Sensory physiology of the Human Louse.
WIGGLESWORTH.

THE SENSORY PHYSIOLOGY OF THE HUMAN LOUSE PEDICULUS HUMANUS CORPORIS DE GEER (ANOPLURA)

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(With 35 Figures in the Text)

CONTENTS

INTRODUCTION

DESCRIPTIONS of the natural history of *Pediculus* (Hase, 1915, 1931; Nuttall, 1917, 1919; Alessandrini, 1919; Buxton, 1939) include a number of scattered observations and experiments on sense organs and behaviour; but, apart from its responses to temperature, the sensory physiology of this insect has never been systematically investigated. In the case of the pig louse, *Haematopinus*, a rather more detailed study has been made by Weber (1929). Later in this paper some of these earlier observations will be discussed in greater detail, but here we may set out briefly the main conclusions reached.

The louse is sensitive to *temperature*: it will pursue a tube of warm water (Martini, 1918), and placed in a temperature gradient it spends most of the time in the region between 25 and 33° C. with a peak at about 29° C. (Martini, 1918; Homp, 1938). *Haematopinus* shows a similar preferred temperature of 28·6° C. (Weber, 1929). Some authors have claimed that the louse has no sense of *smell* (Nuttall, 1917). But *Pediculus* is attracted to the finger even at an air temperature of 36° C. (Martini, 1918) and to cotton-wool impregnated with sweat from the axilla (Pick, 1926); and Weber (1929) showed that *Haematopinus* is repelled by the smell of cedar-wood oil, that it will respond to the finger in preference to an equally warm glass rod and will chose a pig before a dog or a warm oven. There is no experimental evidence in regard to *humidity*, but Nuttall (1917) ascribes the tendency for lice to leave their host in the summer, or during fever, at least in part to the greater humidity of the climate beneath the clothing. *Haematopinus* settles into a state of sleep or akinesis much more readily on a rough surface—an example of thigmotaxis subserved by a sense of *contact*; it is aroused from this state by the vibrations of a tuning fork (Weber, 1929). A definite preference for rough materials is shown by the egg-laying female of *Pediculus* (Hase, 1915; Nuttall, 1917). Both *Pediculus* and *Haematopinus* (Weber, 1929) show an apparent geotaxis; they tend always to climb upwards. But this is probably due merely to the mechanical action of the abdomen (Weber, 1929). As regards *vision*, most authors are agreed that *Pediculus* (Hase, 1915; Bacot, 1917; Nuttall, 1917, 1919) and *Haematopinus* (Weber, 1929) are photonegative and move away from a source of light— though it has sometimes been claimed that this reaction is reversed in the hungry louse (Hase, 1915). *Haematopinus* in a state of akinesis is aroused if exposed to alternate light and shade; and when this louse is moving it may be arrested (akinesis) by sudden exposure to a bright light (Weber, 1929).

What little is known about the sense organs and the mechanism of orientation will be discussed later in this paper.

GENERAL METHODS

The body louse lives normally in the dark on the more or less rough inner layers of the clothing in contact with the warm skin. Under these conditions it doubtless spends the greater part of its life at rest. But in order to show

orientating responses the louse must be moving and it must be visible. The experimental conditions are to that extent abnormal; but there can be little doubt that responses obtained under these abnormal conditions will occur equally in nature.

The method of experiment has consisted in placing the louse in a small circular arena so arranged that one half differs from the other half in a single factor at a time. In most of the experiments the insects have been observed singly: their tracks have been copied on a sheet of paper alongside the apparatus, the position of the louse being marked at 30 sec. intervals. From such tracks it is possible to compare the relative lengths of time spent in either half and to determine whether this is due to the insect (i) coming to rest or moving more
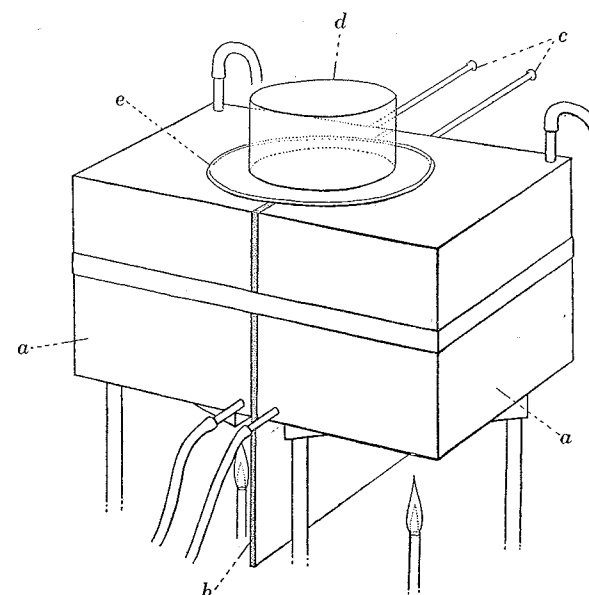

Fig. 1. Explanation in text.

slowly on one side, (ii) changing direction more frequently, or (iii) consistently avoiding one side.

This method has been employed for studying the responses to humidity in *Porcellio* (Gunn, 1937), *Locusta* (Kennedy, 1937), *Blatta* (Gunn & Cosway, 1938), *Culex* (Thomson, 1938) and *Tenebrio* (Pielou & Gunn, 1940) and in studying temperature responses in *Culex* (Thomson, 1938).

The apparatus used is shown in Fig. 1. It consists of two cubical metal containers (*a*) with a side of 15 cm. separated by an asbestos sheet (*b*) 2 mm. thick. Warm or cold water can be passed through the containers or they can be heated from below. Thermometers (*c*) record the temperature of the water immediately below the roof. The arena (*d*) has glass walls and is usually 9 cm. in diameter. The floor is usually of voile stretched on a metal ring (*e*). Except

in the experiments on temperature responses, the arena rests upon one of the containers only, and this is heated to give a temperature on the floor of the arena of about 30° C. Except in the experiments on light responses, the apparatus is exposed to diffuse daylight. Further details will be given as each factor in the environment is dealt with in turn.

Behaviour of the louse in a uniform arena

Most of the experiments have been made on well-nourished adult body lice of both sexes taken directly from breeding capsules worn next to the skin (Buxton, 1939). Hungry lice are sluggish in their movements and sometimes interrupt their course to probe the warm floor of the arena. If females which have not recently had an opportunity of laying eggs are used, they frequently attempt to insinuate themselves between the wall and floor of the arena. Occasionally insects, either fed or unfed, will soon come to rest; but most of the
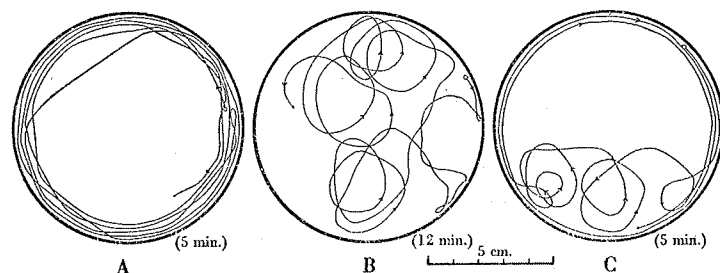

Fig. 2. Tracks followed by lice in a uniform arena.

lice used have continued to crawl without interruption for half an hour or more. Even at the same temperature of 30° C. and with the same voile floor, the rate of movement of different individuals may vary from about 6 to 30 cm. per minute.

The interpretation of the results depends on a knowledge of the behaviour of the louse in a uniform arena. Fig. 2 shows examples of the tracks obtained.

(i) Fig. 2A is the usual type. The louse walks more or less in a straight line; it collides repeatedly with the glass walls, so that the track makes a series of chords in the circle. These chords are usually so short that the track is practically parallel with the circumference;[1] occasionally they cut across the middle of the arena.

(ii) A few insects show a bias towards one side or the other. These follow a spiral course making a series of circles in one direction (Fig. 2B). In some this behaviour is only temporary; but in others it may persist for several days or perhaps permanently. The diameter of the circles varies with the strength of the bias.

(iii) If an insect with a weak left handed bias, for example, moves in a clockwise direction round the arena, it will be prevented by the wall from

[1] In copying these tracks they are shown for the sake of clearness as concentric lines.

turning to the left and will then follow a course around the circumference (Fig. 2C).

REACTIONS TO TEMPERATURE

Method

The two containers (Fig. 1) are brought to the required temperatures and the voile floor of the arena, stretched on a wire ring, placed half on one and half on the other. The arena is open above; its glass walls are 4·5 cm. high; the diameter 9 cm. It rests so that the division between the two containers lies in one diameter. The temperature of the floor is measured by means of a thermocouple resting lightly on the voile.

In most experiments the temperature on one side has been kept at that of the normal environment between the clothes and the skin, 29–30° C.; and the response to temperatures above and below this studied.
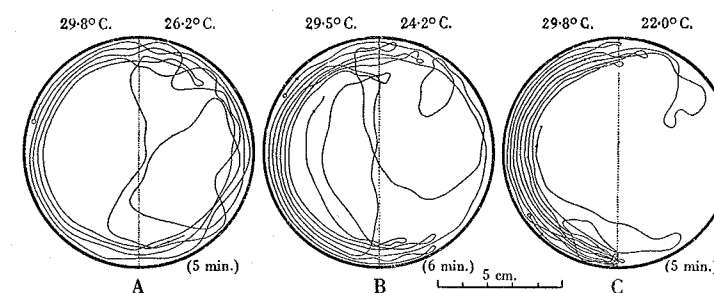

Fig. 3. Tracks followed by a single louse as the temperature in one half of the arena was progressively lowered.

Reactions to alternative temperatures

Some individuals may be indifferent to temperatures as high as 39° C. or as low as 20° C. But these are exceptional. Most show well-marked responses to the change from 30 to 34° C. or from 30 to 25° C.

Fig. 3 shows the reactions of a single louse as the temperature in one half of the arena was progressively lowered. In each case it followed a straight course on the warm side. On passing into 26·2° C. (Fig. 3A) its track was more convoluted and it often turned towards the middle of the arena. On passing into 24·2° C. (Fig. 3B) the reaction was more pronounced and it generally turned back into the warm side after going a short distance. When exposed to 22·0° C. (Fig. 3C) it scarcely crossed the boundary.

Fig. 4 shows some typical reactions of different individuals to rising temperature. Fig. 4A shows the response to 31·8° C. This was the lowest temperature at which an undoubted response was obtained; most individuals were indifferent to this change. Like that to a slight fall in temperature (Fig. 3A) the response shows itself in the tendency of the insect to turn into the arena and to pursue a slightly more convoluted track. Fig. 4B shows a fairly

common type of response to a higher temperature, 35·0° C. The louse follows a straight course at 30° C.; an exceedingly convoluted course at 35° C. Such an insect will spend a far longer time on the adverse side. Fig. 4C shows the usual response to temperatures of 35° C. or higher; the louse turns back instantly on crossing to the warm side. Even where the response fails to cause turning back it may be apparent in the jerky hesitating movements of the insect on entering the adverse side and in occasional convolutions in the trail.

The louse often responds best at the outset and later becomes indifferent (we shall find the same phenomenon in responses to humidity, contact and light). This was well shown in early experiments in which six lice were put together into the arena and with the aid of a stop watch a continuous record made during 10 min. of the number of lice on each side. Offered a choice of 29 and 21° C., out of a total of sixty "louse-minutes" 56·2 were spent at 29° C.,
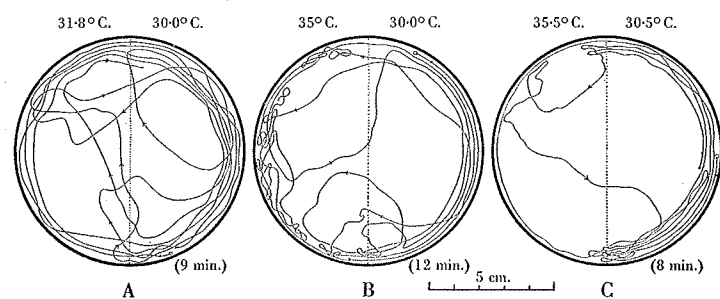

Fig. 4. Tracks followed by different lice when the temperature in one half of the arena was above the optimum.

3·8 at 21° C. On repeating the experiment these figures were 48·5 and 11·5 respectively; and on repeating again 44·9 and 15·1.

The rate of movement is, of course, always greater on the warmer side. For example one insect which appeared indifferent to the temperature change of 31–39° C. moved at an average speed of 27·2 cm. per min. on the cool side, 37·5 cm. per min. on the warm. Under these circumstances the insect of course spends a longer time on the cooler side. Thus one insect which walked continuously round the chamber for 360 sec., spent 220 sec. at 30·5° C., 140 sec. at 39° C.

Once the louse has come to rest it requires a rather high temperature before it is aroused. Ten lice were allowed to settle down into akinesis in a chamber covered with glass. The temperature was then raised slowly during about 20 min. from 32 to 42° C. The lice were aroused at the following temperatures: 39·5, 39·5, 40·0, 40·0, 40·5, 40·5, 41·0, 41·0, 41·0. They do not seem to be aroused by a fall of temperature, at least to 18° C.

