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BEHAVIOURAL AND ELECTROPHYSIOLOGICAL STUDIES OF TASTE DISCRIMINATION BY THE MAXILLARY PALPS OF LARVAE OF *LOCUSTA MIGRATORIA* (L.)

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SUMMARY

1. Behavioural studies show that larvae of *Locusta migratoria* (L.) can discriminate between certain simple chemicals and between chemicals obtained from plant sources.

2. Electrophysiological tests show that within each sensillum the same neurones respond to different chemicals.

3. The frequency of occurrence of sensilla with enhanced specificity to certain chemicals is investigated.

4. Statistical tests confirm that, despite the variability of response, across-fibre analysis could allow discrimination between chemicals provided an adequate number of sensilla are used.

5. The conclusions are discussed in relation to current theories of chemoreceptor functioning.

INTRODUCTION

The sensilla on the domes of 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).

In an electrophysiological investigation of these sensilla, Haskell & Schoonhoven (1969) showed them to be contact chemoreceptors and described their mode of functioning in terms of specific responsiveness of individual neurones within each sensillum to different stimulatory compounds. In a further study, Blaney (1974) has shown that individual neurones respond to more than one type of compound and that there is considerable variability of response, from any given sensillum, to separate stimulations with the same stimulus. He suggested that such specificity of response as exists may be at the level of sensilla rather than of individual neurones and suggested that the differentiation of chemicals from each other involves some form of 'across-fibre' analysis (Pfaffman, 1941, 1955; Erickson, 1963, 1967; Doetsch *et al.* 1969; Dethier, 1973).

In this paper, behavioural experiments are described which investigate the ability of the insect to discriminate between certain simple chemicals and also between chemicals obtained from plant material. Complementary investigations were made of the electrophysiological responses to these chemicals and an attempt is made to describe the neural mechanisms involved in taste discrimination.

MATERIALS AND METHODS

Insects

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

Behavioural experiments

The ability of the insects to discriminate between compounds was assessed on their behavioural responses to the chemicals presented as potential food material (Blaney & Chapman, 1970). Individual insects were fed to repletion on *Poa annua*, then kept without food, in 8 × 2 cm specimen tubes, for precisely known periods between 30 min and 1 h, corresponding to the normal interfeed period (Blaney, Chapman & Wilson, 1973). Insects were then presented with a fresh blade of grass to establish their readiness to feed given suitable food. The grass blade was removed as soon as the insect attempted to eat and replaced with a test strip of Whatman No. 1 filter paper, 100 mm long and 4 mm wide, which had been soaked for 1 min in the test solution and dried in a cold air blast for 15 min. The strips were used within 30 min of being prepared. The insects were observed for 3 min after being presented with the test strip, and palpating and biting activities were recorded. Lack of material prevented the ryegrass and brussels sprouts cuticular waxes being tested in this way. The 'neem + salt' and '*Poa* + salt' solutions were prepared as described below.

Electrophysiological experiments

The methods of preparing the insects for electrophysiology and the electrophysiological techniques involved are described in detail elsewhere (Blaney, 1974). Recordings were made from intact, restrained insects using a modified version of the technique of Hodgson, Lettvin & Roeder (1955) and employing all known means of reducing the variability of experimental procedure (see van der Starre, 1972, and especially Blaney, 1974). The sidewall technique of Morita (1959) was not used because of its variability (see van der Starre, 1972; Dethier, 1972; Blaney, 1974) so all the test solutions were presented with an electrolyte, 0·05 M sodium chloride.

The 'neem' extract was prepared by adding a saturated solution (*ca.* 0·35%) of azadirachtin, the active principle of the neem seed (Butterworth & Morgan, 1968), to an equal volume of 0·05 M sodium chloride. The *Poa* extract was prepared by homogenizing whole leaves in an M.S.E. Ato-Mix blender, filtering and adding the filtrate to an equal volume of 0·05 M sodium chloride. The rye-grass and brussels sprouts waxes were sonicated in a Soniprobe Converter Type 1130/A (Dawe Instruments) for 20 min at 4 °C (0·0041 g per ml of 0·05 M sodium chloride) to give a very fine suspension of the insoluble waxes, thus ensuring their ability to enter the terminal pore of the sensillum.

Table 1. *Frequency with which third-instar larvae of* Locusta *palpated and bit strips of filter paper treated in various ways*

(See text for details of treatment. χ^2 test performed on % palpating and % palpating and biting.)

