ELECTROPHYSIOLOGICAL RESPONSES
OF THE TERMINAL SENSILLA ON THE MAXILLARY PALPS OF *LOCUSTA MIGRATORIA* (L.) TO SOME ELECTROLYTES AND NON-ELECTROLYTES

BY W. M. BLANEY

Zoology Department, Birkbeck College, Malet Street, London, WC1E 7HX

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INTRODUCTION

It has been shown that the maxillary palps of *Locusta migratoria* (L.) play an important part in food selection when the insect has not been deprived of food for a long period (Blaney & Chapman, 1970; Blaney, Chapman & Wilson, 1973). The receptors primarily concerned are those on the flexible dome at the distal tip of the palp, and in the fifth instar larvae of *Locusta* there are about 370 of these sensilla on the dome of each maxillary palp.

The fine structure of these sensilla (Blaney, Chapman & Cook, 1971) corresponds to that generally ascribed to contact chemoreceptors (Lewis, 1970; Slifer, 1970) and a chemoreceptive function has been confirmed by Haskell & Schoonhoven (1969) using electrophysiological techniques.

This paper describes part of an electrophysiological study to determine the role of these receptors in food selection, and in this preliminary investigation an examination is made of the responses of the receptors to some electrolytes and non-electrolytes.

MATERIALS AND METHODS

**Insects**

All the experiments were carried out with male fifth-instar larvae of *Locusta migratoria* (L.) obtained from the normal laboratory stock at the Centre for Overseas Pest Research (Hunter-Jones, 1961) and kept subsequently in 12 l cylindrical Perspex cages at 26-30 °C with about 12 insects in each cage. The insects were marked individually within 12 h of ecdysis and used in the period 2-5 days after ecdysis so that the results were not influenced by the proximity of the moult.

**Recording technique**

Electrophysiological recordings were obtained using a modified version of the technique of Hodgson, Lettvin & Roeder (1955); silver/silver chloride electrodes were used to detect, extracellularly, electrical changes within the sensilla. The indifferent electrode was connected via a back-off d.c. source and calibration source to earth. The back-off source was used to compensate for the potential difference between the
sensillum tip and the tip of the capillary containing the stimulating solutions and the recording electrode. Compensation, which was approximated on adjacent hairs not used for recording, prevented blocking of the amplifier and allowed recording of the earliest impulses elicited by the stimulating solution (see van der Starre (1972) for discussion). The calibration source provided a square wave of 50 mV peak-to-peak with a frequency of 1 kHz.

Electrical signals from the sensilla were fed from the recording electrode through a laboratory built a.c.-coupled pre-amplifier with a cathode-follower input stage giving an input grid current of $< 10^{-12}$ A (Rees, 1968). Amplified signals were displayed on a C.R.O. (Tektronix 502A) and recorded on a tape recorder (Thermionic T 3000). For subsequent analysis the electrical phenomena were printed out using a u.v. recorder (S.E. 3006/DL) or photographed on oscillograph paper.

This method of tip recording prevented the testing of compounds which were not electrolytes except by the addition of an electrolytic substance to the stimulating solution. In practice, all substances other than salts were presented in a solution of 0.05 M sodium chloride. This constraint could have been circumvented by using the sidewall recording technique of Morita (1959); but, besides the difficulty of applying this technique to very small sensilla, when it was successfully applied the level of ‘spontaneous’ firing indicated was very variable (Fig. 1) and was often much higher than that reported in other insects (Rees, 1968, in Phormia; 1969, in Chrysolina; McCutchan, 1969, in Phormia). It seems likely that this represents an injury effect, perhaps arising from interference with the conduction of receptor potentials along the dendrites (Rees, 1967). For these reasons it was decided not to use this technique.

_Solutions and pipettes_

The stimulating solutions were made using Analar or biochemical grade compounds (B. D. H., Hopkins & Williams) in glass-distilled de-ionized water. They were stored when not in use at $-25^\circ$C. The test solution, with the recording electrode, was applied to the sensillum in a glass capillary drawn and cut to give a tip diameter of approximately 10 $\mu$m. There was some tendency for water to evaporate from the tip, so increasing the concentration of the test solution, but this was offset by smoothing the cut end of the capillary by heating and by maintaining the experimental area at
high humidity (R.H. 70–90%). In addition, to ensure that the concentration applied was typical of the solution, fluid was drawn from the tip of the capillary by means of lens tissue immediately before each stimulation.

