Zusammenfassung. Es konnte gezeigt werden, dass elektrische Stimulation des lateralen Hypothalamus mit einer Verzögerung von 2–6 min Fressen auslöst. Selbstreizversuche zeigten, dass diese Stimulation auch belohnend wirkt. Ähnlich verzögertes Fressen kann auch durch Reizung oder spreading depression in anderen Hirngebieten ausgelöst werden. Es wird vermutet, dass alle diese Phänomene auf einem gemeinsamen Mechanismus basieren.

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Cuticular Gas in Marine Decapod Crustacea

A film of gas, perhaps no more than a few microns thick, on the body surface has been suggested as the basis of the pressure sensitivity shown by certain marine crustacea[1], but until recently it has not been possible to establish the existence of such minute volumes of gas experimentally. The ultrasonic techniques currently available are either non-specific for gas[2] or designed to detect moving bubbles using the Doppler shift principle[3,4]. An alternative method[5,6], based on measurement of the harmonic waveform distortion caused by gas in an acoustic field has been developed in the Department of Electronic and Electrical Engineering at the University of Birmingham. This technique, which has the advantage of being specific for gas, is thus suitable for the detection and estimation of small, stationary gas volumes in a liquid medium, and has been used here for the detection of gas on the body surface of decapod crustacea.

Materials and method. Experiments were carried out with the transmit and receive acoustic transducers arranged about 5–7 mm apart (Figure 1a) and immersed in kerosene to avoid electrolysis at the metallic surfaces of the transducers. An acoustically 'transparent' test cell, containing water boiled at reduced pressure to remove any residual air bubbles, was positioned between the two transducers and the apparatus calibrated by generating a known volume of gas electrolytically on the end of a fine copper wire, insulated to the tip and held in the acoustic field. Legs removed from living or freshly killed specimens of two pressure-sensitive species of crab, *Carcinus maenas*[7] and *Macropipus holsatus*[8], were mounted in a rubber

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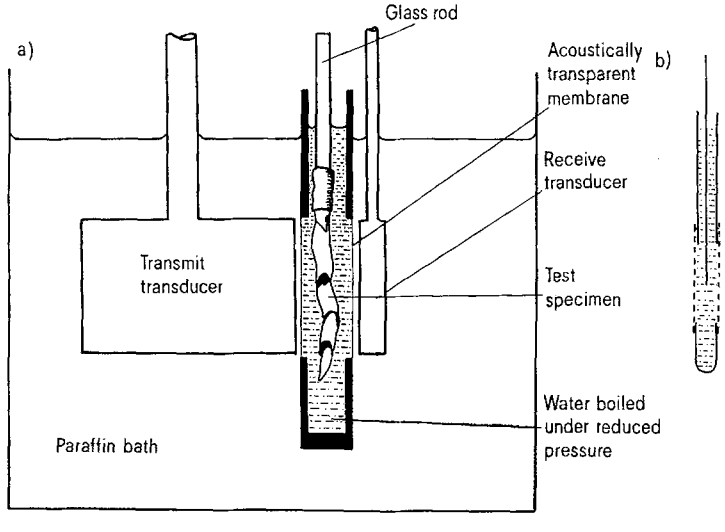

Fig. 1. a) Diagram of the apparatus. The transmit transducer was made from paired lead-zirconate plates mounted on aluminium alloy blocks and enclosed in an aluminium alloy housing while the receiver contained a single plate embedded in araldite in an aluminium alloy block. Kerosene was preferred to water as an acoustic coupling fluid to avoid generating gas electrolytically on the metallic surface of the transducers. The specimen under investigation was lowered into a test cell with acoustically-transparent membrane walls, and containing water boiled under reduced pressure to remove air bubbles. The fundamental and harmonic waveforms were displayed on an oscilloscope and the harmonic distortion component amplified and rectified for monitoring on a pen recorder when required. b) Diffusion cell with dialysis membrane collar.

sleeve on the end of a glass rod and the possible existence of gas on the surface investigated by lowering the leg into the cell between the transducers.

Results and discussion. The resulting acoustic harmonic distortion (Figure 2) indicated gas which ranged in volume from 0.3×10^{-6} to 1.3×10^{-6} ml in the different experiments. Assuming an even distribution, the greatest volume of gas recorded would correspond to a layer no more than 40 nm thick and it seems more probable that the gas is distributed in a mosaic of small pockets. However, it is doubtful whether the gas recorded here was generated as the result of an electric potential difference across the cuticle, as suggested by DIGBY[9]. Similar volumes have been detected on sections of carapace removed from crabs found dead on the bottom of the holding tanks in the Zoology Department aquarium, and on elytra removed from dead and living cockroaches. The acoustic pressure changes generated between the transducers were small, about 10 millibars ($1 kNm^{-2}$) peak-to-peak, and unlikely to effect compression of the veins in the elytra, and it therefore seems probable that the gas detected in these experiments had simply adsorbed on to the surface of the integument.

