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THE DETECTION OF WATERBORNE VIBRATION BY SENSORY HAIRS ON THE CHELAE OF THE CRAYFISH

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SUMMARY

Sensory hairs on the chelae of the Australian freshwater crayfish *Cherax destructor* are grouped together into pits. Electrophysiological recordings from the sensory axons of isolated chelipeds show that the hairs are maximally sensitive to water vibration frequencies between 150–300 Hz. The amplitude threshold is about 0·2 μm water molecule oscillation.

INTRODUCTION

Crayfishes have mechanoreceptive hairs of many different shapes and sizes distributed over almost all surfaces of their bodies and derive a great deal of information about their immediate surroundings via the body surface (Laverack, 1962*a*, *b*; Mellon, 1962; Tazaki & Ohnishi, 1974; Wiese, 1976; Chichibu, 1978).

The sensitivity of the hair receptors on the chelae to different frequencies of water vibration has up to now not been investigated although many marine and freshwater forms are predominantly active at night and the tactile and vibration sensitive sense organs conceivably play a far more important role in the behaviour of the animal than the visual system.

METHODS AND MATERIALS

Crayfish (*Cherax destructor*) of both sexes were caught in ponds near Canberra and kept separately in small tanks in the laboratory.

Measurement of the sensitivity thresholds of mechanoreceptive hairs was made in a sound field in which standing waves and reflexions were excluded. This was achieved by placing the isolated chelae in the body of a 100 cm long, Ringer-filled perspex tube (I.D. 32 mm) with a rubber diaphragm covering one end. The other end was bent up at an angle of 4° to prevent the Ringer solution from flowing out (Fig. 1). The rubber diaphragm was connected by a rod to a loudspeaker and driven from a function generator. To obtain electrical recordings from the sensory organs, a length of the cheliped nerve was exposed by removing the meropodite from the carpopodite. The exposed nerve was then teased into smaller bundles and these were monitored

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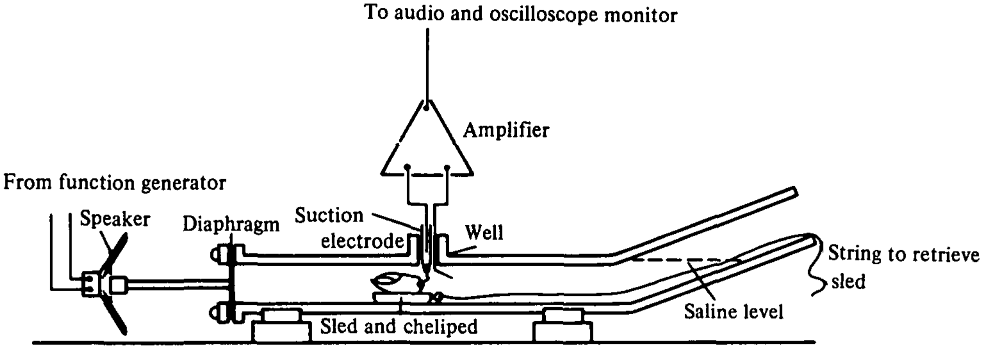

Fig. 1. The apparatus used to stimulate and record from the pit organs on the cheliped of *Cherax*. The cheliped is first removed from the animal and a length of the nerve exposed by taking off the meropodite. The nerve is teased into small bundles and the cheliped is then stapled to a Sylgard-filled sled. The sled is pushed into the tube and positioned below the well through which a suction electrode is lowered. The diaphragm is connected by a rod to a loudspeaker which is driven by a function generator. The upturned open end of the tube prevents the saline in the tube from flowing out and eliminates standing waves and reflections in the tube. The drawing is not to scale.

with a suction electrode, lowered through the well in the tube above the cheliped (Fig. 1). The apparatus was calibrated using a hot wire anemometer (Tautz & Markl, 1978) and a particle-velocity sensitive hydrophone (Veith, 1977). These instruments were calibrated as described previously (Tautz, 1977; Tautz & Markl, 1978).