**Method of preparation**

Before being used in an experiment, normally feeding locusts were taken individually in 350 ml glass jars and observed until they had fed to repletion on fresh grass (Blaney & Chapman, 1970). They were then kept without food for a precisely known period, commonly 2 h, before preparation for electrophysiology. This ensured that a good proportion of the sensilla had regained the readily functional state after feeding (Bernays, Blaney & Chapman, 1972) and avoided any abnormalities arising from unusually prolonged periods without food.

Consistent results were only obtained by using intact but restrained insects; isolated palps or heads frequently gave no results due to the effects of injury (see also Haskell & Schoonhoven, 1969).

Insects were anaesthetized briefly (< 2 min) with carbon dioxide, the legs were restrained and the head and thorax were immobilized as shown in Plate 1, using Cotrell Sticky Wax, care being taken to avoid damage by overheating. The trussed insect was attached with wax to a Perspex cradle so that the left maxillary palp was exposed for recording. The indifferent electrode was inserted into the haemolymph adjacent to the right antennal socket. The Perspex cradle, bearing the connecting terminal for the indifferent electrode, was clipped onto the movable stage of a Leitz microscope, and manipulation of the preparation and recording electrode was accomplished by
combined use of the microscope stage controls and micromanipulators (Narishige).
A schematic diagram of the recording situation is given in Fig. 2.

Attempted movements by the insect during recording were always accompanied by
volleys of impulses due to motor neurones firing. This produced a recognizable sound
on the audio monitor and visually appeared as a burst of low-amplitude impulses
(Fig. 3). When this occurred the record was not used for analysis and any insect
having a tendency to be active was discarded. Further, because of the proximity of
adjacent sensilla on the palp tip, the possibility was investigated of inadvertently
recording spontaneous activity from sensilla other than being tested. With the
recording electrode in place over an adapted and fatigued sensillum, mechanical and
chemical stimuli were applied to adjacent sensilla. At no time was activity from other
sensilla recorded in this way (see also van der Starre, 1972). I am therefore confident
that the results obtained from the terminal sensilla are not influenced by nervous
activity from elsewhere in the body.

RESULTS

General considerations

Three types of sensilla are distinguishable on the basis of their fine structure
(Blaney et al. 1971; Blaney, in preparation) on the tip of the maxillary palp of Locusta
migratoria, and the distinction is confirmed by electrophysiological recordings. About
90 % of the sensilla are approximately 25 μm high with a structure as described by
Blaney et al. (1971). Of the remainder about half, i.e. 5 % of the total, are less than
20 μm high and lack a distal crest (Pl. 2). Le Berre, Sinoir & Boulay (1967) suggest
that these are mechanoreceptors, and this is in accord with the lack of response from
these sensilla on stimulation by the tip-recording method. A further 4–5 % also lack
the distal crest but are about 30 μm high and are readily distinguished on the basis of
their electrophysiological responses. A preliminary study suggests that these sensilla
may mediate the common chemical sense (Blaney, in preparation).

This paper is concerned only with the responses of the first group of sensilla.

Responses to 0.1 M sodium chloride

Representative responses by the terminal sensilla to stimulation with 0.1 M sodium
chloride are shown in Fig. 4. The phasic-tonic response typical of insect chemoreceptors is seen here. Although there is much variation in the absolute and relative
Electrophysiological responses of terminal sensilla of maxillary palps

Fig. 4. Responses of terminal sensilla to stimulation with 0.1 M sodium chloride. In (a) and (b), impulses of one amplitude category are present; (c) and (d) show impulses of two amplitude categories, while in (e) and (f) there are impulses of three amplitude categories. Horizontal bar shows 0.1 sec.

duration and vigour of the phasic and tonic elements, it is always possible to recognize both (Fig. 7).

The traces obtained are, however, very variable with respect to the occurrence of impulses of different amplitudes. Very rarely (in 4 cases out of 192) only one amplitude category appears to exist (Figs. 4a, b; 5a, b). Commonly two (Figs. 4c, d; 5c, d) or three (Figs. 4e, f; 5e, f) discrete amplitude categories are recognizable, but sometimes the
Fig. 5. Frequency histograms of impulse amplitudes during the first second of the responses shown in Fig. 4.

Variation in amplitudes is such that it is not possible to assign them to discrete categories.