Treatment of paper	No. of insects	% palpating only	% palpating and biting	χ^2	P
Fructose + salt	30	0	100	12·4	< 0·001
Salt	28	36	64		
Fructose + salt	30	3	97	28·24	< 0·001
Neem + salt	30	73	27		
Poa + salt	29	4	96	7·77	< 0·01
Salt	28	32	68		

RESULTS AND DISCUSSION

Behavioural experiments

In attempting to elucidate the mechanism of taste discrimination in an insect it is essential, not simply to consider the responses of sensilla to a variety of substances to which they happen to react, but rather to analyse the responses elicited by substances for which behavioural discrimination has been shown to be a reality. In locusts not deprived of food for a long period, palpation on an acceptable substrate leads to biting, whereas an unacceptable substrate may be rejected after palpation alone (Blaney & Chapman, 1970). In the present experiments, 'fructose + salt' and '*Poa* + salt' induced significantly more biting than did either the salt solution alone or the 'neem + salt' solution (Table 1) which were much more frequently rejected at palpation. Thus, with the exception of the plant surface waxes, behavioural experiments reported here have shown clearly that the insects are capable of distinguishing between the pairs of stimuli presented in the electrophysiological tests.

Electrophysiological experiments

The responses to all the stimulus solutions tested showed impulses of one, two, three or more amplitude categories in different sensilla as was previously reported for this preparation (Blaney, 1974). That is to say, there was considerable variability between sensilla. Similarly, there was appreciable variability of response, from any given sensillum, to repeated stimulations with the same solution, even when adequate time (10 min) was allowed for recovery between stimulations. (For a detailed discussion of these phenomena see van der Starre, 1972, and Blaney, 1974.)

Responses to fructose and salt

Blaney (1974) suggested that in the terminal sensilla of the maxillary palps of *Locusta migratoria* (L.), the same neurones may respond to different stimuli and that concept is confirmed by the present study. Approximately 50 sensilla were tested with 0·05 M sodium chloride, followed, after adequate recovery time, by 0·05 M sodium chloride containing 0·025 M fructose. Because of the variability occurring in this preparation (Blaney, 1974), it was not always possible to make clear distinctions between different neurones on the basis of the amplitude and temporal pattern of impulses on traces. However, frequency distributions of the amplitude of all