An attempt was made to see whether the previous exposure of the louse to a given temperature would influence its response to that temperature in the apparatus. A number of lice were kept at 32 and 27° C. for 1–3 hr. and were

then offered a choice of these two temperatures. No good evidence of adaptation could be obtained. Most insects showed a definite preference for 32° C. (Fig. 5A), irrespective of the temperature to which they had been exposed. But some showed a distinct preference for the intermediate zone, turning back towards the mid-line after passing into 27 or 32° C. (Fig. 5B).

The same experiment was made with insects which had been preconditioned at 35–36 and 25–26° C. and then offered a choice of these temperatures. There was again no evidence that the preconditioning had any influence.[1] The avoidance of 36° C. was on the whole greater than that of 25° C. but the lice often turned back in both directions and several insects crawled along the mid-line swinging alternately towards the left and the right (Fig. 5C). This response to the intermediate zone was more pronounced when extreme temperatures such as 39 and 21·5° C. were present on the two sides (Fig. 5D).
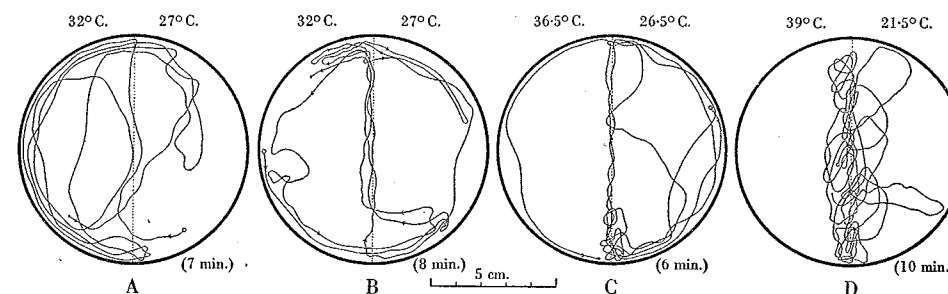

Fig. 5. Tracks of lice when the temperature was above the optimum in one half of the arena and below the optimum in the other half.

Reactions in a temperature gradient

Previous experiments on the response of the louse to temperature have all consisted in observing it in a temperature gradient; sometimes a linear gradient cold at one end and hot at the other (Martini, 1918; Homp, 1938; Weber, 1929); sometimes a concentric gradient around the finger (Hase, 1915) or around a tube of hot water (Homp, 1938). In order to link up the present results with this earlier work the behaviour of lice in a linear gradient has been studied.

The apparatus used is shown in Fig. 6. It consists of an inner trough of sheet zinc (*a*) 45 × 4 × 1·5 cm. with a strip of blotting paper along the floor, supported at intervals by metal trestles (*b*) and an outer trough (*c*), also of sheet zinc 50 × 8 × 8 cm. The space between the two troughs is filled with

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[1] Homp (1938) describes an attempt to influence the choice of temperature in *Pediculus* by previous exposure for several days at 27–29, 40 and 11–20° C. The results showed no differences at the lower end of the temperature range, no differences in the mean, a very slight (and quite unconvincing) difference at the upper end, where those from 40 and 27–29° C. behave alike, those from 11–20° C. do not extend quite so far.

sand (*d*) saturated with water; into this twelve thermometers are inserted at regular intervals, their bulbs level with the floor of the inner trough. The inner trough is closed above by a series of microscope slides. The outer trough rests on an asbestos strip heated by three small bunsen burners, their flames graded from the warm end. Small blocks of ice (*e*) are placed on the sand at the cool end and the excess water siphoned off by means of a strand of cotton wool (*f*) resting on the sand at the warm end. By this means a pretty constant gradient extending from 13 to 45° C. over the distance of 45 cm. could be obtained. The temperatures registered by the thermometers in the sand agree exactly with those shown by thermometers lying on the floor of the inner trough opposite the corresponding points.

A dozen well-nourished female lice were distributed evenly along this gradient and their positions recorded at the end of 15 min. They were then
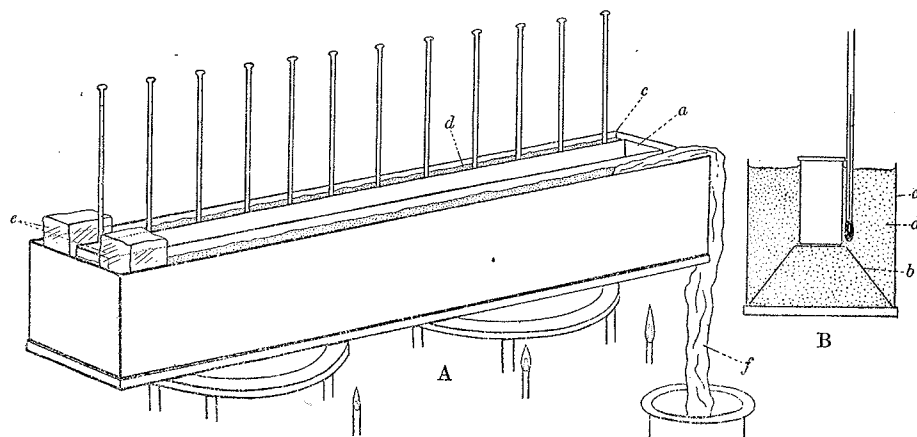

Fig. 6. A, temperature gradient apparatus. B, the same in section. Explanation in text.

removed, evenly distributed again, and the experiment repeated in the same way ten times. At the time of reading, some insects were moving, some at rest. They were observed to come to rest at all temperatures except those above 39° C. (cf. p. 72). Fig. 7 shows the distribution of these lice in relation to the temperature when all the results were summed.

These results confirm those of Martini (1918) in showing the greatest concentration of lice at about 29° C. This has been regarded as the *preferred temperature*. But it is probable that the lice accumulate at this point merely as the result of their avoidance of the upper and lower ranges of temperature. For if individual lice are watched they are seen to crawl for variable distances towards the warm or the cool ends before turning back. Some will turn at 27 or 32° C.; others will continue to 22 or 38° C. Hence at any moment the greater number of insects will tend to be crossing the mean temperature zone of 29–30° C. Moreover, insects approaching from opposite ends of the gradient

tend to huddle together when they meet. This is an additional factor which favours aggregation in the central zone.

Homp (1938) obtained a similar curve for the "preferred temperature". Her curve is based on the relative length of track of individual insects in different segments of the gradient.

Response to radiant heat

Homp (1938) concluded that in the reactions of *Pediculus* to a tube of warm water the air temperature is the important stimulus; experiments to test the effect of radiant heat in the absence of differences in air temperature were unsuccessful. Martini (1918) had concluded that radiant heat, not only from very hot objects but from objects at body temperature, was important
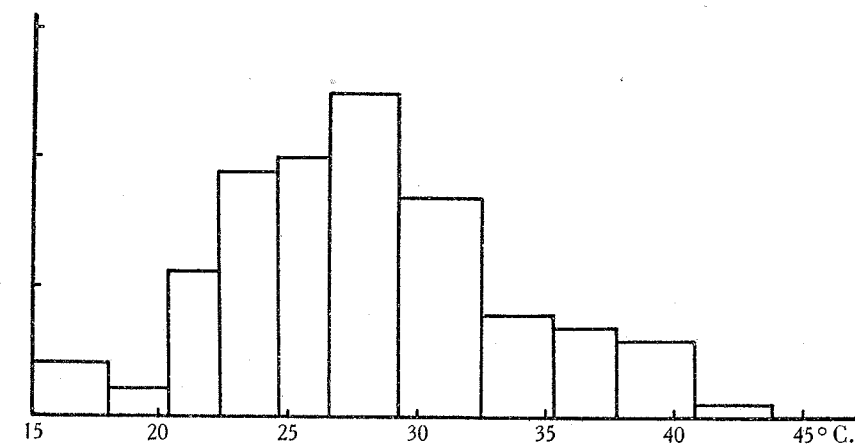

Fig. 7. Relative numbers of lice collecting within different sections of the temperature gradient.

in attracting the louse—but these experiments did not exclude the influence of warm air.

The effect of radiant heat (within the physiological range of temperature) has been reinvestigated as follows. A circular tin 9 cm. in diameter was lined with aluminium foil, and on one half of the wall this was covered with thin cellophane gummed to the surface. The floor of this arena was of blotting paper. It was placed on the bottom of a shallow tin and sealed round the base with plasticine. The whole was firmly secured to the top of the usual container (Fig. 1) through which cold water was passed. Warm water was placed in the tin outside the arena. In this way the walls of the arena were warm while the floor was cooled. In other experiments the outer tin was divided by a partition so that water at different temperatures could be placed in the two halves and thus the wall of the arena heated to different temperatures on the two sides.

The thin cellophane covering makes very little difference to the conduction of heat and consequently to the gradient of air temperature from the walls to the centre of the arena. But it makes a great difference to the radiant heat. The emissivity of the aluminium covered by cellophane is almost equal to that of a dull black surface; the emissivity of the aluminium alone is only about 5 % of this (Crowden (1934) and personal communication).

Results. When the air temperature against the wall of the arena was 29° C. all round and the temperature at the centre of the arena 24·5° C., the lice all made their way to the wall and moved round close to it, showing no difference in the two sides (Fig. 8A). The same result was obtained when air was blown through a funnel above the arena. This reduced the gradient of air temperature, making this 24° C. at the centre, 25° C. against the wall.

When the air temperature against the wall was 43° C. all round and that at the centre 31° C., the lice were repelled and turned away from the wall
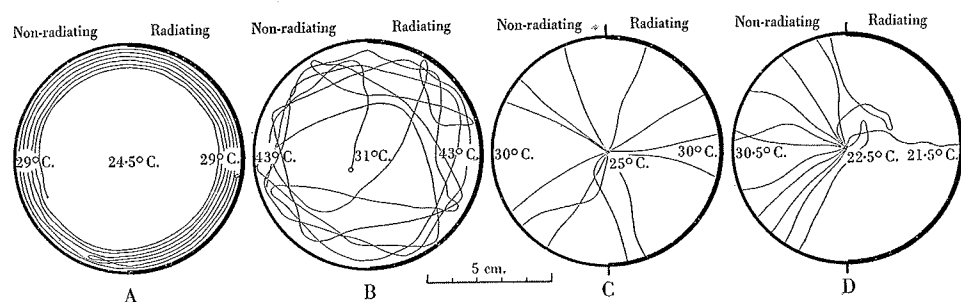

Fig. 8. Reactions of lice to radiant heat.

before actually coming in contact with it. But they came no nearer to the wall when this was covered with aluminium alone (Fig. 8B). In this repellent effect it was clearly the air temperature that was important.

If a number of lice are liberated together in the centre of the arena they crawl over and over one another and then one by one they leave the cluster and migrate to the periphery. When the air against the wall of the arena was 30° C. all round and that at the centre 25° C. the lice moved out in all directions going indifferently to the radiating cellophane surface and the non-radiating aluminium surface (Fig. 8C). Whereas, if the air temperature around the wall is 30·5° C. against the aluminium and 21·5° C. against the cellophane they almost all go towards the former (Fig. 8D).

It is clear that over the range of temperatures used in these experiments, which is that encountered by the louse in nature, in comparison with warm air radiant heat is of no importance in orientation (cf. Wigglesworth & Gillett, 1934b).

REACTIONS TO HUMIDITY

Method

Fig. 9 shows the arrangement of the arena for experiments on atmospheric humidity. A metal base plate (a) 13 cm. square rests on the top of the warm tank. A rod (b) 1·5 mm. in diameter is soldered to the base plate. On either side of this is placed a semicircular pad (c) made up of four thicknesses of blotting paper, which will hold 5 c.c. of the solution for controlling the humidity. A disk of perforated zinc (d) is separated from the pads by four very thin wire rings. The voile floor (e) stretched on a wire ring rests on the perforated disk. The arena is provided by the lid of a Petri dish (f) 9 cm. in diameter, ground down so as to measure 5 mm. deep inside. A glass rod (g) is fastened with plasticine across the roof of the arena so as to reduce the area of contact between one half of the chamber and the other. A large Petri dish (h) 11 cm. in diameter covers the entire apparatus so as to prevent evaporation. With very high humidities, dew may form on the inner cover (f); this is prevented by *slightly* warming the outer cover (h) before each experiment.
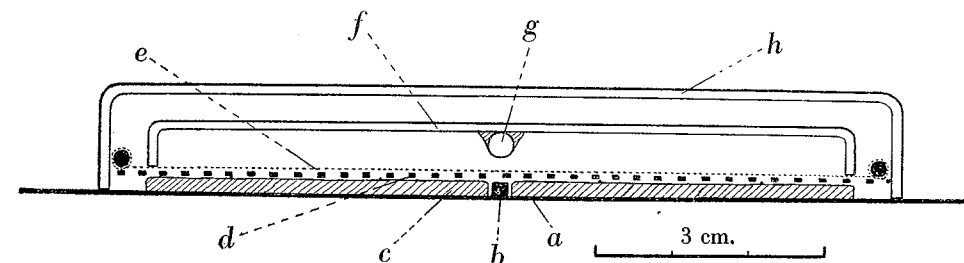

Fig. 9. Arrangement of the arena for experiments on atmospheric humidity, seen in cross-section. Explanation in text.