Fig. 6 shows the adaptation curves for the records shown in Fig. 4, and Fig. 7 expresses the rate of adaptation as derived from Fig. 6. It is apparent that initial, rapid adaptation followed by a tonic level of discharge occurs in all recognizable amplitude classes.

There is great variability in the total number of impulses occurring during the first second of stimulation if the same sensillum is repeatedly stimulated with a given solution at intervals long enough (10 min) to allow complete recovery from the previous stimulation (Table 1). Similarly Fig. 8 shows the variation occurring in these circumstances between successive responses in respect of absolute and relative amplitude classes, and in the relative rate of firing between amplitude classes (see also den Otter & van der Starre, 1967, and van der Starre, 1972). The number of amplitude classes is, however, consistent in any one sensillum for a given stimulus solution.

Table 1 also shows the variation between hairs on initial and subsequent stimulations.
Electrophysiological responses of terminal sensilla of maxillary palps

Fig. 6. Adaptation curves for the first five seconds of responses shown in Fig. 4. △–△, large impulses; •—•, medium impulses; ▼—▼, small impulses.

Table 1. Variability of response in the first second of successive stimulations of five sensilla by 0.1 M sodium chloride solution

<table>
<thead>
<tr>
<th>Sensillum</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
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<tr>
<td>1</td>
<td>M</td>
<td>18</td>
<td>35</td>
<td>27</td>
<td>28</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>17</td>
<td>11</td>
<td>13</td>
<td>12</td>
<td>31</td>
</tr>
<tr>
<td>2</td>
<td>M</td>
<td>54</td>
<td>41</td>
<td>37</td>
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<td></td>
<td>S</td>
<td>17</td>
<td>29</td>
<td>38</td>
<td>31</td>
<td>22</td>
</tr>
<tr>
<td>3</td>
<td>M</td>
<td>49</td>
<td>47</td>
<td>47</td>
<td>39</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>29</td>
<td>24</td>
<td>30</td>
<td>25</td>
<td>43</td>
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<tr>
<td>4</td>
<td>M</td>
<td>42</td>
<td>54</td>
<td>37</td>
<td>73</td>
<td>51</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>16</td>
<td>13</td>
<td>18</td>
<td>38</td>
<td>42</td>
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<tr>
<td>5</td>
<td>M</td>
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<td>46</td>
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<tr>
<td></td>
<td>S</td>
<td>26</td>
<td>18</td>
<td>30</td>
<td>21</td>
<td>30</td>
</tr>
</tbody>
</table>

M = number of medium-amplitude impulses. S = number of small-amplitude impulses.
Fig. 7. Curves derived from Fig. 6 showing rate of adaptation of each amplitude category. Each point, except the first, is expressed as a percentage of the preceding one.

Table 2. The number of impulses in the first second of stimulation of four sensilla with different concentrations of sodium chloride

<table>
<thead>
<tr>
<th>Sensillum</th>
<th>Molarity</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
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<tr>
<td>1</td>
<td>0.01</td>
<td>37</td>
<td>39</td>
<td>64</td>
<td>12</td>
</tr>
<tr>
<td>2</td>
<td>0.05</td>
<td>100</td>
<td>61</td>
<td>52</td>
<td>24</td>
</tr>
<tr>
<td>3</td>
<td>0.075</td>
<td>98</td>
<td>46</td>
<td>55</td>
<td>33</td>
</tr>
<tr>
<td>4</td>
<td>0.1</td>
<td>96</td>
<td>73</td>
<td>12</td>
<td>64</td>
</tr>
<tr>
<td>5</td>
<td>0.25</td>
<td>92</td>
<td>81</td>
<td>21</td>
<td>27</td>
</tr>
<tr>
<td>6</td>
<td>0.5</td>
<td>117</td>
<td>96</td>
<td>34</td>
<td>6</td>
</tr>
</tbody>
</table>

Responses to a range of concentrations of sodium chloride

Individual sensilla were tested with solutions of sodium chloride at six different concentrations (0.01 M, 0.05 M, 0.075 M, 0.1 M, 0.25 M and 0.5 M). The order of application of the stimuli was randomized and at least 10 min were allowed between successive applications of stimulus to any one sensillum.