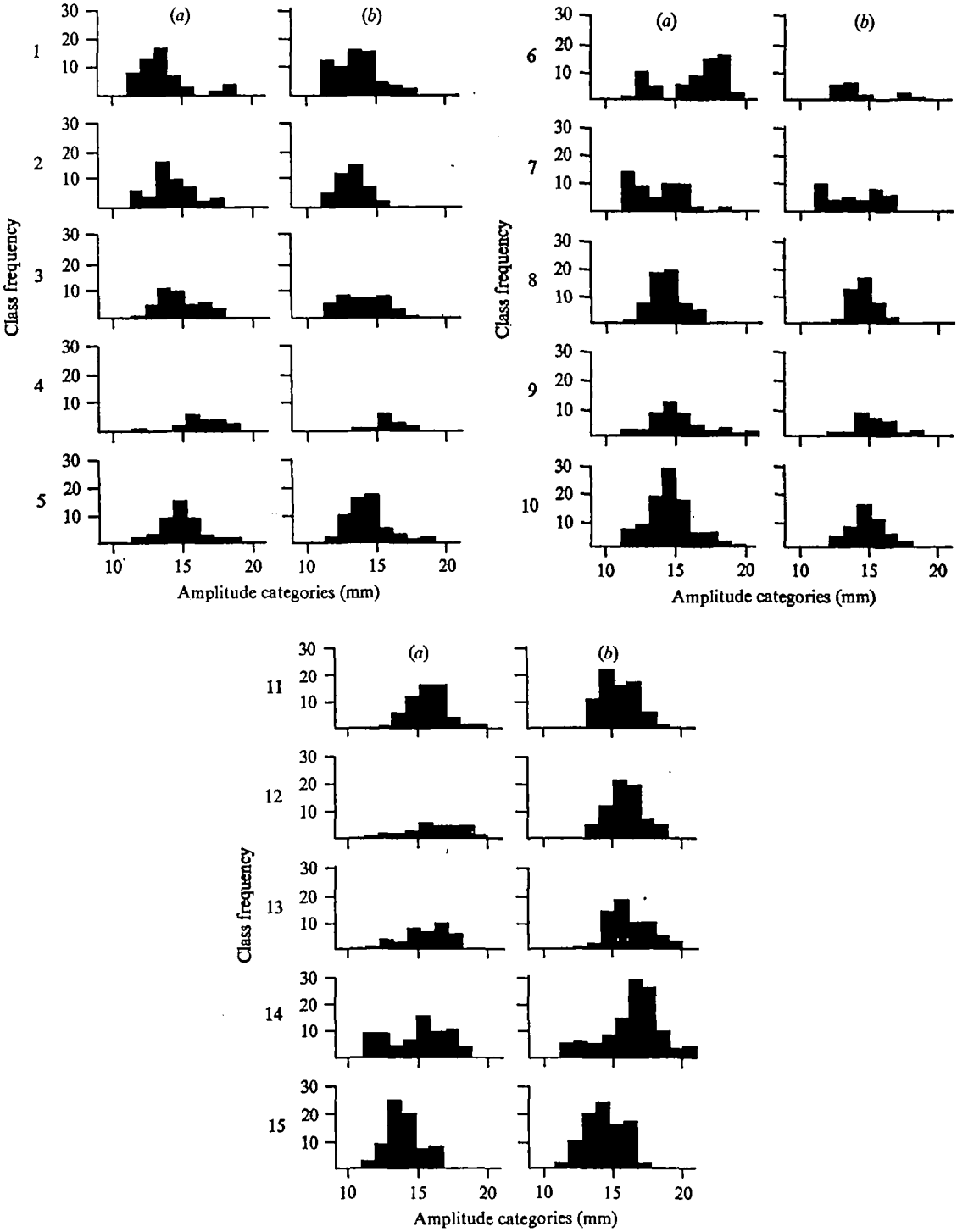

Fig. 1. Responses of 15 sensilla to the first second of stimulation with solutions of (*a*) salt and (*b*) fructose + salt.

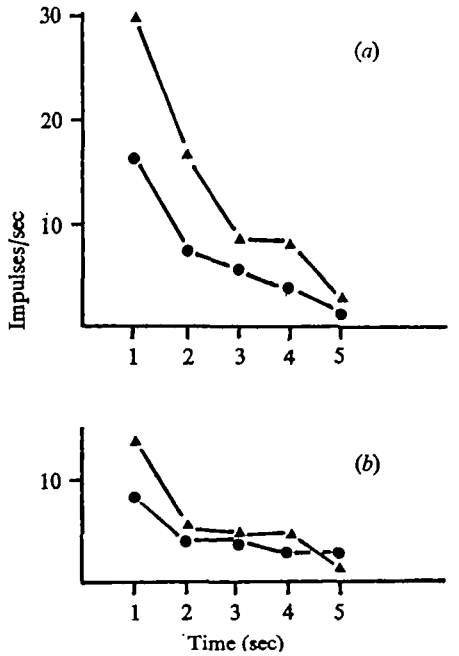

Fig. 2. Adaptation curves (average of five sensilla) for the first 5 sec of a two-cell response to fructose + salt (*a*) with unadapted sensilla (*b*) applied 2 sec after a 5 sec stimulation with salt.

recognizable impulses for the two stimulations of each sensillum were generally similar (Fig. 1), suggesting that the same neurones were involved in both responses.

It is possible, though unlikely, that specialist salt and sugar receptor neurones are involved, which happen to have the same impulse amplitude characteristics. This concept may be tested by an examination of the response to sugar after adaptation by salt (see also van der Starre, 1972). Such responses are shown in Fig. 2 for a group of sugar-sensitive sensilla in which inspection of the traces makes it reasonably certain that only two neurones were involved. It is seen from Fig. 2(*b*) that both neurones show the effects of adaptation resulting from prior stimulation with 'salt' so that the 'fructose + salt' response does not involve the activity of a specifically sugar-sensitive neurone or neurones unresponsive to salt (see van der Starre, 1972, for further discussion).

