

# THE FUNCTION OF THE ANTENNAE IN *RHODNIUS PROLIXUS* (HEMIPTERA) AND THE MECHANISM OF ORIENTATION TO THE HOST

BY V. B. WIGGLESWORTH AND J. D. GILLETT.

(From the Department of Entomology, London School of Hygiene and Tropical Medicine.)

(Received 1st October, 1933.)

(With Five Text-figures.)

ANYONE who has handled the blood-sucking bugs, *Triatoma* or *Rhodnius*, must have observed that they are often attracted to the sides of their jars at places where these have been warmed by recent handling, and that they will probe such spots vigorously with the proboscis. This behaviour suggests that they are attracted to their host mainly by warmth<sup>1</sup>—a belief which is supported by the recent observations of Rivnay (1932) on the bed bug (*Cimex*) and of Hase (1932) on various Triatomidae. Further, the movements of the antennae, which precede the location of the host, suggest that these carry the sense organs concerned; and we were led to undertake the present work because it seemed possible that *Rhodnius* might prove a favourable subject in which to study both the function of the antennae, and the mechanism by which they secure the orientation of the insect in relation to its host. More particularly we hoped to define this mechanism in terms of the current theories of orientation (Loeb, 1918; Kühn, 1919; Fraenkel, 1931).

## GENERAL METHODS.

Most of the experiments have been made in a circular glass vessel (Fig. 1 A), 25 cm. in diameter and 8 cm. deep, with the floor covered with squared paper and the top closed with a disc of stout card. Through the middle of this disc pass two test-tubes, 1.5 cm. in diameter, with their centres 5.5 cm. apart. In front of the test-tubes there is an opening in the cover, through which the insect can be introduced into the vessel. This opening is closed with a glass door, so that the insect may be observed from above. Each test-tube contains water, a thermometer and a U-tube. Their temperature is controlled by passing a stream of hot water through the U-tubes and regulating its rate of flow by means of a screw-clip.

<sup>1</sup> At least at short range, that is, just at the time of feeding. It is possible that they find themselves near their host merely by chance (as suggested by Kemper, 1929, 1932, in *Cimex*), or that they are attracted from a distance by vibrations or other stimuli.

The purpose of this arrangement is to provide standard conditions under which the reactions of the insects can be tested and, meanwhile, to protect them from currents of air, by which they are readily disturbed. The test-tubes provide the source of stimulus. In comparing the response of the insect to two stimuli, it is placed symmetrically in front of the test-tubes with the tip of its head about 4 cm. from each, and its movements recorded.

Fasting adult insects have been used for most of the experiments, because they are more easily controlled and observed than the nymphs and they are more

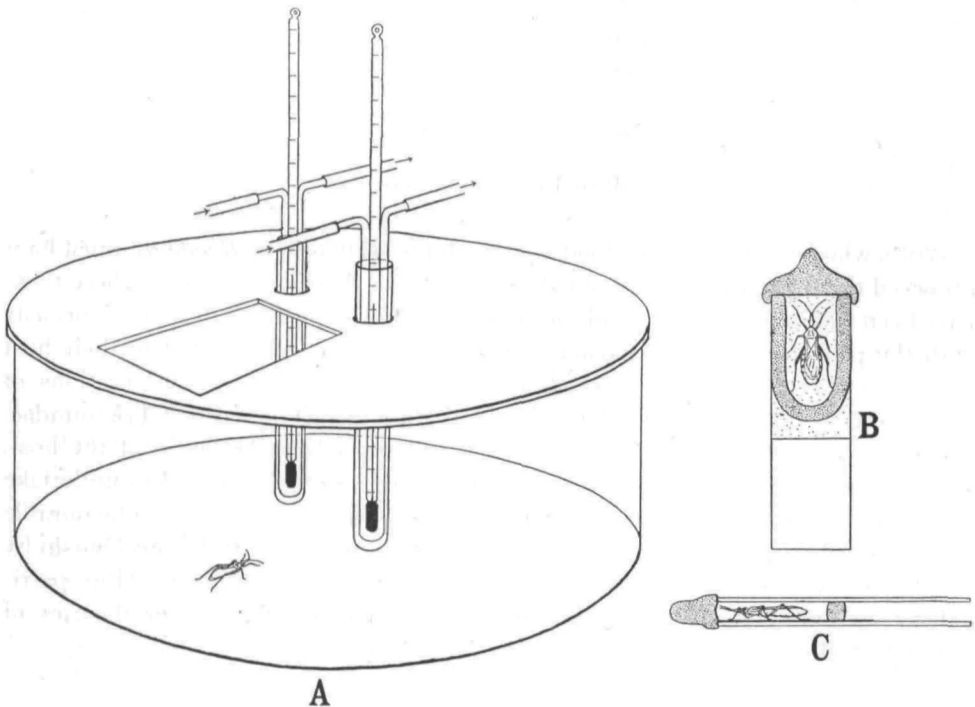


Fig. 1. A, Apparatus for testing the responses of *Rhodnius*. B, C, Plan and sectional view of cell in which the insect is kept before experiment.

easily operated upon. *Rhodnius* are "nervous" insects and are liable to be upset by handling; special methods have therefore been needed to get them into position opposite the test-tubes without disturbing them. For this purpose the small cells shown in Fig. 1 B, C have been used. The floor of the cell consists of a microscope slide covered with blotting paper; the walls and the door are made of plasticine, and the roof of another microscope slide. The insects are transferred to these cells an hour or two before making the experiments. When they have settled down, the cell is placed in position opposite the test-tubes, the plasticine door is removed, and the glass top of the cell is detached, taking with it the plasticine walls and leaving the insect exposed on a little platform of blotting paper.

The insect at rest is normally in a state of sleep or "akinesis" in which it reposes with the body in contact with the ground and the antennae lowered. It is commonly aroused from this state, during the experiment, by the warmth from the test-tubes; it then erects the antennae and rises on its legs with the body well clear of the ground. The insect may be said to have "awakened." This process of "awakening" is a very definite reaction (as has already been noted by Weber (1929) in the louse (*Haematopinus*) and by Rivnay (1932) in the bed bug (*Cimex*)), the insect often waking "with a little jerk," and until it has occurred the normal feeding response cannot be elicited. When the bug does not awake spontaneously, it may be aroused by blowing gently on the antennae or, better, by lightly touching the abdomen with a bristle.

Usually, when the insect has once responded and probed the tube, it is too "excited" to bear a repetition of the experiment without having a period of rest in its cell. But in some cases the same insect may be brought back to the starting-point, and will respond repeatedly; indeed, some of the clearest results have been obtained from such insects. They are best controlled by inverting a glass capsule over them, sliding this into the required position, and removing it when the insect has come to rest.