As before, individual sensilla responded with impulses having one or more amplitude categories. In about half of the sensilla tested there was a tendency for the firing rate to increase as the concentration of salt increased (Table 2, sensilla 1 and 2). Of the remainder, some responded to an increase in salt concentration with a decline in firing rate (Table 2, sensillum 3), but in most the highest firing rate occurred at intermediate concentrations of salt with a decline at either end of the range (Table 2, sensillum 4). Considerable variability was noted, but in general, individual sensilla appeared to have a similar distribution of impulse amplitude categories at all concentrations.
Responses to a range of different compounds

The responses of the terminal sensilla to a number of compounds other than sodium chloride were obtained. The compounds tested were not necessarily at the concentrations at which they occur in plants because that information is not generally available. However, in most cases the concentration chosen was that which had been shown to give an unequivocal response in behavioural experiments (A. G. Cook, personal
Table 3. Responses of ten sensilla to various organic and inorganic compounds

<table>
<thead>
<tr>
<th>Stimulus solution</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1 M sodium chloride</td>
<td>++</td>
<td>+++</td>
<td>+</td>
<td>+</td>
<td>o</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>o</td>
<td>++</td>
</tr>
<tr>
<td>0.1 M potassium chloride</td>
<td>o</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>--</td>
<td>++</td>
<td>++</td>
<td>o</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>0.1 M ammonium chloride</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>--</td>
<td>++</td>
<td>+</td>
<td>o</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>0.025 M glucose</td>
<td>o</td>
<td>o</td>
<td>+</td>
<td>o</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>o</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>0.025 M fructose</td>
<td>o</td>
<td>+</td>
<td>++</td>
<td>++</td>
<td>+</td>
<td>++</td>
<td>++</td>
<td>o</td>
<td>++</td>
<td></td>
</tr>
<tr>
<td>0.025 M xylose</td>
<td>o</td>
<td>+</td>
<td>++</td>
<td>++</td>
<td>o</td>
<td>+</td>
<td>+</td>
<td>o</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>0.025 M maltose</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>++</td>
<td>o</td>
<td>+</td>
<td>-</td>
<td>o</td>
<td>o</td>
<td>+</td>
</tr>
<tr>
<td>0.025 M sucrose</td>
<td>-</td>
<td>o</td>
<td>+</td>
<td>+</td>
<td>o</td>
<td>+</td>
<td>o</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>0.0125 M serine</td>
<td>-</td>
<td>o</td>
<td>++</td>
<td>o</td>
<td>-</td>
<td>++</td>
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<td>0.0125 M alanine</td>
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<td>o</td>
<td>+</td>
<td>o</td>
<td>o</td>
<td>o</td>
<td>o</td>
<td>o</td>
</tr>
<tr>
<td>0.1 M citric acid</td>
<td>-</td>
<td>-</td>
<td>--</td>
<td>o</td>
<td>++</td>
<td>-</td>
<td>o</td>
<td>-</td>
<td>++</td>
<td>-</td>
</tr>
<tr>
<td>0.1 M oxalic acid</td>
<td>o</td>
<td>o</td>
<td>++</td>
<td>++</td>
<td>o</td>
<td>+</td>
<td>o</td>
<td>-</td>
<td>o</td>
<td>o</td>
</tr>
<tr>
<td>1.5% hydrochloric acid</td>
<td>o</td>
<td>+</td>
<td>++</td>
<td>++</td>
<td>o</td>
<td>++</td>
<td>o</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Quinine hydrochloride</td>
<td>o</td>
<td>o</td>
<td>+</td>
<td>+</td>
<td>o</td>
<td>+</td>
<td>o</td>
<td>o</td>
<td>o</td>
<td>o</td>
</tr>
<tr>
<td>Neem</td>
<td>o</td>
<td>+</td>
<td>+</td>
<td>o</td>
<td>-</td>
<td>o</td>
<td>-</td>
<td>-</td>
<td>o</td>
<td>o</td>
</tr>
<tr>
<td>Anthroquinone</td>
<td>-</td>
<td>-</td>
<td>o</td>
<td>-</td>
<td>--</td>
<td>o</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Responses during the first second of stimulation are considered. Those which do not differ from the control level are indicated as o, those showing a marked increase in firing rate are indicated as + + +, those showing a marked decrease as -- --, and the other categories are intermediate.

communication). Otherwise concentrations were chosen so as to avoid being either subthreshold or damagingly high.

To ensure adequate electrical conductivity of the stimulating solution, all the compounds tested were presented in 0.05 M sodium chloride solution and the responses were compared with the average of a number of responses to stimulation with 0.05 M sodium chloride alone.

The results, shown in Table 3, are coded according to the number of impulses occurring in the first second; and, because of the variability inherent in the system, only responses which differed by 20% from the control level were regarded as indicating an effect of the additional stimulant (see also Dethier & Kuch, 1971).

