

THE SIGNIFICANCE OF PALPATION BY THE MAXILLARY PALPS OF *LOCUSTA MIGRATORIA* (L.): AN ELECTROPHYSIOLOGICAL AND BEHAVIOURAL STUDY

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SUMMARY

Palpation increases the amount of sensory input reaching the central nervous system compared with that obtained from sustained contact but that increase is not essential to allow discrimination.

During a meal on favoured food, phagostimulatory input from the palps is not needed to drive feeding. When less favoured food is taken, phagostimulatory input from the palps may enhance feeding. Even with favoured food, the palps are important in registering inhibitory substances.

INTRODUCTION

The sensilla concentrated on the tips of the maxillary palps of Acrididae are contact chemoreceptors (Frings & Frings, 1949; Haskell & Mordue, 1969) and those of *Locusta migratoria* (L.) play an important role in food selection by normally feeding insects (Blaney & Chapman, 1970; Blaney, Chapman & Wilson, 1973). During the testing of potential food, the palps make extensive, rapid vibrations known as palpation. The legs are flexed, the mouthparts come close to the substratum and the terminal sensilla of the vibrating palps touch it. The rapid movement, each cycle being completed in about 0.06 s and repeated 10-15 times/s (Blaney & Chapman, 1970), and the asymmetrical arrangement of the terminal sensilla (Blaney & Chapman, 1969) ensure that a large number of sensilla make frequent tests of the potential food. Blaney & Chapman (1970) suggested that palpation maintains a continuous flow of information to the central nervous system. The present study investigates the validity of that suggestion and considers the role of palpation in providing the neural information necessary for the discrimination of complex plant materials (Blaney, 1975) and also the effect of the sustained sensory input derived from continued palpation during the course of a meal.

MATERIALS AND METHODS

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, London. The insects were used between 2 and 5 days after ecdysis so that the results were not influenced by the proximity of the moult.

Electrophysiological experiments

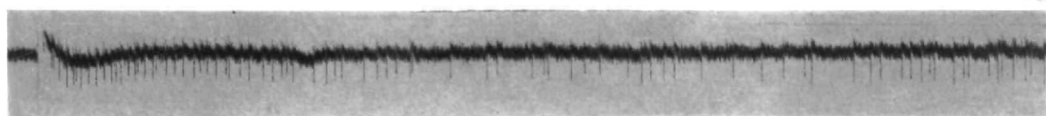
Recordings were made from intact, restrained insects prepared for electrophysiology 2 h after a normal meal. A modified version of the technique of Hodgson, Lettvin & Roeder (1955) was employed to detect, extracellularly, electrical changes within the sensilla by means of silver/silver chloride electrodes. Full details of the pre-treatment of insects and of the recording technique are given elsewhere (Blaney, 1974). The effect of palpation was simulated by bringing the recording electrode into a series of brief contacts with the sensillum under test in rapid succession.

This procedure was found to be more satisfactory when achieved by manual operation of the micro-manipulator than by use of a loudspeaker coil to move the recording capillary. By driving the loudspeaker with a square wave at 10 Hz it was possible to achieve stimulation at a frequency comparable to that of real palpation, but very difficult to adjust and maintain the extent of movement of the capillary so that it was great enough to break the meniscus on withdrawal but not so great as to elicit mainly mechanoreceptor responses. However, a few records were obtained in this way to check that the responses obtained by the more controlled, but slower manual manipulation did not differ materially from those obtained at the frequency of real palpation.

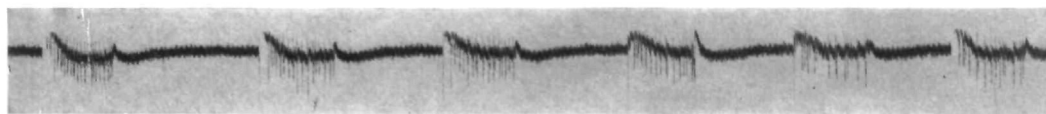
With the manual method, the average length of contact between stimulus and sensillum was 0.38 s ($n = 88$) and the average interval between contacts during simulated palpation was 0.46 s. The stimulating solution in all the electrophysiological experiments was 0.1 M sodium chloride which elicits varying degrees of response (Blaney, 1974) in the contact chemoreceptors, which comprise about 93 % of the sensilla on the maxillary palp tips.

