

Inhibition of oesophageal peristalsis in the lobster after chemical stimulation

PREVENTION of hyperphagia by some mechanism is essential to feeding animals. To date relatively few such control mechanisms have been studied in detail. Termination of feeding by internal inhibitory feedback from stretch receptors is documented for *Phormia regina*¹, *Locusta migratoria*², *Chortoicetes terminifera*³ and *Aplysia californica*⁴. Chemosensory adaptation has been suggested for *Phormia*¹ and *Chortoicetes*³, and in *Locusta* activation of foregut stretch receptors will, through a nervous and hormonal pathway, close the terminal pores of chemosensory sensilla on the maxillary palps⁵. We present here evidence showing that stimulation of a pair of oesophageal contact chemoreceptor organs can slow the ingestion rate and terminate feeding in *Homarus gammarus*.

The anterior oesophageal sensors (AOS) were first described in *Homarus* by Allen⁶ and were described in more detail in the crayfish *Astacus leptodactylus* by Orlov⁷ (for a review of the sensory innervation of the foregut of decapod crustaceans see ref. 8). These sensors are bilaterally symmetrical and their cuticular endings are situated in the clefts between the anterior and lateral lobes of the oesophageal/cardiac sac valve (data not shown). Each anterior oeso-

phageal sensor is innervated by a dorsal branch of the ipsilateral superior oesophageal nerve (SON) and can be divided readily into two populations of receptor neurones; 1, 50–60 bundles of 3–5 small (15–20 μm long axis) uniterminal bipolar neurones; and 2, 250–300 similar small neurones which are present singly. The cuticular modifications associated with the dendrites can be divided similarly (Fig. 1). In addition there are between two and five large (60–80 μm long axis) bipolar neurones whose axons also travel in the anterior oesophageal sensor nerve and whose long dendrites travel over the surface of the cardiac sac and oesophagus in the region of the valve.

Recording and stimulation of selected nerves was carried out with silver wire hook electrodes using conventional techniques. In all experiments the bathing medium was clean, cool seawater. The organ was chemically stimulated with an extract of *Mytilus edulis*. The gills and mantle of a fresh mussel were homogenised in approximately the same volume of seawater. This was applied directly on to the anterior oesophageal sensor with a glass pipette inserted through a hole cut in the cardiac sac. The afferent axons of other chemoreceptors in the area were cut.

The oesophagus undergoes peristalsis for some time after initial dissection, and recordings from the superior oesophageal nerve during this time reveal a complex rhythmical burst which can be shown to occur during oesophageal dilatation. This burst was used as an indicator of oesophageal dilatation during peristalsis. The frequency of bursting is relatively constant at any one time but varies between 0.1 Hz and 0.33 Hz. Suprathreshold electrical stimulation of the anterior oesophageal sensor nerve with a train of rectangular pulses of width 0.6 ms and with a pulse interval of 500 ms has two effects (Fig. 2). In this preparation the burst frequency dropped from its original level (about 0.28 Hz) to approximately 0.1 Hz; this was accompanied by a drop in the number of spikes in each burst. On cessation of stimulation the burst frequency and the number of spikes per burst increased but did not reach their original level. Application of *Mytilus* extract directly on to the anterior

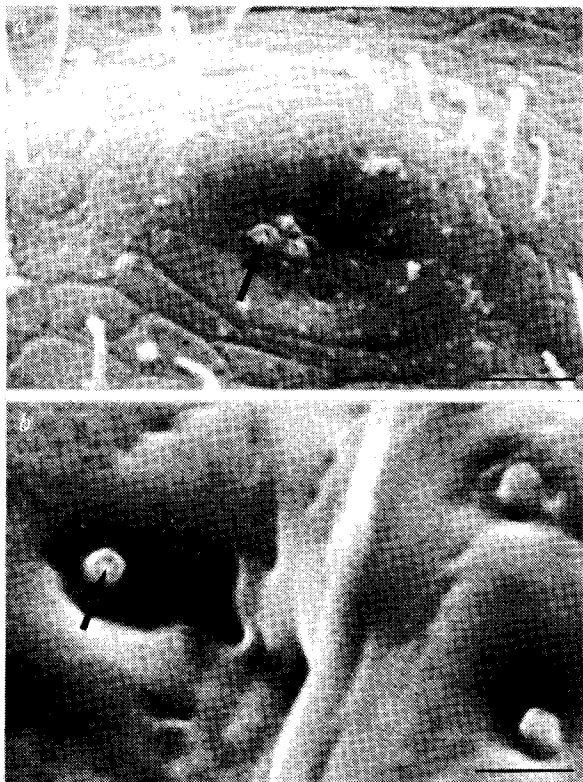


Fig. 1 Scanning electron micrographs of the cuticular modifications associated with the anterior oesophageal sensor. *a*, Grouped endings located in depressions in raised hillocks on the lateral wall of the anterior lobe of the oesophageal/cardiac sac valve. *b*, Single endings present deep in the cleft between the anterior and lateral lobes of the valve. It is possible that the sensilla have terminal pores (arrowed). The single endings bear a marked resemblance to those described for contact chemoreceptors in insects^{9,10}. Scale bar, 10 μm in *a*, 4 μm in *b*.