#### THE NORMAL RESPONSE.

The first response of the insect when placed 3 or 4 cm. from the warm tube is to "awaken"; it raises itself and erects the antennae. It then cleans the antennae by lifting both fore legs and drawing first one antenna and then the other through the small combs on the inner side of the fore tibiae. The antennae are next raised, and lowered, extended outwards, forwards or backwards; the two antennae moving independently, and pausing for a few moments in each position. (The movements recall strikingly the semaphore method of flag signalling.) Finally, the insect advances straight towards the tube, moving the antennae rhythmically up and down; sometimes the antennae move in harmony, sometimes alternately, one being raised as the other is lowered. As soon as one or both antennae touch the tube, the proboscis is extended and pressed vigorously against its surface.

The time occupied by the entire response varies from a few seconds to 20 min. or more. Often, parts of the response are omitted; many insects do not comb the antennae; others will advance at once without going through the "semaphore" movements; and some will extend the proboscis before the antennae actually touch the tube.

The number of fasting insects which will respond in this way varies in an unaccountable manner. The proportion is never great, so that the study of a few insects has taken a long time and the total number of insects studied will appear small. But we have found the observation of a relatively small number of insects under controlled conditions more informative than the general observation of large numbers.

PART PLAYED BY THE EYES, OCELLI, PROBOSCIS AND ANTENNAE  
IN THE NORMAL RESPONSE.

Insects have been blinded by covering eyes and ocelli with a thick coating of black cellulose paint, the proboscis being held extended until the paint is dry. Insects so treated do not run so vigorously as normally, nor are they so readily disturbed by movements. They are, therefore, more easily handled and have been used for many of the experiments. The normal response takes place in them exactly as described, and there is no apparent change in the accuracy with which they can locate the source of stimulus. Many of the insects do, however, show some impairment of the facility with which they can clean the antennae; they raise the legs, but the antennae remain out of reach. After being blinded for a week or so, they usually become adept again at this cleaning process. The converse experiment in which insects with the eyes intact fail to locate the tube although very close to it, will be described later (p. 128).

Insects in which the proboscis has been cut through near the base, also show the normal response; but when they come to the final stage of extending the proboscis, they become confused and agitated and soon cease trying to probe.

On the other hand, insects with the antennae cut off at the base no longer show the normal response. In a typical experiment a *Rhodnius* placed close to the tube at 37° C. responded by probing within a few seconds; after removal of one antenna it probed in 30 sec.; after removal of both antennae it would not respond again.

Observations will be described later (p. 133) which show that under certain circumstances the probing response can be elicited in the absence of the antennae; but the foregoing experiments show clearly that under the standard conditions used, the antennae are the chief and perhaps the sole sense organs concerned in locating the source of stimulus.

THE RESPONSE TO WARMTH ALONE.

Many blood-sucking insects are attracted to their host by the warmth of the body. This is frequently described as a response to radiant heat, but no critical experiments appear to have been carried out to decide whether this is really the case or whether the response is to warm air. Howlett (1910) inclined to the view that in the case of mosquitoes the warm air constituted the effective stimulus. Martini (1917) claims that lice react to radiant heat; but the conditions of his experiments do not exclude a response to warm air.

The question has been tested in the case of *Rhodnius* by having one tube clean and polished, the other covered with lamp-black. Both tubes were kept at the same temperature (ranging from 34 to 39° C.); the relative position of the two tubes was frequently changed, and all the insects used had the eyes blackened.

In one series of twelve experiments on 8 insects: 4 chose the blackened tube, 5 chose the clean tube and 3 failed to locate either. In addition to these, we made a large number of random experiments which were not individually recorded, and in these also the insects showed no preference for either tube.

Now the radiant heat from the blackened tube is many times greater than that from the clean tube, while the conduction and convection of heat from the two tubes will be equal. It is probable, therefore, that the insect is orientated by the warmth of the air and not by the radiant heat.

#### THE RESPONSE TO SMELL ALONE.

To test the response to smell in the absence of warmth, insects were offered the choice of a clean glass tube and a tube covered with a fresh mouse skin<sup>1</sup>, both at room temperature. Adult insects with blackened eyes were used, and they were given 10 min. in which to respond; control experiments being carried out with the same insects, under the same conditions, but with both tubes clean. All the insects were allowed to wake up spontaneously; they were never aroused artificially.

The results were as follows, 10 insects being used:

##### *Out of twenty-three experiments with the skin and clean tube:*

- 12 showed no response at all;
- 9 went through more or less prolonged cleaning movements of the antennae with the front legs, and 2 of these cleaned the proboscis also;
- 9 directed their antennae quite definitely towards the tube covered with skin;
- 3 ultimately walked up to the skin but failed to probe it.

##### *Out of eighteen control experiments with two clean tubes:*

- 14 showed no response at all;
- 4 cleaned legs and antennae for short periods only (never prolonged cleaning of many minutes as in the experimental series).
- None directed the antennae in any definite direction.

The results show clearly that *Rhodnius* can detect the smell of skin, and will respond to this stimulus alone by cleaning the antennae and extending them towards the source of stimulus. (This was observed also by Weber (1929) in the hog louse (*Haematopinus*).) Smell alone (in these experiments) never elicited probing.

#### RESPONSE TO SMELL IN THE PRESENCE OF WARMTH.

The orientating effect of smell in the presence of warmth has been tested in the same way as for smell alone, except that both tubes have been kept at an eq temperature of 35–38° C., the tube without the mouse skin being covered with lamp-black so that it could not be distinguished optically by the unblinded insects from that covered with black mouse skin. The relative position of the tubes was frequently changed. The experiments were performed in four groups.

*Exp. 1.* An early experiment in which the insects were not protected from air currents. They were nearly all "awake" at the commencement of the experiment. All had the eyes blackened.

<sup>1</sup> The insects were normally fed on the rabbit, but they will feed on other warm-blooded animals and man with equal readiness.

*Out of twenty-four consecutive experiments on 6 insects:*

15 went to the skin and probed	}	17 chose the skin.
2 went to the skin but failed to probe		
5 went to the glass and probed	}	5 chose the glass.
0 went to the glass but failed to probe		
2 gave no response.		

*Exp. 2.* Insects with blackened eyes, carefully protected from air currents, and not "awake" at commencement of experiment. If they did not respond they were not artificially aroused.

*Out of thirty-nine consecutive experiments on 15 insects:*

5 went to the skin and probed	}	7 chose the skin.
1 went to the skin but failed to probe		
1 directed the antennae towards the skin		
2 went to the glass and probed	}	3 chose the glass.
1 went to the glass but failed to probe		
26 gave no response.		
3 cleaned antennae but showed no orientation.		

*Exp. 3.* As *Exp. 2*, except that if the insect showed no response it was awakened by touching the hinder end of the abdomen with a bristle.

*Out of ten consecutive experiments on 8 insects:*

1 went to the skin and probed	}	5 chose the skin.
4 went to the skin but failed to probe		
0 went to the glass and probed	}	3 chose the glass.
3 went to the glass but failed to probe		
2 gave no definite response.		

*Exp. 4.* As *Exp. 3*, except that unblinded (and therefore more alert) insects were used.

