threshold curves were obtained by audio monitoring of the response. Threshold was defined as that amplitude which produced a discernible response to at least 50% of the tone bursts presented. Threshold values exceeding 80-dB acceleration were scored as "no response," since levels this high are not found in the field recordings. Data from single units with adequate signal: noise ratios and for which a complete set of stimuli had been presented were digitized on a LINC 8 computer. Frequency-time histograms made from the digitized data were used to plot the adaptation characteristics of the units.

RESULTS

A. ACOUSTIC BEHAVIOR AND SOUND CHARACTERISTICS

Uca pugilator.—The acoustic display of this species has been well documented (Salmon 1965). Briefly, sounds are produced by males when the major cheliped is vibrated against the substrate ("rapping"). Each contact between claw and ground results in a pulse, and there are typically 5–8 pulses per sound. Daytime rapping occurs just outside or within the burrow after a female has been attracted by waving. At night, males position themselves just outside the burrow entrance and rap "spontaneously." Sounds were recorded under both circumstances, using the accelerometer placed within 2.0 cm of the burrow.

Uca minax.—This species produces its sounds by vibrating its walking legs. The "honking" noises which result usually consist of 2–5 pulses per sound. Diurnal sonic activity occurs only when females come near a male's burrow. "Spontaneous" sonic activity during nocturnal periods has not been observed (Salmon and Horch 1973). All our recordings were obtained by forcing females into the burrows of males previously engaged in vigorous bouts of waving.

Ocypode quadrata.—This species makes its sounds deep within the burrow. It has thus far proven impossible to locate the specific burrow beforehand or to observe the animals when they are acoustically active. Recordings are obtained by placing accelerometers in areas where burrows are closely spaced.

The sounds closely resemble those of *U. pugilator* in structure (Horch and Salmon 1969), and on that basis we will refer to them as "rapping." Rapping occurs spontaneously at dawn, but only briefly (20–40 min). This period corresponds to the time when the majority of the population, which feeds at the water's edge during the night, moves up the beach to take over old burrows or dig new ones for daytime shelters. It is likely, but not proven, that the sounds are emitted by males which do not leave their burrows at night. Typically, each sound contains 4–6 pulses.

The pulse duration and repetition rate for the sounds of all species are shown in figure 1. The pulse durations are roughly constant throughout the sound in *O. quadrata* and *U. pugilator* but shorten significantly during the sound in *U. minax*. The duration of the pulses in the latter species is also roughly of an order of magnitude longer than in the former two. Similarly, *U. minax* exhibits