Behavioural experiments

The effect of palpation during a meal was investigated by controlling the stimulation received by the palp tip sensilla while the insect was eating. The palp tip sensilla were prevented from making normal contact with the food by means of open-ended capillary glass tubes slipped over the terminal segments and waxed in position (Fig. 1). Microcap 10 μ l tubes were cut to size and attached with Cottrell Sticky Wax to unstarved insects which had been lightly anaesthetized with carbon dioxide. The sensilla on the tips of the labial palps were waxed to prevent stimulation of these sensilla by chemicals. The insects were released into 1 lb jam jars, screened from each other and from the observer, and allowed to feed *ad lib* for 2 h. They were then deprived of food for 1 h, the normal interfeed period (Blaney *et al.* 1973), and offered a test meal of grass or altar-bread discs soaked for 5 sec in 0.1 M sucrose and dried for 20 min at 40 °C. Immediately prior to receiving the test meal, all the insects were handled briefly and in some experimental groups a test solution was introduced into the capillary tubes by means of an Agla syringe so that the terminal sensilla were bathed in the test solution. Subsequent inspection confirmed that the solution had been retained in the tubes, suggesting that the sensilla had remained bathed throughout the test meal. The size of meal taken by individual insects was determined



(a)



(b)

0.5 s

Fig. 2. Responses of a single terminal sensillum to stimulation with 0.1 M sodium chloride.
(a) Continuous stimulation, (b) simulated palpation.

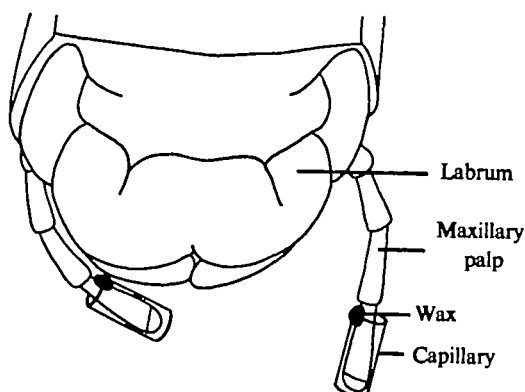


Fig. 1. Diagram of the head of a locust to show the capillary tubes waxed in position on the palps.

mined by weighing the grass or discs immediately before and after the meal. The experimental treatments applied to the palps were:

- (1) No tubes on palps – i.e. normal insects.
- (2) Empty tubes on palps.
- (3) Tubes containing grass extract (1:10 mixture of grass and water by weight blended for 1 min in an M.S.E. Atomix blender).
- (4) Tubes containing 0.1 M sodium chloride.
- (5) Tubes containing 0.01 % azadirachtin.
- (6) Tubes containing 0.1 M sucrose.

RESULTS

Electrophysiological experiments

The response of the terminal sensilla to continuous stimulation with 0.1 M sodium chloride is typical of contact chemoreceptors (Hodgson & Roeder, 1956). An initial brief period with a high rate of impulse initiation, the phasic period, is followed by a prolonged period in which the rate of impulse initiation has reached a lower level, the tonic period (Fig. 2*a*). During simulated palpation, contact with the stimulating/recording capillary is broken whilst the response is still in the phasic period (Fig. 2*b*) and each successive stimulation produces a response typical of the phasic period. In investigating the effects of palpation, comparison is made between the repeated phasic responses of simulated palpation and the phasic/tonic response elicited by a single prolonged stimulation.

Simulation of palpation by manual manipulation was of low frequency (about 2 Hz) whereas real palpation occurs at 10–15 Hz. It could be argued that it is not legitimate to extrapolate to real palpation from these simulations, since the rate of adaptation might be quite different at higher frequencies. However, results obtained from a few successful stimulations at 10 Hz (Table 1) indicate that there is no material difference between the responses obtained to stimulation at 2 Hz and at 10 Hz.

Since, in the low-frequency simulated palpation, the periods of contact and

Table 1. *Comparison of the number of impulses from three sensilla during simulated palpation at 10 Hz and continuous stimulation*

(The number of impulses and duration of each contact in 'palpation' is given, together with the number of impulses occurring in successive periods of equivalent duration from the start of a 'continuous' stimulation.)