*Out of sixteen consecutive experiments on 6 insects:*

5 went to the skin and probed	}	10 chose the skin.
3 went to the skin but failed to probe		
2 directed antennae towards the skin		
1 went to the glass and probed	}	3 chose the glass.
1 went to the glass but failed to probe		
1 directed antennae towards the glass		
3 gave no response.		

It is clear from these experiments that the insect is orientated by smell as well as by warmth (a conclusion already arrived at by Hase (1932) and, in the case of *Cimex*, by Rivnay (1932)); but, as was to be expected from the results recorded in the preceding sections, warmth exerts the greater influence.

This was shown still more strikingly in a series of experiments made with unfed and unblinded nymphs about 10 days after hatching from the egg. In these experi-

ments the centres of the tubes were 3 cm. apart and the insect was placed about 1.5 cm. from their surface. The response in the young nymph is much more rapid than in the adult. The insect rarely waits to do any cleaning; the antennae are moved up and down alternately for a few moments; then the insect turns towards one of the tubes and advances straight to it, both antennae moving up and down simultaneously. The whole response is over in a few seconds.

Out of twenty-seven tests made on 6 insects: 13 chose the skin, 13 chose the glass tube and 1 went between the two. Here, obviously, the orientating effect of smell was completely masked by that of warmth.

#### THE RESPONSE TO MOISTURE.

Krijgsman (1930) and Krijgsman and Windred (1930) have shown that the blood-sucking flies *Stomoxys* and *Lyperosia*, besides being attracted to their host by warmth and smell, are attracted also by moisture. Rivnay (1932) has shown that *Cimex* is repelled by moisture. It was desirable therefore to test whether the moisture of the fresh mouse skin was exerting any influence on the results recorded above.

In order to avoid temperature effects, the experiments had to be done at room temperature. They were carried out in the same way as the tests for response to smell alone (p. 124), one tube being covered with clean dry voile, the other with voile moistened with distilled water.

Of the insects tested, none showed any response to either tube. They sometimes moved the antennae vaguely about, but never extended them in any particular direction. Moisture clearly has no attractive influence; but equally clearly it is not repellent, for the insects would repeatedly probe a warm tube covered with moist voile and would even extend the proboscis into warm water exposed on a glass slide.

#### THE RESPONSE IN INSECTS WITH A SINGLE ANTENNA.

A standard procedure for studying the mechanism of orientation by bilateral sense organs is to observe the effect of extirpating the organ on one side (Loeb, 1918; Kühn, 1919). This experiment has been made on *Rhodnius* deprived of one antenna. A single tube, at 37° C., covered with a fresh mouse skin, has been used as the source of stimulus, and the experiments carried out as before. The responsiveness of insects with a single antenna is much reduced, and those insects which show the feeding response under the standard conditions form a very small part of the total used for experiment. Before summarising the types of response obtained, it will be convenient to describe in full two experiments in which the same insect responded a number of times.

In the one experiment (Fig. 2) an insect with blackened eyes, and with the right antenna removed, was placed about 3 cm. directly in front of the tube, and it responded four times. (i) When placed at *a*, after the usual antennal movements it walked forwards, swinging round to the left. At *b* it turned rather sharply to the left, extended the proboscis and probed the air for some time. (ii) When placed at *c*, it ran forwards (not responding) and stopped suddenly at *d*; here it started to respond,

and after moving the antenna up and down, it extended the proboscis. It then walked very slowly forwards, probing the air and swinging round to the left until it reached the tube, which it probed at *e*. (iii) When placed at *f*, it moved the antenna and walked forwards inclining slightly to the left. At *g* it began to swing round more strongly to the left. At *h* it turned very sharply to the left again, and almost at the same moment probed the air. It then moved backwards slowly round the tube, as shown, probing the air at intervals until the antenna came in contact with the tube, which it probed at *j*. (iv) When placed at *k*, after antennal movements it walked

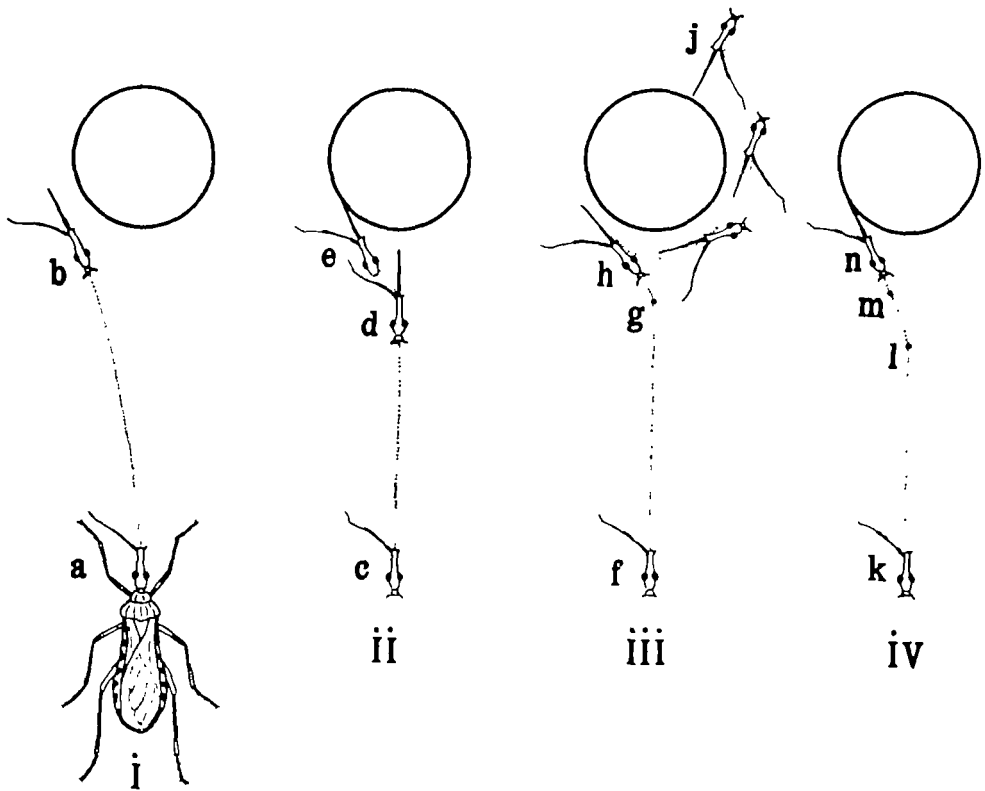


Fig. 2.

straight forwards and at *l* swung slightly to the left; at *m* it began to probe the air; it continued to advance, swinging round still further to the left until its proboscis came in contact with the tube at *n*. The head was definitely flexed to the left from *l* onwards.