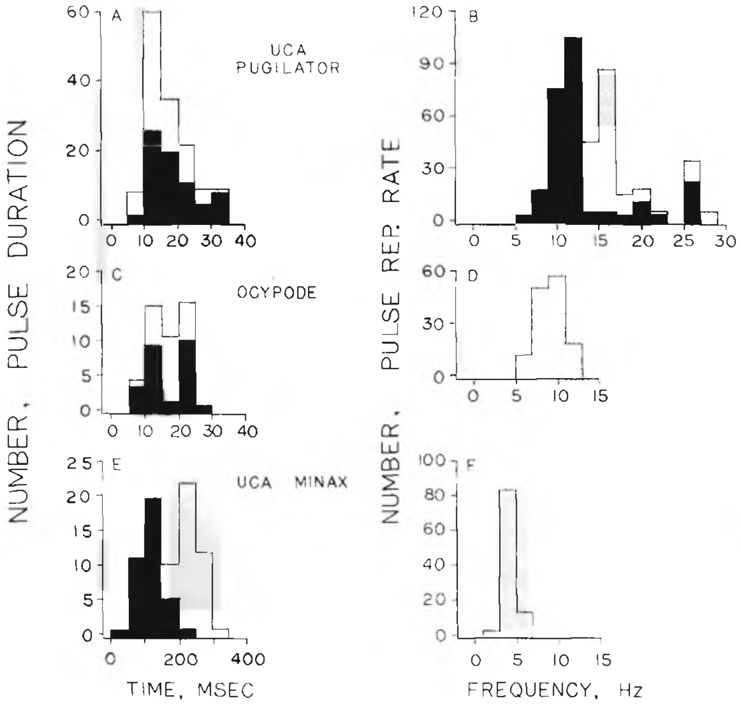

FIG. 1.—Pulse durations (*A*, *C*, *E*) and repetition rates (*B*, *D*, *F*) in the sounds of each species. Pulse durations were measured for the first (open bars) and last (shaded bars) pulses in a series of sounds. Pulse repetition rates were measured as the reciprocal of the interval (onset to onset) between all pulses within a sound. For *U. pugilator*, repetition rate at night (shaded) is distinguished from the daytime rate (open). *A*, 7 crabs, $N = 140$, mean = 15.2 ms. *B*, 3 crabs, 32 sounds (day) and 39 sounds (night), $N = 402$; temperature = 33 C (day) and 24.5 C (night). *C*, 3 crabs, $N = 47$, mean = 14.7 ms. *D*, 3 crabs, 36 sounds, $N = 135$. *E*, 4 crabs, $N = 79$, mean = 174.5 ms. *F*, 3 crabs, 23 sounds, $N = 97$.

the slowest but most regular pulse repetition rate. *Uca pugilator* shows a variable pulse repetition rate and highest mean rate. Note the significant decrease in repetition rate at night. The pulse durations show no such significant and consistent changes from day to night. Pulse repetition rates in *O. quadrata* are intermediate between the two species of *Uca*.

The spectral-energy distribution within the pulses (figs. 2 and 3) is similar for *O. quadrata* and *U. pugilator*. The calls of *U. minax* tend to be about two octaves lower.

B. CLASSES OF INTERNEURONS

Three types of interneurons were found in all species. They are illustrated by the oscillographs in figure 4. These were made from *U. minax* but are typical of all the crabs.

Tonic units are characterized by an excitatory response lasting for the duration of the stimulus. These responses are superimposed upon a varying amount of spontaneous activity, depending upon the cell. In most cases, there was a lag between the end of the stimulus and the resumption of spontaneous activity, if it was present.

Phasic units typically responded with a brief burst of impulses at the onset of each stimulus. These cells never showed spontaneous activity.

Inhibited units always showed spontaneous firing which was reduced or completely absent during stimulation.

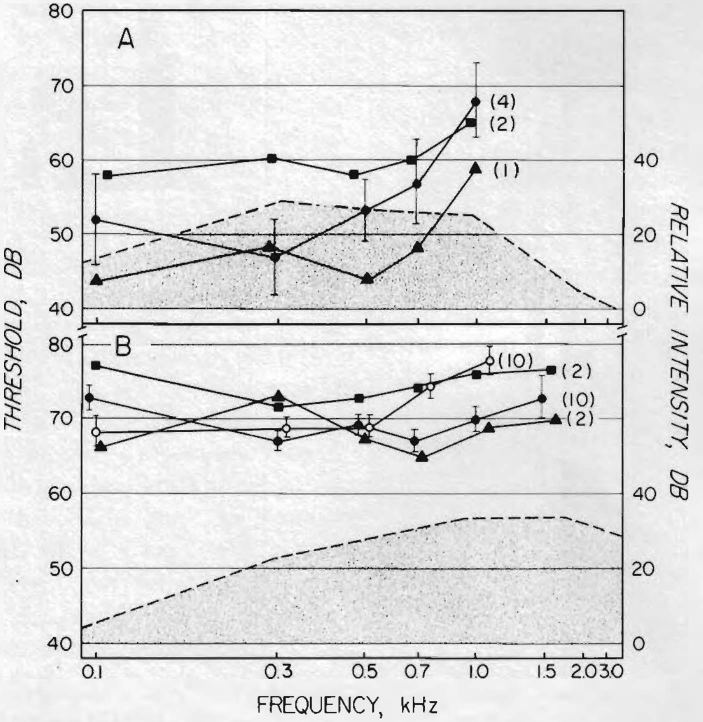

FIG. 2.—Spectral-energy distributions (shaded) of the sounds of *U. minax* (*A*) and *U. pugilator* (*B*), plotted relative to background levels in the field (right scale), and plots of thresholds (mean ± SE) for interneurons in dB re: 10^{-3} cm/s^2 (left scale). Values in parentheses indicate number of cells in the sample. ●, tonic neurons; ▲, inhibited neurons; ■, phasic neurons; ○, tonic neurons when stimuli are presented to a single leg (normally, 2–3 ipsilateral legs are stimulated simultaneously). Background levels: 44 dB (C weighted) and 47 dB (20 KC weighted) for *U. minax* and *U. pugilator*, respectively.

