



# HOKKAIDO UNIVERSITY

Title	Perception of Movement in Compound Eyes Studied by Optomotor Reaction of Mosquitoes (With 17 Text-figures)
Author(s)	SUZUKI, Kenji
Citation	北海道大學理學部紀要, 14(3), 349-380
Issue Date	1960-12
Doc URL	<a href="https://hdl.handle.net/2115/27318">https://hdl.handle.net/2115/27318</a>
Type	departmental bulletin paper
File Information	14(3)_P349-380.pdf



# Perception of Movement in Compound Eyes Studied by Optomotor Reaction of Mosquitoes<sup>1)</sup>

By

**Kenji Suzuki**

(Zoological Institute, Hokkaido University)

(With 17 Text-figures)

## Contents

Introduction .....	349
Material and method .....	351
Experimental results .....	353
I. The relationship of the responses to the velocity of a moving pattern .....	353
II. Responses to various alternate patterns of black and white stripes .....	357
III. Responses to movement of black stripes arranged at various distances on a white ground .....	364
IV. Responses to a definite stripe pattern seen through slits of various widths .....	367
V. Responses when neighbouring ommatidia were each given stimuli of different strengths .....	370
VI. The relationship between responses and resting postures in the glass container .....	372
Discussion .....	375
Acknowledgement .....	378
Summary .....	379
Literature cited .....	380

## Introduction

The use of the optomotor reaction is one of the most effective methods to study the optic reactions in animals. Animals which were placed inside of a rotating cylinder having a pattern of alternate black and white vertical stripes pursue the direction of revolution of the cylinder with heads, eye balls or bodies. Such responses are seen also in animals placed on a turn-table, when the table rotates. This behaviour well known as the optomotor reaction was first described by Radle (1903) in various insects (quoted by Buddenbrock, 1952). Schlieper (1927) established the basis of procedure for studying colour sense of animals by the use of this reaction. Since the time of these two authors, optomotor reaction has been observed in diverse animal groups from the lower invertebrates to the vertebrates. With respect to the mechanism of the optomotor reaction and the biological

---

1) Contribution No. 489 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

*Jour. Fac. Sci. Hokkaido Univ. Ser. VI, Zool., 14, 1960.*

meaning of the response, numerous arguments have been presented up to the present, but the opinions of different investigators seem to be not always consistent. Schlieper considered the essence of the optomotor reaction as a maintenance of a constant visual field, namely, a menotaxis: in other words, in Schlieper's opinion, the optomotor reaction is an accumulation of innumerable small corrective movements by means of which animals tried to keep the image of an object constantly at the same place on the retina. This opinion is still accepted today as a general interpretation of optomotor reaction (Wigglesworth, 1950; Buddenbrock, 1952). However, there is considerable opposition to this view. Gaffron (1933) claimed from the results of experiments on flies and dragonfly larvae that the optomotor reaction is not menotactic, but rather that a rotatory motion of the animal body occurred around the axis of the environmental movement. The grounds of his allegation are as follows: the fly which was accommodated in a small glass tube inclined the body towards the left or right to the direction of the striped cylinder surrounding the tube, and when a glass rod was brought down from the center of the cover into the container, the fly ascended the rod spirally, not vertically, from the lower part of the rod upwards in a direction corresponding to the rotation of the cylinder. Gaffron thought that such a response makes it almost impossible to maintain a constant pattern on the retina. But it does not appear that the inclination of the body on this occasion is not explainable by the principle of photomenotaxis. From the results of the experiments making use of a double cylinder, Hertz (1934) concluded that the optomotor reaction of a fly, *Pollenia* occurs because of the perception of environmental movement and at least, for that fly, displacement of image on the retina by the self-movement does not accord with movement of the outer object. Both Gaffron and Hertz, however, made no extensive experiments quantitatively to support their assertions. In this connection, Shima (1942) presented some interesting data from his experiments on a water-spinner, *Dineutus orientalis*: the velocity of the beetle in motion was never the same as that of his patterned cylinder, and in the velocities of the cylinder greater than 2 seconds per rotation, the beetle always moved faster than the cylinder.

Sälzle (1932) first used the concept of "forced movement" to explain the response of *Aeschna* larvae (dragonfly) to a moving object. *Aeschna* larvae followed the object with their eyes as far as it moved in their visual field. This behaviour may be called a kind of nystagmus. Tonner (1938) regarded nystagmus as a specialized case of optomotor reaction, and distinguished it from the optomotor reaction in the strict sense. According to him, the optomotor reaction is not a response for fixing the object in an area of the most acute vision, 'Forvea centralis' in the frontal area of the eyes (Fixierreaktion), but a response of reacting to changes in the whole pattern of the surroundings in the lateral area of the eyes. Further Tonner says that in insects requiring the visual fixation of some objects in their life (bee, dragonfly etc.), the number of ommatidia in the frontal area is exceedingly abundant, whilst in insects in which fixation is not always indispensable (butterfly, mosquito etc.), the number is almost the same in any sections of the eyes. Therefore, the presumption is derived from Tonner's opinion that mosquitoes are scarcely able to make the fixation response; this needs to be experimentally examined. Analyzing the optomotor reaction of *Drosophila melanogaster*, Gavel (1940) emphasized that the response is a forced horizontal movement of the body axis occurring around the axis parallel to the rotatory axis of the pattern. This might be regarded in some degree as an extension of Sälzle's opinion stated above. But Gavel expressed opposition to Gaffron; the opinion of the latter is that the response is an up-and-down movement of the body axis generated around the axis parallel to the axis of motion of the surroundings.

Recently, in a study of the optomotor reaction of a beetle, *Chlorophanus viridis* by the use of a unique method, Y-maze-globe method, Hassenstein (1958) attached importance to the fact that perception of movement in the eyes of the beetle depends upon an alternation of stimuli in adjacent ommatidia; together with his collaborators, he (1959) attempted to analyze systematically the response to moving patterns by the principle of auto-correlation based upon an information theory.

As stated above, present knowledge related to the mechanism of the optomotor reaction is still far from perfect. The presently described study was carried out with the intention of clarifying the character of the optomotor reaction in mosquitoes and of obtaining a clue for the deduction of a general rule underlying the perception of movement in compound eyes.

**Material and method :** Mosquitoes used for this study were the commonest species in Sapporo, *Culex pipiens pallens* Coquillett and *Aedes vexans nipponii* Theobald: both species were collected in larval stages from the field and reared with yeast products in the laboratory. The most of the experiments were conducted using the females of *Culex pipiens pallens*, while *Aedes vexans nipponii* was employed for comparison with the above species in some experiments.

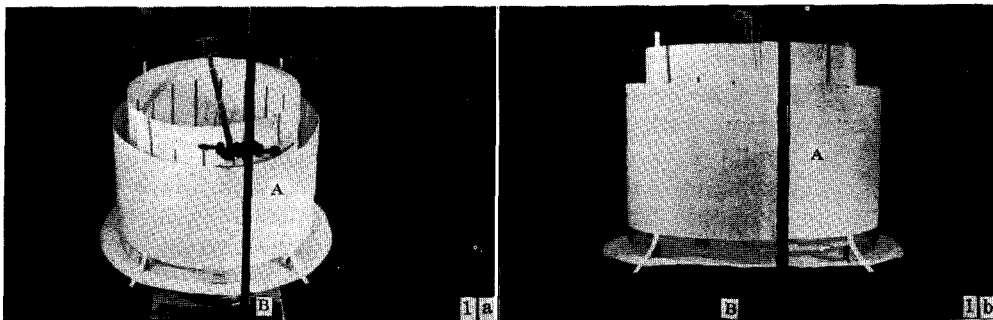


Fig. 1. The apparatus for this experiment (double cylinder system). a, the bird's-eye's view; b, lateral view.