In the other experiment (Fig. 3), an insect with uncovered eyes, with the left antenna removed, was placed in various positions in relation to the tube, and it responded five times. (i) When placed at *a*, it moved the antenna up and down for about 1 min., then turned to the right and probed the tube at *b*. (ii) When placed at *c*, it moved the antenna up and down for 4 min., then slowly worked round to the



left with the proboscis extended, until this touched the tube at *d*, when it began to probe. The antenna did not touch the tube. (iii) When placed at *e*, it moved the antenna up and down for 15 sec., then turned to the right, extended the proboscis, and probed the tube at *f*. (iv) When placed at *g*, it moved the antenna up and down for 45 sec., turned to the left with the proboscis extended, and when this touched the tube at *h* it probed. (v) When placed at *j*, after moving the antenna, it walked straight forwards, and when it was very near the tube it extended the proboscis (so that its tip was almost touching the tube) and then swung suddenly round to the right and probed the tube at *k*.

Although this second experiment happened to concern an insect with uncovered

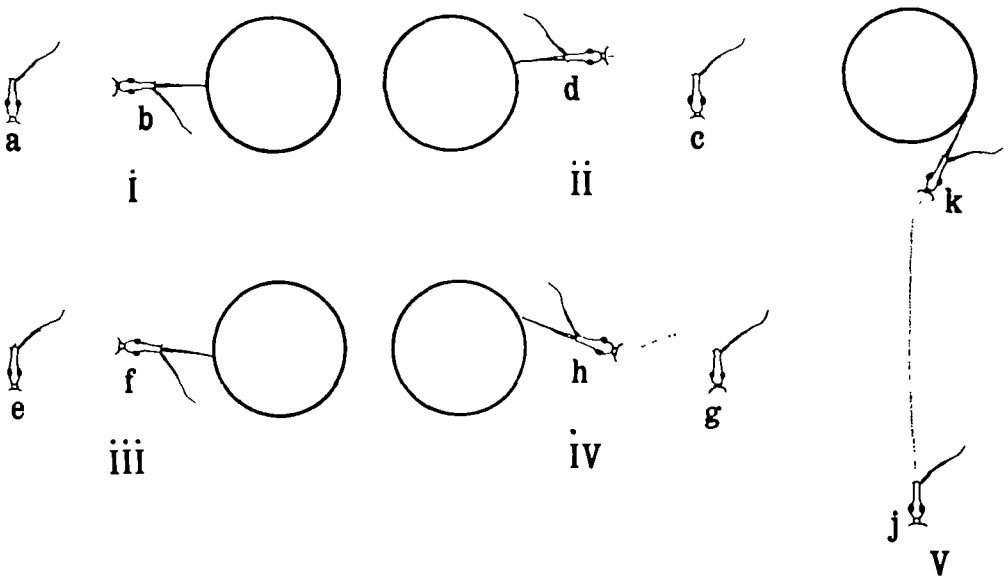


Fig. 3.

eyes, the same responses exactly have been obtained with blinded insects; conversely, the type of response shown in Fig. 2 i, where the insect misses the tube and probes the air, has been obtained with insects that had the eyes uncovered.

The types of reaction obtained in insects with one antenna may be summarised as follows:

(i) As the insect advances, there is a gradual inclination towards the side with the antenna (see Fig. 2 i, iii).

This occurred in 10 cases; the insect walked straight in 3 cases; it inclined towards the side without the antenna in 0 cases.

(ii) As the insect probes, it turns sharply towards the side with the antenna. This movement is often superimposed on a gradual inclination as the insect advances (see Fig. 2 i), but sometimes it occurs in the absence of this (see Fig. 3 v).

This was noted in 9 cases; a sudden turn towards the side without the antenna

occurred in 0 cases. In many cases this sharp turn was not observed; but it is a reaction which could be easily overlooked.

(iii) The insect, placed to the side of the tube with the antenna directed towards it (see Fig. 3 i, iii), turns towards the tube and probes.

The insect turned towards the tube and probed in 8 cases. It turned away from the tube and probed the air in 3 cases.

(iv) The insect, placed to the side of the tube with the antenna directed away from it (see Fig. 3 ii, iv), turns towards the tube and probes.

The insect turned towards the tube and probed in 6 cases. It turned away from the tube in 0 cases.

#### THE MECHANISM OF ORIENTATION.

The attraction of blood-sucking insects to their host by the warmth and smell of the body has often been loosely referred to as a "tropism" (Rivnay, 1932), the term being used in a sense apparently synonymous with "orientation," but without any attempt being made to study the mechanism of this orientation more closely. In recent years most of the suggested mechanisms of animal orientation have been brought together into a single comprehensive theory by Kühn (1919, 1929). It will therefore be convenient to consider which, if any, of Kühn's mechanisms will serve to describe the behaviour of *Rhodnius*.

In the first place, many animals reach their destination without being truly orientated. This may occur in two ways: (i) certain stimuli may have a *kinetic effect* upon the animal and cause it to move at random until, by chance, it enters a region where such stimuli are wanting, and there comes to rest; or (ii) the animal, moving at random, may encounter adverse stimuli which are above or below the optimal intensity; whereupon it shows a reflex "avoiding reaction" and is thereby confined within a zone where the stimuli are optimal. This response Kühn (1919) calls *phobotaxis*. It is obvious that neither of these mechanisms will explain the movements of *Rhodnius* during the feeding response; for these movements are anything but random; they are directed very accurately towards the source of stimulus.

Those movements in which the animal is truly orientated Kühn calls *topotaxis*, and these again fall into two main groups<sup>1</sup>: *tropotaxis* and *telotaxis*. The tropotactic mechanism is synonymous with the "tonus hypothesis" advocated particularly by Loeb (1918), in his later writings, under the name of the "tropism theory<sup>2</sup>"; it implies that the muscular tone on the two sides of the animal's body is proportional to the intensity of stimulus received in bilaterally symmetrical sense organs, and, this being the case, that the animal when it moves is automatically carried towards (or away from) the source of stimulus.

There are two standard methods of proving that orientation is by tropotaxis: (i) when the sense organ on one side is extirpated, and the animal is subjected to the stimulus in question, it moves in a circle towards or away from the intact side;

<sup>1</sup> Kühn's *mnemotaxis* is here excluded.

<sup>2</sup> The terrible confusion that centres around the term "tropism" is discussed by Mast (1915, 1923).

(ii) when the intact animal is subjected to two sources of stimulus, it moves towards a point intermediate between these two sources<sup>1</sup>.

Now it is evident from the behaviour of *Rhodnius*, as described in this paper, that it does not locate its host by tropotaxis to warmth or smell; for when it is offered a choice of two sources of stimuli, it chooses one or the other, and very rarely goes between the two (see p. 125); and when deprived of one antenna it turns towards the source of stimulus whether this be on the normal or the operated side (see p. 128). (To explain the last observation, it might be argued that each antenna is a bilateral sense organ, the right and left surfaces of each determining the tone of the corresponding sides of the body; the insect would then be turned towards the source of stimulus even though deprived of one antenna. Such a point of view might be tenable if the insect were responding to radiant heat, but we have seen (p. 124) that, in fact, it responds to warm air and to smell, and it is difficult to see how these could provide a differential stimulus to the two sides of one antenna.)