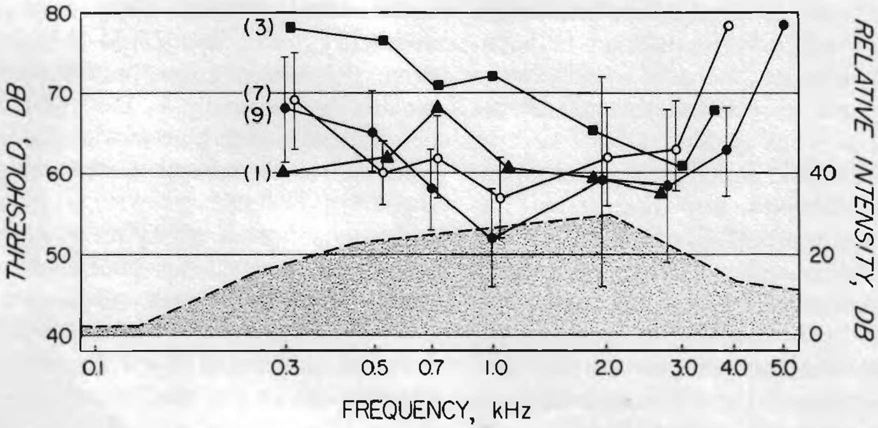

FIG. 3.—Spectral-energy distributions of sound and mean thresholds of interneurons for *O. quadrata*. Format as in fig. 2, except ○ = responses of tonic units to airborne sounds in dB re: 20 μN/m^2. Background levels: 44 dB vibration and 47 dB air (B weighted).