The humidity has been controlled by the use of saturated salt solutions (Buxton, 1931; Buxton & Mellanby, 1934), 5 c.c. being added to a fresh pad each day. The following salts were used, all at 30° C.: $Ca(H_2PO_4)_2$, 95 %; neutral Na-tartrate, 92 %; KCl, 85 %; NaCl, 76 %; NH_4NO_3, 60 %; $Ca(NO_3)_2$, 47 %; $MgCl_2$, 32 %; K-acetate, 16 %; $ZnCl_2$, 10 %. It is assumed that the humidity on the surface of the voile is that given theoretically by the salt mixture which is about 1 mm. below. It may be noted that the area of contact between each half of the chamber and the salt solution is 31·8 sq. cm.; whereas the area of contact between the one half of the chamber and the other is 1·8 sq. cm. Hence the gradient of humidity in the mid-line is probably very steep. This is borne out, as will be seen, by the behaviour of the insect.

Reactions to alternative humidities

Before using controlled humidities with this apparatus some preliminary experiments were made in which a sheet of blotting paper was divided by a line 1–2 mm. wide impregnated with paraffin wax, and one half left dry while

the other was saturated with water. The arena was open above and consisted of a ring of glass prepared from a Petri dish by grinding away the floor.

Fig. 10 A shows a typical result. The louse remained the whole time on the dry side; it often turned away while still a centimetre distant from the moist surface. This response was not due to a difference in temperature. For the temperature as measured by a small thermometer with the bulb resting on the surface was 30·0° C. on the dry side, 30·5° C. on the moist—the improved conduction of heat through the moist paper more than compensating for the cooling effect of evaporation.
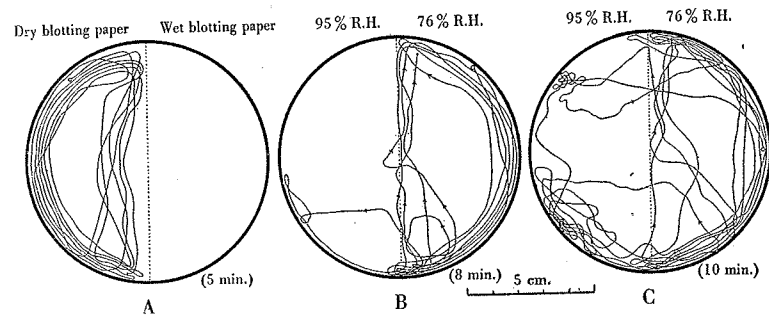

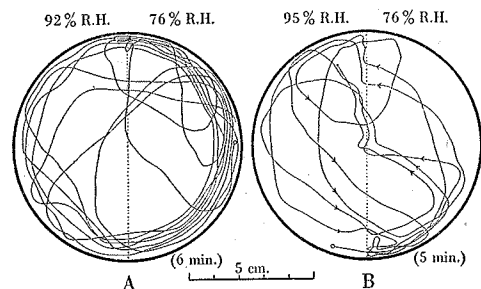Fig. 10. A, response of louse to a wet surface. B, C, responses to atmospheric humidity.

Fig. 11. A, track followed by louse showing a very weak response to high humidity. B, track of louse with left hand bias which showed a fairly strong reaction to humidity.

Fig. 10 B, C, shows the response of lice, taken directly from the breeding capsules, to a choice of atmospheric humidities of 95 and 76 %.[1] There is a very striking avoidance of the higher humidity. Sometimes (Fig. 10 B) the insect turns back immediately on reaching the moist side. If it fails to do so (Fig. 10 C) it frequently pursues a very convoluted course before regaining the drier side. During the periods on the moist side its movements are very agitated.

This reaction to high humidity varies in intensity; sometimes it is absent and the insect is indifferent. Fig. 11 A gives an example of a very weak response to 92 % R.H. in the presence of 76 % R.H. It is apparent only in the

[1] The temperature, as measured by a small thermometer within the closed chamber, was 30·25° C. on each side.

slightly more convoluted course on the moist side. Fig. 11 B is an example of an insect with a weak left hand bias. It regularly turns away on coming to the moist side; but as the result of the left hand bias these turns fail to take it back into the drier side.

When experiments were made at other parts of the humidity range curious inconsistencies became apparent. Many insects would show a very definite reaction to a given pair of alternatives, others would be indifferent under the same conditions, while a few would show an equally definite reaction in the opposite sense. This suggested that the response might be influenced by the conditions to which the insect had been previously exposed.

This was tested as follows. Before each experiment the lice were divided into two groups, usually six or ten in each. Half were exposed for 1–3 hr. to one of the humidities to be used and half to the other. Most of the experiments consisted in offering a choice of 95 % R.H. and a series of lower humidities, or of 10 % R.H. and a series of higher humidities. The following are summaries of the results:
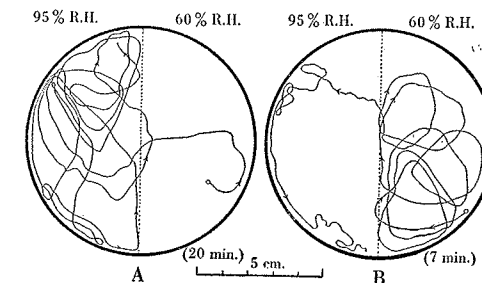

Fig. 12. A, track of louse which had been kept at 95 % R.H. for 2 hr. B, track of same louse after exposure to 60 % R.H. for 10 min.

(i) 95 %/85 %. Insects accustomed to 95 % R.H. show some avoidances of 85 % R.H., but most gradually come to prefer 85 % R.H. and avoid 95 % R.H. Most of those from 85 % R.H. show consistent avoidance of 95 % R.H.

(ii) 95 %/76 %. Accustomed to 95 % R.H. they show at the outset definite avoidances of 76 % R.H.; but later the response is reversed and they avoid 95 % R.H. Those from 76 % R.H. show consistent avoidance of 95 % R.H. or are indifferent.

(iii) 95 %/60 %. Those from 95 % R.H. may avoid 60 %; but this reaction is easily reversed. Fig. 12 gives an example of this. Insects from 60 % R.H. consistently avoid 95 %.

(iv) 95 %/47 %. After exposure to 95 % R.H. the lice usually show at first consistent avoidance of 47 % R.H., though later they may become indifferent. Those from 47 % R.H. show variable responses: some consistently avoid 95 % R.H.; others react in this way at first, but later the response is reversed and they avoid 47 % R.H.

(v) 95 %/32 %. The response is again influenced by the humidity to

which the insects had been exposed; but in both groups they tend to avoid 32 % R.H. eventually.

(vi) 95 %/10 %. Insects from 95 % R.H. avoid 10 % R.H. consistently. Those from 10 % R.H. usually show a number of avoidances of 95 % but later the response becomes reversed and they avoid 10 %.

(vii) 10 %/32 %. One insect after exposure to 10 % R.H. gave some definite avoidances of 32 % R.H. Those from 32 % R.H. were indifferent.

(viii) 10 %/60 %. There was usually no evidence of any preference between these two humidities, but those from 10 % R.H. show occasional avoidances of 60 % R.H.

(ix) 10 %/76 %. The responses are rather weak but avoidances of 76 % R.H. occur in both groups.

(x) 10 %/85 %. Insects from 10 % R.H. consistently avoid 85 % R.H. Those from 85 % R.H. show a few reactions against 10 % R.H., but soon come to avoid 85 % R.H.
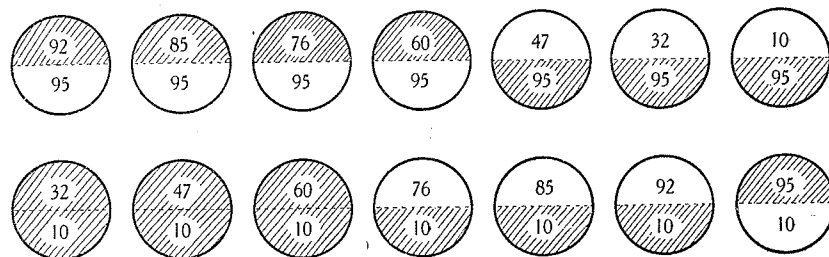

Fig. 13. Diagram summarizing the preferences of the louse when offered two humidities. The shaded side is that usually chosen.

(xi) 10 %/92 %. Lice from 10 % R.H. avoid 92 % continually. Those from 92 % R.H. may be indifferent or react away from 10 % R.H.; but this response is sometimes spontaneously reversed.

(xii) 10 %/95 %. As already described under (vi) insects from both groups come to prefer 95 % R.H. and avoid 10 % R.H.

Thus the response of the louse in the presence of two humidities is greatly influenced by the conditions to which it has previously been exposed. But whatever the conditions it usually comes eventually to prefer the same one of these two humidities.

These results are summarized in Fig. 13. Two points emerge. (i) The louse is usually more or less indifferent to humidity over the drier part of the range—from 10 to 60 % R.H. (ii) The reaction towards a given humidity is influenced by the alternative which it is offered. Thus in the presence of the lower humidities, 10, 32 and 47 % the high humidity of 95 % is preferred; whereas in the presence of the higher humidities, 60, 76 and 85 %, 95 % R.H. is avoided. And whereas 10 % R.H. is preferred in the presence of 85 or 92 % R.H., it is avoided in the presence of 95 % R.H.

The meaning of these differences is not clear. It seems, however, that the insect (a) prefers a low or medium humidity, (b) avoids any change once it has become accustomed to a given humidity. Now it is a general property of hygroscopic substances that they absorb water more rapidly from a very moist atmosphere than they lose it in a dry. If therefore, as seems probable, the sense organs concerned behave like other hygroscopic materials this might explain why the insect comes to prefer 95 % R.H. before 10 % R.H., but to prefer 10 % R.H. before 85 or 92 % R.H. But it is not easy to explain along these lines the striking avoidance of 95 or 100 % R.H. in the presence of 60, 76 or 85 % R.H.

In general the louse shows a greater sensitivity within the higher ranges of humidity. For example the louse is usually indifferent between 10 and 60 % R.H. but may show a striking preference for 92 % R.H. in the presence of 95 % R.H. This was observed also by Thomson (1938) in the mosquito *Culex* and by Pielou & Gunn (1940) in the adult mealworm *Tenebrio*. As these authors point out, it suggests that the sense organs are reacting like hygroscopes to relative humidity (Pielou, 1940).
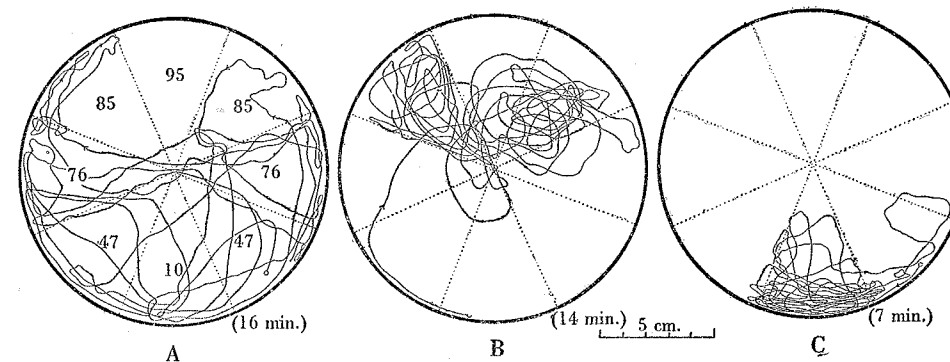
Fig. 14. Tracks of single lice in an arena divided into sectors of different humidity, as indicated in A.

Reactions in a humidity gradient

Some experiments were also made in which the louse was offered a wide range of humidities. A large arena formed by a Petri dish 13·5 cm. in diameter was prepared in the manner already described and divided into eight sections each with four thicknesses of filter paper saturated with salt solution below the perforated zinc. The humidities were arranged as shown in Fig. 14, which gives some typical results on lice taken direct from the breeding capsules.

Fig. 14A represents the most usual response. The insect is apparently indifferent over the range from 10 to 76 % R.H., but avoids 85 % R.H. and still more strongly 95 % R.H.

Fig. 14B is an example of spontaneous adaptation to a high humidity (85 % R.H.) and avoidance of change in either direction. This result was again

obtained on repeating the experiment with the same insect. A few other similar, though less striking examples were obtained.

Fig. 14 C is a very unusual case of adaptation to 10 % R.H. with avoidance of all higher humidities. Later this response was gradually lost and the type shown in Fig. 14 A was given.

Lice were also tested in a linear gradient of humidity. The temperature gradient apparatus (p. 74) heated throughout to 30° C. was used. A glass tube of 1 cm. internal diameter (Fig. 15 *a*) was ground down so as to form a cover 45 cm. long and inverted over a rectangular zinc framework (*b*) with a floor of bolting silk (*c*). Below this was a series of 9 pads, each 5 cm. long, composed of four thicknesses of blotting paper (*d*) enclosed between two strips of perforated zinc (*e*). The gradient consisted of the following relative humidities: 10, 16, 32, 47, 60, 76, 85, 95, 100 %.

A dozen lice were introduced at a time and their positions recorded at 5 min. intervals. In one experiment, after 7 readings in the course of half an hour the summed results were as follows: 10 % R.H. 49; 16 % R.H. 12; 32 % R.H. 6; 47 % R.H. 7; 60 % R.H. 3; 76 % R.H. 4; 85 % R.H. 3; 95 % R.H. 0; 100 % R.H. 0.

The insects obviously avoided 95 % R.H. and in some cases 85 % R.H. They then turned back and continued walking until they reached the dry end. Here they formed a cluster, from which occasional insects would come out, move as far as 85 or 95 % R.H. and then return. The aggregation at 10 % R.H. is thus of no significance. The insects used appeared quite indifferent from 10 to 76 % R.H.