RESULTS

The sensory hairs lying over the inner and outer surfaces of the chelae in *Cherax* are contained in small pits (Fig. 2). Within the pits they are grouped together in complex organs. The number of hairs in each pit is variable within individuals but smaller (younger) animals generally have fewer hairs to each pit than larger (older) ones (Table 1). The greatest number of hairs seen in a pit was 17, the smallest 3. The number of pits does not vary considerably between individuals, so, like some other described crayfish sensory organs (Laverack, 1976), it appears that during growth the sensory complexes do not increase in number but, instead, new hairs are added to the existing pits (Table 1). We found no other types of hairs over the surfaces of the chelae except the short brushlike ones along the edge of the propodite opposed to the dactyl. These resemble hairs in the lobster shown to have chemoreceptive function (Shelton & Laverack, 1970). Examination of the *Cherax* pit organs in freeze dried material with the scanning electron microscope show that there are two 'types' of hair. These are (1) feathered hairs of different lengths and (2) short smooth hairs (Fig. 3). The smooth hairs are not always seen but when present, are in the centre of the pit, the feathered hairs being arranged at the periphery (Fig. 3). When the pit contains large numbers of hairs, most are feathered. The two 'types' of hair may reflect no more than different stages in the development of the feathered hair, which all begin as smooth hairs and become feathered during subsequent moulting. Nevertheless, many pit organs have a longer centrally situated plumose hair which has a more prominent base than [illegible] others (Fig. 3). A comparison of this hair with the integumentary organs of other

Table 1. *Number of pit organs on the chelipeds of four individuals. Also the numbers of single hairs counted in some* (5–12) *pits on comparable regions on the chelipeds are given*

Four individuals	Dactylopodite length (mm)	Number of pit organs			Total number of organs	Number of single hairs counted in some pits (Mean and S.D.)
		On dactylopodite	On propodite	On carpopodite		
1. Left cheliped	9	152	427	152	731	5 ± 2
2. Left cheliped	16	147	462	138	747	7 ± 4
3. Left cheliped	20	165	503	173	841	10 ± 3
4. Left cheliped	25	121	480	156	757	12 ± 4
Right cheliped	25	132	482	144	758	11 ± 3

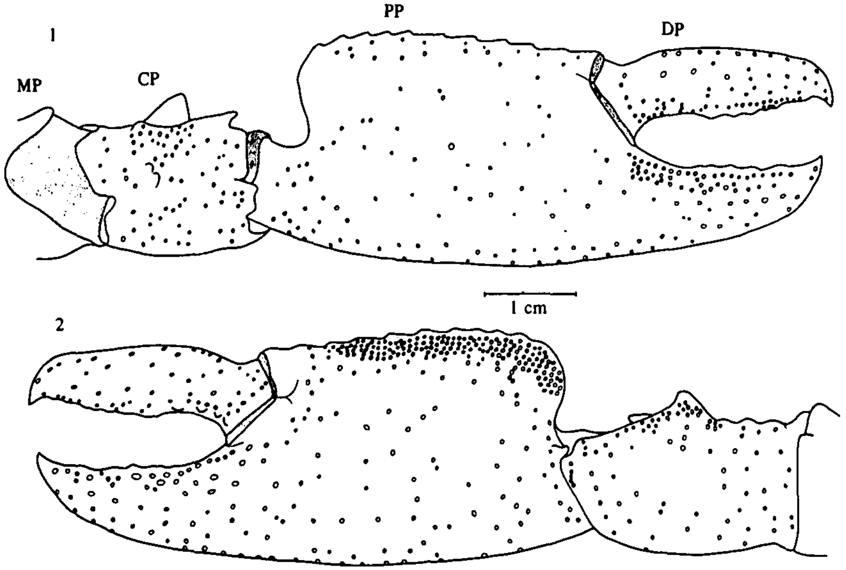

Fig. 2. Distribution of hair pits on the left chelae of *Cherax*. CP, carpopodite; DP, dactylopodite; MP, meropodite; PP, propopodite. 1, inner surface; 2, outer surface.

crustaceans reveals a similarity to the plumose hairs of the antennal hydrodynamic organ of *Palinurus* (Clarac, Vedel & Moulins in Laverack, 1976). We do not regard the hair pit organs of *Cherax* to be the same as the hair fans of *Homarus* (Laverack, 1962*b*). The number of sensory cells belonging to each hair remains open.

The threshold sensitivity of the receptors on the chelae to a range of frequencies was measured in three different ways: (1) from the summed activity of action potentials from several pit organs where individual units could not be separated; (2) from the summed activity from hairs of a single identified pit organ where individual units could not be separated; and (3) from the activity of single units from a single identified pit organ. Identification of a pit organ was achieved by painting over with nail polish all except one from which activity was well represented in the recordings and then, as a control, painting over the remaining organ. Identification of single units in the recordings was based on the size of the action potentials.