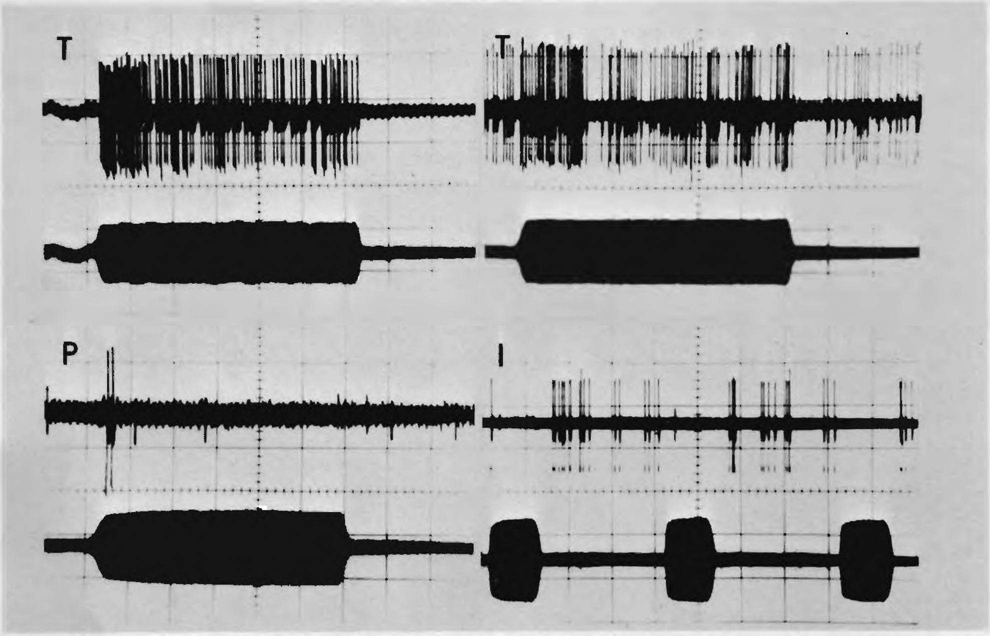

FIG. 4.—Oscillographs illustrating the three classes of acoustically active interneurons found in *Ocypode* and *Uca*. *T*, tonic cells ranging from those with little or no (left) to a relatively high (right) amount of resting or "spontaneous" activity. Tonic interneurons fire for the duration of the stimulus. *P*, phasic units which only fire a brief burst of impulses at the onset of the tone. *I*, inhibited interneurons in which ongoing activity is inhibited by an acoustic stimulus. Recordings were made from *U. minax*. Stimulus frequency and sweep duration: *T* (left), 300 Hz, 2 s; *T* (right), 600 Hz, 1 s; *P*, 300 Hz, 1 s; *I*, 600 Hz, 5 s.

As in the tonic fibers, there was a latent period between the termination of the stimulus and the resumption of spontaneous activity.

The cells were found throughout the central nervous system (CNS), that is, in the thoracic ganglion, circumesophageal connectives, and the brain. The brain was the best recording site, as all the cell types were most easily located in a circumscribed region: the ventral area of the tritocerebrum, between the midline and the juncture of the brain and circumesophageal connectives. None of the cells was found dorsal to the tritocerebrum.

The number of cells found, their latency, and their impulse amplitudes are given in table 1. Tonic neurons were most commonly encountered and, with the exception of *O. quadrata*, showed the shortest latencies. Spike amplitudes varied considerably, depending in part upon proximity of the electrode to the neuron.

All classes of cells were best driven by stimulation of legs on the ipsilateral side of the body and weakly, if at all, by contralateral stimulation. Stimulation was also affected by muscle tonus of the legs. Thresholds varied by as much as 6 dB, depending upon the force with which the subjects pressed their legs against the platform. When tested individually, each leg could effectively drive the interneurons, but maximum sensitivity, especially at the higher frequencies, depended upon simultaneous stimulation of several ipsilateral legs (fig. 2*B*).

Responses of all cell types to acoustic stimulation and their spontaneous activity (if present) were suppressed by voluntary movement. A typical example is shown in figure 5, in which a tonic cell from *U. minax* was studied.

C. SPECTRAL SENSITIVITIES

Thresholds from all interneurons tested are shown in figures 2 and 3. These plots should be compared to the spectral energy present in the crab sounds at the same frequencies.

There were distinct differences between the two species of *Uca* (fig. 2). All *U. minax* neurons were 10–20 dB more sensitive to 100–700 Hz tones than were those of *U. pugilator*. However, the latter responded to 1.5 kHz tones, while *U. minax* did not. The range of spectral sensitivity in *U. minax* covers the distribution of the significant energy present in its sounds, but *U. pugilator* is ap-

TABLE 1

NUMBER, LATENCY, AND IMPULSE AMPLITUDES OF THE UNITS FOUND IN PREPARATIONS

	TYPE OF UNIT		
SPECIES	Tonic	Phasic	Inhibited
Uca minax ($N=18$):			
Number	16	6	7
Latency (ms)	10–20	20–60	14–40
Amplitude (mv)	100–600	200–400	200–250
Uca pugilator ($N=10$):			
Number	12	5	3
Latency (ms)	10–20	15–25	25–30
Amplitude (mv)	50–400	200–250	200–600
Ocypode quadrata ($N=10$):			
Number	9	2	3
Latency (ms)	20–30	15–25	15–35
Amplitude (mV)	200–500	500–750	150–500

parently incapable of detecting frequencies of 2.0 kHz and above. Yet the latter's sounds contain spectral energies between 10–30 dB above background, up to 8.0 kHz.

Ocypode quadrata was sensitive to a higher range of frequencies (fig. 3). None of its neurons responded to 100-Hz tones, and all were sensitive to stimuli up to 4.0 kHz. Greatest sensitivity was shown at frequencies between 0.7 and 3.0 kHz. Tonic units, tested with both air- and substrate-borne sound, yielded parallel and nearly equivalent sensitivities. Finally, this species (like *U. pugilator*) was unable to detect the higher-frequency components of its own sounds, which in our recordings extended up to 11.0 kHz.