The arrangement of the experimental apparatus is shown in Fig. 1. A large transparent cylinder (A; diam. 35 cm, height, 25 cm) of synthetic resin was installed on the rotatory axis of a record player (B): the cylinder revolves only in clockwise direction at a discretionary velocity within the range from 1 to 75 rotations per minute by operation of a transformer connected with an adjuster of the record player. At the center of the cylinder, a small transparent glass tube (diam. 12 mm, height, 45 mm) was hung, containing a single mosquito. From the outside, alternate patterns of black and white stripes in various widths were presented to the mosquito through the transparent surface of the cylinder. Resting postures of mosquitoes in the glass tube are divided as follows: 1. the case of keeping body axis in parallel with the axis of the cylinder, as seen in the mosquito

alighting on the side wall of the container (Fig. 2, A), and 2. the case of retaining body axis vertical to the rotatory axis of the outer cylinder, as seen in the mosquito alighting on the bottom of the container (Fig. 2, B). With the rotation of the patterned cylinder, in general, mosquitoes responded by turning the

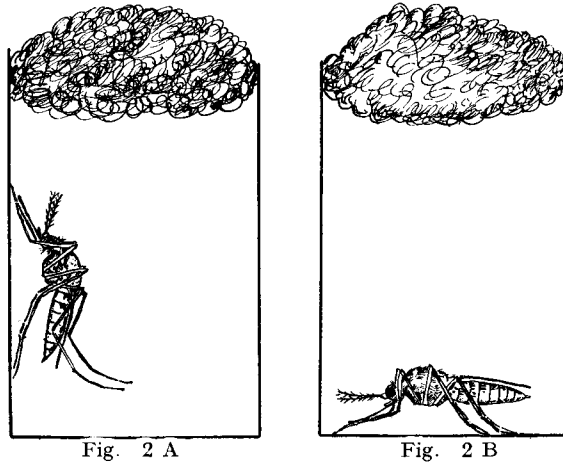


Fig. 2. Main resting posture of mosquitoes in a glass container. a, "vertical posture"; b, "parallel posture."

head, walking or flying in the direction of motion of the cylinder, but in some instances such as extremely high or slow speeds of the cylinder, mosquitoes were often observed to respond by walking or flying opposite to the direction of rotation of the cylinder. The degree of reaction in each experiment was evaluated by calculating the response number of 10 mosquitoes for 100 rotations of the cylinder from the formula,  $[(T-A)/(T+A+O)] \times 100$ , in which T expresses the number of responses to the direction of movement of cylinder, A the number of responses to the reverse direction of moving cylinder, O the number of cases not making any response to any objects in motion. The value calculated from this formula was termed the index of response for selecting direction of movement of object (ISD): positive 100 means that with the rotation of the cylinder, mosquitoes responded always by motion to the direction of rotation of the cylinder, and negative 100 means that responses were made without any exception in reverse direction to the movement of the cylinder. All experiments were conducted in a darkroom of which the temperature and relative humidity ranged from 23°C to 26°C and from 73% to 81% respectively. Illumination for the experiments was taken from four 60 watt accent lamps which were arranged at equal distances in a circle about 20 cm outward from the outer cylinder; the brightness was ca. 50 lux at the periphery of the inside of the cylinder.

### Experimental results

I. *The relationship of the responses to the velocity of a moving pattern*: The minimum angle of ommatidium in both sexes of *Culex pipiens pallens* and in males of *Aedes vexans nipponii* was each measured to be about  $3^\circ$  in the microscopic preparation of the eyes. The experiments were performed by the use of a vertical striped pattern of four black stripes placed at equal distances ( $87^\circ$ ) on a white ground; each stripe corresponds in width to the ommatidial angle of  $3^\circ$ . The results of experiments in females of *Culex pipiens pallens* are shown in Fig. 3.

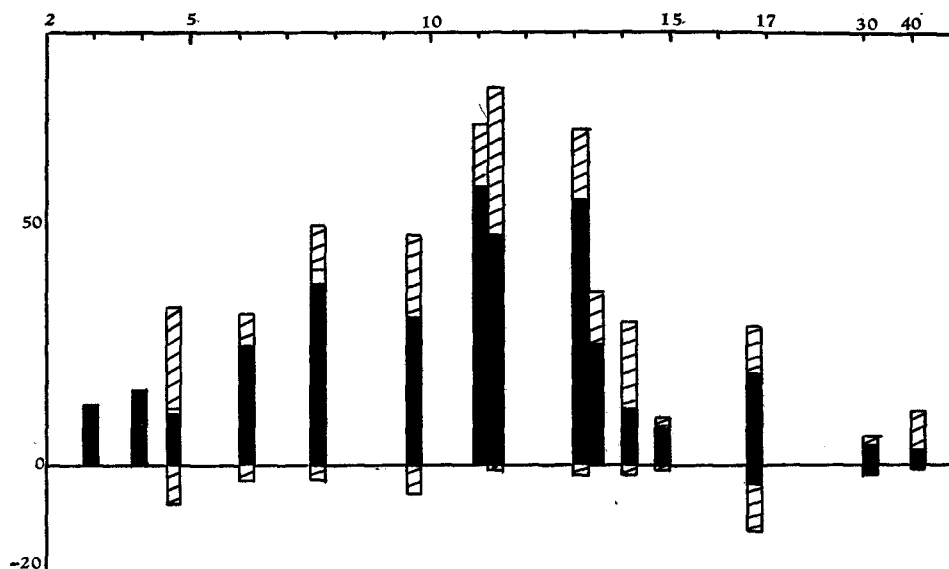


Fig. 3. Responses of *Culex pipiens* females to the rotatory velocity of a stripe-pattern composed of 4 black stripes which were placed quadrantally on white ground; each stripe approximately corresponds in width to the visual angle of an ommatidium. Abscissa, speed of pattern in rotation per minute; ordinate, response frequency (%). The responses to and against the moving direction of pattern are indicated respectively by the histograms above and below the horizontal base. Black, white and rods obliquely striate parts show each responses by turning head, responses by flying and responses by walking. These expressions are used through Fig. 3, 4, 5, 7, 8, 9, 10 and 11.

Optomotor responses of the females increased gradually with the speed-up of rotation of the patterned cylinder, reaching their peak at 11 revolutions per minute. From this point to 15 revolutions per minute, the responses went down rapidly in number, and at 17 revolutions per minute, recovered again to a fair number. To swift rotations such as 30 and 40 revolutions per minute, a few of the females was

well able to respond. Of the responses to every velocity, turning head always showed the highest ratio except in the cases of 4.5 and 14 rotations per minute; walking was the next, and flying was very rare. Furthermore, it was observed as to the direction of movement that the greater part of the optomotor reaction was made to the rotatory direction of the cylinder, while responses to the inverse direction were remarkably few in number. From these results, it may safely be said that optomotor reaction in the female depends greatly upon the speeds of the moving pattern and is mainly carried out with inclination of the head to the direction of movement of the pattern.

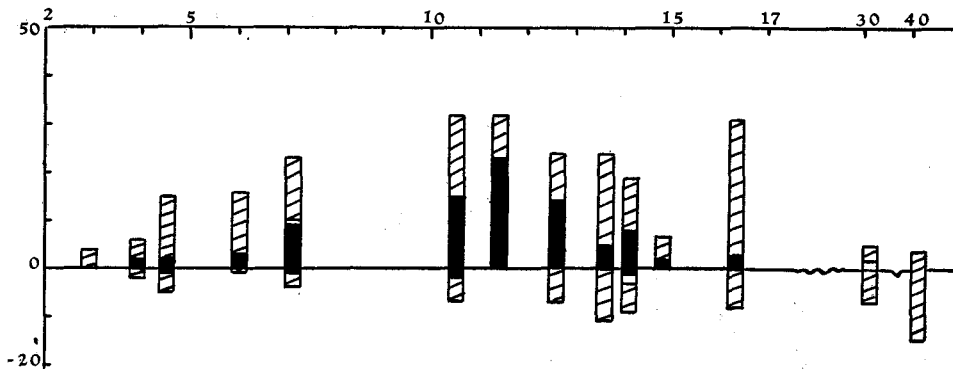


Fig. 4. Responses of *Culex pipiens* males to the rotatory velocity of the same striped pattern as in the females. Explanations as in Fig. 3.

In general, optomotor reaction in males of the same species was low in frequency as compared with the females (Fig. 4). The responses increased in parallel with the velocity of rotation of the patterned cylinder and arrived at a peak in 10.4 revolutions per minute; afterwards, they decreased with oscillation to 15 revolutions per minute and again, formed another peak at 17 revolutions per minute. Also in quicker velocities such as 30 and 40 revolutions per minute, a considerable number of responses was found. Thus, the males resemble the females in relationship of the responses to the velocity of the cylinder, but strikingly differ from the females in the following two qualitative aspects: namely, behaviour and the direction of responses. The males had a tendency to respond by walking inversely against the direction of movement of the cylinder. Especially, at velocities faster than 10 revolutions per minute, the response by movement to the direction in reverse to that of the cylinder were frequently repeated.

As seen in Fig. 5, the males of *Aedes vexans nipponii* are vastly different from *Culex pipiens pallens* described above in the relationship between responses and speeds of the patterned cylinder. The frequency of responses in *Aedes vexans*

*nipponii* was biased towards velocities less than 5.5 revolutions per minute with the peak attained at 2.6 revolutions per minute. From this point to 11 revolutions per minute, the responses gradually dropped against the increase of velocity of the cylinder, then slightly recovered at 17 and 28 revolutions per minute. As to the direction of responses and behaviour, *Aedes vexans nipponii* males formed a marked contrast to *Culex pipiens pallens* females; in the former species, responses by walking were the majority of the optomotor reaction, irrespective of the velocity of movement of the environment; inverse responses to the environmental movement were in particular abundantly observed at slow speeds less than 4 revolutions per minute.