If the lack of neuronal specificity were total and all the neurones of a sensillum responded in unison, then the pairs of histograms in Fig. 1 should be replicas of each other or, where sensitivity to one of the pair of stimulants is enhanced, one histogram should be an enlarged version of the other. That this is not so is patent, but the divergence from this ideal may be due to intra-sensillar variability rather than a lack of unison within the sensillum. This may be assessed by comparing pairs of responses from each sensillum (Fig. 1) with similar pairs of responses in which the *same* stimulus solution was used in each case. A convenient way of doing this is to graph, for each amplitude category in a given sensillum, the response to one stimulus against the response to the other (Fig. 3). Now, the closeness of fit of points to the regression line, as indicated by the correlation coefficient, is an indication of the constancy of the firing pattern of neurones in response to the two stimulations. If *different* neurones,

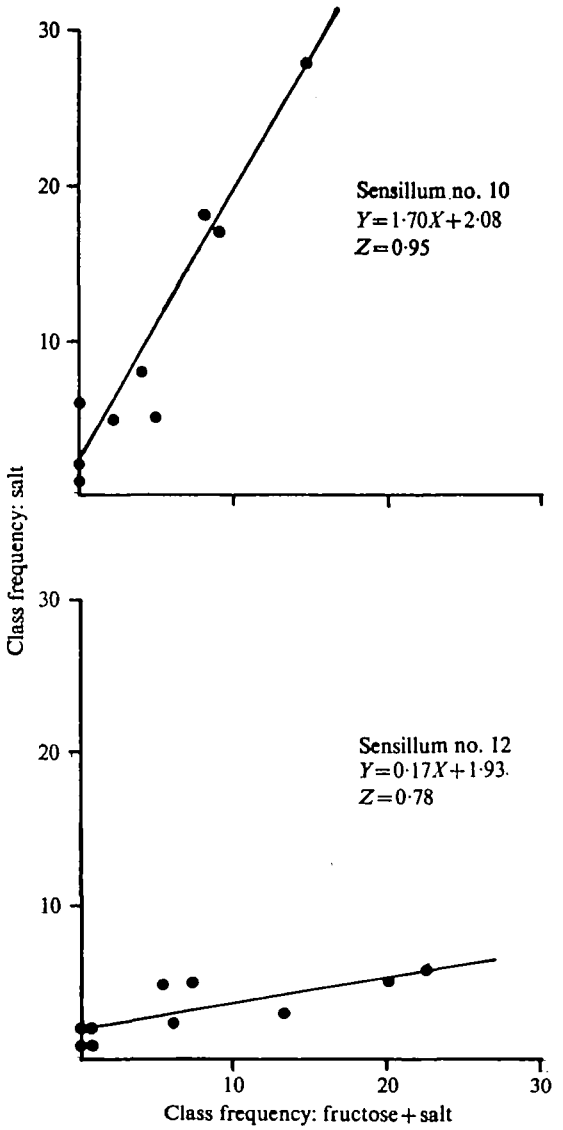

Fig. 3. Amplitude categories in the response of sensilla 10 and 12 (Fig. 1) to stimulation with salt and with fructose + salt. Regression lines constructed from the equations. Z = correlation coefficient.

in a sugar-sensitive sensillum, were responding maximally to 'salt' in the one case, and to 'fructose + salt' in the other case, the correlation coefficient would be low, but if the *same* neurones (same amplitude categories) were responding differentially, and all the neurones responded in the same manner, then the correlation coefficient would approach unity. The equations obtained by regression analysis, and correlation coefficients for the pairs of stimulations of sensilla (represented in Fig. 1), are given in Table 2; and those for an experiment in which 0·1 M sodium chloride was used for both stimulations (data from Blaney, 1974) are given in Table 3. With successive stimulations with the same material (salt/salt) the correlation coefficient varied from

Table 2. *Data relating to responses to stimulations with salt and with fructose+salt as depicted in Fig.* 1 *and derived from graphical comparisons of the amplitude categories in these responses, as shown in Fig.* 3