It was to explain those cases in which the animal, equidistant from two sources of stimulation, does not advance along the resultant between these attractant forces (as expected on the tonus hypothesis) but chooses one or the other, and advances straight to it, that Kühn (1919) introduced the conception of telotaxis. According to this mechanism the animal "fixes" the one source of stimulus with its sense organs, and advances towards it so that a certain region of the receptor apparatus is always acted upon by the chosen stimulus, other sources of stimulus being disregarded. This conception was introduced primarily to explain orientation to visual stimuli; it comes very close to the theory elaborated independently by Mast (1923), according to which the photic orientation of insects is "the result of a series of reflexes specifically related to the location of the stimuli in the eyes."

It has been argued by Warnke (1931) that this mechanism is not applicable to antennal stimulation, because there can be nothing in the antenna to correspond with the "point of clearest vision" or the "fixative reflex" which form the basis of the telotactic response. But the antennae of *Rhodnius* are mobile structures; in the early stage of the response they are moved and extended in each direction in turn, and the condition of maximal stimulation will result when both antennae are extended towards one or other source of stimulus. And if the insect then moves with the antennae so extended, it must go in a straight line to that source. That is what *Rhodnius* does.

This mechanism can be most simply described as a *reflex pursuit of the antennae into the region of optimal stimulation*. It comes very close to the telotactic mechanism of Kühn (1929) which is defined as a series of reflexes, begun and ended by the localisation of the stimulus on the sensory surface. Like the telotactic mechanism, it will explain both the choice of one out of two sources of stimulus, and the location of the source of stimulus after extirpation of the sense organ on one side.

The whole response may, in fact, be regarded as a "chain of reflexes"; the initiation of the response being conditioned by the physiological state of the insect,

<sup>1</sup> It may be noted in passing that Mast (1923) and Clark (1931) have shown that both these reactions may be explained upon a reflex theory without invoking effects on muscle tone.

and each succeeding reflex being conditioned by the reaction which has preceded it<sup>1</sup>.

We have seen (p. 128) that the insects with one antenna, as they advance towards the source of stimulus, commonly incline towards the intact side. Superficially this looks like "tropotaxis"; but if the insect normally "follows its antennae" into the zone where the stimulus is strongest, it is not surprising that in the absence of one antenna it should incline slightly towards the side on which the antenna remains; just as Brecher (1929) observed that cockroaches, trained to turn to the left in a maze, almost invariably go to the right after removal of the left antenna<sup>2</sup>.

We have seen also (p. 128) that at the climax of the response, at the moment when the proboscis is extended, the insect often makes a sharp turn towards the intact antenna, and occasionally the head is flexed in the same direction. Whether this final turn is due to a sudden general increase in tone on the one side, that is, whether it is to be explained on the muscle tonus hypothesis, or whether it is a purposive reflex movement (comparable with the scratch reflex of higher forms, or the response of *Eristalis* to light as explained by Mast (1923)), cannot be decided from the data available.

*Orientation of other insects by the antennae.* The mechanism of orientation by means of the antennae has been comparatively little studied. Barrows (1907) observed circus movements in *Drosophila* with a single antenna, and described this as a "tropism" response—meaning that it is caused by unequal stimulation of bilateral sense organs, but *not* implying that it is due to a direct effect on the muscle tonus of the effector organs. Kellogg (1907), discussing the circus movements of male silkworm moths with one antenna, in the vicinity of the female, is equally non-committal, but seems to imply a reflex movement towards the side with the antenna. Schaller (1926) describes how the water beetle (*Dytiscus*), in finding an object by smell, feels about with its antennae until these are directed towards the source of stimulus, that is, until they are both most strongly stimulated, and then swims forward. He does not attempt to explain this behaviour in terms of mechanistic physiology. Glaser (1927) describes how, when a piece of cheese is held near the head of a cockroach, the antennae follow its movements "like the pursuit of a magnet by a piece of iron." Murr (1930) concludes that the parasitic wasp (*Habrobracon*), which finds its prey (the larva of *Ephestia*) by smell, is orientated mainly by phobotaxis (though there is no evidence of any "avoiding reaction"); but since this insect moves in a straight line during the last few centimetres of its approach, and since the insect with one antenna turns more frequently towards that side than the other, she concludes that tropotaxis is superimposed on phobotaxis when the stimulus is strong. Valentine (1931) describes circus movements in the male mealworm beetle (*Tenebrio*) with one antenna, in the presence of the female, but does not discuss the nervous mechanism of this response. Finally, Warnke (1931) has studied in great detail the mechanism of orientation of the dung beetle (*Geotrupes*) in locating dung.

<sup>1</sup> This is well illustrated by the following observation. Normally, if the antenna of *Rhodnius* is touched by a cold object it is quickly withdrawn and the insect retreats. But if touched by such an object while the insect is advancing towards a source of stimulus, the proboscis is at once extended.

<sup>2</sup> As Brecher remarks, "*P. americana* läuft ihrer Antenne nach."

His conclusions are similar to those of Murr; that when the stimulus is weak the beetle is directed by phobotaxis (although there is no evidence of the "avoiding reactions" demanded by the phobotactic mechanism), but that when the stimulus is strong, that is when the insect is close to the dung, it is orientated by "tropotaxis." He notes that insects with a single antenna usually (in about 75 per cent. of cases) turn towards that side as they approach the dung; but this is not always so; many of them still advance in a straight line, and he explains this by invoking the "effort" ("Bestreben") of the insect to reach the source of smell. On this goal-seeking effort is superimposed the tropotaxis, and this, when there is only one antenna, tends to draw the insect to one side as it advances.

In all these insects, the behaviour observed is more or less similar to that of *Rhodnius*, and all the cases could be explained upon the same mechanism as we have proposed: a reflex pursuit of the antennae, or, in other words, a special form of telotaxis. Where an attempt has been made to explain the behaviour by random movement supplemented by tropotaxis (Murr, Warnke), it has been necessary to introduce the factor of volition ("Bestreben," "Reizsuchung"). This, of course, is perfectly legitimate; indeed, from the psychological standpoint, all these reactions can be adequately described as typical goal-seeking or conative behaviour; but to introduce such psychological conceptions into the mechanistic theory of animal orientation is to bring back the very elements which that theory has been devised to eliminate.

#### BEHAVIOUR OF *RHODNIUS* DEPRIVED OF BOTH ANTENNAE.

Further light has been thrown on the functions of the antennae in *Rhodnius* by comparing the general behaviour of normal insects with that of insects without antennae. Series of normal insects have been placed separately in Petri dishes with a floor of filter paper, and compared with a corresponding series of antenna-less insects.

Immediately after amputation of the antennae there is no obvious difference between the natural movements of the normal and the operated animals. An hour or two later, when all have settled into a state of sleep or "akinesis," those without antennae are definitely more torpid. The normal insects are readily awakened or caused to start by slight currents of air; those without antennae give no response even when blown upon strongly.