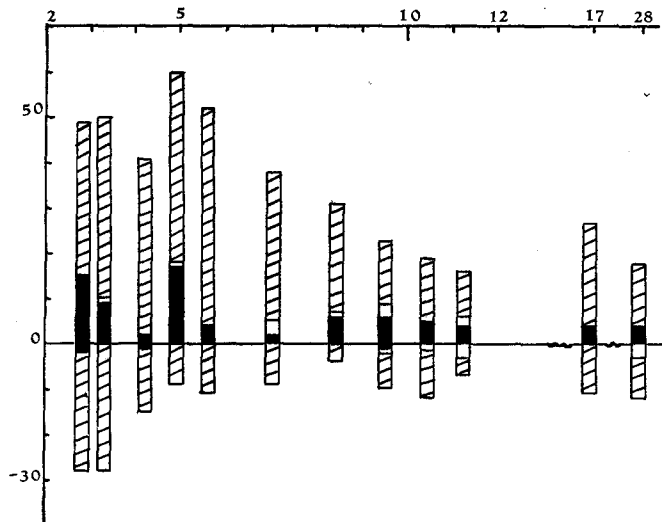


Fig. 5. Responses of *Aedes vexans* males to the revolving velocity of the same striped pattern as in *Culex pipiens* females. Explanations as in Fig. 3.

Fig. 6 illustrates the relationship between velocity of moving pattern and strength of optomotor responses expressed by ISD in *Culex pipiens pallens* females and males, and *Aedes vexans nipponii* males. According to the figure, ISD in each species of mosquitoes showed always positive values excepting the responses of *Culex pipiens pallens* males to quick rotations of the patterned cylinder (30 or 40 rotations per minute). This means that in velocities less than 30 rotations per minute, the mosquitoes used to respond selectively to the direction of movement of the cylinder (normal response), and in velocities above 30 rotations per minute, only *Culex pipiens pallens* males responded predominantly to the inverse direction to the movement of the cylinder. From a closer examination of the figure, it is revealed that responses of *Culex pipiens pallens* females indicated a unimodal

distribution at about the velocity of 11 rotations per minute of the cylinder within the range 2.5 to 40 rotations per minute; the males of the same species quite resembled the females in the progress of response frequency. On the other hand, normal responses in *Aedes vexans nipponii* males concentrated around the speed of 5 rotations per minute; consequently, distributed fairly slantingly towards slow velocities below 10 rotations. In the experiments on the optomotor reaction of a beetle, *Chlorophanus viridis*, Hassenstein (1959) observed a unimodal distribution of the responses to the alternate pattern of black and white stripes moving in

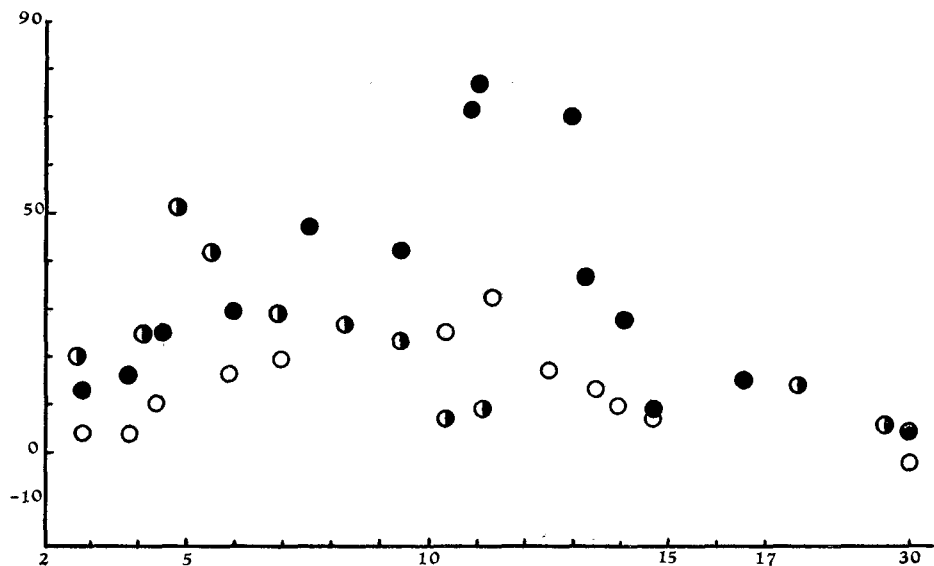


Fig. 6. The relationship between velocity of moving pattern and strength of responses expressed by ISD (see in text). The pattern used is explained in Fig. 3. Solid, open and semi-open circles indicate each results of females of *Culex pipiens*, males of the same species and of *Aedes vexans*. Abscissa, rotation number of pattern per minute; ordinate, ISD. Positive ISD shows that responses to the moving direction of pattern outnumbered those to the inverse direction and negative ISD the reversed instances.

various velocities of 1 to 82 rotations per minute, and explained this result by the addition and reduction of contour of moving striped pattern. The present writer holds the following opinion as to the change of responses to velocity of movement of pattern. Simultaneously with the rotation of an alternate pattern of black stripes on a white ground, a stimulus which was caught by a given ommatidium, constructs in the center of perception, the "field of impression", i.e., the expanse of impression. At slow rotations, intervals between stimuli are comparatively long, and the impression of a stimulus grasped previously by a certain ommatidium disappears

before the arrival of the next on-coming stimulus to the ommatidium in question; therefore, the impression of each stimulus is separately without accompanying the mutual connection sensible in the center of perception, hence, the perception of movement does not arise. With the increase of velocity of rotation of the pattern, the intervals between stimuli become shortened, and the fields of impression of each stimulus which are built up in the center of perception expand gradually up to the point of mutual contact in the peripheries of the fields; in other words, each single stimulus is followed by the next one before the first one has disappeared, thus the fade-out and -in of impressions continue alternately, which results in the clear perception of movement. In too quick rotations, before the field of preceding impression is formed with a sharp outline in the perception center, the next impression arrives at the center and unites the preceding obscure impression, thus two successive stimuli are perceptible as the almost simultaneous appearance of impressions. In this way, by mediating the spatial indication of stimuli to the appropriate temporal indication, the mosquitoes have ability to seize precisely the movement of surroundings. The divergence of peaks of the responses between two species used in this experiment may suggest that the rotatory velocities of the pattern suitable to the perception of movement vary according to the species.

*II. Responses to various alternate patterns of black and white stripes:* a) Experiments with various stripe patterns of which the black stripes were of width corresponding to 3 ommatidia ( $9^\circ$ ) and placed at equi-distances on a white ground. The experiments were executed with *Culex pipiens pallens* females by revolving the patterns at 11 rotations per minute. The mosquitoes responded sluggishly to the movement of black stripes placed at equi-distances of  $9^\circ$ ; inverse responses against the rotatory direction of the pattern occurred as many times as normal responses, that is, responses to the proceeding direction of the pattern (Fig. 7, the upper part). As a result of widening the distances between stripes, the normal responses increased and occurred exclusively in the range of distances from  $27^\circ$  to  $171^\circ$ ; the responses abruptly decreased at the distance of  $371^\circ$ , namely, in the pattern with a single black stripe on a white ground.

b) Experiments with various stripe patterns of which the white stripes were of width corresponding to 3 ommatidia and arranged at equi-distances on a black ground. As seen in the lower part of Fig. 7, responses underwent a striking change with changes of distances between stripes. The mosquitoes already responded 100% to a stripe pattern consisting of white stripes of  $9^\circ$  and distances of  $18^\circ$ . The responses declined numerically to a conspicuous degree at distances from  $89^\circ$  to  $351^\circ$ ; at this point, the result was greatly different from that of experiment a.

Interesting facts were observed by the comparison of the results of the above experiments a and b. When the ratio of width of stripes to distances was 3 : 18, responses to the pattern of white stripes on a black ground were by far better

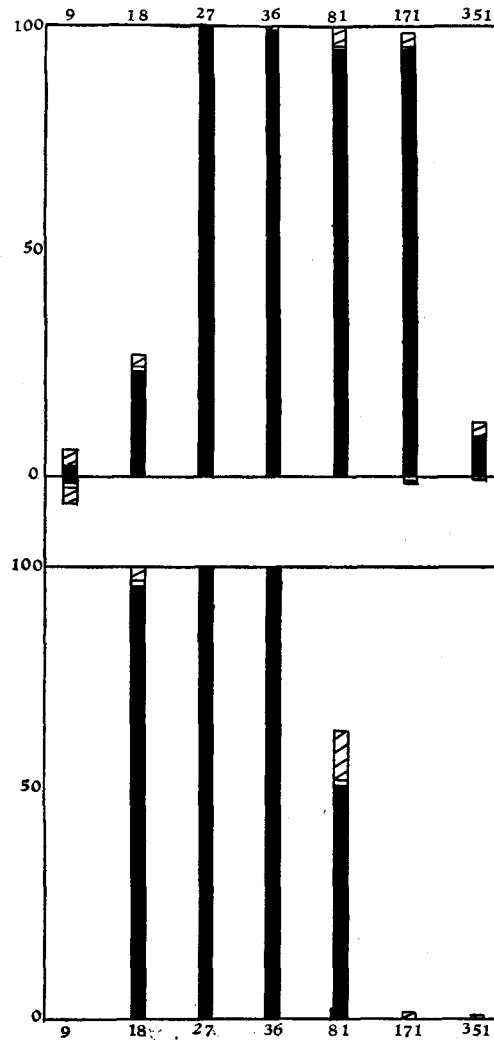


Fig. 7. Upper part; responses to various striped patterns of which black stripes were of width corresponding to the visual angle of 3 neighbouring ommatidia and arranged equi-distantly on white ground. Abscissa, width of distance between stripes; ordinate, response frequency (%). Lower part; responses to various striped patterns with white stripes on the black background arranged with the same proportion as in Upper part.