Sensillum no.	Equation obtained by regression analysis	Correlation coefficient
1	$Y = 0{\cdot}73X+0{\cdot}77$	0·82
2	$Y = 0{\cdot}60X+2{\cdot}91$	0·74
3	$Y = 0{\cdot}51X+2{\cdot}59$	0·37
4	$Y = 0{\cdot}70X+0{\cdot}86$	0·86
5	$Y = 0{\cdot}60X+1{\cdot}42$	0·81
6	$Y = 0{\cdot}61X+5{\cdot}78$	0·20
7	$Y = 1{\cdot}52X+1{\cdot}23$	0·86
8	$Y = 1{\cdot}18X+1{\cdot}07$	0·93
9	$Y = 1{\cdot}03X+1{\cdot}94$	0·81
10	$Y = 1{\cdot}70X+2{\cdot}08$	0·95
11	$Y = 0{\cdot}69X+1{\cdot}14$	0·92
12	$Y = 0{\cdot}17X+1{\cdot}93$	0·78
13	$Y = 0{\cdot}42X+1{\cdot}36$	0·74
14	$Y = 0{\cdot}39X+2{\cdot}17$	0·68
15	$Y = 0{\cdot}87X-1{\cdot}02$	0·83

Table 3. *As in Table 2 but both stimulations with salt*

(Data from Blaney (1974).)

Sensillum no.	Equation obtained by regression analysis	Correlation coefficient
1	$Y = 0{\cdot}59X+1{\cdot}12$	0·68
2	$Y = 0{\cdot}83X+0{\cdot}90$	0·70
3	$Y = 0{\cdot}81X+0{\cdot}46$	0·86
4	$Y = 0{\cdot}74X+2{\cdot}48$	0·36
5	$Y = 0{\cdot}84X+1{\cdot}05$	0·74
6	$Y = 0{\cdot}50X+1{\cdot}82$	0·52
7	$Y = 1{\cdot}07X+0{\cdot}79$	0·64
8	$Y = 0{\cdot}60X+1{\cdot}10$	0·70
9	$Y = 0{\cdot}35X+2{\cdot}48$	0·26
10	$Y = 0{\cdot}22X+2{\cdot}94$	0·44
11	$Y = 0{\cdot}98X+1{\cdot}12$	0·72
12	$Y = 0{\cdot}45X+3{\cdot}07$	0·65
13	$Y = 0{\cdot}39X+2{\cdot}67$	0·36
14	$Y = 0{\cdot}71X+1{\cdot}90$	0·75
15	$Y = 1{\cdot}00X+1{\cdot}15$	0·85

0·26 to 0·86, and 11 out of 15 sensilla gave a coefficient greater than 0·5. When the second stimulus was sugar instead of salt (salt/sugar) the range of correlation coefficient was similar, with 13 greater than 0·5. The association between neurones was then at least as good as with the same material. This provides further strong evidence for the unspecialized nature of the responses of individual neurones.

The slope of regression lines varied from 0·17 to 1·52. A slope of 1·0 indicates that the sensillum is equally sensitive to both stimuli, a slope of $> 1{\cdot}0$ indicates greater sensitivity to the first stimulus, whilst a slope of $< 1{\cdot}0$ indicates greater sensitivity to the second stimulus. Thus sensillum 10 (Fig. 3*a*) has enhanced sensitivity to salt whilst sensillum 12 (Fig. 3*b*) has enhanced sensitivity to sugar. In about half the sensilla tested there was no significant difference in the rate of firing elicited by 'salt' or 'fructose+salt' (i.e. 'neutral' sensilla, e.g. Fig. 1, sensilla 9, 15). Of the remainder,

Table 4. *Frequency of occurrence of different sensillum types round the apex of the maxillary palp tips of six insects*

	Sensillum type		
	'Salt'	'Sugar'	'Neutral'
	3	4	13
	6	3	11
	6	6	8
	5	7	8
	4	5	11
	3	6	11
Average	4·50	5·17	10·33

some responded with a decreased rate of firing in response to 'fructose+salt' compared with 'salt' (i.e. 'salt' sensilla, e.g. Fig. 1, sensilla, 7, 10), whilst others had a higher rate of firing in response to 'fructose+salt' than in response to 'salt' (i.e. 'sugar' sensilla, e.g. Fig. 1, sensilla 12, 14). Since the existence of sensilla with differing sensitivity is likely to be significant in the determination of taste quality, the frequency of occurrence of these three types was investigated (Table 4).