This shows that the antennae are sensitive to air currents, and that air currents are one of the chief stimuli which alarm *Rhodnius*, awaken it, and bring it into a responsive state. (We did not obtain any evidence that air currents themselves had any orientating effect, such as was observed by Warnke (1931) in the dung beetle *Geotrupes*, but *Rhodnius* did not prove amenable to suitable experiments.)

But it is not only to stimuli normally perceived by the antennae that the antenna-less insects are refractory. The normal insect when asleep is readily disturbed by vibrations, and if the hind end of the abdomen is touched with forceps, it usually runs rapidly away. The antenna-less insect is often most difficult to arouse by

either of these stimuli; even if the abdomen is strongly pinched with forceps, it will only take a step forwards and then settle down again. On the other hand, the antenna-less insect can ultimately be aroused, but even then its movements are less active than those of the normal insect.

This torpor cannot be a "shock" effect caused by the amputation of the antennae; for it is not apparent immediately after the operation, nor does it occur when wings, legs or proboscis are cut off. Both v. Frisch (1921) and Schaller (1926) have emphasised the complete absence of any shock effect when the antennae of insects are amputated.

Clearly, an important function of the antenna in *Rhodnius* is a "kinetic function," to keep the central nervous system in such a state that it will respond readily to stimuli (what is often unfortunately called a state of "tone"). Air movements probably provide the chief stimuli concerned in this function.

It has been observed by Brecher (1929) that removal of the antennae in the cockroach lowers the threshold for stimulation of the photo-receptors; and this observation finds a parallel in the very striking response shown by antenna-less *Rhodnius* towards moving objects. After being aroused by repeated stimulation, the antenna-less insect will often follow an object, such as a pencil, in every direction—so mechanically, sometimes, as to resemble a compass needle following a magnet. If the pencil is brought to rest for a moment, the insect rushes at it with the proboscis extended. It will sometimes follow and probe at normal insects moving near it, and will often walk round the Petri dish, probing at its reflection in the glass. This behaviour is not shown by normal insects, which are alarmed by a pencil moved near them and retreat from it, as indeed do antenna-less insects sometimes.

The pursuit of moving objects is a common phenomenon among insects (Baldus, 1924) and is believed to depend upon the "fixation reflex," the insect tending always to keep the image of the object that has attracted attention upon the corresponding point of the retina in both eyes. It is probable, therefore, that the response is latent in normal *Rhodnius*, but that it cannot be elicited so readily as in those deprived of antennae because they are distracted and alarmed by incidental stimuli. That this view is correct was shown in the following way. Normal insects were placed in a jar with folded blotting paper, upon which they rested, standing vertically in it. A ball of red wax about 1.5 cm. in diameter was suspended from a thread and allowed to swing to and fro above the blotting paper. Several insects were attracted by it, advancing to it and probing; while some probed the surface of the blotting paper as they moved forward. (A comparable "release" of visual responses, following extirpation of the antennae, is seen in the case of homing bees, which, if their hive is displaced, normally collect in a swarm at the site it previously occupied; whereas if they are deprived of their antennae, they make straight for the hive in its new position (Bethe, 1898; Wolf, 1926).)

The antenna-less insect placed on the hand makes no response. If a pencil is moved in front of it, it runs after it and extends the proboscis. If, in the course of the pursuit, the tip of the proboscis chances to touch the skin, it stops and begins to probe and will suck blood. Once it has begun to probe the skin, it will pay no further

attention to moving objects; but if the proboscis is forcibly removed from the skin it will again run after the pencil as before.

This experiment, which can often be repeated many times with the same insect, shows that in the antenna-less insect the feeding response is elicited more readily by movement than by warmth or smell. It is interesting to consider whether this response, latent in the normal insect, may not reflect the predaceous ancestry of *Rhodnius*, for it is likely that the Reduviidae, to which *Rhodnius* is related, hunt mainly by sight.

It is uncertain whether any response to warmth and smell persists after removal of the antennae. The antenna-less insect at rest upon the hand may, very rarely, extend the proboscis without any movement near it. But antenna-less insects are very prone to extend the proboscis without apparent cause; perhaps as the result of distant visual stimuli. On the other hand, Minnich (1929) and Abbott (1932) have shown that extension of the proboscis in various insects can be brought about by chemical stimulation of the legs, and of other parts of the head besides the antennae; and *Rhodnius*, in common with other Hemiptera (v. Rath, 1888), has a few sensilla at the tip of the proboscis which, on structural grounds, are regarded as chemoreceptors.

Antenna-less insects with the eyes blackened, placed on the hand, do not show any response. But if the skin is scratched with forceps close to them, they will sometimes extend the proboscis and probe the skin; and sometimes they will probe whatever they are resting upon if this is lightly tapped.

These experiments show that the feeding response in *Rhodnius* may be elicited by visual stimuli and by vibration; and although in the normal insect (under the standard conditions we have used in our experiments) these factors are masked by the effects of warmth and smell acting upon the antennae, it is possible that all these stimuli may play a part in the free-living insect in attracting it to its host from a distance. In this our results agree with the observations of Minnich (1929), who has shown that the proboscis response in butterflies may be brought about by many factors: currents of warm, moist air, or mechanical stimuli, or chemical stimuli acting upon the antennae or the tarsi, or visual stimuli, or various internal stimuli; some of these becoming effective only through association. And Nash (1930) has shown that in the tsetse fly (*Glossina*), although the antennae are usually necessary to call forth the probing response, if the insect is very hungry it will probe in the absence of antennae.

#### THE STRUCTURE OF THE ANTENNAE AND THEIR SENSILLA.

The structure of the antennae was studied in the hope that the different types of sensilla might have a different distribution, and that it might thus be possible to study the function of each by cutting the antennae at different levels. But all the types proved to be generally distributed, and only indirect evidence of the function of each can be produced.

The antenna (Fig. 4 A) consists of four segments (not counting the minute intercalary segments in the flagellum): a stout scapus and a very long pedicellus,

which together comprise almost half the antenna, and two flagellar segments. The pedicellus bears stout feathered bristles, like other parts of the body surface, and a few long hairs; internally, at its apex, it has a well developed Johnston's organ (Fig. 4 B). The first flagellar segment in its proximal third resembles the pedicellus, but in the distal two-thirds the cuticle is pierced by innumerable trichoid sensilla. The second flagellar or terminal segment resembles the distal part of the first flagellar segment (Fig. 4 C).