No single sensillum would seem capable of differentiating between compounds nor even classes of compounds, yet it is clear that many sensilla are capable of responding in some way to a larger number of compounds than there are neurones in the sensilla. The full extent of this effect may be masked by the conservative interpretation of response level; some compounds recorded as ineffective may in fact be weakly stimulating or inhibiting.

Mechanoreception

In addition to the effects of chemical stimulation, those of mechanical manipulation were investigated. Sensilla which were already being stimulated by a 0.1 M solution of sodium chloride were displaced laterally by the stimulating capillary.

The response, when it occurred, was always the same and consisted of a burst of impulses whose amplitude was considerably greater than that of impulses elicited by chemical stimulation (Bernays, Blaney & Chapman (1972), fig. 4). The response was
strongly phasic as reported by Haskell & Schoonhoven (1969); but, whereas these authors found it to occur in all the sensilla which they tested, in the present investigation only 47% of 390 sensilla (on 13 insects) responded.

**INTERPRETATION OF RESULTS**

The uncertainty in identifying the responses of individual neurones by inspection of the amplitude and temporal pattern of impulses on traces is compounded with the variability of response between different sensilla, between subsequent stimulations of the same sensillum with the same solution and between stimulations of the same sensillum with different concentrations of the same stimulant.

It is generally assumed that impulses of characteristically different and constant amplitudes derive from different neurones (Dethier & Hanson, 1965; Dethier & Hanson, 1968; Hodgson, 1968), but it does not necessarily follow that impulses of the same size derive from the same neurone. Unusually large impulses occurring infrequently appear to result from a temporal coincidence and consequent summation of two or more smaller impulses. This diagnosis may be confirmed by inspection of traces when pairs of different-sized impulses may be seen to occur successively closer together, finally to be replaced by one or more larger impulses before reappearing as separate, smaller impulses again. Significantly, this phenomenon may occur with pairs of similar-sized impulses which, but for the coincidence, would otherwise be regarded as deriving from one neurone.

Clearly this event occurs most frequently when the overall rate of firing is high. In many cases in the present study the rate of firing is low compared with that reported for other insects and may well be too low for the coincidence effect to be apparent. It is therefore impossible to ensure that the traces shown in Fig. 4, and others like them, in fact represent the activity of the number of neurones that they seem to indicate.

Further, the terminal sensilla each contain at least six neurones (Blaney et al. 1971); the total range of amplitude from the largest to the smallest impulses recorded commonly did not exceed 20 mm, and the range of variation in impulses of one amplitude category was seldom less than 6 mm, hence the chance of 6 neurones firing without overlap is remote.

Firm conclusions regarding the number of cells responding at any time are therefore unwarranted; and it appears that, while it is fairly certain that in some cases (during stimulation with 0.1 M sodium chloride) at least three neurones are firing, in none of the records is there unequivocal evidence for less than three neurones firing.

It is arguable that some of these neurones were firing spontaneously at a tonic level unrelated to the application of the stimulus under investigation, but Figs. 6 and 7 show that all the neurones, identified on the basis of impulse-amplitude categories, initially show rapid rates of adaptation consistent with a response to the stimulus (Rees, 1968).

The same holds true for other stimulating substances; in every case the response appears to involve a number of neurones.

The variation of impulse-amplitude categories associated with the application of different concentrations of sodium chloride solution to a given sensillum (Fig. 9a) might indicate the activity of different neurones at different concentrations. However
Fig. 9 (i) and (ii). For legend see facing page.
Fig. 9. Frequency histograms of impulse amplitudes during the first second of stimulation of four sensilla, (i)–(iv), with sodium chloride solution at the concentrations indicated. (a) Impulse amplitudes as recorded; (b) amplitude corrected by the calibration factor. For further details see text.
when the calibration pulse was passed through the preparation during recording and its height used as a correction factor to standardize the impulse amplitudes, the variation was largely eliminated (Fig. 9b), and must have arisen through some characteristic of the preparation/stimulus system which varied with concentration of electrolyte. There is, however, still considerable misalignment when the recorded calibration pulse was of low amplitude, i.e. especially at 0.01 M concentration.

That this was not an effect of low electrolyte concentration on the recording of the calibration pulse was shown by recording the amplitude of the calibration pulse without the preparation in circuit (Fig. 10). The amplitude increases at low concentrations in parallel with the equivalent conductance curve (Weast, 1964). Thus the misalignment is associated with the preparation.