While tonic and inhibited neurons were equally sensitive in all species, phasic units tended to show the highest thresholds, especially at the lower frequencies. However, all determinations were made with tone bursts containing gradual on- and offsets, and phasic units were most sensitive to stimuli with instantaneous onsets.

D. ADAPTATION PROPERTIES

The time course of adaptation of individual tonic units from each of the three species is shown in figure 6. The average frequency was determined by dividing the response period into time bins and counting the number of impulses occurring in each bin for several repetitions of the stimulus. The mean frequency equals the number of impulses per bin per repetition divided by the bin width. The bars show the tone duration. The tonic interneurons are capable of maintaining a response to tones with durations of an order of magnitude at least longer than the duration of the pulses in the sounds of the animals (see

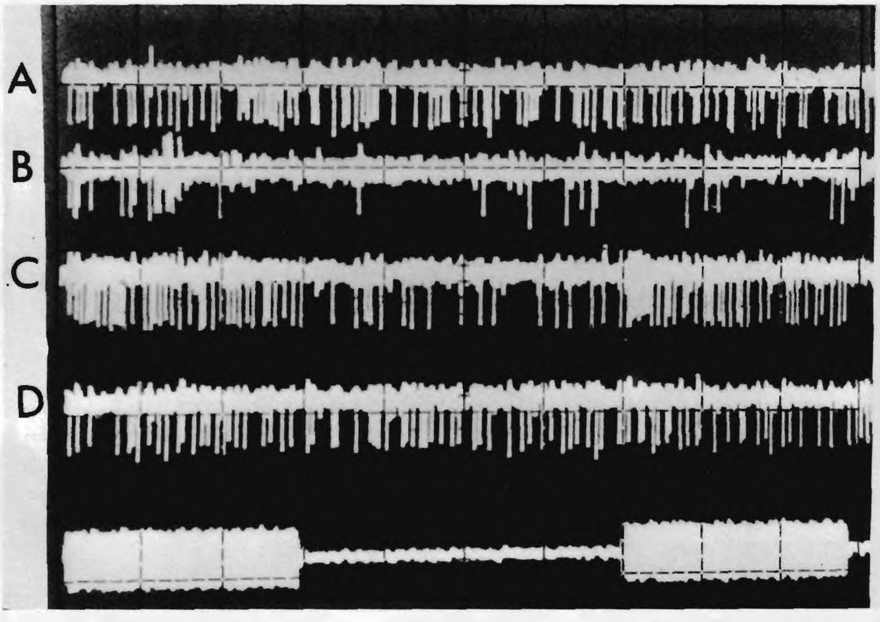

FIG. 5.—Effect of movement on responses of a tonic interneuron in *U. minax*. Stimulus (bottom trace): 500 Hz, presented at 500-ms intervals. *A*, stimulus off, animal motionless with legs resting on platform. *B*, stimulus on and animal moving, 20 s later. *C*, record 5 s after movement ceased with the stimulus present. *D*, stimulus on, but platform moved so that it no longer contacts the legs of the motionless crab.

fig. 1). Figures 6*A* and *B*, in which the levels of spontaneous activity are plotted, illustrate the inhibition of spontaneous activity which often follows the termination of the stimulus.

Phasic interneurons, which fire only a few impulses at the beginning of a tonal stimulus, adapt very rapidly.

The inhibited interneurons are much like the tonic units in their adaptation properties (fig. 7). (Quantitative study of these interneurons was not done with *O. quadrata*, but qualitatively they were the same as those in *Uca*.) Note that some period of time must pass after the termination of the stimulus before spontaneous activity returns to the prestimulus level.

