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(v. Thiel), and their possible function in relation to the attraction of

female mosquito to man

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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

it quite impossible to test one single type alone towards the attracting stimulus or stimuli, in order to know its proper function. This distribution forces us to combine the morphological and histological findings, the distribution and number of sense organs on the different flagellar segments and the reaction changing with the progressive elimination of the flagellar segments. By such combinations only indirect evidence of the possible function of each type of sense organ can be suggested.

According to the structure of the different types of sensilla, in the form of hairs, we can classify them into two groups. In the first group, each organ has an external thick-walled cuticular process, one sense cell (long and short bristles, Types I and II respectively), and is articulated in a distinct socket. The second group has thin walls, innervated through more than one sense cell and possesses no sockets: sensilla trichodea (Types III and IV); sensilla basiconica (Type V) and sensilla coeloconica (Type VI).

The first group has been classified (WIGGLESWORTH, 1953) as tactile receptors, and from their structure and distribution there seems to be no doubt that these sensilla are responsible for perceiving contact. They stand out in all directions, beyond the other types of sensilla in two circles, the long bristles in the outer circle projecting from the base of the segments and the short bristles in the inner circle, so as to prevent any object from coming in contact with the more delicate sensilla with which the antennae are richly equipped. Possibly these two types are also responsible for the perception of air movements as proposed by WIGGLESWORTH & GILLETT (1934) in *Rhodnius prolixus*.

The perception of body odour, moisture and heat mostly concerns the second group of sensilla, and Table 13 includes the number of these sense organs ⁹ remaining on each antenna with the progressive elimination of the flagellar segments as well as the corresponding reaction intensity of female mosquitoes towards the three combinations of factors. The number of sense organs (in per cent) remaining on the antennae with the progressive elimination of the flagellar segments is illustrated in Fig. 17.

Sensilla coeloconica and basiconica.

These two types of sense organs are distributed on the flagellar segments in a special manner; sensilla coeloconica is concentrated on the basal segments and sensilla basiconica on the terminal ones. The following findings and results would reveal in an in-

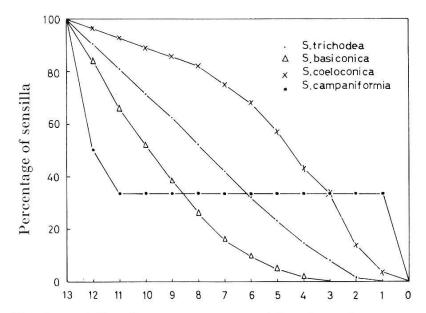
⁹ Sensilla campaniformia is also included in the table.

TABLE 13.

The number of sensilla coeloconica, basiconica, trichodea, and campaniformia remaining on the antennae of the amputated mosquitoes and the corresponding index of reaction intensity with the three combinations of factors.

| | | ur, | .C. | | | | | | A | | | | | | |
|--|--------------------------------------|--|----------------|-----|----------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-----|
| | Index of reaction intensity (I.R.I.) | Body odour, 75–85 % R. H. and 25–26 °C. | | 100 | 126.3 | 113.4 | 97.2 | 88.7 | 54.3 | 1 | 35.4 | 1 | 22.8 | Ι | 7.3 |
| | | 75–85 % R. H. and 34° C. | | 100 | 75.8 | 59. | 45.4 | 37. | 14.7 | 1 | 12. | 11.6 | 6.5 | 4.5 | 1 |
| | | Body odour, 75–85 % R. H. and 34° C. | | 100 | 94.2 | 83.3 | 67.4 | I | 47.2 | 35.6 | I | 14.4 | 1 | 6.7 | 1.8 |
| | Sensilla | Average of sensilla campaniformia | in per cent | 100 | 20 | 33.33 | 33.33 | 33.33 | 33.33 | 33.33 | 33.33 | 33.33 | 33.33 | 33.33 | 0 |
| | | | in number | 9 | 3 | 2 | 7 | 2 | 2 | 5 | 2 | 2 | 2 | 2 | 0 |
| | | Average of sensilla trichodea | in per cent | 100 | 90.45 | 71.68 | 52.10 | 41.91 | 31.88 | 22.98 | 14.72 | 7.93 | 1.62 | 0 | 0 |
| | | | in number | 618 | 559 | 443 | 322 | 259 | 197 | 142 | 91 | 49 | 10 | 0 | 0 |
| | | Average of sensilla basiconica | in per cent | 100 | 83.87 | 51.61 | 25.81 | 16.13 | 89.6 | 4.84 | 1.61 | 0 | 0 | 0 | 0 |
| | | | in number | 62 | 52 | 32 | 16 | 10 | 9 | 3 | - | 0 | 0 | 0 | 0 |
| | | Average of sensilla coeloconica | in per cent | 100 | 96.43 | 89.29 | 82.14 | 75.00 | 67.86 | 57.14 | 42.86 | 28.57 | 14.29 | 3.57 | 0 |
| | | | in number | 28 | 27 | 25 | 23 | 21 | 19 | 16 | 12 | 8 | 4 | - | 0 |
| | Number of | Number of flagellar segments remaining in each antenna | | | 12 | 10 | ∞ | _ | 9 | īĊ | + | 33 | 73 | - | 0 |
| | | | | | 37772-33 | | | | | | | | | | - |

¹ Average of 5 antennae.