Contact numbers ...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Sensillum 1																				
'Palpation'																				
Impulses	6	5	5	6	4	5	3	3	2	4	5	5	3	4	5	3	5	6	6	2
Duration (ms)	50	60	60	60	60	60	50	60	40	60	60	60	50	60	60	40	60	60	60	40
'Continuous' impulses	6	7	4	3	2	3	1	1	1	1	1	0	1	0	1	1	0	1	0	1
Sensillum 2																				
'Palpation'																				
Impulses	2	1	1	0	2	2	1	2	2	3	2	2	1	1	3	3	3	3	2	1
Duration (ms)	50	50	60	70	60	60	60	70	60	70	60	80	50	60	60	60	50	60	60	50
'Continuous' impulses	2	0	2	2	1	2	2	1	2	2	0	0	0	0	0	0	0	0	0	0
Sensillum 3																				
'Palpation'																				
Impulses	7	8	7	5	8	6	7	8	6	6	5	5	5	6	4	5	6	5	6	7
Duration (ms)	50	50	60	60	50	50	60	60	50	60	60	50	60	60	50	60	50	50	60	60
'Continuous' impulses	5	3	3	3	3	2	2	2	2	1	1	2	0	1	0	0	0	3	2	1

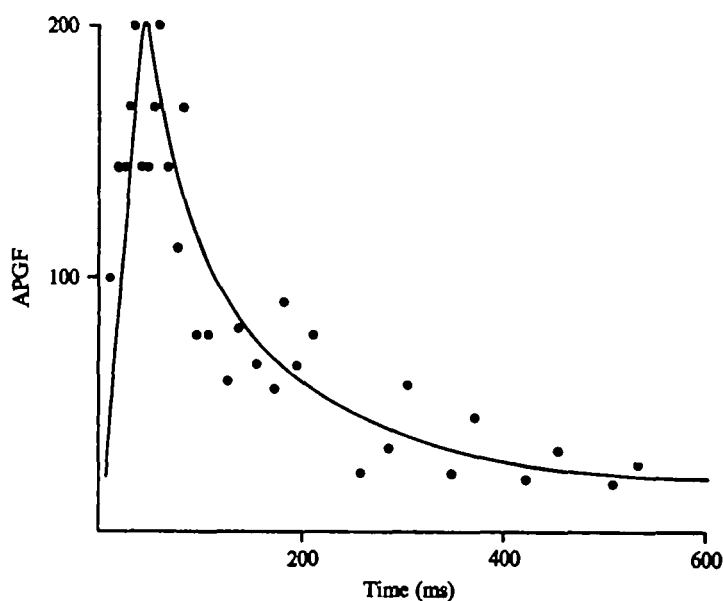


Fig. 3. Action potential generation frequency of terminal sensilla in response to 0.1 M sodium chloride. Derived from responses of 17 sensilla.

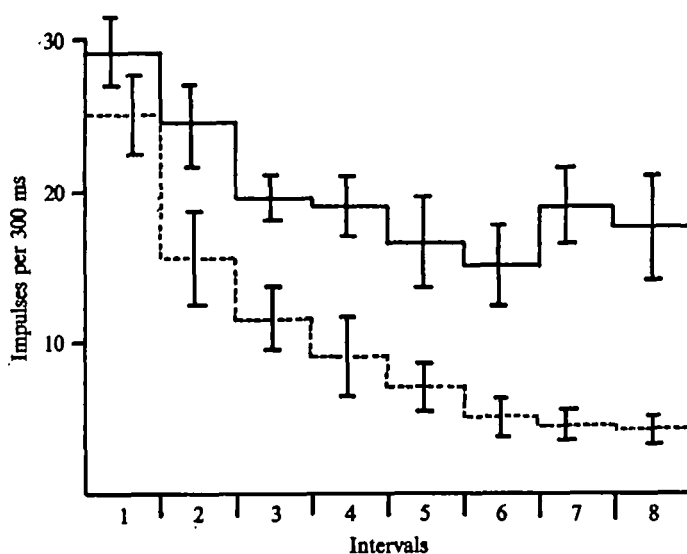


Fig. 4. Histogram comparing the number of impulses occurring during the first 300 ms of each succeeding 'palpation' contact (solid line) with those occurring in successive 300 ms periods of continuous contact (broken line). Derived from 11 sensilla. Range bars show \pm s.e. of mean.