The threshold curves of summed activity from several hair pits show a maximum sensitivity in the frequency range 150–300 Hz, with a water particle displacement

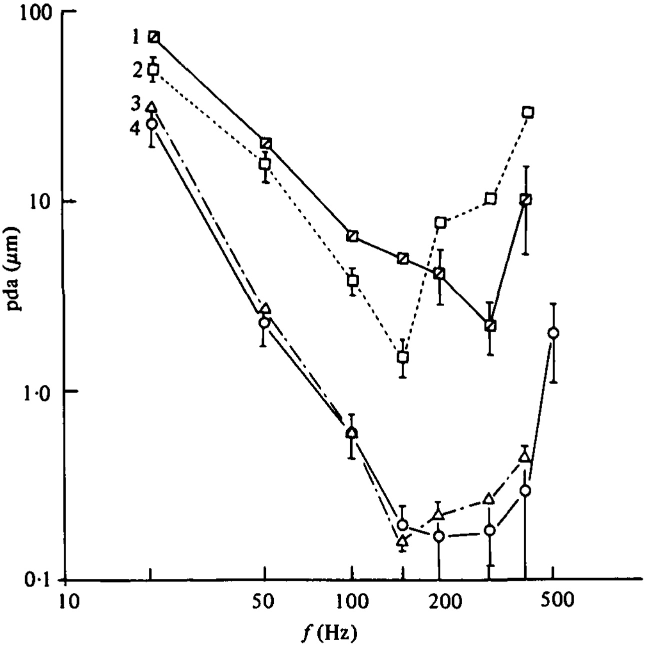

Fig. 4. Threshold curve of impulse initiation for hair pit organs. Abscissa: stimulation frequency. Ordinate: particle displacement amplitude. Tuning curves are shown for two individual units from one pit organ (1: solid line, 2: dotted line), for the summed activity from several units from one hair pit (3: dot-dashed line) and the summed activity from several pit organs (4: solid line). Means and standard deviations from 15 measurements.

amplitude (i.e. half peak to peak motion) of about 0·2 μm (Fig. 4). This curve is closely matched by the summed activity from a single organ, but threshold curves from single or smaller populations of units from within a single pit organ are more sharply tuned (Fig. 4). Threshold tuning curves for mechanoreceptors are not altered, in terms of the optimal frequency of the signal, when the direction of the signal is changed. It was, therefore, not necessary to orient the cheliped to the stimulus before measuring its tuning curve.

DISCUSSION

The sensitivity of hair receptors in crayfish to waterborne vibrations was described earlier by Laverack (1962*a*, *b*). Offutt (1970) determined in behavioural experiments (conditioning heart beat rate) the sensitivity of *Homarus americanus* to sound in the frequency range 10–150 Hz. He found at 75 Hz a threshold of $8{\cdot}1 \times 10^{-4}$ μm particle displacement amplitude (p.d.a.) and at 150 Hz $2{\cdot}9 \times 10^{-4}$ μm p.d.a. (calculated by the authors from the given particle velocity). This value lies 3 decades below the receptor thresholds given in the present paper and leads to the conclusion that receptors other than those on the chelae were involved in Offutt's experiments. Wiese (1976) investigated telson hairs in *Procambarus clarkii* in the frequency range 0·05–150 Hz with the hairs tightly coupled to the stimulator. For a free oscillating hair he calculated a threshold of 0·1 μm p.d.a. at 100 Hz, which is less than the directly measur threshold of 0·6 μm p.d.a. at 100 Hz in the case of *Cherax*, but it must be consider