Number of flagellar segments remaining in each antenna

Fig. 17. Proportion of each type of sensilla trichodea, basiconica, coeloconica and campaniformia remaining as the flagellar segments of Anopheles maculipennis are progressively amputated symmetrically.

direct way the possible function of each. We repeat first the results obtained in the combinations used in our experiments.

- 1) The reaction intensity decreased considerably with six segments left in each antenna when mosquitoes were tested towards:
 - a) Moisture content of 75-85% R.H. and temperature of 34° C.
- b) Body odour combined with moisture content of 75-85% R.H. and temperature of 25-26 $^{\circ}\mathrm{C}.$
- 2) When body odour was added to the moisture content of 75-85% R.H. and temperature of 34° C, the reaction intensity decreased gradually with the progressive elimination of flagellar segments, even the six basal ones.
- 3) On the six basal segments there are averages of: 197 trichoid sensilla from the total of 618 on the whole antenna (about one-third) and 6 basiconic sensilla from the total of 62 (one-tenth) and 19 coeloconic sensilla from the total of 28 (about two-thirds).

These results enable us to draw the following conclusions:

a) For the Sensilla coeloconica.

If the mainly basal coeloconic sensilla were responsible for the perception of heat and/or humidity (result 1 a), the perception of such factor or factors would be more likely not to decrease con-

siderably when the flagellar six basal segments are still present, because these contain about two-thirds of the total number of sensilla coeloconica. In adding body odour, as shown in result 2, progressive amputation provoked gradual decreasing reaction. This seems to indicate that the sensilla coeloconica are the sense organs responsible for the perception of odour.

The morphological and histological structure of this type also provides further evidence to support this idea. They are peg organs with very thin walls, and they are protected by being sunken into pits. The floor of the pit being thin increases the surface of perception. Every sensillum innervates through about six sense cells, relatively larger than the sense cells of the other types of sensilla.

b) For the Sensilla basiconica.

The reaction intensity decreased considerably (result 1 a) when only 6 segments were left. It seems that the number of receptors for heat and/or humdity on the six basal segments is less than that required to mediate a clear response (PIELOU 1940, ROTH & WIL-LIS 1951 b, 1952). It is more reasonable to consider that sensilla basiconica, which have about one-tenth of their total number left on the six basal segments, are responsible for the big decrease rather than trichoid sensilla which still have a considerable number, about one-third 10. The results with the addition of body odour and the decrease of temperature to 25-26°C (result 1 b), also showed a considerable decrease when 6 segments remained in the antenna. Heat in this case would not have a great influence on the responses of mosquitoes as long as it is equal to the degree of ambient temperature. Laarman (1955) wrote about the influence of the milieu on the responses of mosquitoes: ".... one should always bear in mind the possibility that Weber's Law may here be applicable: if the stimulus is to be perceived by the insect, there must be a certain relationship between it and already existing, similar stimuli." Moreover, Bates (1949) mentioned that the critical temperature below which attraction of mosquitoes does not occur seems to be 28° C. From this we can conclude that the basiconic sensilla are possible hygroreceptors.

c) For the Sensilla trichodea: (Types III and IV).

This kind of sensilla is different from the coeloconic and basiconic sensilla in being distributed on all the flagellar segments with no special concentration on any. For this reason it is quite

¹⁰ Trichoid sensilla, Types III and IV on the six basal segments are nearly equal in number.

difficult to correlate any considerable change in reaction intensity with the number of sense organs present on the antenna. But their great number, combined with the sensitivity of the antenna to warmth, suggests that they may act as thermoreceptors; but we have no other experimental evidence for this, nor for stating which one of these two types of trichoid sensilla is responsible, or if both are. The last probability, however, is not likely owing to the big difference in structure and cellular elements.

d) For the Sensilla campaniformia.

This type of sensilla is not included either in the first or in the second group of sensilla, as it possesses no external process in the form of hair. It has the fewest number of sensilla: two in the basal flagellar segment, one in segment 12 and 3 in the terminal one. For the possible function of this type there are two probabilities:

1) According to Wigglesworth (1953), almost all authors agree that the campaniform sensilla are sensitive to mechanical stimuli. The distribution of the sense organs in the female and male antenna may fit in with this idea, and the following explanation would support it. It is known that the female mosquitoes normally travel upwind, but they take off much more readily when the wind carries host stimuli and, according to the same principle, the males would be expected to react as well in order to reach their source of nutrition such as nectar and plant juices. In this case females and males are almost in equal need of receptor organs for detecting air movements.

The presence of two campaniform sensilla in the terminal end of the antenna with a third one just beneath (one-half of the total number) would be highly satisfactory for such a function. On the basis of the histological studies, if only one of the cells is receptive in function, this would give further support for this possible function.

2) The experimental results when the temperature decreased to $25\text{-}26^{\circ}\text{C}$ and was combined with the body odour and moisture content of 75-85% R.H. showed that the reaction intensity with one segment missing was considerably higher than in the controls. This leads us to think that there could exist a kind of inhibiting sense organ which prevents the mosquitoes from responding to such a lower degree of temperature. The campaniform sensilla having half of its total number on the last segment could be responsible for such changes, but there is no further evidence to support this idea.