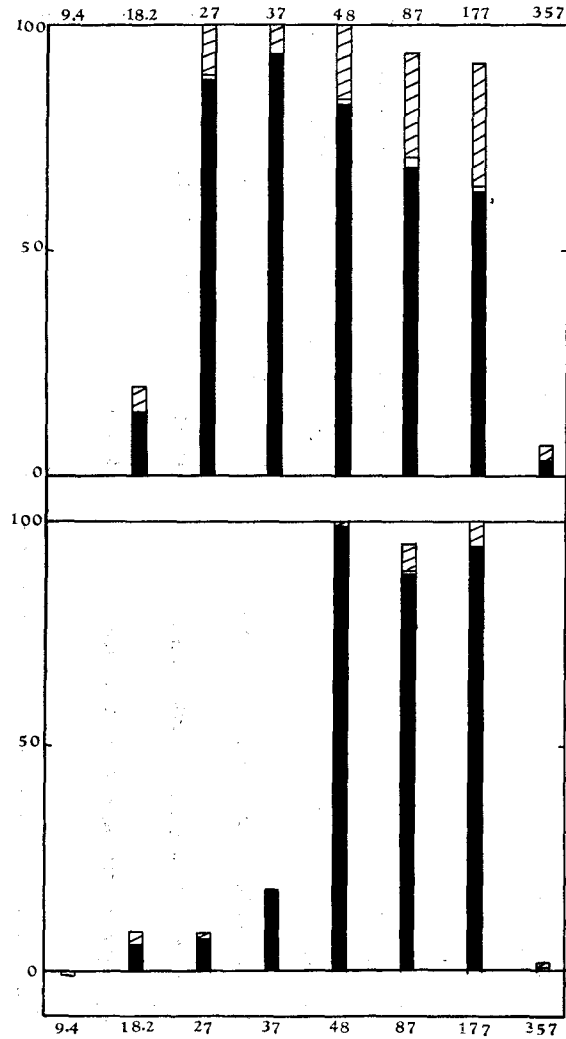


Fig. 8. Upper part; responses to various striped patterns of which white stripes were of width corresponding to the single ommatidial angle and placed equi-distantly on black background. Abscissa; width of distance between stripes; ordinate, response frequency (%). Lower part; responses to various striped patterns with black stripes on the white background arranged with the same proportion as in Upper part.

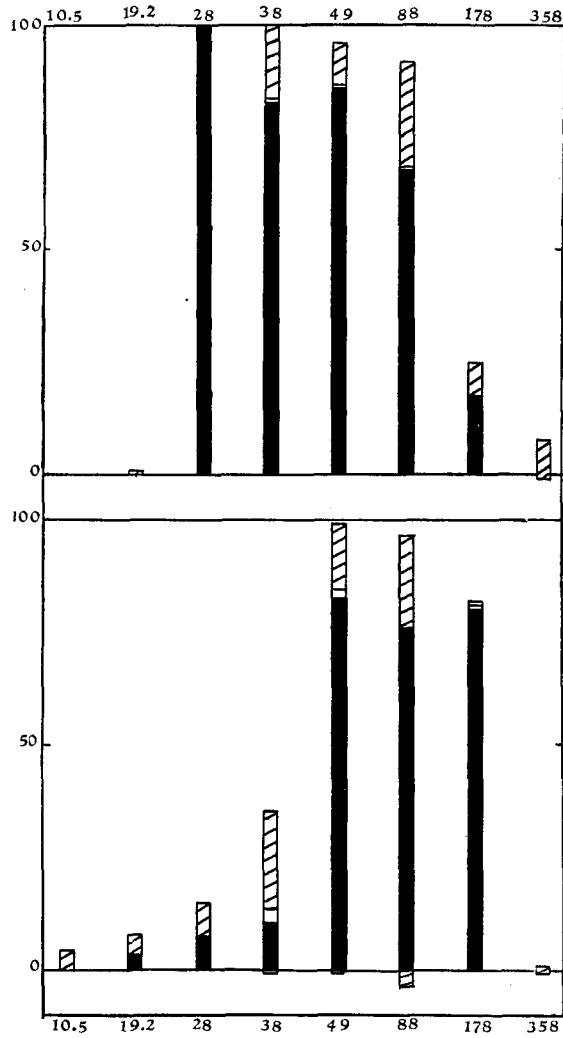


Fig. 9. Upper part; responses to various striped patterns of which white stripes were of width corresponding to  $2/3$  of the ommatidial angle and placed equidistantly on black background. Abscissa, width of distance between stripes; ordinate, response frequency (%). Lower part; responses to various striped patterns with black stripes on the white background arranged with the same proportion as in Upper part.

than those to the reversed black/white pattern. But in the cases where the ratios are 3 : 81 and 3 : 171, responses to movement of black/white pattern exceeded numerically those to movement of the reversed white/black pattern. The former instance shows that when the distances between stripes are narrow, the mosquitoes are more sensitive to movement of white stripes on a black background than to movement of black stripes of the same width on a white background. On the other hand, the latter instance reveals that in the striped patterns with very wide distances, movement of black stripes superimposed upon a white ground is more sharply perceptible to the mosquitoes than movement of white stripes on a black ground.

c) Experiments with various stripe patterns with the white stripes of width corresponding to a single ommatidium ( $3^\circ$ ) and placed equi-distantly on a black ground. Responses showed high frequency at distances from  $27^\circ$  to  $177^\circ$ , while they manifested low frequency at distances of  $18.2^\circ$  and  $357^\circ$  (Fig. 8, the upper part).

d) Experiments with various stripe patterns of which the black stripes were of width corresponding to a single ommatidium and arranged at equi-distances on a white ground. Frequency of responses rose up in a quadratic curve to the increase of distances between  $9.4^\circ$  and  $48^\circ$  and reached to 100% at  $48^\circ$  and  $177^\circ$ , but decreased to 95% between them (Fig. 8, the lower part).

From comparison of the results of experiments c and d, it may be said that the mosquitoes responded to the pattern of white stripes on a black ground better than to the reversed black/white pattern.

e) Experiments with various stripe patterns with white stripes of width corresponding to  $2^\circ$  and arranged at equi-distances on a black ground. Generally speaking, the process of responses resembles that in experiment c (Fig. 9, the upper part). The responses were very frequent in cases where the distances between stripes are the width from  $28^\circ$  to  $88^\circ$  and, dropped rapidly at greater distances. But in contrast to experiment c, the responses to distance  $178^\circ$  were less frequent than to those at  $177^\circ$  in c.

f) Experiments with various stripe patterns of which the black stripes were of width corresponding to  $2^\circ$  and arranged at equi-distances on a white ground. The relationship of responses to distances  $10.5^\circ$  to  $49^\circ$  graphed as a typical sigmoid curve; the same relationship was already found in experiment d (Fig. 9, the lower part). The responses occurred without failures at distances of  $49^\circ$  and  $88^\circ$ , but showed a swift fall at distances of  $178^\circ$  to  $358^\circ$ .

g) Experiments with various stripe patterns of which the white stripes were of width corresponding to  $1.5^\circ$  and arranged equi-distantly on a black ground. Responses followed a fairly irregular course in which two peaks of responses were each found to patterns of white stripes on a black ground separated by equi-distances of  $29^\circ$  and  $50^\circ$  respectively (Fig. 10, the upper part). Furthermore, the responses at distances between  $29^\circ$  and  $179^\circ$  were considerably lower than responses to the same range of width in other experiments. Such a general dropping of responses

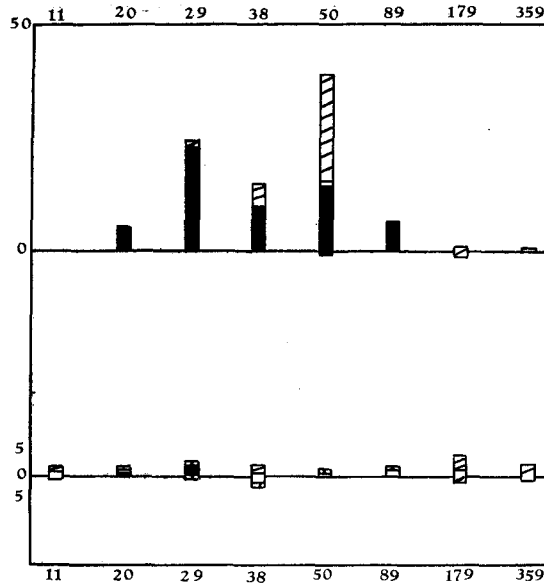


Fig. 10. Upper part; responses to various striped patterns of which white stripes were of width corresponding to  $1/2$  of the ommatidial angle and placed equi-distantly on black background. Abscissa, width of distance between stripes; ordinate, response frequency (%). Lower part; responses to various striped patterns with black stripes on the white background arranged with the same proportion as in Upper part.