Experiments have shown that during palpation there are seldom less than 30 sensilla brought into use at each contact (Blaney & Chapman, 1970). These presumably have a range of sensitivities and it thus seemed imperative to examine the output from a substantial number of sensilla at the same time. This approach was taken by Yamada (1971) in an investigation of odour encoding in the olfactory lobe of *Periplaneta americana* but, whereas he combined the responses from several insects, I felt that to have a true picture of the neural input available to the C.N.S. of the locust, the sensilla chosen should be from the same palp of one insect and that the whole of the experiment should be carried out on the same occasion. It is not yet technically possible to stimulate and record from many sensilla at the same time and, in practice, the number of sensilla which could be identified with certainty for repeated stimulation was limited to about 20, of which a few sometimes failed to respond at some stage of the experiment and had to be discarded. Nevertheless, the sample obtained was a reasonable approach to that normally used by the insect. In order to assess the effect of variability, each stimulus was applied to each sensillum a number of times. The number of impulses in the first second of each stimulation is shown in Table 5.

It is clear from an examination of the data in Table 5 that, in many cases, taste discrimination is not possible on the basis of the output from individual sensilla (e.g. Table 5, sensilla 11–20, which do not show any particular sensitivity to either the 'salt' or the 'fructose+salt' stimulations). Some of the 'specialist', sugar-sensitive sensilla may show sufficient disparity of response to 'salt' and to 'fructose+salt' to allow a distinction between the two stimuli to be made (e.g. Table 5, sensilla 1, 3, 4 and 5), but even amongst this group of sensilla there may be an overlapping response range due to the variability (e.g. Table 5, sensilla 2 and 6).

The situation is further complicated in that a sugar-sensitive sensillum may produce the same range of response when stimulated with a low concentration of sugar as it does when stimulated with a high concentration of salt. Thus the insect can only discriminate between these two stimuli when the output from sugar-sensitive sensilla

Table 5. *The number of impulses occurring during the first second of stimulations of 20 sensilla with salt and with fructose + salt*

Stimulus	Stimulus sequence	Sensillum 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Salt	1	56	56	31	14	29	20	16	21	30	24	13	13	12	18	20	42	15	22	10	24
	3	23	55	52	13	17	10	11	19	17	19	16	14	13	14	24	25	19	17	14	22
	5	32	63	51	14	21	5	15	17	21	23	13	13	8	14	11	30	17	17	8	23
	7	51	60	64	9	21	10	4	14	21	30	19	8	7	14	13	23	13	12	12	26
Fructose +salt	2	98	113	123	96	58	25	11	12	7	21	12	14	8	20	25	46	21	19	13	30
	4	96	105	128	82	41	22	8	8	6	10	25	11	16	15	21	20	12	27	9	23
	6	114	59	107	78	48	14	8	5	10	11	14	9	6	16	14	16	14	15	11	27
	8	95	108	121	75	38	14	6	10	6	6	17	13	4	17	16	30	15	14	15	26
Sensillum type ...		'Sugar'						'Salt'				'Neutral'									

Table 6. *Analysis of variance computed on data given in Table* 5

(S.S. = sum of squares, D.F. = degrees of freedom, M.S. = mean of squares.)

Source of variation	S.S.	D.F.	M.S.	
Between stimuli	5664·40	1	5664·40	•••
Between sensilla	83234·03	19	4380·74	•••
Interaction	26454·35	19	1392·33	•••
Error	6464·00	120	53·87	
Total	121816·78	159		

••• Highly significant.

Table 7. *The number of impulses during the first second of stimulations of* 15 *sensilla with fructose + salt and neem + salt*

Stimulus	Stimulus sequence	Sensillum 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Fructose + salt	1	21	34	110	34	14	12	18	73	38	41	52	26	12	14	44
	3	35	49	59	37	16	14	35	35	56	33	30	50	21	17	18
	5	24	41	63	38	13	13	20	65	43	31	46	24	21	13	36
	7	19	38	82	31	19	8	17	76	42	37	58	30	27	8	28
Neem + salt	2	122	26	56	75	47	27	18	103	122	35	95	41	22	35	20
	4	73	41	44	54	45	39	25	129	134	30	121	27	20	29	17
	6	98	24	31	61	41	33	16	112	169	27	102	29	17	32	19
	8	87	30	51	73	48	25	15	121	125	31	93	39	19	27	11

is examined in conjunction with the output from other sensilla whose sensitivity is different. That is to say, the code for taste quality consists of the relative amounts of activity produced simultaneously in many neurones in different sensilla.

This concept of 'across-fibre' analysis was proposed by Pfaffmann (1941, 1955) and developed by Erickson (1963, 1967) and Doetsch *et al.* (1969) in respect of mammalian gustatory systems, and has recently been restated in some detail by Dethier (1973) with reference to gustation in lepidopterous larvae. The basic tenets of this theory are firstly that receptors should have unique but overlapping action spectra, and secondly that each substance discriminated generates a unique total pattern of response.