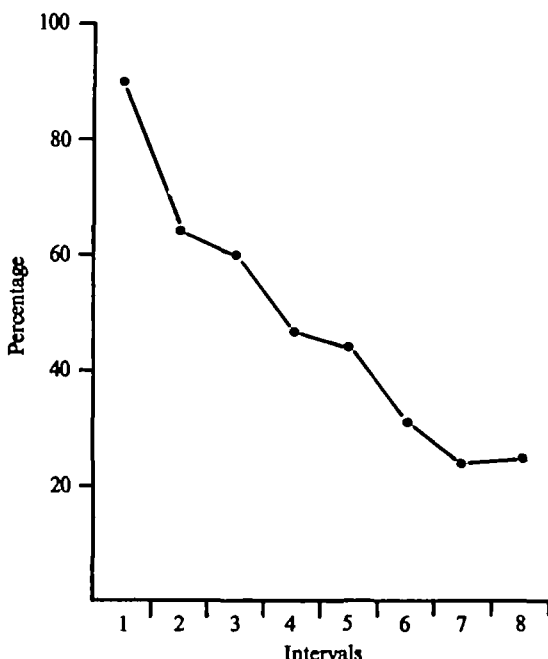


Fig. 5. Data derived from Fig. 4 with response to continuous stimulation expressed as a percentage of the response to palpation over successive 300 ms intervals.

intervals between contacts were not of uniform duration, it was useful, arbitrarily, to select for consideration a constant period at the start of each brief contact. To this end, the mean action potential generation frequency (Rees, 1968) for a number of sensilla was investigated. Most of the phasic activity occurs during the first 300 msec of response and, since palpation involves the phasic part of the response, it was decided to use this as the standard period for comparison. Thus in comparing the effects of palpation and continuous stimulation on the same sensillum, the first 300 msec of each succeeding palpation contact are compared with successive 300 msec periods of a single continuous stimulation. The results obtained by this method from eleven sensilla are shown in Figs. 4 and 5.

It is clear that while, in the simulated palpation, some adaptation does occur, or alternatively recovery from adaptation is incomplete, nevertheless the loss of neural input due to adaptation is much less than that occurring during continuous stimulation (Figs. 4, 5).

Behavioural experiments

In this investigation of the effect of palpation during a meal, it was important to ensure that the attachment of capillary tubes to the palps did not in itself impose such a constraint on the behaviour of the insect as to mask any effect of the test situations additionally applied. To this end, 25 insects, treated in the same way as the test animals but without tubes on the palps, were compared with insects which had empty tubes covering their maxillary palps. The mean meal sizes (mg) of these groups were 109.65 ± 5.79 and 110.05 ± 6.25 respectively. It may therefore be concluded that the capillary tubes alone do not have a significant effect on th

Table 2. *The effects of various treatments of the palp tip sensilla on meal size (mg) and ingestion rate (mg/min)*

(Insects, with tubes in place, were starved for 1 h before treatment and testing at 30 °C.)

Expt	Treatment	Food	No. of Insects	Meal size (mean \pm s.e.)	<i>t</i>	<i>P</i>	Ingestion rate (mean \pm s.e.)	<i>t</i>	<i>P</i>
1	Empty tubes Tubes + grass extract	Grass	{ 24 }	137.30 \pm 11.60	0.21	N.S.	15.60 \pm 1.85	1.5	N.S.
				134.20 \pm 8.62			12.10 \pm 1.14		
2	Empty tubes Tubes + 0.1 M sodium chloride	Grass	{ 18 }	106.40 \pm 8.24	2.12	0.05	9.81 \pm 0.73	1.27	N.S.
				82.4 \pm 7.72			10.94 \pm 0.54		
3	Empty tubes Tubes + 0.01 % azadirachtin	Grass	{ 11 }	115.90 \pm 9.65	5.32	0.001	9.41 \pm 1.09	0.17	N.S.
				47.0 \pm 8.41			9.69 \pm 1.15		
4	Empty tubes Tubes + 0.1 M sucrose	Altar bread	{ 13 }	4.45 \pm 1.67	3.41	0.01	2.96 \pm 0.96	0.51	N.S.
				13.63 \pm 2.08			2.60 \pm 0.28		

insects' feeding. In each experiment involving chemical stimulation, meal size (mg) and ingestion rate (mg/min) of test insects were compared with those of control insects (with empty capillary tubes) which were taken from the same batch of insects and fed on the same food material (Table 2).