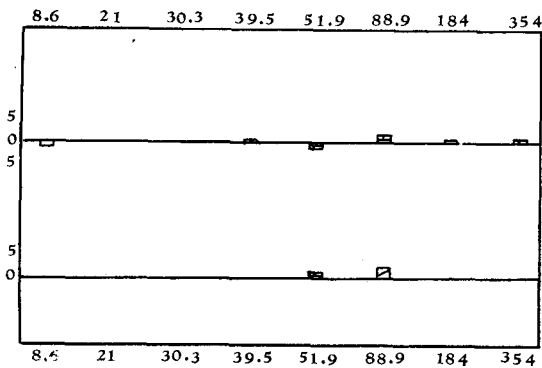


Fig. 11. Upper part; responses to various striped patterns of which white stripes were of width corresponding to the visual angle of  $0.6^\circ$  and placed equi-distantly on black background. Abscissa, width of distance between stripes; ordinate, response frequency (%). Lower part; responses to various striped patterns with black stripes on the white background arranged with the same proportion as in Upper part.

seems to be brought about by the fact that the visual angle subtending the white stripe is only a half of the minimum angle of the ommatidium.

h) Experiments with various stripe patterns with the black stripes of width corresponding to  $1.5^\circ$  and arranged equi-distantly on a white ground. Responses to these patterns oscillated around the line of 0% within the limit not exceeding  $\pm 5\%$ , and never occurred at a particularly high frequency in any cases of patterns in experiment h (Fig. 10, the lower part). Hence, it is presumable that movement of black stripes similar to the visual angle of  $1.5^\circ$  is scarcely perceptible by the mosquitoes, irrespective of distances between stripes.

i) Experiments with various stripe patterns with the white stripes of width corresponding to  $0.6^\circ$  and placed equi-distantly on a black ground, and experiments with stripe patterns in which black was replaced by white. As seen in Fig. 11, the upper part, only a few mosquitoes responded sporadically to white/black patterns without showing a remarkable rise or fall of responses resultant from increasing distance. The same tendency in responses was also recognized in black/white patterns (Fig. 11, the lower part). The failure of responses in these experiments seems to be ascribable to the visual angle of the stripes which was markedly smaller than the minimum ommatidial angle.

From the results of the above ten experiments, the following conclusions were deduced with respect to the optomotor reaction of mosquitoes to the alternate patterns of black and white stripes of various widths.

- 1) Perception of movement of stripes is exceedingly difficult for mosquitoes when the visual angles are smaller than half of the minimum ommatidial angle.
- 2) Movement of stripes is, as a rule, clearly perceived when the visual angles are greater than  $2^\circ$ .
- 3) When the visual angles of stripes are larger than one half of the ommatidial angle and the distances between neighbouring stripes are relatively narrow, responses to the movement of white stripes superimposed upon a black ground are distinctly better than those to the movement of black stripes on a white ground. In his experiments concerning the vision of honeybees, Sakagami (1956) ascertained that bees which were trained to a black circle on a black-white checkered pattern come to a yellow circle but refuse to alight on a white circle placed on the same pattern, that is, bees dislike white. According to this opinion, the superiority of responses in white/black patterns with narrow distances to responses in black/white patterns may be explained from the fact that the ratio of black to white in the former patterns is greater than that in the latter ones. But it is not a general principle useful for the explanation of difference in optomotor reaction to the movement of stripe patterns of varied widths because when distances between stripes are so extremely wide as  $90^\circ$  or  $180^\circ$ , responses to white/black patterns are numerically inferior to responses to black/white patterns, notwithstanding black predominates over white in the ratio. The perception of movement in the alternate patterns of stripes wider than the half of the ommatidial

angle is, therefore, influenced by the relative relationship of width between the stripes and ground, i.e., the degree of contrast of black and white between the stripes and ground, but not by a one sided preference for black.

4) Concerning the stripes used in the experiments described above, responses to movement of a single stripe on the background equal to visual angle of  $360^\circ$  were very low, irrespective of the width of the stripe (below 15%). Such a result is not expected if the optomotor reaction takes the form of merely continuing to watch a single moving object because the contour line of a single black stripe on a broad white ground is highly distinct. Therefore, it is inferred that the mosquitoes are unable to fix the movement of the stripe in the same area of the eyes. Reduction of frequency in the responses to a single stripe on a white background indicates that some other causes may participate in the optomotor reaction.

5) As observed in the experiments concerning the velocities of revolution of the striped cylinder, *Culex pipiens pallens* females have a tendency to respond by turning the head towards the direction of progression of the cylinder. Such a tendency was confirmed also in the experiments conducted at a constant velocity with various black and white stripe patterns consisting of visual angles greater than  $2^\circ$ . The meaning of head turning will be referred to later in relation to the resting posture of mosquitoes in the glass container.

*III. Responses to movement of black stripes arranged at various distances on a white ground:* Experiments were conducted with patterns in which 2, 3 and 4 black stripes were arranged at various distances on a white ground respectively; width of each stripe was  $3^\circ$  throughout the trials, that is, approximately equal to the visual angle of an ommatidium and the rotatory speed of the pattern always 11 rotations per minute. The results are graphed in Fig. 12. Considering selection of direction of moving pattern, the intensity of responses is expressed by ISD. In the case of two black stripes (Fig. 12, b-g) ISD rose in parallel with the increase of the distances between the stripes reaching nearly 100% at the distances over  $62^\circ$ . In the case of three stripes, ISD was still passably low when the stripes were placed at distances of and less than  $49^\circ$  (Fig. 12, h, i), but it was conspicuously high at  $49^\circ$  plus  $152^\circ$  (Fig. 12, j).

The mosquitoes responded very actively to the pattern of four black stripes, each arranged on two diagonal lines crossing at an angle of  $49^\circ$  (Fig. 12, k). On the contrary, responses were markedly low to the pattern of four stripes arranged side by side at the same distances of  $49^\circ$  (Fig. 12, l). The responses to the four stripes which were placed on two diagonal lines declined greatly when the angle between the diagonal lines was  $9^\circ$  (Fig. 12, m).

The most noteworthy results were obtained as for the perception of movement of two stripes placed at extremely narrow distances. When the distance was  $12^\circ$ , namely, similar to the combined visual angles of three contiguous ommatidia,

the responses were 5%, but with decrease in the width of distances, they increased gradually, arriving at 100% at below 1.5°, i.e., less than half of the ommatidial angle (Fig. 12, n-s).

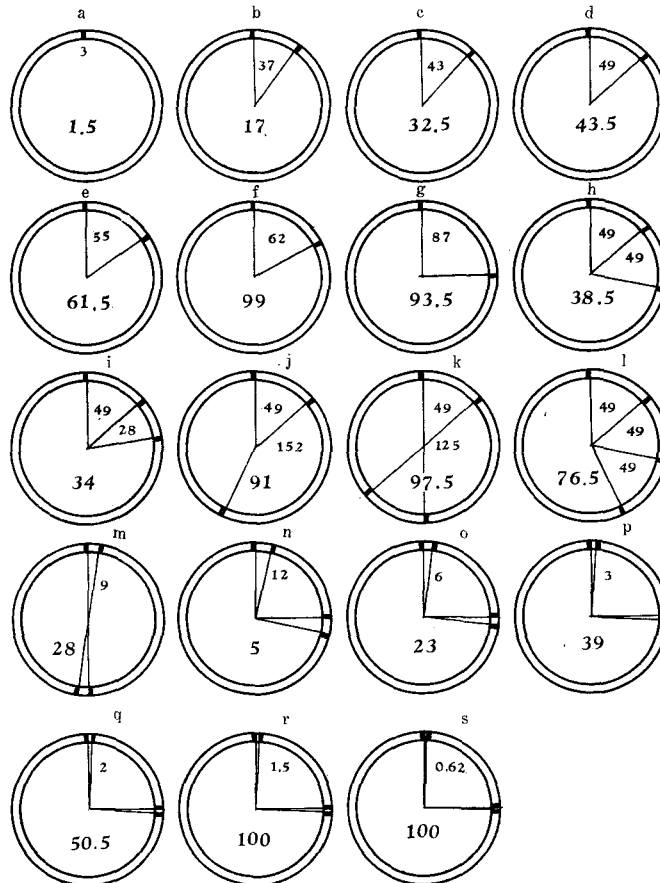


Fig. 12. Responses to movement of the patterns in which the black stripes of width corresponding to the ommatidial angle were arranged at various distances on white ground. Large figures show responses expressed by ISD. Small figures indicate width of distances between stripes in angular degree.