Fig. 15. Section of humidity gradient apparatus. Explanation in text.

REACTIONS TO SMELL

Method

For experiments on smell the arena is open above and consists of a ring of glass made from a Petri dish by grinding away the bottom. The rest of the apparatus is the same as that used in the humidity experiments, the blotting-paper pads being replaced by whatever materials are to be tested. The floor of the arena is always at about 30° C. Under these conditions it is assumed that the warm odours will be carried upwards by the convection currents and produce in still air a pretty sharp boundary between the two halves.
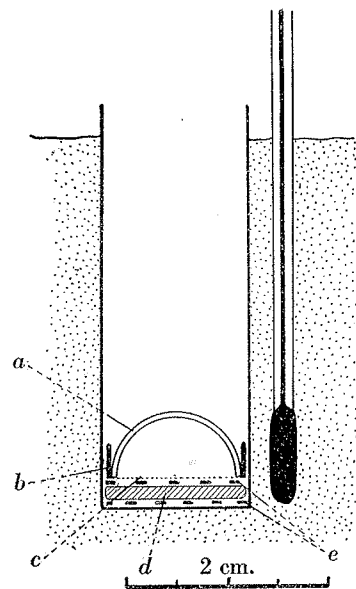
Results

A double layer of cotton stockinet was placed below each side, that on one side being clean, that on the other having been pinned inside the shirt and worn next the skin for a week or 10 days. Fig. 16 A shows the insect returning to the man-scented side almost immediately after crossing into the neutral side. Fig. 16 B shows the track of a louse which followed a straight course on the man-scented side, a convoluted course on the neutral side. Fig. 16 C represents a more extreme example of the same type.

The same experiment was repeated using stockinet which had been well rubbed on a dog, together with some of the dog's hair. Most of the lice proved
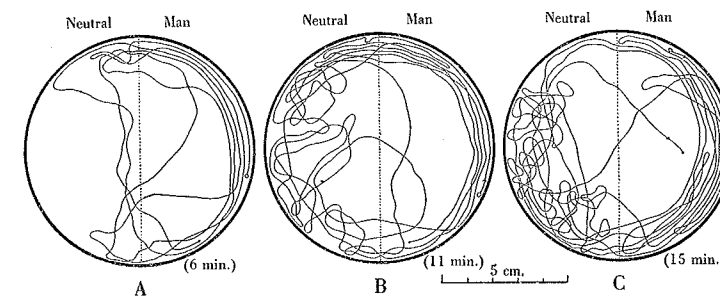
Fig. 16. Reactions of lice to the smell of man.
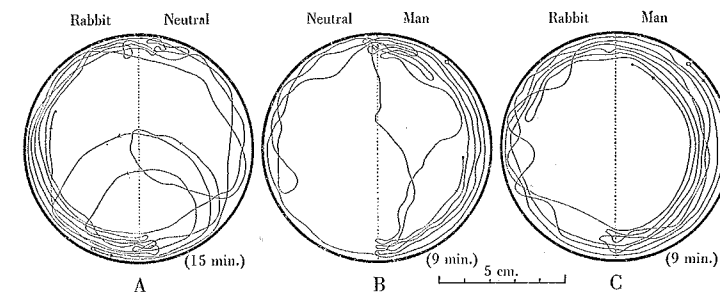
Fig. 17. Reactions of the same louse to the smell of man and rabbit.

indifferent; a few showed a very slight preference for the dog-scented side. When lice were offered a choice of a man-scented side and a dog-scented side they showed a preference for the former quite as great as that shown in Fig. 16 A, where one side was neutral.

The response to the odour of rabbit was tested in the same way. (To the human sense this odour comes much closer to that of man.) Most lice show a quite definite preference for the rabbit-scented side when the other side is neutral. The reaction to human scent is, however, stronger. And when the rabbit-scented side is exposed alongside the man-scented side there is a definite preference for the latter. Fig. 17 shows the reactions of the same insect when offered these three alternatives.

6-2

An attempt was made to see whether lice would show any detectable preference for the odour of the individual human host on which they had been reared. A series of lice reared throughout on S. A. S. and another series reared on V. B. W. were offered the choice of stockinet worn for several days under the clothing of these two hosts. No evidence was obtained of the one host being more attractive than the other, or of the lice being more strongly attracted by the odour of the host on which they had been reared. But the experiments were not extended to other human hosts.[1]

Other odours which might be expected to contribute to the normal environment of the louse are those from other lice or from their excreta. A Petri dish exactly the same size as the arena was ground down so as to be only 4 mm. deep inside. Clean filter paper was placed on the bottom and it was divided in the middle by a partition of celluloid. Thirty-six female lice were introduced into one side of this container. The voile disk was placed on the top, and on this the open arena. Fig. 18 A, B shows two examples of the tracks followed
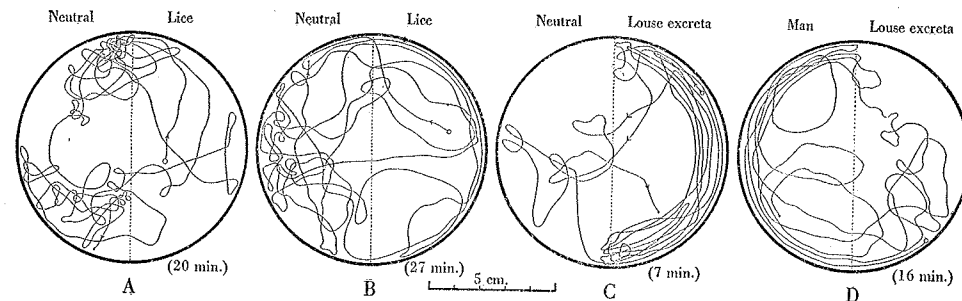

Fig. 18. A, B, tracks of single female lice when half the arena covered a chamber containing other female lice. C, reaction to the smell of louse excreta. D, reaction to smell of man when the other half of the arena contained louse excreta.

by single female lice placed in the arena. They follow a much more convoluted course above the empty side than above the side containing the other female lice. During the experiment the latter laid a number of eggs at various points in the chamber. (Bacot (1917) and Nuttall (1917) have shown that females tend to lay their eggs where they or other females have already deposited them.) The lice in the container also produced a small amount of excreta.

The response to excreta was tested by covering a pad of blotting paper with excreta and cast skins collected from the breeding capsules, moistening this layer and then allowing it to dry. The material contains much incompletely digested blood; on warming to 30° C. it gives off a slight and somewhat disagreeable smell. It was compared with a clean pad of blotting paper. Fig. 18 C shows a very striking response, this insect being almost confined to the side above the excreta. If a piece of man-scented stockinet is placed below the

[1] There are many inconclusive statements in the literature about individuals who are said to be repellent or particularly attractive to lice (Frickhinger, 1916; Alessandrini, 1919; Pick, 1926).

opposite side the lice come to prefer this side and avoid that above the excreta. Fig. 18 D shows an example of this.

It was interesting to see whether the attractiveness of human odour was enhanced when the smell of lice and their excreta was added to it. A piece of man-scented stockinet was divided and half placed in each side of the chamber described above. In addition, one side contained thirty-six lice of mixed sexes and a large quantity of excreta. As shown in Fig. 19 the lice in the arena show a slight preference for the side containing the lice and excreta.

In the past many experiments have been made with the practical object of discovering a repellent which will prevent the biting of lice when applied to
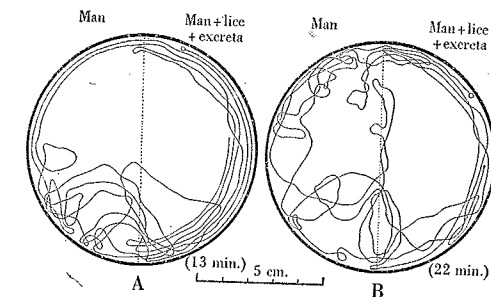
Fig. 19. Tracks of lice where half arena provided smell of man and half that of man plus lice and excreta.
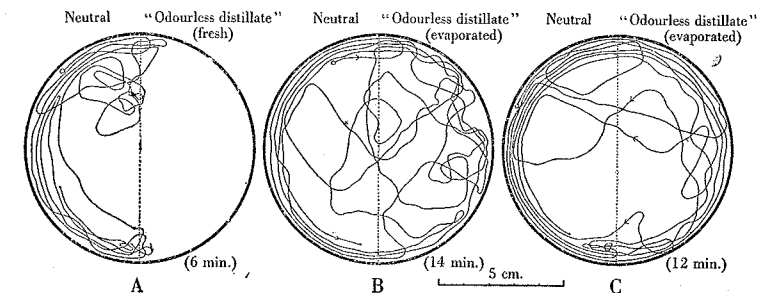
Fig. 20. Reactions of lice to the smell of petroleum ("odourless distillate"). A, fresh; B, C, after exposure for 18 hr.

the skin. These tests have proved consistently negative and have even led some authors (Nuttall, 1917) to question whether lice possess a sense of smell. But a variety of substances, light oils, creosote, naphthalene, etc., will serve as repellents when studied by the present technique. A rather mild repellent chosen for the experiments described was "Shell odourless distillate". This is a highly refined petroleum oil, containing less than 1 % of aromatics, with a boiling point range of 198–257° C. It has a faint smell of petroleum, which disappears from a thin film after exposure to the air for some hours.

A few drops of "odourless distillate" were applied to filter paper below one half of the arena, clean filter paper was placed below the other half. Fig. 20 A shows the response of a louse to the fresh oil; this is almost completely

avoided. Figs. 20 B, C show responses after the film had been exposed to the air at room temperature for 18 hr. and no longer had a smell detectable by man. The insect now merely follows a more convoluted course on the side above the evaporated oil.

REACTIONS TO CONTACT

Method

Most of the experiments were on the same lines as before. Materials of graded roughness were secured with gum to glass plates. These were placed side by side, warmed to 30° C., and a small Petri dish 6 cm. in diameter inverted over them to form the arena. The materials used were glazed paper, unglazed paper, blotting paper, smooth silk, cotton stockinet and coarse woollen stockinet. The texture of the last three in relation to the louse is shown in Fig. 21.
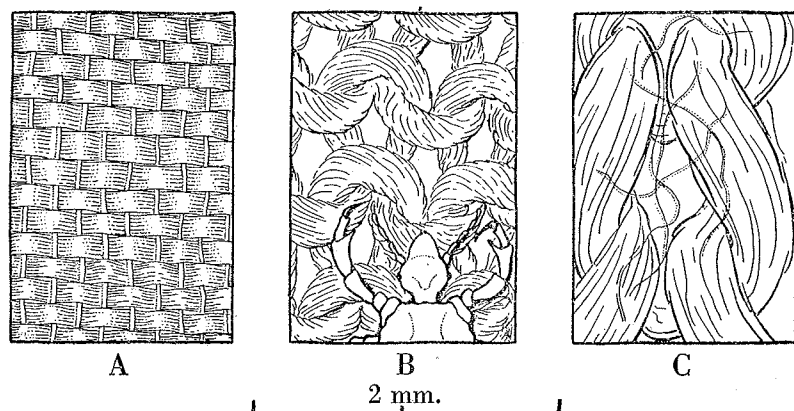

Fig. 21. Texture of materials used in relation with the louse. A, silk; B, cotton stockinet; C, woollen stockinet.

Results

Lice cannot hold to glazed paper. When on any rougher material they will usually avoid glazed paper absolutely. If they do walk onto it they struggle actively, their claws slipping over the surface, until they get back to the rougher material (Fig. 22 A).

When offered a choice of other materials they show a varying degree of preference for the rougher. Fig. 22 B shows the track of a rather slow-moving insect offered woollen stockinet and smooth unglazed paper; it never left the woollen stuff. Fig. 22 C is the track of a louse offered this woollen material and smooth silk. It seldom left the margin of the wool; and when it did so it showed great agitation in its movements, followed a convoluted course, and soon returned. Fig. 22 D shows the response to woollen stockinet and fine cotton stockinet. The reaction is not so strong; the louse often gets on to the cotton stuff and there follows a somewhat convoluted course. Fig. 22 E is the

trail of an insect in the presence of this same cotton stockinet and smooth silk. It repeatedly gets onto the silk, and then twists and turns in all directions before returning to the cotton. Fig. 22 F is a response to the cotton stockinet and blotting paper. On the cotton the louse follows a straight course; on the blotting paper it changes direction repeatedly and pursues a highly convoluted trail.