E. AMPLITUDE, DURATION, AND RATE CODING

It can be seen in figures 6 and 7 that the larger the stimulus, the greater the

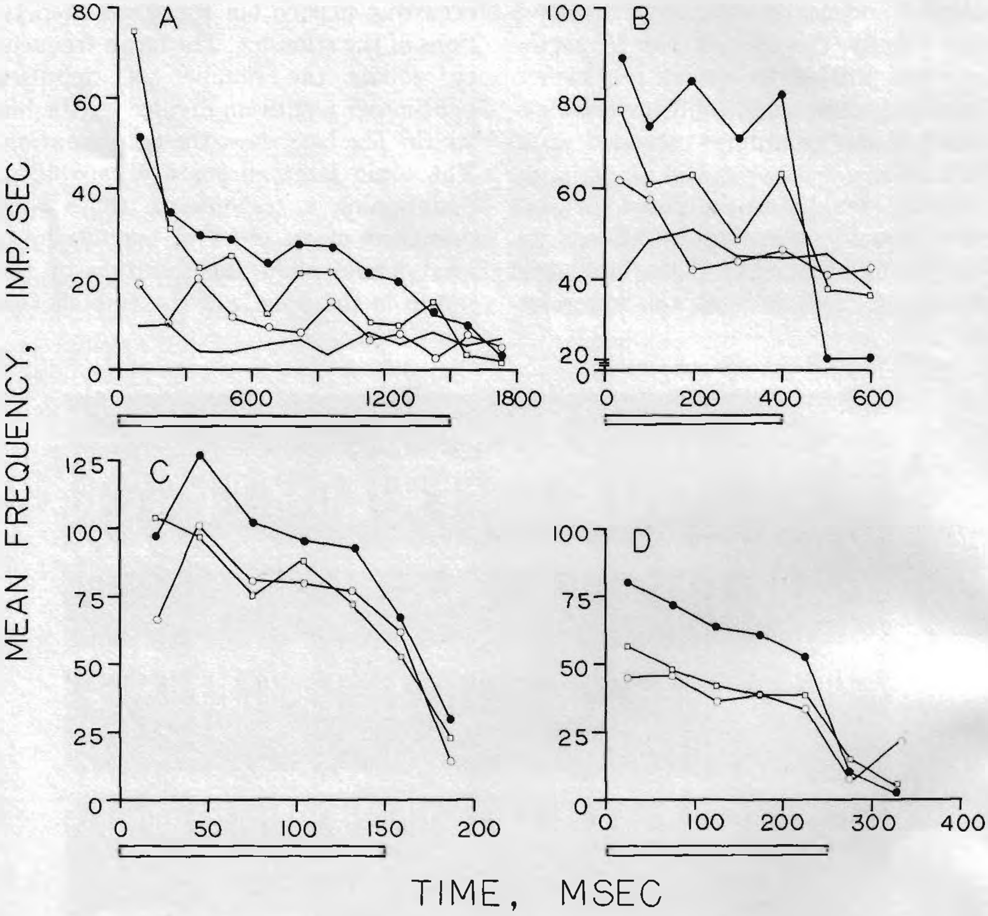

FIG. 6.—Adaptation properties of tonic interneurons. Mean frequency was determined by counting the number of impulses in each bin for several repetitions of the stimulus. Bars show the duration of the vibrational stimulus. Increasing stimulus strength shown by the sequence of symbols: ○, □, ●. (——) = spontaneous activity during sweeps with no stimulus present. *A*, *U. minax*. Each curve is the average of 4–6 repetitions at 39-, 50-, and 56-dB stimulus amplitudes, using 600-Hz tones. *B*, a different *U. minax;* average of 8–10 repetitions at 52, 57, and 66 dB, 400 Hz. *C*, *O. quadrata;* average of 15 at 68, 71, and 74 dB, 1 kHz. *D*, *U. pugilator;* average of 10–11 at 68, 74, and 80 dB, 500 Hz.

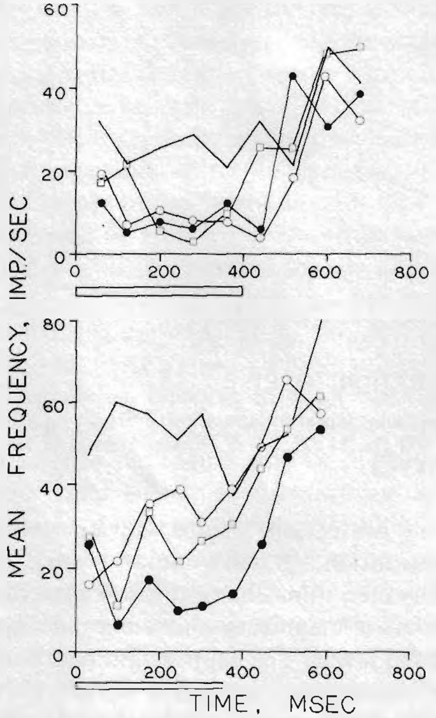

FIG. 7.—Adaptation properties of inhibited interneurons. Format as in fig. 6, except (——) is the weakest stimulus given, not spontaneous activity. Upper graph: *U. minax*, average of 5–7 at 48, 53, 58, and 63 dB, 300 Hz. Lower graph: *U. pugilator*, average of 9–11 at 65, 70, 74, and 80 dB, 1 kHz.

