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perature, in combination with body odour and humidity, has more effect on the alighting reactions than changes in the other two factors. This explains what happens in nature: at a distance odour alone is the factor reaching the mosquito and guiding it to its host, in the vicinity of the host the effect of odour is increased by the addition of body moisture. Warmth, then, is the factor responsible for the actual alighting, followed usually by the probing action.

VIII. Reactivity of Female Mosquitoes with Progressive Amputation of their Antennal Flagellar Segments towards the Attracting Factors.

The three combinations of factors which showed the high attractive effect with the normal unoperated mosquitoes were tested against groups of mosquitoes with progressive symmetrical amputation of their antennal flagellar segments. In each operation an equal number of segments from both antennae were eliminated. It was hoped that the study of the change in reaction intensity with different amputated groups of mosquitoes, would reveal the possible function of the sense organs distributed on the antennae.

In order to estimate the change in reaction caused by progressive amputation, each group of operated mosquitoes was tested with a parallel control group of unoperated mosquitoes. In each group of operated mosquitoes the number of mosquitoes involved was between 35 and 40, whereas the number of accompanying controls was fixed at 40.

When comparing the corresponding reactions we were restricted by the following facts:

- 1) Owing to mortality, the number of operated mosquitoes used finally in the reaction experiments was not always the same.
- 2) Variations due to the uncontrollable interfering factors from one experiment to another or one day to the next (see p. 34).

Hence a standard basis was necessary, in which the influence of these factors was eliminated and consequently direct comparison possible. So in each series of experiments the reactions of the operated mosquitoes were corrected to give a value corresponding to the number of control mosquitoes (40).

To exclude as far as possible the influence of the other uncontrollable interfering factors, the reactions of the operated mosquitoes were corrected with reference to a constant reactivity value (100). This procedure would allow us to compare the influence of progressive amputation on reactivity.

To illustrate this, we would give the following example for body odour, moisture content of 75-85% R.H. and temperature of 34°C.:

Mean reactivity of amputated mosquitoes (8 exp.)	3
Mean reactivity of accompanying controls (8 exp.)	168
A constant reactivity value	100

Accordingly, the theoretical reactivity of the amputated mosquitoes (both flagella completely eliminated) under these testing factors would be $\frac{100 \times 3}{168} = 1.8$. From now on this value will be referred to as "Index of Reaction Intensity (I.R.I.)" and will be adopted in investigating the effect of progressive amputation on reactivity, and later on to find a correlation between the sense organs and the possible functions.

Results of the three combinations of factors are given in Tables 10, 11 and 12 and graphically represented in Figs 14, 15, 16 respectively.

Combination of body odour, moisture content of 75-85% R.H. and temperature of 34°C.

TABLE 10.

The reaction intensity of female mosquitoes towards body odour, moisture content of 75-85% R.H. and temperature of 34°C with the progressive symmetrical amputation of the antennal flagellar segments.

Number of flagellar segments remaining in each antenna	Mean reactivity of amputated mosquitoes and accompanying controls (8 exp.)		Index of Reaction Intensity (I.R.I.)
	Amputated	Controls	
12	130	138	94.2
10	150	180	83.3
8	120	178	67.4
6	85	180	47.2
5	52	146	35.6
3	20	139	14.4
1	10	149	6.7
0	3	168	1.8