These figures provide a fair sample of the results obtained. But there is a great deal of individual variation. It is obvious that the course followed upon a given material depends upon what alternative material is offered. If any of the materials is present alone, the trail soon becomes straight. And it is
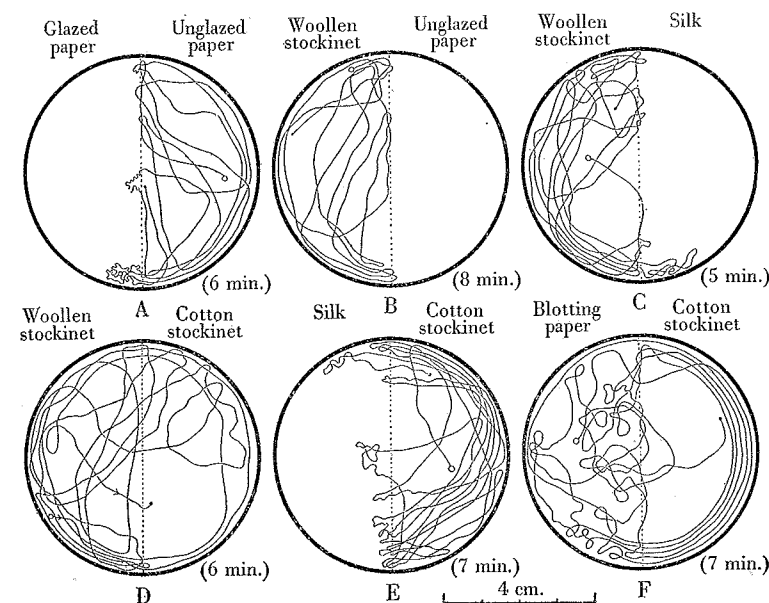
Fig. 22. Reactions of lice to contact with rough and smooth materials.

quite common for the insect to be completely indifferent even when two very dissimilar materials are present; or for it to become indifferent and follow a straight track on both sides in the course of an experiment.

The general response of turning back from a smooth material is seen equally when a narrow strip of khaki flannel is placed on blotting paper (Fig. 23 A); or even when a strip of frayed flannel is laid, like a seam in the clothing, upon a floor of the same material (Fig. 23 B). On the other hand, the louse shows little tendency to move along in contact with a smooth surface. It often turns and leaves it almost at once (Fig. 23 C). And most of the time that it walks round the Petri dish it is not in contact with the walls nor does it touch the wall with its antennae. As described already (p. 70) it follows a series of short chords in the arena.

Some other tactile responses may be mentioned. Lice show a great tendency to creep into narrow clefts of rough material. This is particularly so in the egg-laying female. On the other hand they do not seem inclined to insinuate themselves beneath smooth surfaces, such as a coverslip, whether on smooth or rough material. They tend to come to rest (akinesis) more readily on rough material and scarcely ever on a glazed surface. This has already been noted in *Haematopinus* by Weber (1929).

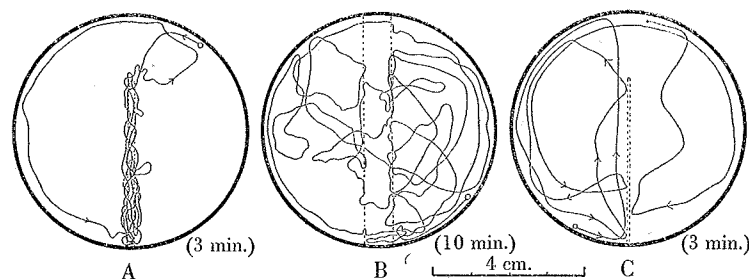Fig. 23. Tracks followed by lice: A, a strip of flannel on blotting paper; B, a frayed strip of flannel on a flannel surface; C, a vertical strip of metal on blotting paper.

Reactions to moving air

Air currents provide another form of mechanical stimulus which might be important in the orientation of the louse; although the relative shortness of the antennae and the sparseness of slender tactile hairs makes this unlikely. The effect was tested in an arena 9 cm. in diameter and 4·5 cm. deep, open above and with a voile floor. This was divided by a vertical card extending from
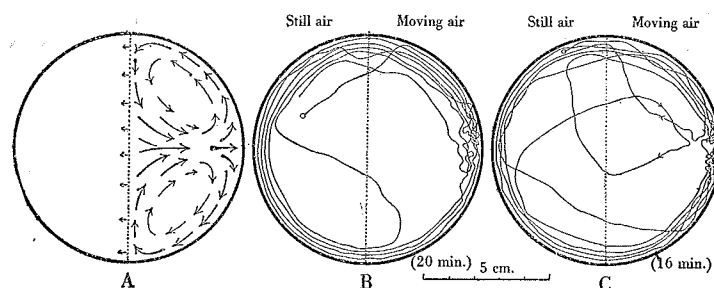

Fig. 24. A, the course of air currents in the arena. B, C, tracks of lice in such an arena.

the top to within 3 mm. of the floor. A jet of compressed air blown through a pipette was directed downwards and outwards at an angle of 45° on one side of the arena, setting up a violent turbulence there. The direction of the currents was mapped out by means of the parachute of a dandelion seed (Fig. 24 A). Opposite the jet the current was so strong that the louse was blown violently

away on a smooth surface. Only very weak air currents pass below the partition to the other side. The floor of the arena was at room temperature, about 20° C.

Fig. 24 B, C, gives typical results obtained. The louse shows no response until it enters the very strong current close to the jet. It then stops and turns in all directions and frequently retreats.

REACTIONS TO LIGHT

Method

The reactions so far considered (apart from those to radiant heat) have all concerned diffuse stimuli. Such stimuli may show a gradient of intensity; but the insect, at a given point in the gradient, cannot detect, without further exploration, in which direction it is rising or falling. In the case of light, however, it is important to differentiate between the effects of general light intensity and the effects of directed light. As Ullyott (1936) has shown, it is very difficult to arrange an arena with a large difference in illumination on the two halves without at the same time introducing differences in the amount of light reflected from the surroundings.

In observing the track of the insect, however, there is no need to use a divided chamber; because the intensity of light can be changed instantly all over the arena. To test the effects of light intensity an open glass ring with walls 1 cm. high, painted a dull black inside, was used. This was exposed in a darkened room to a screened lamp vertically above the centre and the light intensity varied by interposing a number of pieces of stout white card below the lamp. The intensity of the surface illumination was measured approximately with an "Avo" photoelectric cell (Automatic Coil Winder and Electrical Equipment Co., Ltd.); approximate values for the lowest illuminations lying outside the range of this instrument were arrived at, by extrapolation, from the number of cards interposed.

Other methods will be described below.

Reactions to changes in light intensity

Lice were kept in the dark for an hour or so and then exposed in the arena to a surface illumination of less than 0·01 metre candle. At this illumination it is just possible to follow the trail of the louse. The illumination was then suddenly increased to 500 metre candles.

(i) The most constant response is for the movements of the insect to be arrested by the sudden increase in illumination. It may stop only for a few seconds or it may remain for many minutes in a state of akinesis. This response is described by Weber (1929) in *Haematopinus*. When the louse advances again, spontaneously or after being disturbed by touching, it usually moves at a slower pace and often hesitates or stops. Eventually it becomes accustomed to the light and regains its normal activity. Thus in one experiment the louse

at an illumination of 0·008 metre candle moved round the arena for 5 min. at an average rate of 25·4 cm. per min. On exposing it to 500 metre candles it stopped for 10 sec.; advanced 5 cm. and came to rest again. It was disturbed by touching after 5 min. It went once round the arena at a rate of 18·8 cm. per min. and stopped once more. It was aroused by touching after 5 min., and then continued around the arena at an average of 22·6 cm. per min. during the next 5 min.

(ii) But there is a second type of response in which the movements of the insect are not notably retarded but the course becomes convoluted on exposure to the bright light (Fig. 25). This is the type of response we have seen already in the presence of slightly adverse stimuli of temperature, humidity, smell and contact.
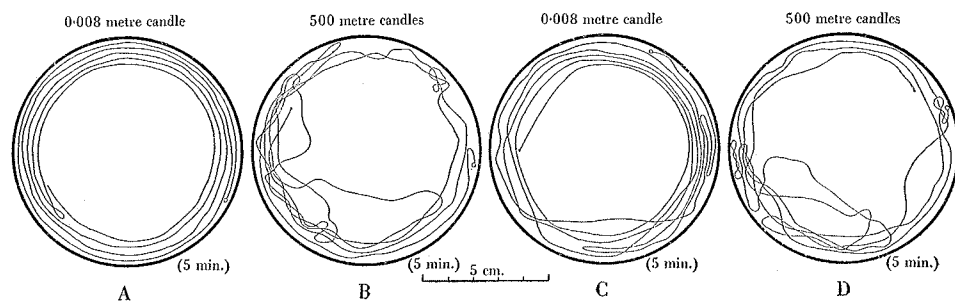

Fig. 25. Consecutive tracks of a single louse when the surface illumination was changed abruptly from 0·008 metre candle in A and C to 500 metre candles in B and D.

Reactions to directed light

It has repeatedly been observed that lice move away from the light (Hase, 1915; Nuttall, 1917; Weber, 1929). If the arena is placed unshaded before the window the tracks of the lice are mostly on the opposite side (Hase, 1915). In this reaction, however, the intensity of the diffuse light to which the louse is exposed will have an important effect. For, as Ullyott (1936) points out, in accordance with the Weber-Fechner law the threshold value of the orientating stimulation should be a function of the total stimulation to which the animal is subjected.

This effect is readily demonstrated by having one half of the arena with the wall dull black, the other half with white paper on the outside of the uncovered glass. It is illuminated from above so as to give a uniform surface illumination of 500 metre candles. A black card is then arranged so as to throw that half of the arena with black walls into deep shade (less than 0·1 metre candle).

Fig. 26 shows the result of such an experiment. When the arena is bright all over (Fig. 26 A) the louse walks closely round the black wall, but tends to swing away from the white wall into the middle of the arena. Whereas when

the black-walled side is shaded (Fig. 26 A') the louse may be entirely confined to the dark side, often turning back well before it enters the bright light. But if it does stray into the bright side it follows the same type of course as before— merely swinging away from the white wall (Fig. 26 B).

It is evident therefore that the light reaching the louse horizontally from different directions is chiefly important in its orientation. This can also be seen when a relatively small part of the wall of the arena is darkened. In the experiment shown in Fig. 27 the arena was placed in front of the window. It
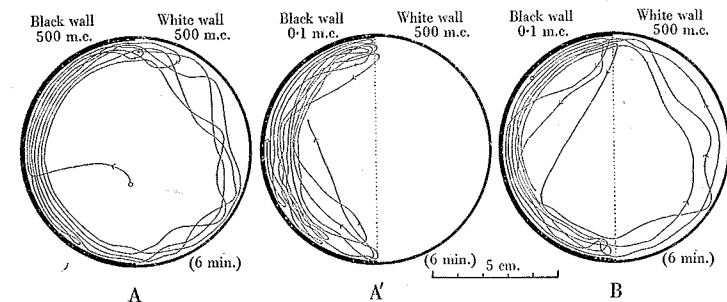
Fig. 26. Reactions of the louse to light reflected from the walls of the arena. A, entire arena light; A', track of same louse with black-walled half of arena shaded; B, track of another louse under the same conditions.
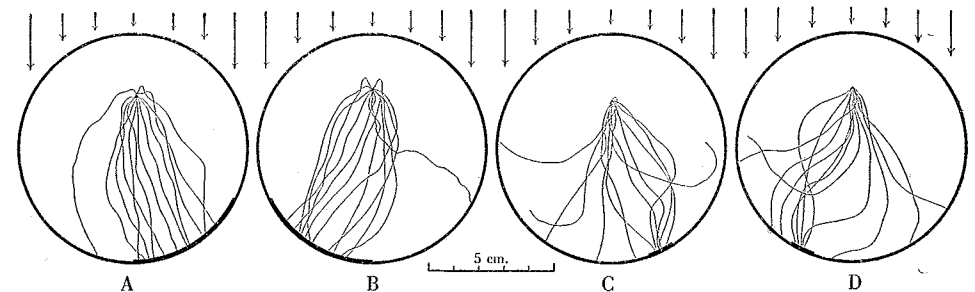
Fig. 27. Tracks of lice liberated in the middle of an arena with a black segment in the otherwise white walls. The arrows show the direction of the light.

was lined with white paper save to one side or the other of the pole opposite the window, where there was a dull black segment 5 cm. wide. The wall was 1·5 cm. high. Twelve lice were liberated in turn at a point in the arena; and as can be seen in Fig. 27 A, B, almost all went to the black region as they moved away from the window.

When the black segment was reduced to 1 cm. wide lying 1·5 cm. to one side or the other of the mid-line, the deflection of the tracks towards the black region is still apparent—particularly when they come close to it (Fig. 27 C, D). Bacot (1917) has already described how lice will turn towards dark objects and Homp (1938) observed that they will avoid a glass rod set in their way as

they move from the light. (Here they are presumably repelled by the reflected light.)

A response described by Weber (1929) in *Haematopinus* occurs also in *Pediculus*—the louse in a state of akinesis is awakened by alternating the light from bright to dark every few seconds.

According to Hase (1915), starved *Pediculus* become "positively phototropic"—except when disturbed, in which case they are negative as usual. I have been unable to confirm this observation. Twenty lice starved for 18 hr. at 28° C. and then for 24 hr. at 22° C. were placed in the centre of an arena formed by inverting a 13 cm. Petri dish on voile in front of a window, with the half away from the window shaded with black paper. When placed in the arena all the lice moved to the shaded half. Here they wandered for some time and all eventually settled down, mostly in the shade. Left undisturbed for 6 hr. they still remained in the same resting places; none moved toward the light.

Nuttall (1919) showed that lice offered black and white cloth, collect chiefly on the black. Under these conditions both directed light and general light intensity will be operative.

Sense organs

Antennae

Fig. 28 A shows the antennae of the adult louse. I can detect no constant differences between the sexes. It consists of five segments which bear three types of sensillum.