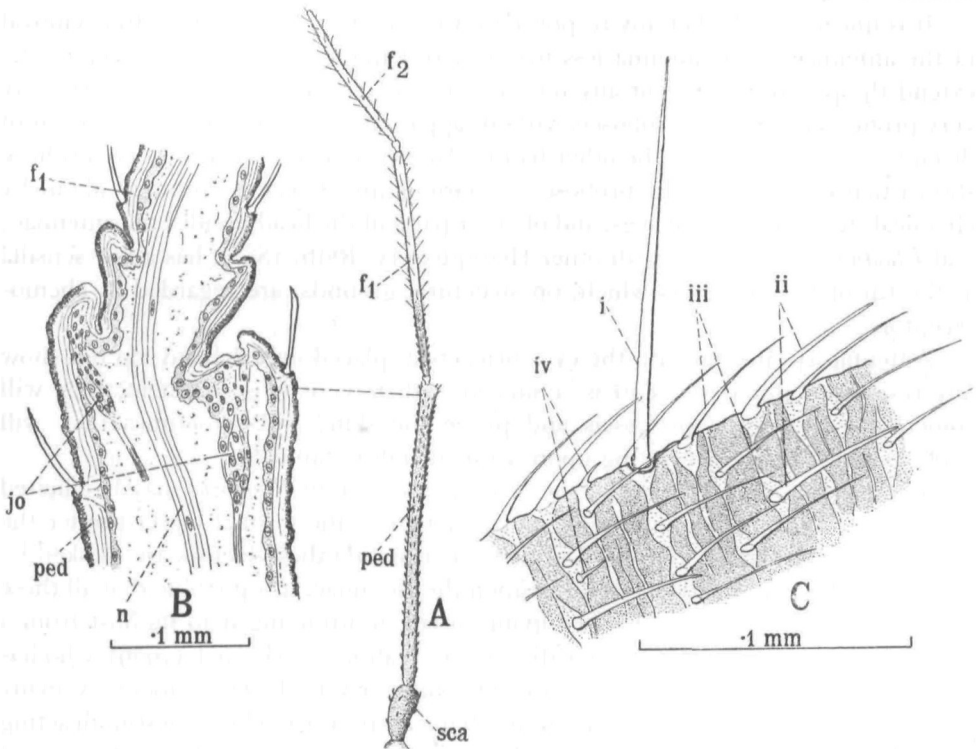


Fig. 4. A, Antenna of *Rhodnius*. B, Longitudinal section of distal end of pedicellus to show Johnston's organ. C, Part of terminal segment of antenna.  $f_1$ ,  $f_2$ , first and second flagellar segments;  $jo$ , Johnston's organ;  $n$ , antenna nerve;  $ped$ , pedicellus;  $sca$ , scapus; i, ii, iii, iv, the four types of sensillum.

The sensilla present in the flagellar segments are of four types. Type i are relatively large bristles, slightly divided at the tip, arising from a distinct socket, and projecting well out from the antenna. Type ii are fine curved structures very much smaller than the last, rounded at the tip, lying close to the surface of the antenna, and not articulated at the base. Type iii are very like type ii in general form and size, but they are somewhat more slender and they end in a sharp point; this is the most numerous type. Type iv are like type iii in thickness, but only about one-fifth their length; they are very sparse.

The structure of the sensilla has been studied in celloidin and paraffin sections  $3\mu$  to  $7\mu$  in thickness.



Fig. 5 A shows type i. The bristle is thick-walled and rigid. Two large cells lie at its base; of these one is presumably the trichogen cell, the other the socket-forming or tormogen cell (Wigglesworth, 1933) sometimes called the membrane cell (Snodgrass, 1926). Running from the margin of the socket is a fine filament which passes through the trichogen cell, enlarges somewhat, and leads to a rather large cell, presumably a bipolar nerve cell.

Fig. 5 B shows type ii. It is an exceedingly thin-walled hollow structure which evidently contains fluid during life, for in sections the contents are faintly staining and vacuolated. At the base there is a very large "glandular cell" (homologous

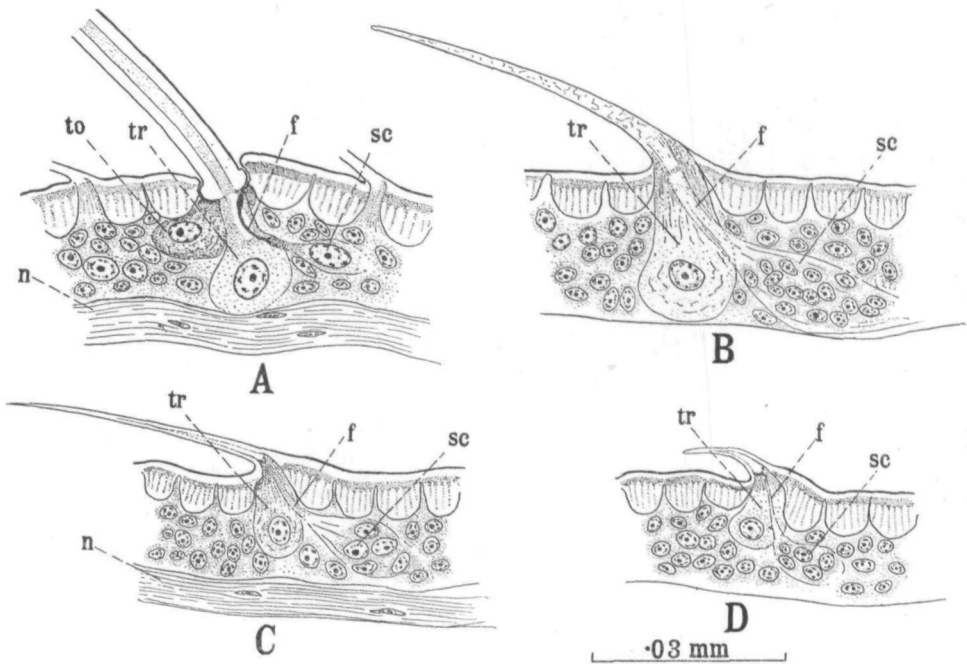


Fig. 5. Longitudinal sections through sensilla on flagellar segments of antenna. A, Type i. B, Type ii. C, Type iii. D, Type iv. *f.* distal filament from sense cells; *n.* antennal nerve; *sc.* sense cells; *to.* tormogen, socket-forming or membrane cell; *tr.* trichogen or glandular cell.

presumably with the trichogen cell) which extends into the cavity of the sensillum, and a large fusiform group of about fifteen nerve cells, which also give off delicate filaments running into the sensillum. The nerve comes off from this fusiform mass, but the exact relation of the individual nerve fibres to the individual cells has not been worked out. This type has no socket, and no tormogen cell can be detected at its base.

Fig. 5 C shows type iii. Though very slender it is relatively thick-walled with only a very small central cavity. The same cellular elements are present as in type ii, but the "gland cell" is much smaller, and the group of nerve cells far fewer, numbering only five or six. Type iv differs from type iii only in the size and shape of the bristle; the cellular elements are the same.

We have seen that *Rhodnius* perceives with its antennae contact, air movements, smell and warmth. There is no doubt that type i sensillum is that responsible for perceiving contact; for it projects far beyond the others and effectively protects them from contact with outside objects (Fig. 4 A). If the antenna of a living insect (suitably attached to a glass slide) is observed under the microscope, and a small glass rod brought in contact with it, the antenna is withdrawn immediately the rod touches the type i sensillum, and when it is still remote from the other types.