The above results may be analysed from both the numerical aspect and the arrangement of stripes. Number of stripes is related with the number of ommatidia stimulated simultaneously. The responses increased with the increase in number of stripes from 1 to 4 placed at equal distances of 49° (Fig. 12, a, d, h, l). This indicates that perception of movement is intensified by the accumulation of each

impression obtained simultaneously in different ommatidia, that is, the summation of stimuli is concerned in the optomotor reaction of the mosquitoes. But the number of stripes is not the sole determinant factor but their arrangement is also of crucial importance for the optomotor reaction. In the case of two stripes, the responses were simply proportional to the distances between the stripes; the limit of distance in which the movement of the stripes is most clearly seen is surmised to be about  $60^\circ$  (Fig. 12, b-g). In the arrangement of 3 and 4 stripes, the circumstances become highly complicated. The relative relationship of distances between stripes will be one of the most prominent factors in releasing the optomotor reaction. For instance, responses to three stripes apart each other at distances of  $49^\circ$  and other discretionary widths were subjected to the great influence of the discretionary distance, and increased almost proportionally to the width of distances close to  $49^\circ$  (Fig. 12, h, i, j). A similar result was gained in responses to four stripes (Fig. 12, k, l). The conditions indispensable for releasing optomotor reaction are, therefore, not merely numerical increase of distance of  $49^\circ$ , but the manner of spatial arrangement of the third and the fourth stripes. The importance of arrangement of stripes was pointed out by v. Buddenbrock and Friedrich (1933) in their experiments upon the optomotor reaction of the crab, *Carcinus maenas*. They supposed four centers of perception of movement corresponding to the spatial arrangement of stimuli and considered that the degree of perception varies with the manner of connection between the centers; unfortunately, experiments with an electric model to test the above assumption failed. Apart from the absolute number of the centers assumed by them, however, this view is worthy of attention because it indicates the existence of a perception center. In the present writer's opinion, impressions of stimuli given to ommatidia in different areas of eyes are sent to the perception center and construct the respective fields of impression. As previously touched upon in relation to responses to the change of rotatory velocities of a definite stripe pattern, there occurs an interaction between the fields of impression; the degree of interaction is affected by the spatial distance between stimuli. When the distance is short, the fields of impression formed by the motion of stimuli greatly overlap and strongly interfere with each other; consequently, the motion of the stimuli is perceived as a simultaneous appearance of stimuli, thus the perception of movement does not result. The fields of impression of two stimuli adjoining at an extremely narrow distance (below  $1.5^\circ$ ) overlap almost completely and are no longer distinguishable from one another; finally, the movement of the two stimuli is perceived like the movement of band of a fairly broad width (Fig. 12, r, s). With the increase of distance between stimuli, the mutual interference between the fields of impression becomes weak, and movement of each stimulus is gradually separately perceptible; so far as the stripe pattern rotates at the velocity of 11 revolutions per minute, the distances between stripes in which the clearest movement is seen seem to correspond to the visual angles between  $60^\circ$  and  $180^\circ$ . In this way, responses to the change of distances between



out in normal arrangement from the sector corresponding to a single ommatidium in the visual angle.

The results of experiment j are depicted in Fig. 13. Intensity of responses is expressed by ISD. With increase in the width of slits, ISD under normal arrangement of slits drew a complicated curve; ISD rapidly increased up to the width of  $3^\circ$ , dropped at  $5^\circ$  and again quickly rose at  $8^\circ$ . ISD under combined arrangement of slits was similar to that under normal arrangement. But there is a distinct difference in the magnitude of ISD between the two cases; ISD was always greater in normal arrangement of slits than in combined arrangement excepting the cases of both  $5^\circ$  and  $7^\circ$ .

Judging from the results noted above, it is concluded that optomotor

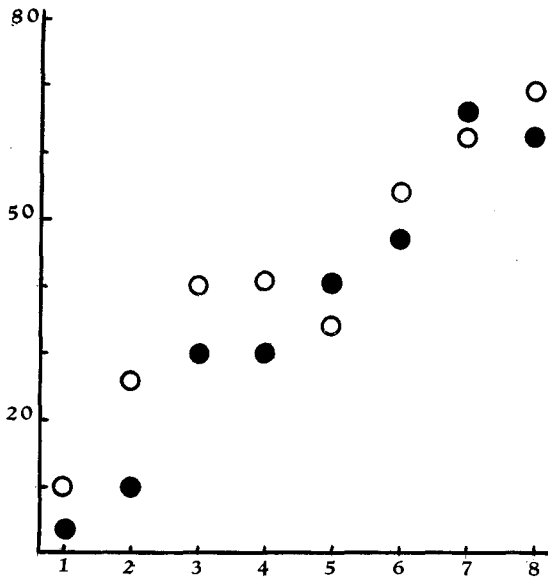


Fig. 13.

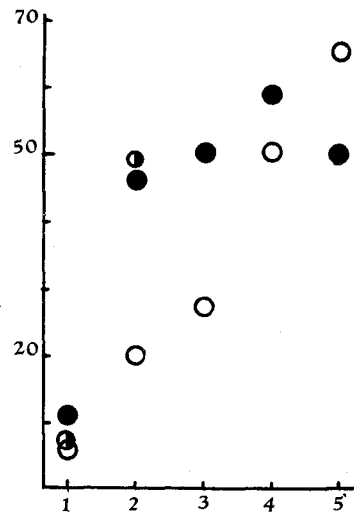


Fig. 14.

Fig. 13. Responses to movement of stripes seen through slits which were cut out from the sector corresponding to 3 adjoining ommatidia in the visual angle. Solid and open circles represent responses in combined or normal arrangement of slits respectively. Abscissa, width of slits cut out from the sector of  $9^\circ$ ; ordinate, response expressed by ISD.

Fig. 14. Responses to movement of stripes seen through slits which were cut out from the sector corresponding to 2 ommatidia in the visual angle, and responses to the movement seen through slits which were cut out from the sector of the single ommatidium. Solid and open circles show respectively responses under combined arrangement and under normal arrangement of slits clipped out from the sector of  $6^\circ$ . Semi-open circles indicate responses under normal arrangement of slits cut out from the sector of  $3^\circ$ .

responses are released very frequently with the increase of slit widths, that is to say, by the gradual exclusion of any obstruction which disturbs the vision of ommatidia in a row. This means probably that the responses depend upon the degree of mutual communication of stimuli between 3 adjoining ommatidia. Generally speaking, responses under combined arrangement of slits were very slight compared with responses under normal arrangement; especially, in slits of widths less than  $4^\circ$ , such inactiveness was conspicuous. There are sufficient reasons to provoke this fact. As seen from the schemata of procedure given at the beginning of this section, slits in combined arrangement are in number only one-half those in normal arrangement as the result of putting together the neighbouring slits at a definite distance, although the width total of slits is equal in both sorts of arrangement. In other words, the chances to catch the stimuli in combined arrangement of slits are only half those in normal arrangement, when stimuli of the same number were given. Responses under combined arrangement of slits narrower than  $4^\circ$  accepted a more remarkably inhibition than responses in normal arrangement due to the lack of chances as just mentioned. Another interpretation is also possible. The slit newly built up by combination of two slits below  $4^\circ$  is at the maximum width corresponding to 2.5 ommatidia. Therefore, it will be more difficult for the mosquitoes to pursue movement of stimuli in such combined narrow visual fields than to seize flicker of stimuli appearing frequently from the slits of normal arrangement. In slits greater than  $5^\circ$ , responses under combined arrangement numerically surpassed in some instances ( $5^\circ$ ,  $7^\circ$ ) those from normal arrangement. Visual fields seen through combined slits are sufficiently wide compared with those through the slits normally arranged, and equal in the minimum width to the visual angle of 3 contiguous ommatidia. Therefore, the above observations of responses to the slits larger than  $5^\circ$  may indicate that in some instances, the width of the visual fields in combined slits can compensate to some degree the numerical reduction of the slits in bringing about the optomotor reaction.