(i) *Peg organs.* These form a group arising from the thin cuticle at the apex of the 5th segment. There are nine or ten on each antenna: three sharply pointed, lying dorso-lateral, and six, or usually seven, of varied length, with rounded tips, lying medial and ventral. In section they are seen to be exceedingly thin-walled (Fig. 28 D). Below each is an elongated group of about six sense cells, the distal processes of which unite to form a filament that can be traced into the cavity of the peg.

(ii) *Tuft organs.* These were named and figured by Keilin & Nuttall (1930) but not fully described. In the adult louse there are three tuft organs on the dorso-lateral aspect of the fifth segment and one at the tip of the fourth segment on its outer side. Each consists of a minute cone arising from the floor of a saucer-shaped depression. At the apex of the cone there is a tuft of four tiny delicate hairs which stain weakly with haematoxylin.[1] These hairs appear to arise from a delicate membrane. Below this is a little oval cavity through which runs a deeply staining rod or filament attached at the point where the four hairs unite. A curved tubular thread connects this rod with a group of five or six sense cells (Fig. 28 C).

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[1] The pits and cones alone are mentioned by Alessandrini (1919).

(iii) *Tactile hairs.* These are of the usual type and consist of a slender bristle arising from a socket below which are trichogen and tormogen cells and a single sense cell with axon fibre (Fig. 28 B). They vary somewhat in number, but there are usually 5–7 on segment 1, 8–10 on segment 2, 5–7 on segment 3, 3–4 on segment 4, 3–4 on segment 5.

(iv) *Scolopidial organs.* In segment 2 there are Johnston's organ and some chordotonal organs, which will not be described in detail.
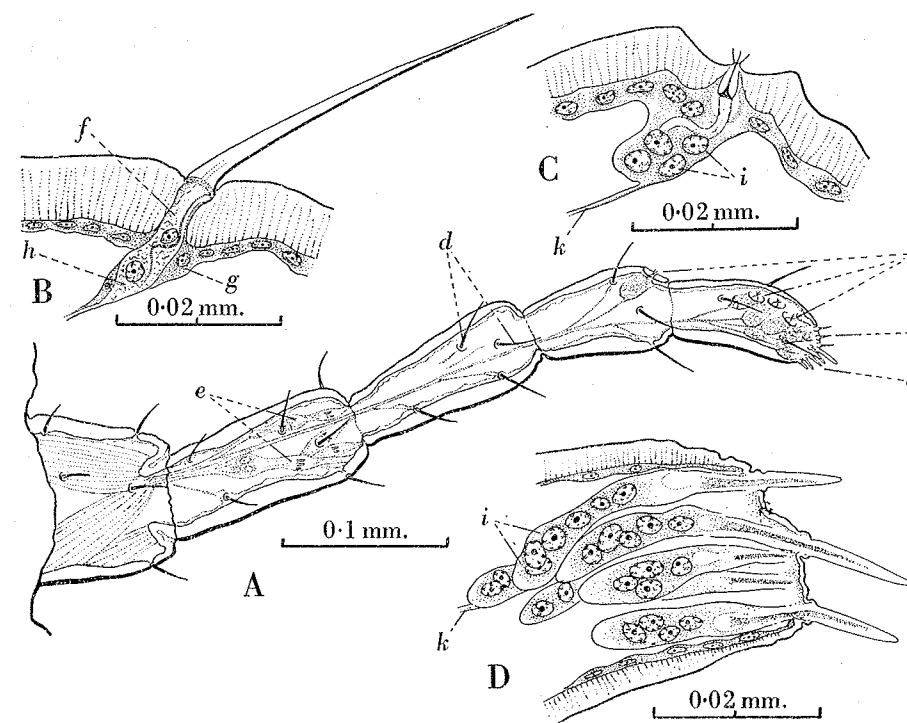
Fig. 28. A, dorsal view of left antenna. *a*, peg organs with rounded tips; *b*, peg organs with sharp tips; *c*, tuft organs; *d*, tactile hairs; *e*, scolopidial organs. B, detail of tactile hair. *f*, trichogen cell; *g*, tormogen cell; *h*, sense cell. C, detail of tuft organ. D, detail of peg organs. *i*, sense cells; *k*, nerve.

Sense organs elsewhere in the body

(i) *Tactile hairs* of the type described are widely scattered over the body. According to Brühl (1871) quoted by Müller (1915) there are about 150 on the whole insect. They are particularly numerous around the mouth parts and on the legs.

(ii) *Campaniform organs.* On the lower surface of each trochanter there are five sense organs, two anterior and three posterior (Fig. 29 A) pointed out by Keilin & Nuttall (1930) as a "new type of sensory organ of unknown function". In section these appear to be typical campaniform organs, con-

sisting of a thin dome with a deeply staining rod inserted into it and a sense cell with accessory cells below (Fig. 29 B).

(iii) *Chordotonal organs* occur in the femur, tibia and tarsus of each leg. They have been figured by Keilin & Nuttall (1930).

Fig. 29. A, ventral view of leg showing the campaniform organs (*a*) in the trochanter. B, section through these campaniform organs. *b*, dome; *c*, scolopale; *d*, sense cell; *e*, accessory cell; *f*, membrane-forming cell; *g*, nerve. C, horizontal section through eye. *h*, corneal lens; *i*, corneagenous cells; *k*, rhabdoms; *l*, pigment; *m*, nuclei of retinal cells.
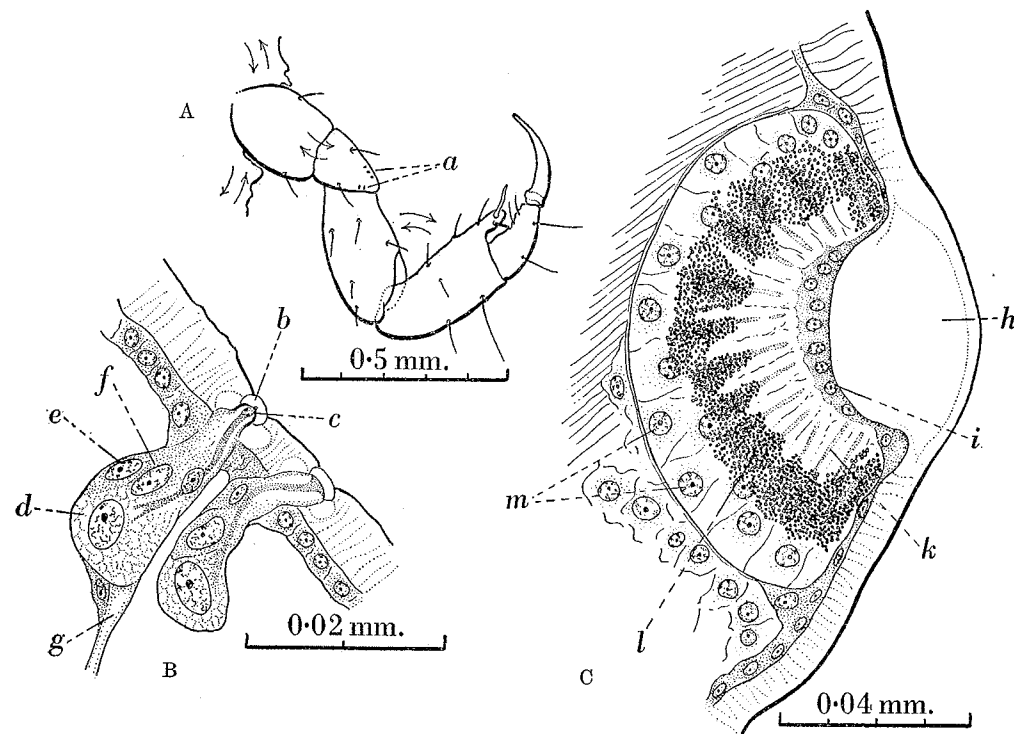
Eyes

The eyes lie at the sides of the head and are directed exactly laterally. Fig. 29 C shows a horizontal section. The structure, which has been briefly described by Müller (1915), is similar to that of many insect ocelli. Below the biconvex corneal lens is the layer of corneagenous cells, and below these again the cup-shaped retina. This is made up of elongated visual cells with basal nuclei. The rhabdoms occupy the distal two-thirds of these retinal cells; their distal halves are clearly visible in section; but their proximal halves are closely invested by the pigment granules which fill the middle region of the retinal cells.

LOCATION OF THE SENSES

Antennal movements

Lice have been observed under the binocular microscope in a small arena 2 cm. in diameter in which alternative stimuli were offered in the two halves on the same lines as before. As the insect walks the antennae make continuous and more or less synchronous horizontal movements. They are occasionally raised or lowered. Often the head makes slight side to side movements at the same time.

On passing from 30 to 40° C. the antennal vibrations become so rapid that the individual movements cannot be followed. The insect then turns round and retreats.

On coming from 30 to 15° C. the antennal movements become very slow. Often both antennae are extended forwards together. The insect then turns round. It does not usually test the surface by contact with the antennae, though it may occasionally do so.

If the voile floor of the arena rests on the arm, one-half being separated from the skin by metal foil, the antennal movements occur as before. But on the side exposed to the skin the louse occasionally stops and reaches downwards with the antennae. When allowed to walk on the skin it soon stops and probes and sucks blood. During this process the antennae are spread out and in close contact with the skin.

If the floor rests on a warm stage at 30° C. with wet and dry blotting paper below the two halves respectively, the louse often stops dead for a few moments when the antennae *alone* extend into the moist side; it then retreats backwards or turns round.

When one half of the arena is covered with woollen stockinet and half with silk, the same antennal movements take place. As the louse walks it is evident that the antennae and the legs are constantly being stimulated by contact with upstanding fibres in the wool; whereas on the silk, only the tips of the legs are in contact, and the antennae on the rare occasions when they are lowered to the surface.

Senses of smell and humidity

These observations suggest that the senses of smell and humidity are located in the antennae. The antennae were therefore removed from a number of insects proximal to the basal segment, and it was found that reactions to smell and humidity had disappeared. A detailed study of the antennae in relation to these senses was therefore carried out. The humidity sense was tested throughout by offering a choice of 95 % and 76 % R.H. The sense of smell was tested by means of the avoidance of "odourless distillate" (p. 85) to which very few normal insects are indifferent.

In preliminary experiments the fifth antennal segment on both sides was cut through with scissors in a number of lice under ether. In some cases the

segment was only partially removed, but in all the thin-walled sensilla at the tip were eliminated. These insects were tested 18 hr. later. In all of them the reaction to the smell of "odourless distillate" had been eliminated, but in several the humidity reaction still remained. This suggested that the peg organs at the tip are the organs of smell (as Müller (1915) supposed) and that the tuft organs are the organs of humidity. This idea was therefore tested systematically.

The lice were lightly etherized and the sensilla covered with cellulose paint applied by means of the finest entomological pin bent at the point into a minute hook. The insects were in two groups: (i) with the apical peg organs alone covered, (ii) with the dorso-lateral aspect of the fourth and fifth segments covered but the peg organs left exposed. The accuracy of covering was confirmed with the high power of the microscope and those insects discarded in which the paint had not the desired distribution. The insects responded normally 3 or 4 hr. later; the reactions were often confirmed after 24 hr.

Table 1

Treatment	No. of lice	Humidity +	Smell +
Peg organs covered, tuft organs exposed	25	20	1
Tuft organs covered, peg organs exposed	20	0	19

Table 1 summarizes the results obtained and Fig. 30 gives two typical examples. Five out of twenty-five insects were indifferent to humidity although the tuft organs were exposed, and one out of twenty was indifferent to the smell of "odourless distillate" when the peg organs were exposed; but the results strongly support the conclusion that the tuft organs are sensitive to humidity and the peg organs to smell. There was one exception in which the peg organs were covered and the insect still reacted quite definitely to odourless distillate. The covering in this case was certainly complete, the result is therefore unexplained; but the covering was exceedingly thin at some points; possibly the odour penetrated through this thin layer to the sense organs.

An attempt was made to see if the tuft organs show any visible change when exposed to alterations in humidity. Lice killed with chloroform were placed in the small gas chamber previously described (Wigglesworth, 1930, 1935) and air first at 0 % R.H. and then at 95 % R.H. passed over them while the tuft organs were watched under the 4 or 2 mm. objective of the microscope. No movements in the fine hairs of the tuft could be detected with certainty.

In few insects has the humidity sense been located. Pielou (1940) has shown that in the adult mealworm beetle *Tenebrio* it is strictly confined to the antennae, and by amputation of the antennae at different levels has concluded that the pit peg organs and peg organs are the sensilla responsible. These are also regarded as the true olfactory organs. The results therefore suggest that the apparent response to humidity in this insect may perhaps be a response

to the altered perceptions of the olfactory organs in the drier or moister air; or alternatively, that changes in the humidity of the air may so affect the thin-walled olfactory sensilla as to serve as stimuli to them. In spiders, also, Blumenthal (1935) concludes that the "tarsal organ", a deep pit with one or several peg organs arising from the floor, responds to both humidity and smell.