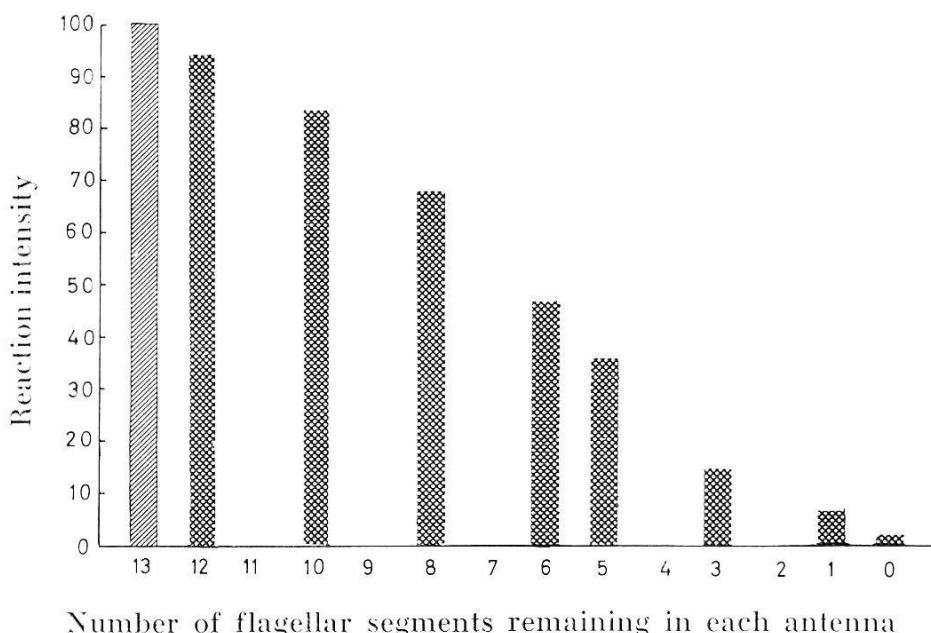


Fig. 14. The reaction intensity of female mosquitoes towards body odour, moisture content of 75-85% R.H. and temperature of 34°C with the progressive symmetrical amputation of the antennal flagellar segments. The reaction intensity with 13 flagellar segments represents the mean reactivity of control mosquitoes (56 exp.).

When female mosquitoes were tested against this combination of factors, the control experiments showed a mean reactivity (\bar{x}) of 157 (100%) (cf. Table 5). Table 10 shows that with the gradual elimination of the flagellar segments the reaction intensity decreased gradually and no considerable change occurred between any successive eliminations of segments. When one segment was eliminated, the I.R.I. fell to 94.2%, and then decreased gradually with the progressive elimination of the flagellar segments to 83.3% when 10 segments remained in each antenna and to 67.4% with 8 segments remaining; when 6 segments (about half of the total number) were left, the reaction intensity was also about one half (47.2%). With the elimination of the whole flagellum there was a reaction intensity of 1.8%.

In *Anopheles maculipennis* the flagellectomized females are practically not able to respond any more to the combination of body odour, moisture content of 75-85% R.H. and temperature of 34°C. This proves that the antennae are the organs responsible for directing the female mosquito to the source of attraction from a distance; these results agree with the findings of ROTH (1951) and RAHM (1958) on *Aedes aegypti* and *Anopheles quadrimaculatus*.

The gradual decrease in the reaction intensity with the progressive elimination of the flagellar segments shows that the sense organs which locate the source of the stimuli—body odour, hu-

midity and temperature—are distributed on the flagellar segments in such a way that their combined effectiveness at perceiving the different stimuli seems also to be distributed equally on the different segments.

Since the scape and pedicel do not carry sense organs (as seen in the morphological and histological studies) which could be responsible for the location of the tested stimuli, the small value of response with the flagellectomized mosquitoes (1.8%) is probably due to other sense organs existing on other parts of the insect's body.

*Combination of moisture content of 75-85% R.H.
and temperature of 34°C.*

TABLE 11.

The reaction intensity of female mosquitoes towards moisture content of 75 to 85% R.H. and temperature of 34°C with the progressive symmetrical amputation of the antennal flagellar segments.

Number of flagellar segments remaining in each antenna	Mean reactivity of amputated mosquitoes and accompanying controls (8 exp.)		Index of Reaction Intensity (I.R.I.)
	Amputated	Controls	
12	75	99	75.8
10	65	110	59
8	58	128	45.4
7	43	116	37
6	17	116	14.7
4	12	99	12
3	11	95	11.6
2	9	139	6.5
1	4	89	4.5

When the moisture content of 75-85% R.H. combined with the temperature of 34°C was used without the body odour, the reaction intensity of amputated mosquitoes did not decrease in the same gradual manner as in the first combination (with body odour). In this combination the mean reactivity of control mosquitoes (\bar{x}) was 111 (100%) (Table 6). Table 11 shows that when one segment was eliminated and 12 segments remained in each antenna, the reaction intensity decreased considerably to 75.8%. By the progressive elimination of the next flagellar segments the intensity decreased gradually to 59% with 10 segments remaining