Fig. 14 illustrates the results of experiment k. The values of ISD under normal arrangement of slits rose almost rectilinearly to the increase of slit width. On the other hand, ISD under combined arrangement of slits rapidly grew for the increase of slit width from  $1^\circ$  to  $2^\circ$ , thereafter, dropped in the growth rate, describing finally a convex curve. Excepting the case of  $5^\circ$ , ISD in combined slits was always greater than in slits normally arranged. From the results just stated, it is not too much to say that in the case of stimulation of every pair of ommatidia, the width of visual field more greatly contributes to the evocation of optomotor reaction than the growth in number of slits. As to this point, the results are entirely different from those of experiment j, i.e., stimulation of every group of three ommatidia.

In the successive stimulation of every single ommatidium (Fig. 14), responses in normal arrangement of slits were subjected to the serious influence of slit width. ISD was increased from 9% to 49% by the change in width of slits by only  $1^\circ$  to

2°. This observation suggests that the visual ability is probably proportionate to the magnitude of stimulus received by a single ommatidium.

V. *Responses when neighbouring ommatidia were each given stimuli of different strengths*: The double cylinder system and the stripe pattern used in experiments described in Chapter IV were employed for this experiment, too. In order to obtain stimuli of various strengths, three different slits were devised:

i) Slit of width corresponding to visual angle of  $3^\circ$ , i.e., a single ommatidium. Black stripes seen from this slit were perhaps the strongest stimulus given to the ommatidium; it is expressed as degree III.

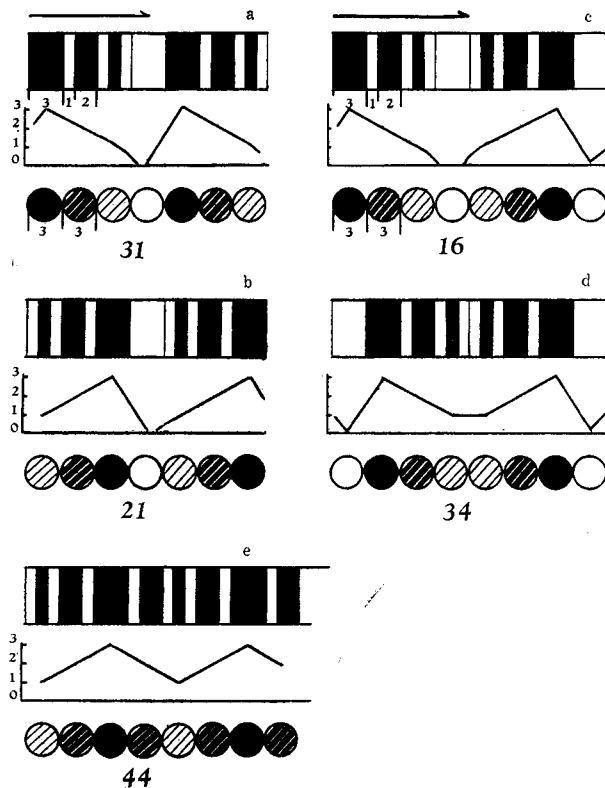


Fig. 15. Responses to movement of black stripes with the visual angle of  $3^\circ$  which is seen through consecutive slits of different widths cut out from the sector of 3 ommatidia. Arrows show the direction of moving pattern. Illustrations indicate from the above downward 1) width of stripes seen through slits, 2) the corresponding change of strength of stimuli and 3) the extreme impression in each occasion. Large letters, responses expressed by ISD; small letters, strength of stimuli and angular degree.

ii) Slit made by cutting out 2/3 of the width corresponding to visual angle of  $3^\circ$ . As the strength of the stimulus given through this slit is next to the strength of stimulus III, it was expressed as degree II.

iii) Slit made by cutting out 1/3 of the width corresponding to visual angle of  $3^\circ$ . The strength of the stimulus appearing from this slit is the weakest among stimuli used in these experiments: it is expressed as degree I. Various manner of stimulation was obtained by the combination of these three slits.

According to the number of ommatidia which are stimulated simultaneously, two sets of experiments were designed as follows:

m) Successive stimulation of every 3 neighbouring ommatidia.

n) Successive stimulation of every 2 neighbouring ommatidia.

The outer cylinder with a pattern of black stripes placed quadrantly on a white ground was moved at the velocity of 11 rotations per minute.

Fig. 15 illustrates various manner of stimulation and intensity of responses expressed by ISD (large letters in space below the diagram) in experiment m. As seen in the figure, ISD to the decreasing stimulus which proceeded from III to I in strength was greater than ISD to the increasing stimulus advanced oppositely I to III (Fig. 15, a, b). When these two ways of stimulation were combined together at a distance similar to visual angle of  $3^\circ$ , the minimum value of ISD in experiment m was obtained (Fig. 15, c). By the elimination of such intermediate distance, ISD again ascended to 34% (Fig. 15, d). Further, responses were caused to attain to the highest value of ISD in experiment m by the continuous stimulation of three different strengths, resulting from exclusion of distances equal to width of  $3^\circ$  from the cylinder with slits (Fig. 15, e).

Considering the results noted above, mosquitoes are able to perceive movement varying from the strong to weak stimulus more easily than movement of reversed arrangement. When two stimuli of mutually inverse directions in strength were continuously given at a definite distance, the mosquitoes responded with difficulty. Removal of the intermediate distances could improve the ability to perceive the movement. Thus it was ascertained that perception of movement in the compound eyes is profoundly influenced by the manner of stimulation received by adjacent ommatidia.

Fig. 16 shows the various manners of stimulation and strength of responses expressed by ISD in experiment n. The mosquitoes responded to the change of degree III to I with a higher frequency than to the reverse change (Fig. 16, a, b). By interposition of distance of  $3^\circ$  between the two stimulation manners, the minimum responses in experiment n were gained (Fig. 16, c). Responses became again vigorous as a result of the abolition of the intermediate distance (Fig. 16, d), moreover, they were increased numerically to a striking degree by the resulting alternate stimulation of both stimuli III and I of complete removal of distances equal to the visual angle of a single ommatidium from the cylinder with slits (Fig. 16, e). The same tendency of responses was already found in the

previous experiment m.

The results of the experiments made by the combination of stimuli III and II are similar to the results which were obtained by the use of stimuli III and I. ISD to the movement from degree II to III was inferior to ISD to the reversed stimulation III to II (Fig. 16, f, g). By the combination of these two modes of stimulation, ISD was caused to grow by far compared with the case of separate use of each mode of stimulation (Fig. 16, h). This was quite unexpected, judging from the results hitherto described (Figs. 15 and 16, c). Consideration upon the numerical growth of responses in this case will be offered in the last chapter.

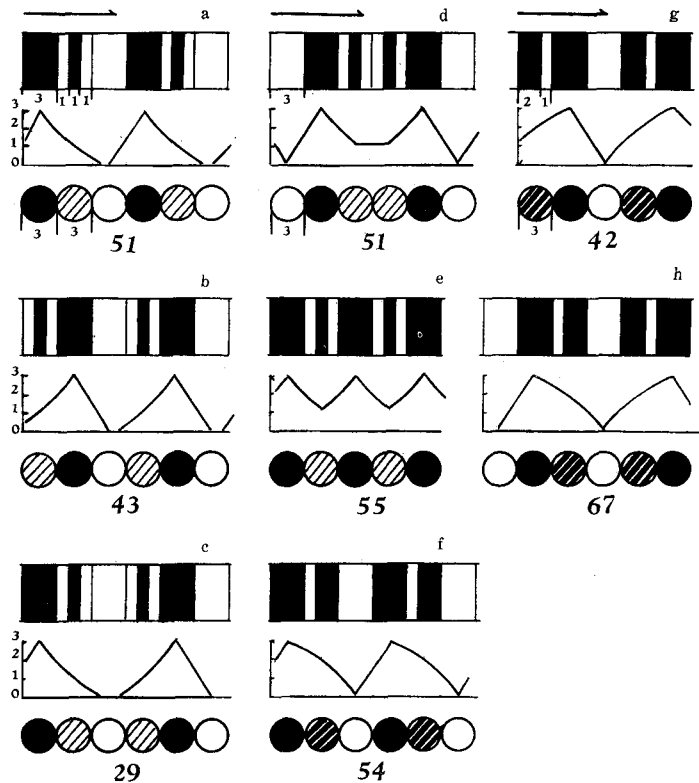


Fig. 16. Responses to movement of black stripes with the visual angle of  $3^\circ$  seen through consecutive slits of different widths clipped out from the sector of 2 ommatidia. Explanations as in Fig. 15.

VI. *The relationship between responses and resting postures in the glass container:* As illustrated in Fig. 2, the resting postures of mosquitoes in the glass tube are roughly classified into two types: 1. keeping body axis in parallel with

vertical side wall of the container (Fig. 2, a) and 2. keeping body axis vertical to the side wall of the container (Fig. 2, b). The former was termed the "vertical posture" because the rotatory axis of body is vertical to the axis of the environmental movement, and the latter the "parallel posture" as the rotatory axis of body runs parallel to the axis of the environmental movement.