The correlation between impulse frequency and calibration-pulse amplitude is high ($Z = 0.89$, Fig. 11). It may be that the recorded changes in amplitude of calibration pulse and of nerve impulses are related to changes in the dendritic membrane resistance which is in series with the recording electrode (Bernard & Guillet, 1972; Rees, 1967). Thus a high rate of firing would reflect a high degree of depolarization of the receptor membrane and increased electrical conductivity of the dendritic membrane. That would reduce the series resistance in the recording pathway and increase the amplitude of the recorded events.

Alternatively Morita & Takeda (1957) working on tarsal receptors of *Vanessa* and Stürckow (1971) on chemoreceptors of *Calliphora* suggest that changes in resistance may be related to different amounts of viscous material present at the tip of the sensillum. This material is also present in *Locusta* but the apparent changes in resistance observed here occur too rapidly to be accounted for by changes in the amount of viscous material. The electrical properties of this material may vary when subjected to different osmotic potentials but no evidence of this is presently available.

Varying osmotic potential might also have an effect on resistance pathways by
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opening or closing of the distal pore of the sensilla. Scanning electron-microscope studies (Blaney & Chapman (1969), on Schistocerca gregaria and (unpublished) on Locusta) have shown that the distal pores on these sensilla are capable of being opened and closed, and Stürckow, Holbert & Adams (1967) describe a similar phenomenon in chemoreceptor hairs of Phormia regina. However, no evidence was found here of any change in degree of conductivity during stimulation when solutions of different osmotic potential were applied successively (see also Bernays et al. 1972). Thus it seems highly unlikely that the degree of opening could be affected by the osmotic potential of the stimulus solution since this would take some measurable time to have its effect.

It is apparent that certain difficulties of interpretation remain unresolved. It would be possible, by rejection of anomalies and conservative selection of reproducible data (Gillary, 1969), to present a picture of chemoreception by the terminal sensilla along conventional lines (see, for example, Haskell & Schoonhoven, 1969); but in so doing much usable and valuable information would be lost, not least the magnitude and extent of occurrence of variability.

It seems best to use analysis at the neuronal level where it is warranted, but otherwise analysis at the level of total output of individual sensilla is probably valid (see also Dethier & Kuch, 1971), particularly where the equivalent of 'across-fibre' analysis is being considered.

**DISCUSSION**

This study confirms the original findings of Haskell & Schoonhoven (1969) that the terminal sensilla on the maxillary palps of Locusta migratoria act as contact chemoreceptors, responding to a wide range of chemicals of different chemical classes. It is also clear that, in some cases at least, individual neurones are capable of responding to more than one type of compound. This characteristic, together with the variability
of results following stimulation with a constant stimulus, suggests that these sensilla do not respond in the manner commonly accepted for chemoreceptors.

It is generally considered (Rees, 1968; Haskell & Schoonhoven, 1969) that the response of sensilla to a salt solution involves different neurones for each of the modalities (the 'salt' and 'water' neurones of most authors and the 'Type 1' and 'Type 3' neurones of Rees). In the present study it is clear that salt and water invoke activity from more than two neurones in many cases, and there is no evidence to suggest that this is not so in all cases.

Similarly, den Otter & van der Starre (1967) and van der Starre (1972), working on *Calliphora*, and van der Starre (1970), on *Phormia*, have shown that water alone can elicit activity in more than one neurone in sensilla where it was previously thought that only one water-sensitive neurone existed. Further, Dethier (1973), studying the responses of the maxillary taste receptors of seven species of caterpillars, commonly found that in addition to a 'major salt receptor' neurone, up to three other neurones also responded to salt and that some 'salt receptors' responded to other chemicals as well, e.g. amino acids. Other reports of compounds stimulating more than one cell have been given by Schoonhoven (1969) and by Dethier & Kuch (1971).

These data do not suggest general applicability of the concept of specialized neurones for each stimulus modality. It seems more likely that many neurones respond to a range of stimuli, though perhaps with differential sensitivity. Instances of neurones responding to only a single modality would then be regarded as extremes of this differentiation.