Fig. 3

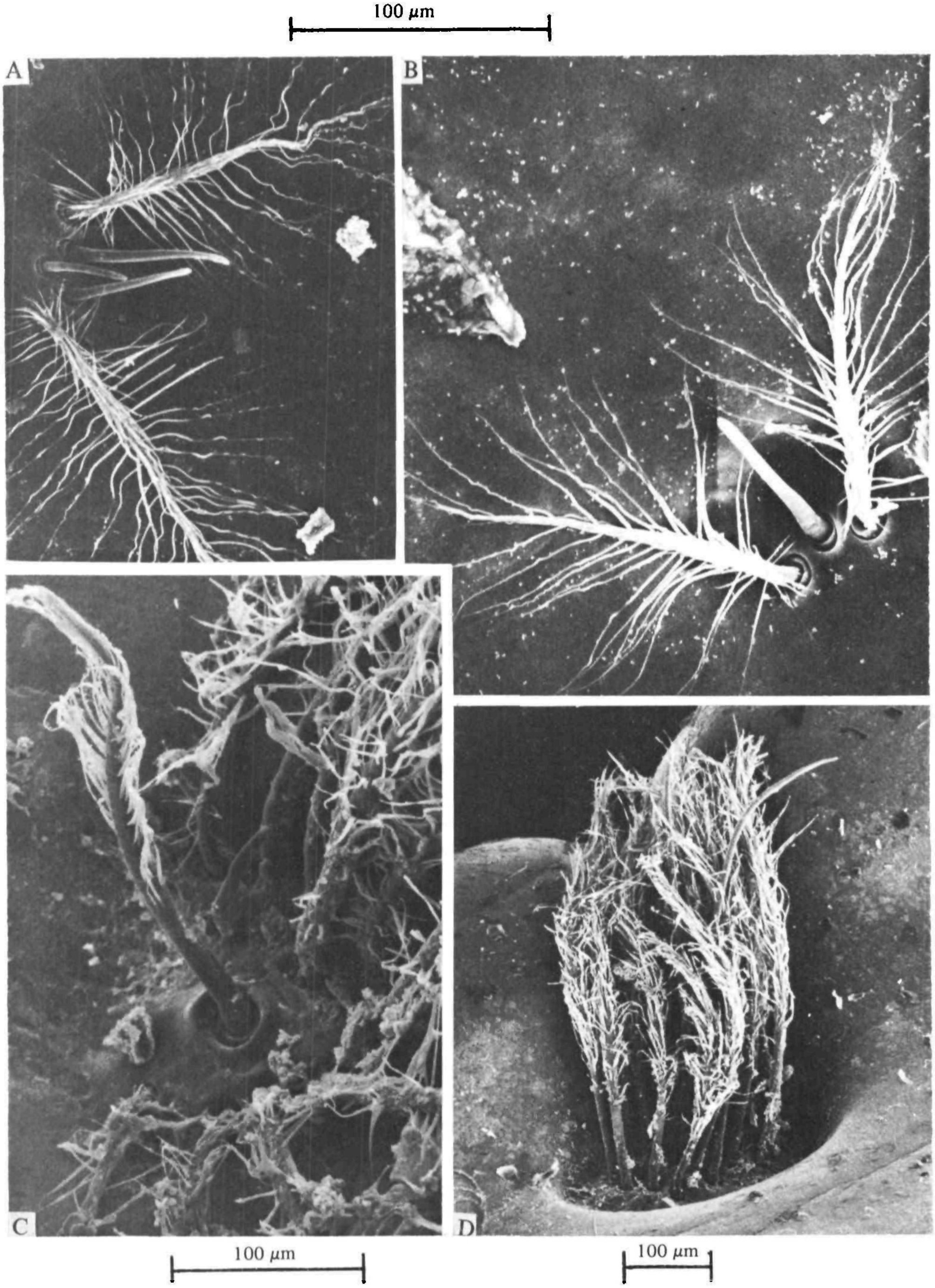

Fig. 3. Scanning electron micrographs of hair pit organs. A and B: pit organs containing few hairs (from a young animal). C and D: pit organs with a ring of feathered hairs. A larger central plumose hair can be seen in C, and several smooth hairs project from the centre of the pit in D.

that *Cherax* chelae are most sensitive in the range 150–300 Hz with a threshold of 0·2 μm p.d.a. Tazaki & Ohnishi (1974) found for hair receptors on the antennal flagellum of *Panulirus japonicus* that only low frequency oscillations (< 5 Hz) are effective. They give no values for sensitivity. Chichibu, Tani & Tsukada (1978) found in sensory hairs of the 1st antennae of *Procambarus clarkii* responses of the sensory cell to stimulation up to 300 Hz. In the present investigation the innervation pattern of the receptor hairs was not investigated and it remains open if all hairs of the composed organ are pure mechanoreceptors and that chemoreceptors are not also present.

To be effective mechanoreceptors in water, sensory hairs can be much shorter than those detecting movements in the air, because the frequency dependent boundary layer in water is about 1000 times smaller than in air (e.g. at 150 Hz: in air, 126 μm in water, 0·1 μm). Hairs on the chelae of *Cherax* which are only 20 μm long (the smallest found) are, therefore, also effective receptors for the detection of vibration in water. Additionally, it is not necessary for the hairs to be critically balanced, as is the case with detectors of airborne vibrations, because the specific weight of the crayfish hairs is nearly the same as that of the surrounding water (see Tautz, 1979).

As the near field of a sound source spreads five times as far in water as in air, it can be seen that the receptors on the chelae of *Cherax* are extraordinarily effective in the detection of vibrating sources in the surrounding environment. For example, a sphere 1 cm in diameter, and pulsating with an amplitude of 1 mm, can be detected at a distance of 35 cm. (This can be calculated from $a_n = a.r_0^2/r^2$, r = distance from the centre of the sphere, r_0 = radius of the sphere, a_n = p.d.a. at distance r, a = p.d.a. at the surface of the sphere, see e.g. Markl & Tautz, 1975). Larger objects can be detected from proportionately greater distances.

The importance of water borne vibration in the behaviour of unrestrained animals has been confirmed in many cases and recently we have been able to demonstrate that crayfish can be conditioned to search for food given a stimulus of a particular frequency and amplitude of water vibration (J. Tautz & D. C. Sandeman, in preparation).

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