The gustatory system described in this paper could function on the basis of across-fibre analysis provided that the variability of response is not such as to make either or both of these conditions unattainable. This may be tested by computing an analysis of variance on the data in Table 5. The results of that analysis are given in Table 6. The variance between sensilla is highly significant, indicating that sensilla differ from each other in their response – the first tenet of the across-fibre hypothesis. The variance between solutions is also highly significant, indicating that, on the total information available in each case, the insect can differentiate between solutions – as was predicted by the behavioural experiments. Further, there is a highly significant variance due to interaction, which indicates that different sensilla respond in different ways to the two stimulus solutions. That is to say, each solution generates a different total pattern of response – the second tenet of the across-fibre hypothesis. Thus, despite the variability, the neural output generated by the palp-tip sensilla is such as to allow discrimination so long as the responses of a population of sensilla are considered.

Table 8. *The number of impulses occurring during the first second of stimulations of* 18 *sensilla with* Poa+*salt and salt*

Stimulus	Stimulus sequence	Sensillum 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Poa+salt	1	29	52	88	19	66	35	73	37	19	81	99	28	45	12	32	49	72	13
	3	36	48	49	31	69	46	77	29	16	51	89	50	55	30	26	44	68	19
	5	21	50	85	27	56	32	53	32	26	45	93	50	37	19	16	56	66	20
	7	51	62	43	22	53	35	66	23	18	51	82	43	46	17	33	58	64	27
Salt	2	38	48	59	23	28	25	71	24	20	29	58	9	26	11	26	41	10	8
	4	33	74	84	24	33	49	53	25	29	59	62	24	29	21	16	44	43	6
	6	43	57	73	18	26	21	42	23	23	51	56	22	27	15	34	43	39	10
	8	36	31	44	11	27	32	51	28	24	35	40	30	22	17	32	37	46	9

Table 9. *The number of impulses occurring during the first second of stimulations of ten sensilla with salt, salt + rye grass and salt + brussels sprout*

Stimulus	Stimulus sequence	Sensillum 1	2	3	4	5	6	7	8	9	10
Salt	1	48	13	53	26	61	39	43	72	86	169
	4	48	13	43	25	57	47	53	83	106	125
	7	49	13	42	26	61	33	61	85	112	94
Salt + rye grass	2	84	43	31	53	51	50	51	73	102	121
	5	70	43	38	62	57	46	57	78	91	123
	8	77	41	37	54	65	58	64	54	93	111
Salt + brussels sprout	3	56	53	59	34	52	62	76	69	101	67
	6	64	46	62	29	57	63	45	81	95	80
	9	61	58	61	39	57	56	65	70	98	64

Table 10. *Analysis of variance computed on data given in Table 7*

Source of variation	S.S.	D.F.	M.S.	
Between stimuli	12444·03	1	12444·03	•••
Between sensilla	70821·45	14	5058·68	•••
Interaction	34716·72	14	2479·77	•••
Error	9759·50	90	108·44	
Total	127741·70	119		

••• Highly significant.

Responses to other stimuli

A similar, though less detailed, study was made of the responses to neem, extract of *Poa* leaves and the cuticular waxes of ryegrass and brussels sprout plants. The same general characteristics of responses were observed and a special study was made of the responses of a group of sensilla from an individual palp to a pair of stimulating solutions. The results for fructose and neem are given in Table 7, for *Poa* and salt in Table 8 and for the cuticular waxes and salt in Table 9.

In these experiments the sensilla were chosen at random, so that the distribution of sensilla with differing sensitivity in the sample does not necessarily reflect that in the total population of sensilla on a palp tip. The number of sensilla with special sensitivity to neem is higher than that reported previously by Blaney (1974) but not so high as that reported by Haskell & Schoonhoven (1969). Some sensilla also exhibited a tendency to respond very strongly to *Poa* extract but there was no indication of any 'specialist' in the case of the surface waxes.

The results of analyses of variance on these data are given in Tables 10–12. In all cases, both the variance between sensilla and the variance due to interaction are highly significant, thus satisfying both requirements of the across-fibre hypothesis. The variance between solutions is highly significant except with the surface waxes, where only a small sample was taken, and even there it is significant at the 5% level. Thus these experiments confirm that, provided a sufficiently large population of sensilla is involved, discrimination is possible on the basis of the total neuronal output.