response. A similar effect was seen with the phasic units, although in the latter case stimulus-onset rate, as well as stimulus amplitude, was important in determining the vigor of the response. The level of spontaneous activity could markedly affect the response to a given stimulus, especially in the inhibited interneurons. In the upper graph of figure 7, for instance, apparently less inhibition was caused by a 63-dB stimulus (○) than by a 58 dB stimulus (●). However, the level of resting activity was 49 impulses/s at the time the 63-dB stimulus was given, but only 42 impulses/s when the 58-dB tone was used. In terms of the depression of spontaneous activity, then, the 63-dB tone was actually more effective than the 58-dB stimulus. This implies that stimulus-amplitude coding in these interneurons may be based on a relative change in frequency, not on the absolute firing rate.

Stimulus duration is well coded by the tonic interneurons. For a given stimulus strength, the number of impulses evoked during a stimulus is nearly linearly related to the stimulus duration in these units for tones comparable to the pulse durations in the calls (fig. 8). For the inhibited interneurons, the slow recovery of spontaneous activity masks termination of the response to longer tones.

All crabs showed essentially similar, nonhabituating responses to rapid pulse trains. In these tests, pulses varied from 5–30 ms in duration and were presented at rates of 10–30 Hz. Tonic units of all species coded these faithfully. Phasic units, however, failed to follow pulses delivered at rates above 5 Hz. Since the latter responded most vigorously to pulses with rapid onsets and since these tests were done using sounds which took 1–3 ms to reach full amplitude, it is unclear whether these findings reflect their full potential for rate coding.

Inhibited cells responded to short (15-ms duration) tones, but their slow recovery of spontaneous firing precluded discrete responses to bursts delivered faster than 10 per s.

DISCUSSION

We identify the three types of cells described here as interneurons for the following reasons. First, their responses are clearly different from those recorded in the primary afferents (Salmon and Horch 1973). Second, the cells receive convergent input from all the ipsilateral walking legs. However, we cannot say on the basis of our experiments here

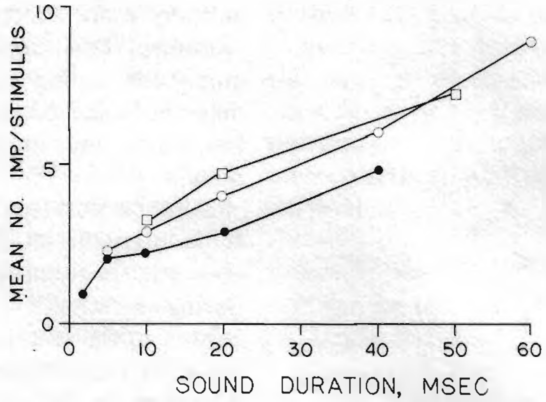

FIG. 8.—Number of impulses evoked in tonic interneurons by vibratory stimuli of different durations. ●, *O. quadrata*, average of 20–23 repetitions per point, 700 Hz, 84 dB. ☐, *U. minax*, average of 15–16, 300 Hz, 55 dB. ○, *U. pugilator*, average of 9–13, 500 Hz, 85 dB.

whether these cells represent ascending or descending systems.

The present experiments have yielded threshold values for all species which are lower than our previous reports (Horch 1971; Salmon and Horch 1972). We attribute this primarily to better coupling between the walking legs and the platform. The crabs typically extended their legs to the platform and pressed down, often with enough force to dampen stimulus levels. Another factor was the use of living preparations (in recordings from the sensory nerves, the crabs were eviscerated, and all CNS activity soon ceased). Ideally, one would prefer to record from the entire system (sensory cells and interneurons) using free-moving crabs. Such a preparation would probably show even greater sensitivity, but this "ideal" is not yet technically feasible.