In *Pediculus*, however, the two senses seem quite distinct. The "tuft organs" are an entirely new type of humidity receptor. The rounded "peg organs" on the other hand, are the commonest type of olfactory organ. Whether the sharply pointed organs have a different function has not been determined (cf. p. 98).
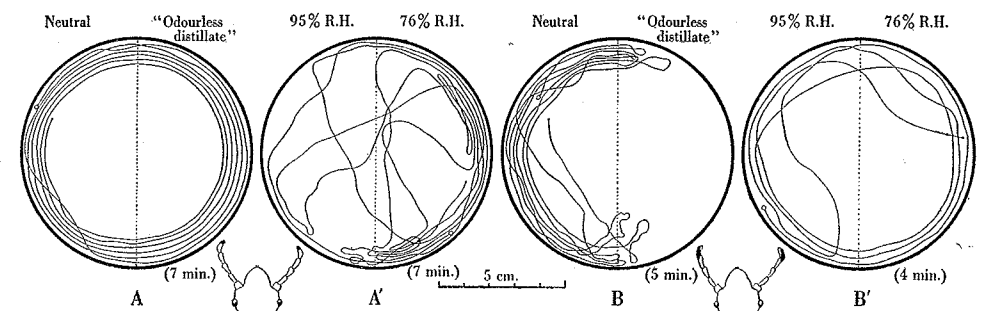
Fig. 30. A, A', reactions of louse, with peg organs alone covered, to smell and humidity. B, B', reactions of louse, with the tuft organs alone covered, to smell and humidity.
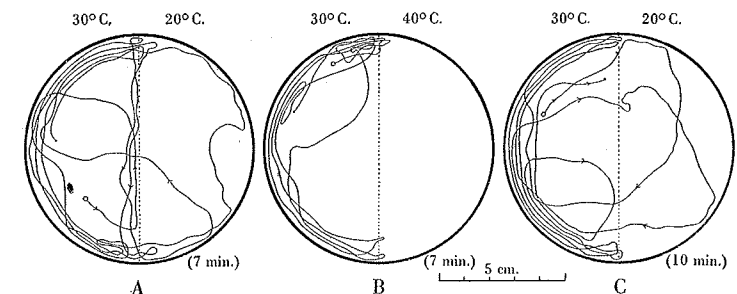
Fig. 31. A, B, reactions to temperature in lice deprived of both antennae. C, reaction to temperature in louse deprived of both antennae and anterior part of head.

Sense of temperature

The temperature sense is not confined to the antennae. Fig. 31 A shows that in a louse in which the antennae had been removed 24 hr. previously, exposed to 30° C./20° C., the avoidance of 20° C. may be as efficient as in the normal insect. And Fig. 31 B shows efficient avoidance of 40° C. in a louse similarly treated. Even when the antennae are removed and the head cut through with scissors in front of the antennal sockets (the wound being sealed with paraffin) there may be complete avoidance of 20° C. (Fig. 31 C).

Thus the sense organs responding to temperatures above and below the optimum certainly occur elsewhere besides the antennae. The effect of removing the antennae on the delicacy of the responses has not been systematically tested. But the sensitivity to high temperatures at least is certainly reduced. Thus in the normal louse avoidance of 40° C. is almost complete; but in lice without the antennae it is absent more often than not. Homp (1938) likewise observed that lice deprived of their antennae come closer to a very hot object; and Weber (1929) noted that *Haematopinus* without the antennae wander more widely in a temperature gradient, particularly at the hot end.

The temperature sense therefore resides probably in the antennae as well as elsewhere; but the sense cannot be ascribed to any particular sensilla. In
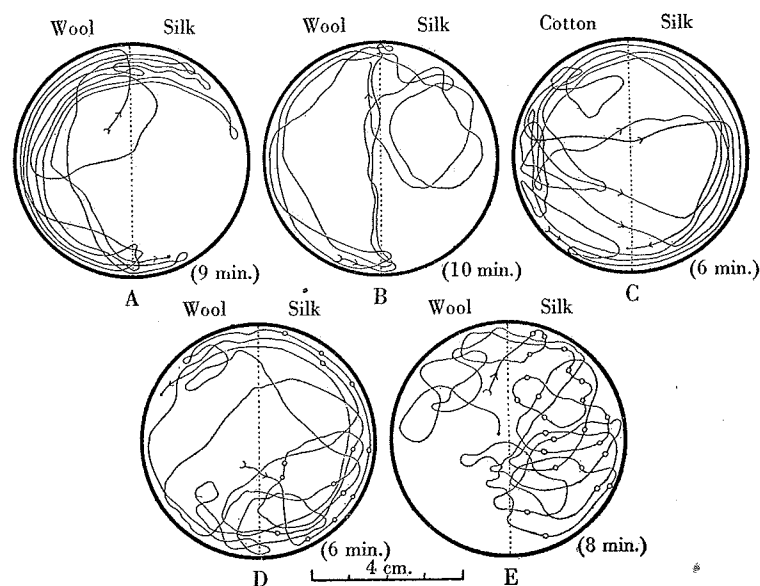

Fig. 32. Reactions to contact in lice deprived of both antennae. In B the anterior part of head also removed. The circles in D and E indicate the spots where the louse stopped and probed.

the bug *Rhodnius*, in which there is a very delicate temperature sense confined to the tips of the antennae, there is some evidence that the sense organs concerned are the innumerable finely pointed, relatively thick-walled hair sensilla (Wigglesworth & Gillett, 1934*a*). It is just possible that the pointed members of the group of peg organs on the fifth antennal segment have this function in *Pediculus*.

Sense of contact

We have seen that when the louse moves on rough material the antennal hairs are constantly being stimulated. But after removal of the antennae (Fig. 32 A) or of the antennae plus the anterior part of the head (Fig. 32 B) the preference for woollen stockinet as compared with silk still persists; although,

as in the normal louse, this response may disappear in the course of an experiment.

A response seen several times in the louse without antennae, though never in the normal insect, was a preference for the smoother material (Fig. 32 C). This is probably associated with the feeding reaction. Homp (1938) observed and I have confirmed that lice without antennae will repeatedly probe a warm smooth surface, whereas intact lice nearly always need the additional stimulus of smell.[1] Thus Figs. 32 D, E, show the tracks of lice without antennae, which had an obvious preference for the silk. The points where they stopped and probed the surface are indicated by circles. Later these insects became indifferent and ceased probing.

In these reactions to contact, therefore, organs all over the body are concerned, and orientation by contact stimuli is possible without the antennae.

Function of chordotonal and campaniform organs

These are generally regarded at the present time as proprioceptive organs recording the position of the appendages or the strains set up in them by their own movements (Wigglesworth, 1939).

We shall see that the appreciation by the insect of its own antennal movements is probably an important factor in the orientation of the louse at the boundary of a steep gradient of humidity or smell. The Johnston's organ and chordotonal organs in the second antennal segment probably serve this function.

In the movements of the legs, abduction and adduction occurs proximal to the coxa; flexion occurs chiefly between coxa and trochanter and between femur and tibia (Fig. 29 A). The campaniform organs, lying ventrally and laterally at the distal end of the relatively fixed trochanter, are well placed to detect strains in the limb caused by any resistance to these movements (cf. Pringle, 1938).

MECHANISMS OF ORIENTATION

Introduction

We must now attempt to define the mechanisms by means of which the louse orientates itself in relation to the various stimuli we have been considering.[2]

Simple mechanisms of orientation are classified as: (i) *kineses*—effects exerted by stimuli on the *rate* of random movements of the animal, and (ii) *taxes*—movements which result from a discrimination of the *direction* of stimulation.

[1] Homp calls attention to the analogous behaviour of ticks which will feed on any host if their Haller's organ is removed (Hindle & Merriman, 1913). A somewhat similar response is shown by *Rhodnius*, which will probe moving objects of all kinds when deprived of the senses of temperature and smell by removal of the antennae (Wigglesworth & Gillett, 1934*a*).

[2] In this section I have made extensive use of the modified classification of mechanisms of orientation drawn up by Fraenkel & Gunn (1940). I am greatly indebted to Dr D. L. Gunn for allowing me to use the proofs of this work in advance of publication.

Kinesis may be subdivided into (*a*) simple effects of the intensity of stimulation on the rate of movement (*orthokinesis*), and (*b*) effects on the frequency of turning, that is, on the rate of change of direction of movement (*klinokinesis*).

Taxes or directed movements may be subdivided into (*a*) movements whose direction is dependent on the comparative intensities of stimulation acting simultaneously on bilateral sense organs (*tropotaxis*), and (*b*) movements whose direction is dependent on the comparison of intensities of stimulation on each side by regular deviations of the body or the antennae; that is, by the comparison of intensities which are successive in time (*klinotaxis*).

In the past klinokinesis and klinotaxis have been included together under the terms "avoiding reaction", "trial and error" or "phobotaxis" (Kühn, 1919; Fraenkel, 1931); but the fact that in the former the movements are random, while in the latter the movements are directed, is considered by Fraenkel & Gunn (1940) a sufficient reason for their separation.

In the movements of an animal the mechanism of orientation may of course change from moment to moment; and even at the same instant more than one mechanism may be operating.

Orientation to light

Sudden exposure to bright light causes an arrest or reduction in the movements of the louse (p. 89). This is an example of negative "orthokinesis". Acting alone it would tend to keep the louse exposed to the light; but since this insect remains chiefly in darkness, it cannot be an important element in the light response.

Some individuals exposed to a bright light begin to change direction frequently and follow a convoluted course (Fig. 25). This is an example of "klinokinesis". As will be seen below it will tend to restore the insect to the dark.

It is obvious, however, that orientation to light is primarily a directed response determined by the comparison of the light coming from different directions. If one eye is covered with black cellulose paint and the louse is then exposed in an arena uniformly lit from above so as to give a surface illumination of 500 metre candles, it circles continuously towards the covered side (Fig. 33). It is clearly the simultaneous comparison of stimulation in the two eyes which is important in determining the direction of movement—an example of "tropotaxis". As in other insects, the circus movements become progressively weaker as the exposed eye becomes adapted to the light; they have generally ceased in half an hour or so. The circus movement is much more pronounced in an arena with white walls (Fig. 33 A); in an arena with black walls the louse tends to cling to the dark surface (Fig. 33 A'); indeed the dark wall may eliminate the circus movement altogether (Figs. 33 BB').

These results emphasize once more the importance of horizontal light in

the orientation of the louse. This is doubtless correlated with the position of the eyes, which are exactly lateral.

The orientation of an insect to a relatively small dark object (Figs. 27 C, D) is sometimes termed "skototaxis". Probably, however, in the louse at least, it is merely another manifestation of the tropotactic response. The formation of images by the eyes must be almost non-existent; but the dark spot in the horizontal plane will reduce the total light stimulation in one visual field so that the insect is deviated towards it. The effect naturally increases as the object comes nearer (cf. Fig. 27 D).
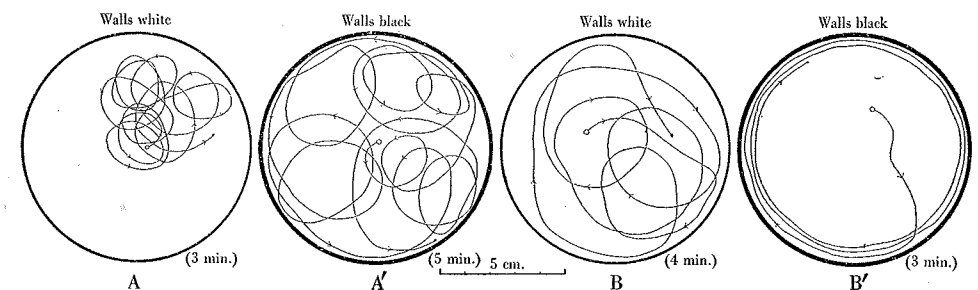

Fig. 33. Circus movements in lice with one eye covered. A, left eye covered, walls of arena white. A', the same, walls of arena black. B, right eye covered, walls of arena white. B', the same, walls black.

Orientation to smell and humidity

The methods of orientation to these two stimuli agree in almost every respect; they may therefore be considered together. On entering a mildly unfavourable region (Figs. 16 B, C; 20 B, C) the louse no longer walks straight round the periphery of the arena but follows a convoluted course, changing its direction repeatedly. This is an example of "klinokinesis". Under the conditions of experiment here used it may cause the insect to remain much longer than it otherwise would on the unfavourable side. But after a time it becomes adapted to the weak adverse stimulus; it then goes straight once more and so regains the favourable side.

If the louse is more reactive or the adverse side of the arena more repellent, the insect may turn round instantly on reaching the boundary or may walk backwards (Fig. 10 B; 17 B; 20 A). This is the limiting case of "klinokinesis"; it is often referred to as the "shock reaction" or "avoiding reaction". But as Ullyott (1936) points out in the case of the planarian *Dendrocoelum*, and as is obvious from an inspection of the tracks of lice given here (e.g. Fig. 10 C; 16 C), there are all intermediate stages between the two reactions—if the insect turns soon enough and sharply enough it will regain the favourable side; if the turn is delayed or insufficient it may remain in the adverse half of the arena.

It is obvious in some experiments, however, that the response at the

boundary, where there is a steep gradient in the intensity of stimulation, is a *directed response*. This is most evident when the insect approaches the boundary obliquely. It is true that it may occasionally turn into the adverse zone—as would be expected if the direction of turning were entirely random as in "klinokinesis"—but in the vast majority of instances the louse inclines away from the boundary and back into the favourable side. Fig. 10 B is a typical example.[1]

What is the nature of this directed response? If it is by tropotaxis, the elimination of the sense organs on one side ought to cause the insect to turn always towards this side on reaching the boundary or to circle always to this side in the adverse half of the arena.