In Expt 1 the presence of grass extract in the tubes had no significant effect compared with the empty tubes. In Expt 2 the effect of 0.1 M sodium chloride was to reduce the size of meals taken, although the ingestion rate was not significantly different when compared with the effect of empty tubes on that occasion. Similarly, the effect of azadirachtin (Expt 3) was to reduce the meal size, but again the rate of ingestion was not significantly different from that of the empty tube group.

Altar-bread discs, containing only wheat flour, are much less palatable to *Locusta migratoria* than grass, and smaller amounts are eaten. Stimulation of the palps with 0.1 M sucrose during the meal (Expt 4) increased the amount eaten but the rate of ingestion was not significantly different.

DISCUSSION

The electrophysiological evidence reported here indicates that palpation may be more effective than continuous, sustained contact in maintaining a flow of information to the central nervous system. Because of the very rapid movements involved, it is impossible exactly to mimic palpation by the locust. However, it is clear that the effect of repeated, short contacts between sensilla and stimulating material is to keep the sensilla responding in the relatively unadapted, phasic mode, and so to increase the overall rate of generation of impulses.

In normal palpation by the insect, the period of contact of the terminal sensilla with the leaf surface at each movement of the palps is probably less than 20 msec (Blaney & Chapman, 1970) so that, with 15 contacts/s, the total contact time would not exceed 300 ms/s. It has been shown (Blaney, 1974) that the spectra of sensitivity and specificity of neurones in the terminal sensilla and of the sensilla themselves, overlap to an appreciable extent. Thus cognition requires some degree of computation; an analysis must be made of the output of many neurones (Pfaffman, 1941, 1955; Erickson, 1963, 1967; Dethier, 1973; Blaney, 1975). No precise data are available on the amount of neural information needed for cognition but the interval between the start of palpation and head lowering, the next stage in the feeding sequence, is 1 s or less. As a result of palpation, very little sensory adaptation will have occurred during this time.

It seems likely, however, that a sustained, high level of neural input is not essential for discrimination. Lacher (1967) has suggested that the time for a response indicating discrimination of food material by the honey bee, *Apis*, is 500 ms. A number of similar times are given in the literature for the blowflies: 100 ms or less for the labellar sensilla of *Phormia* (Dethier, 1955; 1968; Dethier, Solomon & Turner 1965), 43–54 ms for the same sensilla (Gettings, 1971), 30–70 ms for the labellar sensilla of *Calliphora* (den Otter, 1968) and 125–2000 ms with a mean just under 500 msec for tarsal sensilla of *Calliphora* (van der Starre, 1972). Halpern & Tapper (1971), working with rats, have shown that animals conditioned to avoid drinking 300 mM sodium chloride solution are able to recognize and reject this solution withi

250–600 ms of the onset of stimulus, a period containing the phasic portion of the peripheral neural response. They point out that this corresponds to reports of human taste quality reaction time.

These reaction times encompass discrimination and central nervous activity leading to an overt response. Obviously the time needed for discrimination alone is shorter and it seems reasonable to assume that, in most cases, only about 100 ms of peripheral input is needed for discrimination (see also van der Starre, 1972). That means that, if the same situation obtains in the locust, the coding for taste quality is contained in the phasic part of the response and could be adequately obtained from a single sustained contact.

The work of Blaney (1974, 1975) indicates that the palp tip sensilla constitute a very noisy receptor system. That is, there is much overlap of receptor sensitivity and specificity, and variability of response. To decipher the neural message in such a system it is necessary for the insect to measure the average impulse frequency over a sufficiently long time before and during stimulation. However, this constraint is alleviated by the multiplicity of sensory channels in use, the insect seldom using less than 40 sensilla on each palp at each contact (Blaney & Chapman, 1970). If the signal to noise ratio of each channel is q and the time required to register a significant change in average frequency is t , the corresponding parameters when n channels are involved are qn and t/n respectively (Aidley, 1971). Thus, unless the process of integration is in some way less efficient in the locust, it cannot be argued that palpation, as opposed to a single sustained contact, is essential for discrimination, provided contact is easily made with appropriate materials (see below).