The suppression of interneuronal response to external stimuli during voluntary movement is particularly interesting. A similar effect has been reported, by Taylor (1968) for antennal mechanoreceptors in the crayfish, and for other sensory systems (Collett 1974). In our crabs, suppression may serve as "overload protection," since, during normal locomotion, Barth's organ would be subjected to mechanical forces of several orders of magnitude above normal vibrational levels. The suppression may occur at the receptor level (see Horch 1971), or it may involve central inhibition. We favor the latter as a working hypothesis, since movement affected not only the response to external stimulation but also spontaneous firing by the interneurons (fig. 5). Whatever the mechanism, the result suggests that, when the crabs walk, they are unable to detect the sounds of conspecifics. Thus acoustic discrimination and localization, if they occur, must take place during pauses between periods of locomotion.

The tonal stimuli used were designed to determine if interneurons could respond to temporal patterns comparable to those present in the crab's sounds. The results indicate that the most obvious of these—pulse repetition rate, pulse duration, sound duration, and intersound interval—can be resolved. Tonic units, which were the most frequently found, encode all these parameters faithfully. Phasic units should respond to the presence of transients in the sounds, such as the leg-striking components of "honking" noises whose timing varies characteristically with each species (Salmon and Atsaides 1968). Our rate-coding trials indicated phasic units were incapable of resolving individual, brief tone bursts with smooth onsets presented at rates comparable to those occurring in the rapping sounds of *Uca pugilator*. However, when "clicks" were substituted for the tones, the neurons followed these rates. Finally, inhibited interneurons, because of their slow recovery after stimulation, are not likely to resolve individual pulses. However, they could encode sound duration and intersound interval. Since both inhibited and tonic interneurons yield graded and complementary responses, the two units together could provide some information on the sound-intensity changes which occur when a crab moves toward or away from an acoustically active conspecific.

However, all these predictions must be confirmed by experiments in which natural sounds serve as the stimuli. These tests are in progress.

The spectral-sensitivity curves of the three species differ, especially when *U. minax* is compared with the rapping species. In the former, sensitivity is most obviously related to the sound spectrum received near the male. In the rapping species, which emit their noises spontaneously, the animals may be matching their sensitivities to the frequency composition of weaker, more distant sounds. Measurements of sound transmission in these species (Horch and Salmon 1972; Salmon and Horch 1972; Horch 1975) show that the higher frequencies attenuate rapidly with distance from the crab source. It is just these frequencies which the crabs cannot detect. In any event, it would clearly be of interest to know how differences in spectral tuning, such as those occurring in our crabs, are built into the detection system.

We should emphasize that our catalog of acoustic interneurons may not be complete. There may be present cells which respond only to crab sounds generally or to the sounds of conspecifics. These neurons would not, of course, have been located by the search stimulus used in the present experiments.

Studies of vibration reception in other crustaceans have centered on behavioral correlates and on temporal analyses of the signals (Altevogt 1964; von Hagen 1967; Klaassen 1973). We know of no other reports in which interneurons sensitive to substrate vibration were examined. While many other arthropods respond to vibration (Markl 1973), little is known about further processing of sensory input. Dambach (1972*a*, 1972*b*) found tonic fibers in the circumesophageal connectives of crickets (*Gryllus campestris* and *G. bimaculatus*) which responded most strongly to stimulus onset and showed greater tuning to certain frequencies than the sensory cells. An important property of these cells was their "habituation" upon repeated stimulation. These properties are ideal when the primary role of the system is that of warning, as he suggests. While fiddler and ghost crabs also use vibrational cues to detect potential predators, it is clear that the transformations made by the three classes of interneurons studied here exceed the demands of a simple warning system. Rather, they show many similarities to the nonhabituating interneurons processing sensory input during acoustic courtship of crickets (Zaretsky 1971; Stout and Huber 1972) and grasshoppers (Rheinlaender 1975), in which discrimination of species-typical sounds is known to occur.

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