

SHORT COMMUNICATION

VIBRATION SENSITIVITY IN THE STATOCYST OF THE
NORTHERN OCTOPUS, *ELEDONE CIRROSA*

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Accepted 12 August 1987

The question of whether cephalopods have a sense of hearing has recently received renewed attention in the literature (Moynihan, 1985; Hanlon & Budelmann, 1987). However, the scarcity of physiological data (Maturana & Sperling, 1963; see also Budelmann, 1977) has meant that both those taking the view that cephalopods are deaf (Moynihan, 1985) and those of the opposing view (Hanlon & Budelmann, 1987) have relied almost entirely on morphological and behavioural evidence. Unfortunately, the morphological evidence cannot be conclusive and some behavioural experiments indicate no reaction to sound by cephalopods (Hubbard, 1960), although this is contradicted by other observations (Maniwa, 1976).

The statocyst in octopus has been shown to be a detector system for gravity and angular acceleration (Budelmann & Wolff, 1973; Williamson & Budelmann, 1985) and, as pointed out by Young (1960), this organ could also serve as a vibration or sound detector in a way analogous to the vibration/sound sensitivity of the vertebrate vestibular system (for a review see Hawkins & Myrberg, 1983). The following experiments were undertaken to test this hypothesis.

Intact statocysts, still entirely embedded in cartilage, were removed from the octopus, *Eledone cirrosa*, and placed in a small bath mounted on a vibrator system. The bath was vibrated by an electromagnetic vibrator (Derritron type V.P.2) driven by a function generator programmed to provide 300 ms bursts of stimuli with 50 ms rise and decay times. The vibrations were sinusoidal, within the range 10–200 Hz and with particle velocities of 1 to $5 \times 10^4 \mu\text{m s}^{-1}$. The stimuli were monitored by a miniature geophone (Sensor Nederland). The statocyst was mounted in the upright position in the bath (see Messenger, 1967) such that the vibrations were in the anterior–posterior direction. The responses from the statocyst were obtained by a suction electrode recording from the cut end of the statocyst crista nerve at the point where it emerges from the cartilage to enter the brain cavity; this nerve is composed of the anterior and medial crista nerves. Attempts were also made to record from the macula nerve but these proved unsuccessful.

A representative example of a stimulus and the response obtained is shown in Fig. 1. Here two units, neither of which showed spontaneous activity, can be seen

Key words: statocyst, octopus, vibration sensitivity.

responding to the stimulus. This clearly demonstrates that the statocyst crista can respond to vibration. To test whether this was a non-specific response, or whether the magnitude of the vibration was being coded, stimuli of increasing amplitude were applied at a fixed frequency of 80 Hz (Fig. 2). It can be seen that the response from the statocyst increases with increasing stimulus amplitude up to a velocity of about $3 \times 10^3 \mu\text{m s}^{-1}$ and thereafter levels off to a plateau. It was also found that additional units were recruited with increasing stimulus amplitude, implying that different units have different sensitivity thresholds.

The frequency sensitivity of the statocyst was investigated by applying a range of different frequencies and steadily increasing the stimulus amplitude until a response was obtained. This point was taken as the threshold response for this frequency. A



Fig. 1. Recording of activity from the statocyst crista nerve in response to a tone burst. The tone burst is at a frequency of 80 Hz and of 300 ms duration with 50 ms attack and decay times.

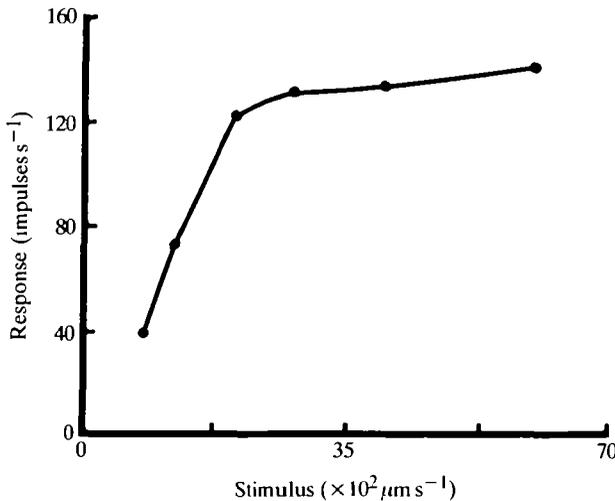


Fig. 2. Statocyst response plotted against stimulus amplitude. The response is given as the maximum spike firing frequency obtained at each stimulus amplitude. The stimuli are expressed as particle velocities.