Such a situation would yield less precise information than that commonly described for the blowflies and other insects but this limitation may be overcome in the case of the terminal sensilla on the maxillary palps of *Locusta* by virtue of the large number of sensilla available to test the environment at any one time. This, and the effect of palpation (see Blaney, in preparation), may allow the acquisition of adequately detailed information, particularly if some form of 'across-fibre' analysis is used by the insect. Further, the lack of differentiation may have a positive advantage in that, by having broad band sensitivity, the palpal chemoreceptors are able to perceive a wide range of potential food materials.

Such specificity as exists in this system appears to be more at the level of sensilla than at the level of neurones; some sensilla have a notably vigorous over-all response to salt, some to water, some to sugar (see also Blaney, in preparation, and Stürckow, 1970). This would appear to reflect the presence in these sensilla of one or more neurones having their differential sensitivity particularly biased towards a specific modality. The significance of this in terms of neural integration is not yet clear.

The mechanism by which the insect determines different modalities and different degrees of the same modality and how it distinguishes between these two conditions is not clear from this study, but the indications are that the code for taste quality consists of the relative amounts of activity produced in many neurones according to the model proposed by Pfaffmann (1941, 1955) and developed by Erickson (1963, 1967) and Doetsch *et al.* (1969) in respect of mammalian gustatory systems. An investigation of these problems is the subject of further studies (in preparation).

It is surprising that there was not a more distinct response to neem which is known to be a powerful feeding deterrent for locusts (Sinha & Gulati, 1965). Haskell &
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Schoonhoven (1969) have reported that the terminal sensilla contain a neurone specifically sensitive to neem. However, the response to neem is less marked when it is applied to the palps than to the sensilla of the cibarial cavity (Blaney, unpublished). If, as seems likely, sensitivity to a particular compound is not universally distributed among sensilla, the small number of sensilla tested with neem in the present study may account for the failure to obtain an unequivocal response.

Gilbert, Baker & Norris (1967, 1968) and Norris (1969) have established the role of certain quinones as inhibitors of gustation in a number of insects. In the present study the effect of anthroquinone was to reduce the activity of neurones previously responsive to sodium chloride and water. This cannot, however, be regarded as the typical response elicited by a deterrent substance as other such substances had a markedly different effect. Similarly Ishikawa (1966) working on Bombyx mori, and Dethier (1973) with seven species of lepidopterous larvae, have shown that inhibition is not a unitary modality.

Haskell & Schoonhoven (1969) have reported that all of the terminal sensilla they tested could act as mechanoreceptors; in the present study this property has only been found in 47% of the sensilla tested. Blaney et al. (1971) and Blaney & Chapman (1969) studying the fine structure of these sensilla and similar sensilla on Schistocerca gregaria found a differentiated region of dendrite near the base of some sensilla and, following other authors (Thurm, 1965; Nichlaus, Lunquist & Wersall, 1967) associate this with a mechanoreceptor neurone. This region was not found in all sensilla examined by these authors, but failure to find it cannot be regarded as significant. Haskell & Schoonhoven (1969) do not record how many sensilla they tested for the mechanoreceptor response. It may be that the present findings reflect the absence of a mechanoreceptor neurone in many sensilla, or alternatively it may result from a failure of response in many sensilla at the time of recording. This would be in general agreement with the variability of response shown by these sensilla. In either event, the density of sensilla on the palp tip is such that mechanoreceptor sensitivity, say as a means of monitoring hardness of grass (Haskell & Schoonhoven, 1969), is unlikely to be impaired significantly by the non-functioning of 50% of sensilla.

SUMMARY

1. Three morphologically and functionally different types of sensilla on the maxillary palp tips of Locusta migratoria are distinguished and an electrophysiological study is made of the most commonly occurring type.
2. Responses to stimulation with 0.1 M sodium chloride show impulses of one, two or three amplitude categories in different sensilla.
3. Variability of response to a constant stimulus is appreciable, both between and within sensilla.
4. Tests with a range of compounds indicate that individual neurones are capable of responses to compounds of different chemical classes.
5. Specificity of sensilla is more marked than specificity of neurones.
6. Methods of interpretation of results are evaluated and the results are discussed in the context of discrimination of food plant materials.
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EXPLANATION OF PLATES

Plate 1

(a) Microscope stage to show cradle (C), locust (L), indifferent electrode (I.E.) and recording electrode (R.E.). (b) Locust in position for recording, showing method of restraint. (c) Palp tip exposed for recording.

Plate 2

Scanning electron-micrograph of part of tip of maxillary palp showing several normal sensilla (N), and one small sensillum (S.S.). so = socket of sensillum, c = crest.