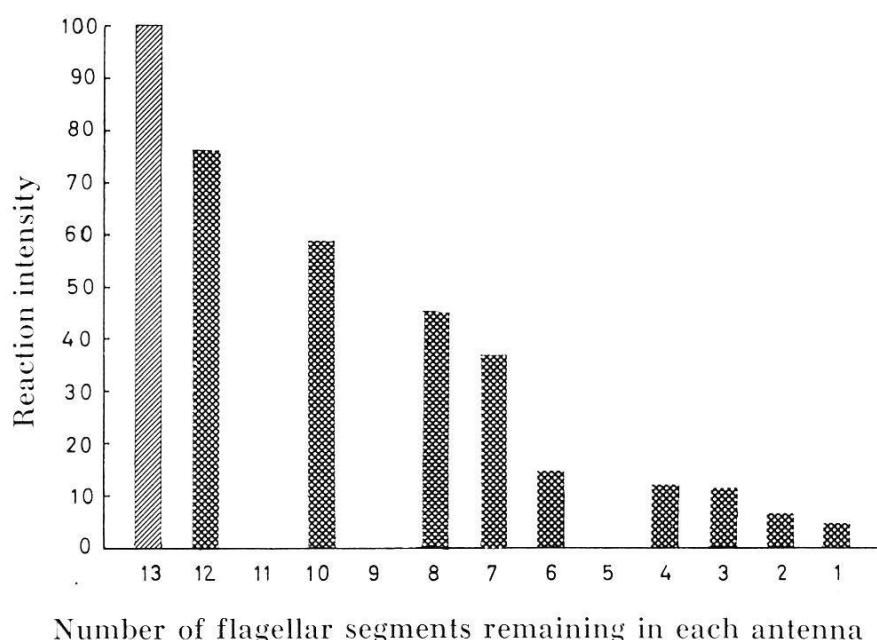


Fig. 15. The reaction intensity of female mosquitoes towards moisture content of 75-85% R. H. and temperature of 34°C with the progressive symmetrical amputation of the antennal flagellar segments. The reaction intensity with 13 flagellar segments represents the mean reactivity of control mosquitoes (56 exp.).

in each antenna, 45.4% with 8 segments and 37% with 7 segments; then when one more segment was eliminated and 6 remained, the intensity decreased again considerably from 37 to 14.7%. The intensity with 4 and 3 segments remaining gave nearly the same value as that with 6 segments, i.e. 12% and 11.6 respectively, and then decreased to 6.5 with 2 segments remaining and 4.5% with one segment.

The considerable change in reactivity with the elimination of the last flagellar segment (terminal) from each antenna suggests that this segment plays an important role in the location of humidity and/or temperature.

With the elimination of 3, 5 and 6 segments (10, 8 and 7 remaining), the mosquitoes showed a clear response to the source of stimuli, which suggests that there are sufficient receptors on the remaining segments to mediate the stimuli. Also the gradual decrease in reaction intensity with the elimination of those segments shows that the responsible hygroreceptors and/or thermoreceptors are distributed quantitatively on the terminal segments.

The big decrease in reaction intensity with the elimination of 7 segments (6 remaining) and the persistence of this low intensity with gradual elimination of the basal segments suggests that the hygroreceptors and/or thermoreceptors on these basal segments cannot mediate and consequently cannot show a significant response to the source of humidity and/or temperature.

*Combination of body odour, moisture content of 75-85% R.H.
and temperature of 25-26°C.*

TABLE 12.

The reaction intensity of female mosquitoes towards body odour, moisture content of 75-85% R.H. and temperature of 25-26°C with the progressive symmetrical amputation of the antennal flagellar segments.

Number of flagellar segments remaining in each antenna	Mean reactivity of amputated mosquitoes and accompanying controls (8 exp.)		Index of Reaction Intensity (I.R.I.)
	Amputated	Controls	
12	78	62	126.3
10	76	67	113.4
8	69	71	97.2
7	55	62	88.7
6	32	59	54.3
4	23	65	35.4
2	19	83	22.8
0	4	55	7.3