Possibly type i serves also for the perception of air movements; but it is more likely, as suggested by Eggers (1924), that the Johnston's organ at the apex of the pedicellus is responsible for this function. The pedicellus in *Rhodnius* is exceptionally long, and the flagellar segments are very light and delicate—features which should make the Johnston's organs in this insect particularly efficient receptors for air movements. Weber (1930) has noted the extreme sensitivity to air currents in the antennae of *Reduvius personatus*, which is allied to *Rhodnius*, and has suggested that here the Johnston's organ subserves a "Ferntastsinn" on the borderline between touch and hearing.

The fact that type ii sensillum is very thin-walled and is provided with a large "glandular cell" and a massive clump of nerve cells, makes it highly probable that this type is olfactory. Its structure agrees closely with that of the sensilla trichodea olfactoria and the sensilla basiconica as described by Vogel (1923) in bees and wasps, and regarded by him as olfactory organs.

The great abundance of type iii, combined with the remarkable sensitivity of the antennae to warmth, suggests that this type may perceive thermal stimuli; but we have no other evidence for this, nor for the function of type iv. (The thermal sense of the bugs *Pyrrhocoris* and *Lygaeus* was shown by Herter (1924) to be located chiefly in the antennae, and that of Collembola was shown by Strebelt (1932) to be similarly localised; but neither of these authors throws any light on the receptor organs concerned. Cappe de Baillon (1932) has described a sense organ, in the antennae of certain Phasmids, specifically adapted to thermal impressions. This organ is devoid of hairs, and consists simply of a mass of sense cells below specialised cuticle.)

#### SUMMARY.

*Rhodnius prolixus* is attracted to its host from short range mainly by the warm air diffusing from it, but partly by the smell of the skin. No evidence was obtained of either attraction or repulsion by moisture.

The olfactory and thermal senses reside chiefly in the antennae, which serve also to perceive air currents and contact. Under the conditions employed in our experiments, the location of the source of stimulus seems to be effected solely by the antennae, the eyes playing no part.

In the presence of two sources of stimulus, *Rhodnius* chooses one or the other and does not make for a point between the two. After removal of one antenna, it is still able to locate the source of stimulus in whatever direction this may lie. These

observations are not compatible with orientation by the muscle tonus mechanism or tropotaxis.

The direction of the source of stimulus is usually inferred only after the antennae have been extended in every direction in turn, and it is suggested that orientation consists in a reflex pursuit of the antennae into the zone of optimal stimulation. This mechanism comes closest to the telotaxis of Kühn, or to the co-ordinated reflex mechanism of Mast. But it is pointed out that the factor of volition has not been definitely excluded.

After removal of both antennae, *Rhodnius* becomes inert and torpid, showing that these have a "kinetic" function. In the antenna-less insects, the feeding response can be readily elicited by moving objects, which are actively pursued. In antenna-less insects with the eyes covered, the feeding response may be elicited by vibration. Vision and vibration may therefore be accessory factors in enabling the normal insect to find its host.

The structure of the antennae and their sensilla is described.

#### REFERENCES.

- ABBOTT, C. E. (1932). *Ann. Ent. Soc. Amer.* **25**, 241.  
 BALDUS, K. (1924). *Zeitschr. f. wiss. Zool.* **121**, 557.  
 BARROWS, W. M. (1907). *Journ. Exp. Zool.* **4**, 515.  
 BETHE, A. (1898). *Arch. f. ges. Physiol.* **70**, 15.  
 BRECHER, G. (1929). *Zeitschr. f. vergl. Physiol.* **10**, 495.  
 CAPPE DE BAILLON, P. (1932). *C. R. Acad. Sci.* **195**, 557.  
 CLARK, L. B. (1931). *Journ. Exp. Zool.* **58**, 31.  
 EGGERS, F. (1924). *Zeitschr. f. Morphol. u. Ökol. Tiere*, **2**, 259.  
 FRAENKEL, G. (1931). *Biol. Rev.* **6**, 36.  
 v. FRISCH, K. (1921). *Zool. Jahrb. Abt. allg. Zool. u. Physiol.* **38**, 449.  
 GLASER, R. W. (1927). *Psyche*, **34**, 209.  
 HASE, A. (1932). *Zeitschr. f. Parasitenk.* **4**, 585.  
 HERTER, K. (1924). *Zeitschr. f. vergl. Physiol.* **1**, 221.  
 HOWLETT, F. M. (1910). *Parasitology*, **3**, 479.  
 KELLOGG, V. L. (1907). *Biol. Bull.* **12**, 152.  
 KEMPER, H. (1929). *Zeitschr. f. Desinfektion*, **21**, 1.  
 — (1932). *Zeitschr. f. Gesundheitstechnik u. Städtehygiene*, **24**, 379.  
 KRIJGSMAN, B. J. (1930). *Zeitschr. f. vergl. Physiol.* **11**, 702.  
 KRIJGSMAN, B. J. and WINDRED, G. L. (1930). *Zeitschr. f. vergl. Physiol.* **13**, 61.  
 KÜHN, A. (1919). *Die Orientierung der Tiere im Raum*. Jena.  
 — (1929). *Handbuch d. normalen u. pathologischen Physiol.* **12**, i, 17.  
 LOEB, J. (1918). *Forced Movements, Tropisms, and Animal Conduct*. Philadelphia  
 MARTINI, E. (1917). *Zeitschr. f. angew. Entom.* **4**, 34.  
 MAST, S. O. (1915). *Arch. f. Entw.-Mech.* **41**, 251.  
 — (1923). *Journ. Exp. Zool.* **38**, 109.  
 MINNICH, D. E. (1929). *Zeitschr. f. vergl. Physiol.* **11**, 1.  
 MURR, L. (1930). *Zeitschr. f. vergl. Physiol.* **11**, 210.  
 NASH, T. A. M. (1930). *Bull. Ent. Res.* **21**, 201.  
 v. RATH, O. (1888). *Zeitschr. f. wiss. Zool.* **46**, 413.  
 RIVNAY, E. (1932). *Parasitology*, **24**, 121.

- SCHALLER, A. (1926). *Zeitschr. f. vergl. Physiol.* **4**, 370.  
SNODGRASS, R. E. (1926). *Smithsonian Misc. Coll.* **77**, No. 8.  
STREBEL, O. (1932). *Zeitschr. f. Morphol. u. Ökol. Tiere*, **25**, 31.  
VALENTINE, J. M. (1931). *Journ. Exp. Zool.* **58**, 165.  
VOGEL, R. (1923). *Zeitschr. f. wiss. Zool.* **120**, 281.  
WARNKE, G. (1931). *Zeitschr. f. vergl. Physiol.* **14**, 121.  
WEBER, HEINZ (1929). *Zeitschr. f. vergl. Physiol.* **9**, 564.  
WEBER, HERMANN (1930). *Biologie der Hemipteren*. Berlin.  
WIGGLESWORTH, V. B. (1933). *Quart. Journ. Micr. Sci.* **76**, 269.  
WOLF, E. (1926). *Zeitschr. f. vergl. Physiol.* **3**, 615.