In a further series of experiments legs were amputated from *Carcinus* and transferred to the acoustic chamber under water. Potential differences of 35–50 mV, inside negative, had been previously recorded across the integument of the leg, and gas could conceivably originate electrolytically under these conditions. Only on one occasion was gas detected and then in much smaller quantities than above. The amputee had been kept submerged for about a week prior to the experiment, but had been exposed previously in transit, and it is possible that minute quantities of air could have survived over this period in microcavities in the cuticle[10].

Although the periodic exposure of littoral animals could thus confer upon them a mechanism of pressure transduction, it would appear unlikely that such an important environmental variable should be perceived so fortuitously. Many pressure-sensitive animals are planktonic[11–13] and are not normally exposed to the air.

DIGBY postulated an electrogenesis of gas at the body surface on the basis of a series of experiments in which he demonstrated how the potential difference recorded across the integument of the prawn *Palaemonetes varians*, and between diffusion cells of different ionic concentrations varied with changes in ambient pressure. These experiments are readily repeated. Using copper electrodes (cf DIGBY) pressure-induced changes in potential have been recorded from isolated legs of *Carcinus*, stage 2 larvae of the lobster *Homarus*, and also from a comparable diffusion cell[14]. These results are consistent with the compression of a gas phase but it is difficult to ascertain whether this is located at the surface of the integument (or diffusion cell membrane) or on the surface of the metallic electrode itself. We have attempted to locate the gas in a model cell system in which sea water was separated from slightly saline tap water by a collar of dialysis membrane (Figure 1b). The potential difference developed across the membrane was found to be 70–80 mV, inside negative, and a further −15 mV was recorded at the junction between the copper wire cathode and the sea water within the cell. Overall potential changes of up to 20% had been previously recorded from similar cells following an increase of pressure of up to 1250 mb (125 knm^{-2}). In our experiments the cell was positioned with the membrane collar in the centre of the acoustic field and a weak current passed between the electrodes. Gas was detected only when the tip of the copper cathode was located within the acoustic field. No gas was recorded when the electrode was partially withdrawn from the cell to a position outside the acoustic field, suggesting that in this experiment the gas was generated primarily at the surface of the metallic electrode. However, as DIGBY[15] has more recently pointed out, if the membrane is too porous any gas produced at its surface would be removed by electro-osmotic effects. Crustacean cuticle is much less porous, and has been shown to function as an intermediate electrode at which hydrogen is generated when a current is passed across it, but the evidence that gas is generated electrolytically at the body surface in the natural situation appears inconclusive.

Résumé. On a décelé la présence d'une couche de gaz d'àpeuprès 40 nm d'épaisseur sur la cuticule de certains crustacés décapodes marins en enregistrant la distorsion harmonique que ce gaz a causée lorsqu'on le soumet à un champ acoustique. Quoiqu'on ait démontré que le gaz pourrait être adsorbé sur la surface, une origine électrolytique est à la limite du possible.

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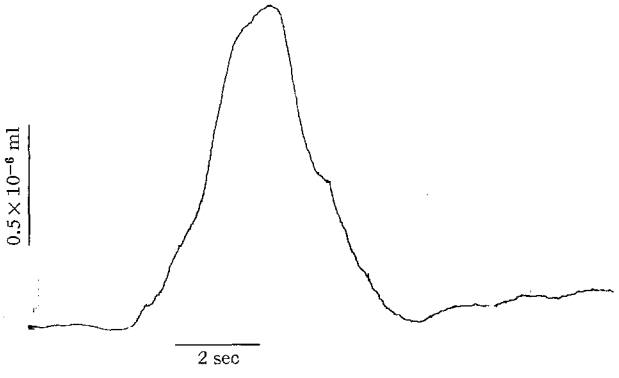

Fig. 2. Trace obtained on lowering the 3rd walking leg of the shore crab *Carcinus maenas* into, and subsequently removing it from, the acoustic field. The leg was positioned manually and the harmonic distortion caused by gas was found to be proportional to the amount of leg located between the transducers, suggesting a uniform distribution over the surface of the integument. The volume of gas involved is indicated by the extent of the vertical deflection.

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[16] Part of this work was carried out by one of us (E.M.) while at the Marine Biological Station, Port Erin. It is a pleasure to recognize the hospitality of the Director and his staff.