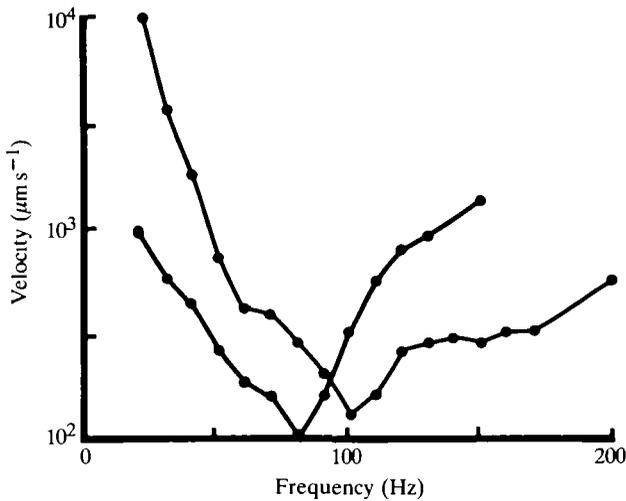


Fig. 3. Threshold response curve from two statocyst afferents. Abscissa: stimulation frequency. Ordinate: particle velocity on a logarithmic scale.

graph of some typical frequency response thresholds is shown in Fig. 3. All units examined ($N = 17$) showed peak sensitivity at about 70–100 Hz. The most sensitive unit responded at a stimulus velocity of $60 \mu\text{m s}^{-1}$.

These results show that the octopus statocyst is sensitive to vibration with a maximum sensitivity representing a particle displacement of $0.12 \mu\text{m}$. This compares well with the vibration sensitivities of other aquatic invertebrates; for example, the sensory hairs of the crayfish *Cherax destructor* have a threshold of $0.6 \mu\text{m}$ (Tautz & Sandeman, 1980) and *Procambarus clarkii* has a threshold level of $0.1 \mu\text{m}$ (Wiese, 1976). However, these values are much less sensitive than the levels found in marine fish: *Gadus* has an otolith displacement threshold of $0.5 \times 10^{-4} \mu\text{m}$ (Chapman & Hawkins, 1973) and *Salmo* a threshold of $3 \times 10^{-4} \mu\text{m}$ (Hawkins & Johnstone, 1978). Thus the octopus crista is three or four orders of magnitude less sensitive to vibration than the auditory systems of fish and so, in comparative terms, cannot be classified as an auditory sense organ.

However, this does not necessarily imply that the octopus is 'deaf' for it may be that the statocyst macula is more sensitive to vibration than the crista. The otolith-like structure of the macula should have a higher acoustic impedance, and therefore a greater sensitivity, than the crista/cupula system, but without direct physical measurements it is difficult to estimate the sensitivity of the system. It may be that improved recording techniques will allow recordings to be obtained from the macula nerve.

In addition, vibration sensitivity need not be confined to the statocyst. Young (1960) has indicated that octopuses with their statocysts removed can still respond to vibration and a variety of mechanoreceptors, which may be vibration sensitive, have been found in cephalopods (e.g. Boyle, 1976; Kier, Messenger & Miyan, 1985).

Finally, this and other octopuses are benthic, often living close to the shore, where a high level of background noise can be expected (Myrberg, 1978); it may be that open-water cephalopods have more sensitive detection systems for vibration.

RW is a Wellcome Senior Research Fellow.

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