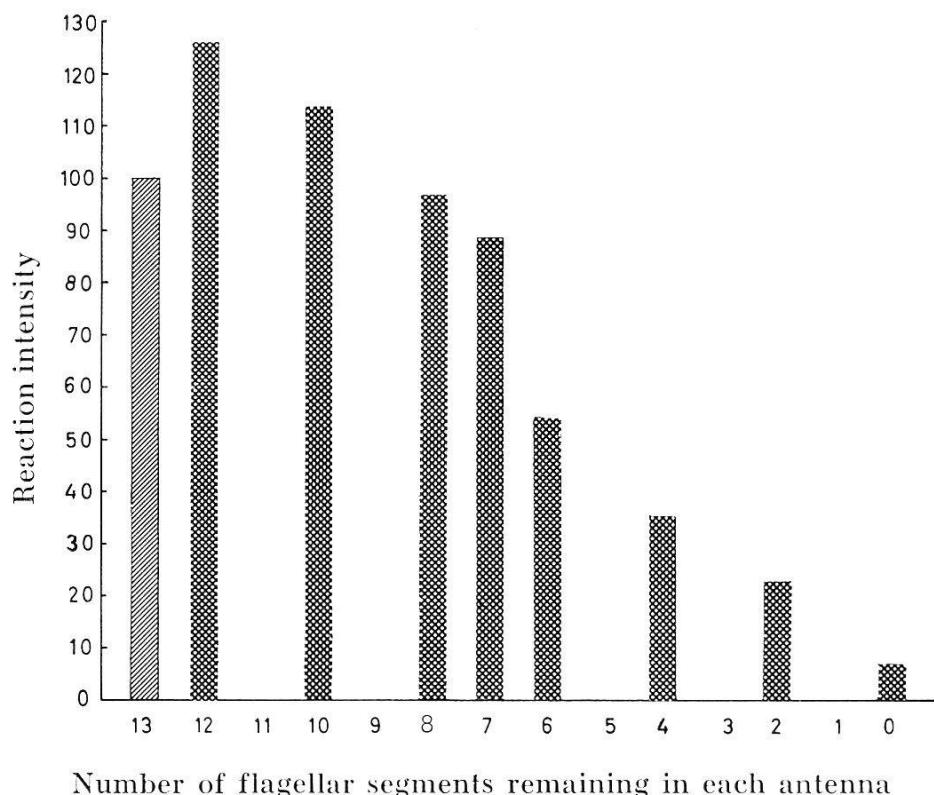


Fig. 16. The reaction intensity of female mosquitoes towards body odour, moisture content of 75-85% R.H. and temperature of 25-26°C with the progressive symmetrical amputation of the antennal flagellar segments. The reaction intensity with 13 flagellar segments represents the mean reactivity of control mosquitoes (56 exp.).

When body odour was used with a moisture content of 75-85% R.H. and a temperature of 25-26° C, the reactivity of the amputated mosquitoes unexpectedly changed in a different way. By comparing the values of the reaction intensity with the gradual elimination of the flagellar segments we find that with the elimination of one segment, the reaction intensity, instead of being decreased, increased from 100% (equivalent to 66, the mean reactivity of the controls) to 126.3%, and then gradually decreased with the progressive elimination of the flagellar segments to 113.4% with 10 segments remaining in each antenna, 97.2 with 8 segments and 88.7 with 7 segments. When only 6 segments were left in each antenna, the reaction intensity decreased considerably from 88.7% to 54.3%, and then the decrease became gradual again with the progressive elimination of the rest of the segments. When the whole flagellum was eliminated a considerable intensity was still obtained (7.3%).

The possible explanation for the increase of reaction intensity with the elimination of the terminal segments is that there might exist a type of sense organ on the last flagellar segment which has an inhibiting function, preventing the female mosquitoes from showing a high response to such a combination of factors. Since the body odour and this moisture content (75-85% R.H.) proved very attractive in the other combinations, it would be expected that the lower degree of temperature was the factor responsible for such a change.

With the elimination of 7 segments, the sense organs left on the remaining 6 segments which are responsible for mediating one or more of these factors show a considerable decrease in function.

In contrast to the second combination of factors, the responsible sense organs still showed a sufficient response in spite of the fact that the intensity of reaction was considerably decreased with the elimination of 7 segments. Also with the progressive elimination of the basal segments, the reaction intensity decreased gradually.

The response obtained with the elimination of the whole flagellum from each antenna demonstrates the existence of sense organs on other parts of the insect's body which play a role in the attraction.

IX. Possible Function of the Sense Organs.

The specific function of the sense organs would have been clearly demonstrated if each type was limited to special segments. But they are scattered over the flagellar segments in a way that makes