The analysis does not, of course, indicate how the central nervous system of the

Table 11. *Analysis of variance computed on data given in Table* 8

Source of variation	S.S.	D.F.	M.S.	
Between stimuli	4646·69	1	4646·69	***
Between sensilla	39162·89	17	2303·7	***
Interaction	5437·06	17	319·83	***
Error	10608·00	108	98·22	
Total	59854·64	143		

*** Highly significant.

Table 12. *Analysis of variance computed on data given in Table* 9

Source of variation	S.S.	D.F.	M.S.	
Between stimuli	614·49	2	307·25	*
Between sensilla	45016·27	9	5001·81	***
Interaction	12594·40	18	699·69	***
Error	5515·33	60	91·92	
Total	63740·49	89		

* Significant at 5 % level. *** Highly significant.

insect decodes the message for taste quality, merely it shows that the message is adequate. It would be naive to conceive of a computer-like programme for analysis of variance in the central nervous system of the insect. The true activities of interneurones at higher levels awaits investigation.

Conclusions in relation to chemoreceptor function

The interpretation placed on the data obtained in these experiments poses some problems of fundamental interest in the functioning of contact chemoreceptors, namely the occurrence and significance of variability within sensilla, the lack of neuronal specificity and the possibility of neurones firing in unison within a sensillum.

The degree of intrasensillar variability is considerable and it is impossible to determine accurately to what extent this represents variation of output by the sensillum and to what extent it is attributable to artifactual influences. However, the problem has been studied by van der Starre (1972), Blaney (1974) and Dethier (1974) and all are agreed that a large element of the variability is a real representation of the activity of the sensilla. Indeed, as Dethier (1974) points out, 'Contrary to popular conceptions the responses of receptors to single stimuli are not very uniform. They are extremely ragged. This is even true of responses of such stable receptors as the visual cells of *Limulus* for which the stimulus can be impeccably controlled.'

Examples in which the same neurones responded to different stimuli have been reported in the blowflies by van der Starre (1972) and Morita (1967) and in various species of lepidopterous larvae by Schoonhoven (1969), Dethier & Kuch (1971) and Dethier (1973). The investigations reported here, especially adaptation tests, and those reported in a previous paper (Blaney, 1974), offer further evidence of this lack of specificity at the neuronal level and suggest that such specificity as exists is at the level of sensilla rather than neurones.

The concept of specificity occurring at the level of sensilla rather than neurones is not new. Stürckow (1970) stresses the significance of the viscous substance in front of

the dendritic endings for the reception of the stimulus and predicted that, 'the direction of investigations will change from the search for *cells* with more or less specialized dendritic membranes to the search for *sensilla* with more or less specialized receptive membranes'. Nevertheless, reports of this phenomenon in the literature are rare and the mechanism involved is quite unknown. The viscous substance in the maxillary palp tip sensilla of *Locusta* is almost certainly secreted into the basal cavity of the neurilemma cell (Blaney, Chapman & Cook, 1971). Numerous authors have reported similar basal cavities formed by a neurilemma cell and several have shown that substances do exude from the pores of chemoreceptors (see Blaney *et al.* 1971, for lists of references). Moulins & Noirot (1972) point out that this material is an obligatory intermediate between the receptive surface and the stimulating solution. It is possible that this material is the agency which determines the specificity of the entire sensillum.

Alternatively, or in addition, interactions between neurones may account for their apparent synchrony within the sensillum. In a study of the fine structure of these sensilla, Blaney *et al.* (1971) have shown that the distal ends of the proximal region of the dendrites may not be ensheathed by the neurilemma cell but, instead, may be in contact with each other and bound together by a zonula adhaerens (see their fig. 6). Similarly, regions of the perikarya of the neurones are sometimes in direct contact instead of being separated by folds of the neurilemma cell. This latter condition is also described in gustatory organs of the buccal cavity of *Blabera craniifer* by Moulins & Noirot (1972) and these authors suggest that the 'windows' in the glial sheath which allow direct contact between neurones may be sites of electrotonic coupling between cells, such as that occurring at the morphologically similar gap junctions in smooth and cardiac muscle where there is rapid electrical flux. Thus the presence of either or both the viscous fluid and the interneuronal contacts could account for the responses described here.

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