Eight lice were lightly etherized and the fifth antennal segment and the terminal half of the fourth segment covered with cellulose paint, on the right side in four insects, on the left side in four more. They were then exposed in an arena with "odourless distillate" below one half; their tracks were copied
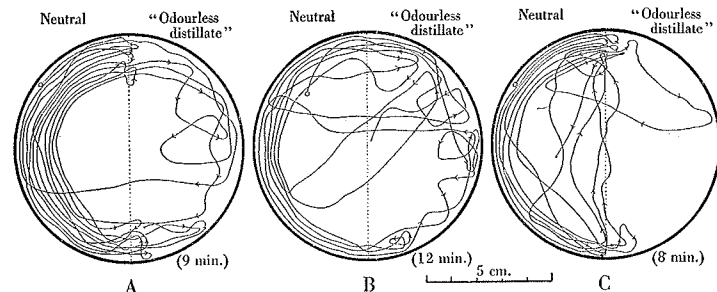

Fig. 34. Tracks followed by lice, with the organs of smell on one side covered, in the presence of a repellent odour. A, right antenna covered; B, C, left antenna covered.

and the number of turns made in each direction observed. As can be seen in Fig. 34 they turn indifferently towards the exposed or the covered antenna. This is so during the abrupt turns at the boundary (Fig. 34 A) and during the sinuous movements after entering the adverse side (Fig. 34 B). Out of a total of 116 turns[2] made in the course of these records sixty were towards the covered side, fifty-six towards the uncovered side. In tests with 95 %/76 % R.H., out of forty-three turns in the adverse half, 23 were towards the covered antenna, twenty towards the exposed.

In these experiments, with the sense organs on one side completely out of action, the difference in stimulation on the two sides must be far greater than anything encountered by the intact insect. Yet this has no significant effect on the direction in which the louse turns on encountering an adverse stimulus.

[1] Hase (1915) has described the pursuit of the finger by the louse "like a hound on the trail"; here also the orientation appears to be directed.

[2] Each deviation from the normal straight course has been counted as a turn—whether this causes the insect to go through 180° and reverse its direction or whether it merely causes it to incline 90° from its previous course.

Further, it is evident, from Fig. 34 C for example, that the louse with a single antenna still retains the faculty for directed orientation at the boundary.

One must therefore conclude that this orientation is effected not by the comparison of simultaneous stimuli in the bilateral sense organs (tropotaxis), but by comparison of stimuli at successive moments (klinotaxis). Gunn & Pielou (1940) obtained similar results in the orientation of *Tenebrio* to humidity. In this reaction the swinging of the antennae and head from side to side (p. 95) is doubtless important. The scolopidial organs in the second antennal segment probably serve as proprioceptors to indicate the position of the antennae at the moment of greatest stimulation (cf. Sioli (1937) on *Cimex*). A similar method of orientation was described in *Rhodnius* (Wigglesworth & Gillett, 1934a); but here the long antennae are moved independently, so that the orientation can be effected by the insect at rest.

An important factor in the behaviour of the louse is the adaptation shown in a constant field of stimulation. As Ullyott (1936) has pointed out, if the animal merely went straight in a favourable zone and followed a sharply convoluted course on entering an adverse zone, this would result in its being trapped in the unfavourable region. In fact it gradually becomes adapted, makes increasingly long excursions before turning (unless it should chance to enter a still more unfavourable region) and finally goes straight. On reaching a favourable zone it continues to go straight.

This adaptation to an adverse field of stimulation is well seen in Fig. 10 C. In the case of the high humidity of 95 %, the "adaptation" may be so complete after prolonged exposure that the response is reversed and turning may occur on entering the 76 % R.H. side. Indeed, what constitutes an "adverse" region depends to a large extent upon the experiences in the immediate past; that is, on the state of adaptation. Blotting paper or smooth silk cause increased turning only if the louse has been on rough material (p. 87); clean voile constitutes a favourable zone if the other half of the arena contains "odourless distillate"; it forms an adverse zone and induces active turning if the other half lies above man-scented cloth (pp. 83, 85). The response may be regarded as an elementary form of memory.

Orientation to temperature and contact

Orientation to temperature is clearly of the same kind as to humidity and smell; that is, "klinokinesis" (Figs. 3, 4). Homp (1938) likewise concluded that this orientation was chiefly "phobotactic". But she suspected that there was a directed element in the response when close to the source of stimulus; and on the assumption that the antennae are the chief site of the temperature receptors she removed the antennae from one side in twelve lice. When these were exposed to a uniform temperature of 29° C., seven of them turned more frequently towards the intact side, five towards the operated side. She interprets these results as indicating "tropotaxis", but the figures are quite unconvincing.

I have repeated the experiments and obtained the same results. Removal of one antenna is very liable to induce a bias and cause the insect to circle in some cases towards and in some away from the injured side. But, allowing for these insects, no evidence could be obtained that the louse turned more frequently away from the intact antenna upon entering an adverse temperature of 20 or 40° C., or towards the intact antenna in a favourable temperature of 30° C.

The directed orientation that occurs along the boundary between the temperatures is therefore again probably "klinotactic". As we have seen (Fig. 31 A) it may be shown by lice deprived of both antennae. Tropotaxis would be more likely to occur in response to radiant heat. But as we have seen (p. 76) within the range of temperatures employed the louse does not react to radiant heat.

The mechanism of *orientation to contact* appears to be the same as that to the other stimuli. It consists of an increased frequency of turning upon a smooth surface (klinokinesis), provided that the insect has recently experienced a rough surface. Combined with this is an orthokinetic effect—the louse moves more actively and is less disposed to settle down and come to rest on a smooth surface.

SENSORY RESPONSES AND THE NORMAL ENVIRONMENT

The warmth, the smell and perhaps the smooth surface of the skin are important factors in inducing the feeding response in the louse. But the reactions dealt with in this paper are those shown by fully gorged lice; they are the responses concerned with keeping the louse within its normal environment.

These responses have an obvious bearing on many familiar facts about the habits of the human louse. The optimal zone of temperature, 28–31° C., is that which exists between the skin and the clothing (Martini, 1918). The humidity below the clothing in men at rest is rather low, 23°–70 % R.H. (Mellanby, 1932; Marsh & Buxton, 1937); it will increase in the outer layers of the clothing as the air is cooled, and will increase during sweating. It has been observed by Dr John MacLeod and Dr H. J. Craufurd-Benson (personal communication) that the number of lice on the inner garments of infested labourers decreases markedly after work entailing profuse sweating; and Nuttall (1917) has attributed the reduction in the number of lice in summer, at least in part, to the increased moisture beneath the clothing. Lice tend to leave a patient with fever (Lloyd, 1919); here the high temperature and increased humidity may both operate. The preference of *Pediculus* for the smell of man (p. 83) is in accordance with the rarity with which this louse is found on other hosts. The attraction to rough materials, and to the smell of other lice and of their excreta explains the aggregation of lice in the seams of clothing. And the orientating effect of light reaching the eyes horizontally

explains the comparative rarity with which the louse strays onto the exposed parts of the body.

But beyond these obvious uses of the reactions studied the experiments throw some light on the methods by which the louse reaches environments favourable to it. Fig. 35 is the hypothetical track of a louse approaching a centre from which emanates some favourable diffuse stimulus of temperature, smell or humidity. The louse has become adapted to the unfavourable environment and therefore goes approximately straight. On entering the zone which provides the favourable stimulus it shows *no* response. But once having experienced this stimulus it makes turning movements as it leaves the zone again. Thus the insect, turning when the intensity of stimulus falls, keeping
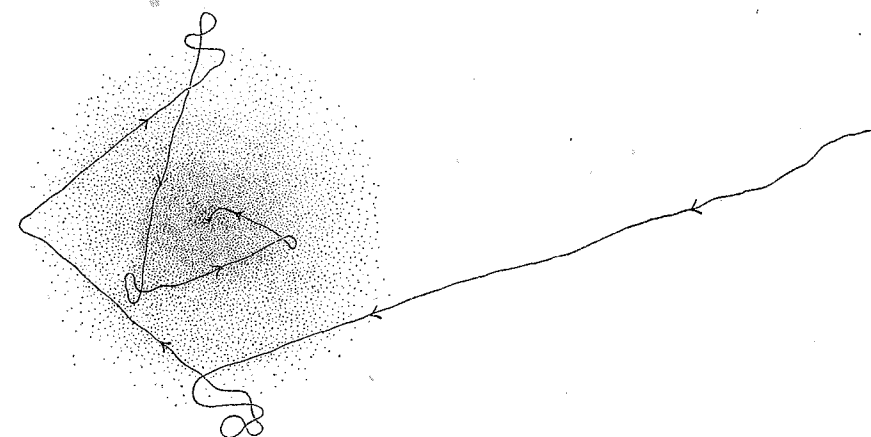

Fig. 35. Hypothetical track of louse approaching the centre of some favourable diffuse stimulus.

straight while the stimulus remains constant or increases, is led to the centre of the favourable zone. When the gradient is steep, directed responses effected by the comparison of stimulation in each direction in turn are also added (p. 103).

In this way the louse will be led by successive stages into those sites where the stimuli of temperature, smell, humidity and contact are optimal. In respect to light, the same mechanism operates to some degree; but here the directed element in the stimulus is far more important; it is particularly effective when the louse is already in the dark (p. 90).

Finally, it may be emphasized once more that, except perhaps in a very steep gradient, the louse shows no sign of being *attracted* by a favourable stimulus. It simply makes turning or avoiding movements when such a stimulus ceases to operate; just as it makes avoiding movements on encountering a stimulus that is repellent.

SUMMARY

(i) *Sensory responses*

The reactions of the body louse to temperature, humidity, smell, contact and light have been tested in an arena divided into two halves.

Temperature. A temperature of 29–30° C. is preferred before 32° C. or 27° C. As the alternative temperature rises above 32° C. or falls below 27° C. the avoidance becomes increasingly strong. Different individuals vary in sensitivity.

These results are in accordance with those observed in a linear gradient of temperature, in which the lice collect chiefly in the region from 28 to 31° C.

The response is always to air temperature; there is no response to radiant heat from objects at 20–45° C.

Humidity. The louse is generally indifferent to humidity over the range from 10 to 60 or 75 % R.H. Higher humidities are avoided. But when offered two humidities the choice is greatly influenced by the conditions experienced by the louse in the immediate past; it avoids any change; hence different individuals may show quite different responses. Moreover, when offered the choice of very moist air (95 % R.H. or over) and very dry (47 % R.H. or under) the louse becomes more readily adapted to the moist air and begins to avoid the dry.

Smell. The louse prefers cloth that has been in contact with human skin to clean cloth or cloth smelling of dog or rabbit. The smell of other lice and of their excreta is also attractive. Many substances serve as repellents; a refined petroleum with a very faint odour has been chiefly used for the experiments.

Contact. When offered smooth and rough materials the louse chooses the latter. It moves more rapidly on smooth materials and does not come to rest so readily. It shows little response to air currents unless very strong, when they are avoided.

Light. The movements of the louse are arrested or retarded by sudden exposure to a bright light, and sometimes it may show avoiding movements. But the movement of the louse towards dark places is mainly a response to directed light received by the horizontally placed eyes. Slight differences in the light received from different directions exert a much greater effect if the louse is exposed to a low level of general light intensity.

The movement of the louse towards relatively small dark objects is probably a manifestation of the same response.

(ii) *Sense organs*

The antenna bears three types of sensillum. (i) *Tactile hairs* on all segments. (ii) *Peg organs* at the tip of the fifth segment; these are shown to be olfactory receptors. (iii) *Tuft organs* on the fourth and fifth segments; these are shown

to be humidity receptors. There are also a Johnston's organ and chordotonal organs in the second antennal segment.

Tactile hairs occur around the mouth parts, and on the legs, etc.; *chordotonal organs* in the femur, tibia and tarsus of each leg; and there is a group of five *campaniform organs* on the lower surface of each trochanter.

The *eyes* are described.

The temperature sense is widely distributed over the body; orientation to high or low temperatures still occurs after removal of the antenna and the anterior half of the head, although the sensitivity is reduced.

(iii) *Mechanisms of orientation*

The mechanism of orientation to the diffuse stimuli of temperature, humidity, smell and contact is the same. It consists in an increase in random turning movements upon entering a zone of adverse stimulation (phobotaxis or klinokinesis). This may result in an immediate return to the favourable zone if the response is strong and immediate, or in a long convoluted course in the unfavourable zone if the response is weak or delayed.

Sensory adaptation is very important in this response. For the increased rate of turning disappears after prolonged exposure to the unfavourable stimulus and only appears again after a favourable stimulus has been experienced.

There is no evidence that the louse is "attracted" by a favourable stimulus. It shows only an avoidance of zones where a "repellent" is present or where a favourable stimulus (recently experienced) is absent.

Where there is a steep gradient between the adverse and favourable zones the louse may show a directed orientation. This appears to be brought about by a comparison of successive stimulation to right and left by swinging the body and antennae from side to side (klinotaxis). There is no evidence that the comparison of simultaneous stimulation in the antennae (tropotaxis) plays any part.

In orientation towards darkness, increased turning in a bright light (klinokinesis) plays a small part. The comparison of stimulation by horizontal light received in the two eyes (tropotaxis) is far more important. If one eye is covered the louse makes circus movements towards this side.

The relation of these responses to the biology of the louse is discussed.

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