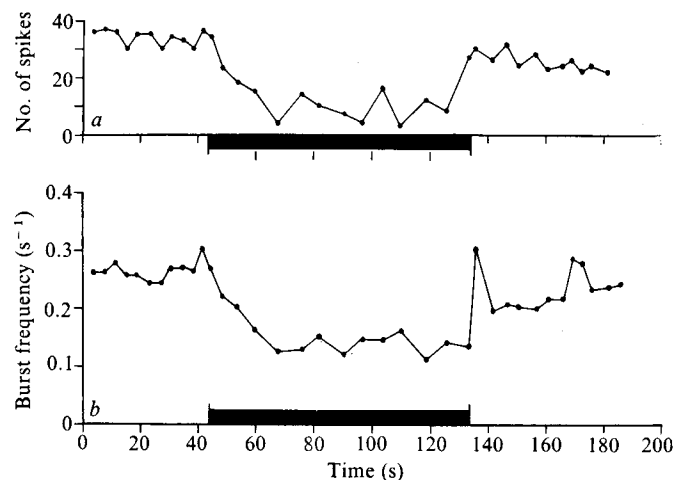


Fig. 2 Effect of electrical stimulation of the anterior oesophageal sensor nerve (black bar) on rhythmic bursting in the SON. The number of spikes in each burst (*a*) and the burst frequency (*b*) are plotted against the time of occurrence of each burst. Burst frequency is calculated as the reciprocal of burst interval which is measured from the start of one burst to the start of the succeeding burst.

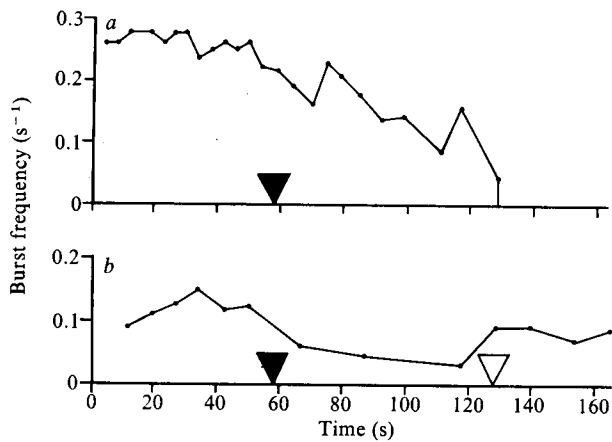


Fig. 3 Effect of chemical stimulation of the anterior oesophageal sensor on rhythmical bursting in the superior oesophageal nerve. (a) and (b) are different experiments. Application of *Mytilus* extract (solid arrow) slows and stops bursting (a). In (b) burst frequency increases on removal of the pipette (open arrow) but without washing the organ.

oesophageal sensor mimics the effect of electrical stimulation of the sensory axons by reducing the burst frequency (Fig. 3), although there is no reduction in the number of spikes per burst. Continued application can terminate bursting, and to be effective the extract must be closely and continuously applied.

The anterior oesophageal sensors are classified as contact chemoreceptors on morphological grounds and direct experimental evidence is not yet available. The positions of the receptor organs are such that they become available

for stimulation only when the cardiac sac is filled to capacity and the oesophageal/cardiac sac valve is stretched open. The solitary endings lie deep in the cleft between the lobes of the valve while the grouped endings spread on to the lateral walls of the anterior lobe. It is unlikely that these positional differences reflect functional differences, the more complex arrangement of the grouped endings probably serving to prevent causal stimulation during feeding. The observed difference between electrical and chemical stimulation can be explained by the presence in the anterior oesophageal sensor nerve of the axons of the small group of large bipolar neurones. These are presumptive mechanoreceptors that may respond to stretch in the region of the oesophageal/cardiac sac valve and could also be involved in the control of the peristaltic rhythm.

These observations suggest an alternative control mechanism for feeding processes, dependent upon chemical rather than mechanical feedback to higher centres. It is possible that such methods of controlling food ingestion will be found more commonly, especially amongst decapod crustaceans.

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