It is noteworthy that, whatever the method of discrimination, it is often the phasic portion of the response which is acted upon. Unless suitable precautions are taken (Blaney, 1974; van der Starre, 1972), recording of the phasic element is often hampered by the occurrence of electrical artefacts. Commonly this portion of the record is discarded or grouped with the tonic component, by students of taste quality coding, both in vertebrate (Erickson, 1967; Doetsch *et al.* 1969; Sato, Yamashita & Ogawa, 1969; Frank & Pfaffman, 1969) and insect systems (Schoonhoven, 1967; Haskell & Schoonhoven, 1969; Ma, 1972; Gothilf, Galun & Bar-Zeev, 1971) with consequent loss of information.

Behavioural experiments have shown that, when favoured food is being eaten, phagostimulatory input from the palps is not needed to drive feeding. Barton-Browne, Moorhouse & van Gerwen (1975) have suggested that when *Chortoicetes* is fed on solutions of single chemicals, meal size is regulated by sensory adaptation. Similarly, Bernays & Chapman (1974) point out that sensilla within the cibarial cavity of the locust are continually bathed in fluid during a meal and presumably become fully adapted, whereas with the palps this does not occur. They suggest that feeding is driven by the continued input from the palps. However, it is clear from the experiments described here, in which the empty tubes prevented chemosensory input from the palp tip sensilla, that meal size is not reduced by that lack of input, at least while the insect is feeding on a favoured food such as grass. In such a case, presumably, the level of phagostimulatory input from other mouthpart sensilla is adequate to maintain feeding at the normal level. Thus, as one might expect, there was no significant increase in meal size on grass when grass extract

was added to the tubes since the insects were already receiving sufficient phagostimulatory input to ensure that a normal meal was taken.

When a non-favoured food is being eaten, phagostimulatory input from the palps may enhance feeding. Thus stimulation of the palp sensilla with 0.1 M sucrose increased the consumption of altar bread discs. Similarly Mordue (1975) has shown that fifth-instar larvae of *Schistocerca* eat only small meals of filter paper impregnated with sucrose, but that they eat even less if the palps have previously been amputated. However, the intake of insects without palps is increased if they are presented with the sucrose paper in the presence of grass odour. Mordue suggests that the increased sensory input, presumably perceived via the antennae, heightens the feeding drive. Whether this represents an increase in a specific feeding drive or an increase in central excitatory state (Moorhouse, 1969) is not clear.

Even when favoured food is being eaten, the palps are important in registering feeding inhibitors. Thus addition of sodium chloride and azadirachtin to the tubes resulted in a decline in meal size. Both these substances act as feeding deterrents and azadirachtin is particularly effective in this respect (Haskell & Schoonhoven, 1969). Apparently then, input from the palp tip sensilla during the course of a meal can affect meal size but it is unlikely that this input has a significant effect in driving feeding behaviour when favoured food is being eaten.

It is apparent that when meals are smaller than normal, this results from an earlier termination of feeding. In no case was there a significant difference in rate of ingestion between test and control groups of insects. The present results differ in this respect from those of Bernays & Chapman (1972), who report an ingestion rate of 3 mg/min in fifth-instar larvae of *Locusta migratoria* fed on *Trifolium* compared with a rate of 7 mg/min for similar insects fed on *Agropyron*. However, ciné-film analysis of mouthpart movements during feeding on a palatable and a less palatable plant showed that the rate of mandibular movement in *Locusta migratoria* was constant (E. A. Bernays, personal communication) and that the differences arose from pauses towards the end of the meal on less favoured food. A more detailed study is necessary to resolve this issue.

Apart from any role in modifying a feeding drive, continued palpation during a meal provides a continuous monitoring of food quality before the food enters the cibarial cavity. In this function, and indeed in initial sampling prior to biting, palpation ensures that a larger area of the potential food material is sampled than would be possible with few and sustained contacts. This may be of particular value if the significant chemicals in the plant surface (Bernays *et al.* 1975) are discontinuously distributed. Perhaps the percussive mode of contact between sensilla and substrate employed in palpation is advantageous in sampling a solid but irregular surface (Martin & Juniper, 1970) from which, presumably, some of the surface materials must be taken up in the tips of the sensilla.

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