Table 1

			VH	VW	VF	PH	PW	PF	
Males of <i>Aedes vexans nipponii</i>	Responses to velocity of pattern	+	39	135	7	38	190	6	
		-		50	2	3	94	6	
		Total	39	185	99	233	41	284	12
		%	16.7	79.4	3.9	100	12.1	84.1	3.8
Males of <i>Culex pipiens pallens</i>	Responses to velocity of pattern	+	42	52	2	47	110	1	
		-		26		4	46	2	
		Total	42	78	2	122	51	156	3
		%	34.4	63.9	1.7	100	24.2	74.2	1.6
Females of <i>Culex pipiens pallens</i>	Responses to velocity of pattern	+	263	87	2	112	78	2	
		-	6	23			15		
		Total	269	110	2	381	112	93	2
		%	70.6	28.8	0.6	100	54.1	44.9	1
	Responses to normal arrangement of slits	+	388	95	4	117	33		
		-		6			10		
		Total	388	101	4	493	117	43	160
		%	78.7	20.5	0.8	100	73.1	26.9	100
	Responses to combined arrangement of slits	+	427	77	8	32	5	10	
		-		15	1		5	10	
		Total	427	92	9	528	32	5	47
		%	80.8	17.4	1.8	100	68	10	22
Responses to stimuli of different strength	+	285	68	3	199	28	2		
	-		9			9	1		
	Total	285	77	3	365	199	38	240	
	%	78	21	1	100	82.9	15.8	1.3	

V: Vertical posture, P: Parallel posture, H: Response by turning head, W: Response by walking, F: Response by flying. VH means response by turning head from vertical posture. Other symbols like VW, PH etc. have corresponding meanings. Plus and minus express respectively response to the rotatory direction of pattern and response to the inverse direction.

Table 1 summarizes the body postures observed in the experiments so far described. *Aedes vexans nipponii* males chiefly responded with the parallel rather than the vertical posture, and the majority of the reactions was aroused by walking responses; responses which took the form of turning of head were next to the walking responses in number, and responses by flying were the minimum. This pattern of responses emerged also in case of *Culex pipiens pallens* males. Reaction of the males originated mostly from the parallel rather than the vertical posture,

and responses in the form of walking were carried out at the ratio of over 60% of responses in each posture. Thus so far as concerns these experiments, males are inclined to respond with walking from the parallel posture in both species. In this respect, *Culex pipiens pallens* females presented a vivid contrast to the males mentioned above. Turning of head in the vertical posture predominated over any other responses without exception in the experiments upon the females summarized in Table 1.

The difference of responses between the different sexes may arise in the following manner: The mosquitoes resting on the vertical side wall of the container cannot but respond by turning of head in order to adjust themselves as soon as possible to the change of the environmental movement. On the other hand, for the mosquitoes alighting on the bottom of the container, responses by walking will be the most appropriate manner to adjust themselves to the change of the environmental movement. *Culex pipiens pallens* females usually rested on the side walls of the container at the starting of the experiment, while males of *C. pipiens pallens* and *A. vexans nipponii* alighted on the bottom of the container. Thus the mosquitoes of different sexes showed different responses; so to speak, casual resting postures at the starting of the experiment gave rise to the responses between the two sexes.

von Gavel judged optomotor reaction as the revolving movement which arose around the axis parallel to the axis of environmental movement. This may be exactly applied to the cases of males of the two species employed here. There is another mode of responses, namely, a rotatory movement about the axis vertical to the axis of environmental movement, as seen not infrequently in *C. pipiens pallens* females used for this experiment. The latter behaviour cannot be explained on the basis of the definition of optomotor reaction by Gavel. The question whether intrinsic differences lie between such two modes of responses or not has not yet been solved. However, the present writer emphasizes the occurrence of responses of both "vertical posture" and "parallel posture".

According to the widely accepted opinion, responses by turning of head may be regarded as an optical nystagmus. The nystagmus in a strict sense is diphasic, that is, animals return the head or eye balls quickly to the incipient position as soon as the watched object disappears outside of their visual field. The mosquitoes in this experiment never restore the head to the onward direction of the pattern, as far as the pattern is not revolved inversely. This obviously monophasic reaction appears as if a forced movement. Consequently, reaction by turning of head in the mosquitoes distinctly differs from nystagmus in a strict sense, and may be a characteristic response independent nystagmus.

It is certain that a moving object is not confined constantly to one and the same ommatidium in the optomotor reaction of mosquitoes. In the course of the experiments, discrepancy between the speed of movement of the mosquitoes and the rotatory velocity of pattern was repeatedly observed; particularly, such

discrepancy was enormous in responses which took the form of walking or flying. In the forced movement mentioned above, a stimulus is naturally not maintained in the same place of the eyes. Further, this inference is supported by the fact that responses to the moving pattern of a single black stripe on a white ground were utterly sluggish, regardless of width of the stripe (Exps. in Chapt. II). Hence, optomotor reaction of the mosquitoes, in the writer's opinion, is the response to "movement" of the environment, not the response for the purpose of fixation of an object in the eyes. The mosquitoes probably gain impression of "movement" by mutual communication between the neighbouring ommatidia, of resultant excitation from spatial or temporal migration of sequential stimuli. The marked decrease of responses to the movement of the single stripe on a broad background may be ascribed to the lack of summation of impressions by sequential stimuli.

### Discussion

*Culex pipiens pallens* females could respond to various patterns of black stripes which were arranged at suitable distances (above  $48^\circ$ ) on a white ground; each stripe was the same width as the visual angle of  $3^\circ$  (Fig. 8). Identical results were obtained in response to the movement of stripe pattern of black stripes of  $2^\circ$  on a white ground (Fig. 9). On the other hand, responses to the movement of black stripes narrower than  $1.5^\circ$  were arrested at 10% in the highest value of ISD, without regard to the spatial arrangement of the stripes (Figs. 10 and 11). The minimum visual angle of a single ommatidium in the female mosquito is calculated as ca.  $3^\circ$  from microscopic examination. From these observations, it is reasonably concluded that the female mosquito can clearly perceive the movement of black stripes wider than  $2/3$  of the ommatidial angle, and that a single ommatidium is a functional unit in the vision of the mosquito.

There is a considerable amount of experimental evidence and theoretical considerations to indicate that the ommatidium is a functional unit of compound eyes (Hecht and Wolf, 1929; del Portillo, 1932; Hassenstein, 1951; Barlow, 1952; Bauers, 1953). On the other hand, some observations have been reported which suggest that constituent structures within an ommatidium may perform different functions (Hanström, 1927; Power, 1943). Different types of intraommatidial sense cells of *Limulus* lateral eyes functionally differ in sensitivity to light (Waterman and Wiersma, 1954). Whether the same principle can be applied to the ommatidium in all arthropod compound eyes or not is quite unknown. In this connection, it is interesting that Autrum (1950) classified compound eyes into two physiologically different types from the character of potential generated by exposure to light.

The results of experiments by the use of various slits upon the optomotor reaction of *C. pipiens pallens* females can be evaluated from number and width of slits. Frequency of responses to normal arrangement of slits is proportionate to the slit width when the number of slits is equal, but the frequency depends upon the number of slits when they are of the same width. For instance, as shown in Figure 17, when the visual field was divided into sectors equal to the width of 3 ommatidia adjoining in a horizontal direction, responses increased approximately

in parallel to the increasing width of the slits cut out from the sectors. The same results were produced in both cases when the sectors were divided into widths of one or two ommatidia. On the contrary, the comparison of responses to slits of equal width in the above experiments revealed that, in general, the responses are roughly in inverse proportion to the size of the sector, that is, the responses are inclined to be better with the subdivision of the sector. Consequently, it is inferable that with the subdivision of sector, chances to recognize the movement of an object were increased and the responses were released easily.

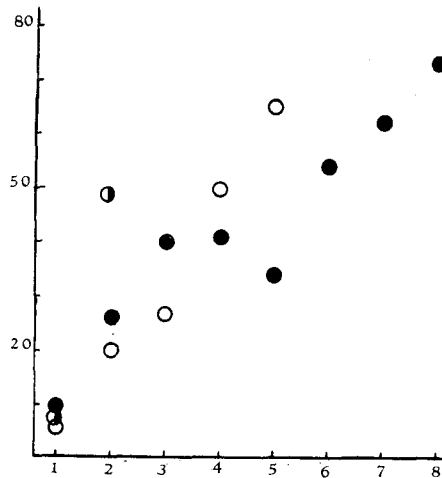


Fig. 17. Comparison of responses in normal arrangement of various slits. Solid, open and semi-open circles show each responses to movement of stripes seen through slits clipped out from the sectors of 3, 2 and 1 ommatidia. Abscissa, width of slits cut out from each sector; ordinate, responses expressed by ISD.

Perhaps the responses described above are carried out through a peculiar mechanism based upon the morphological characteristics of compound eyes, that is to say, the transmission of impression by a continuous stimulation of neighbouring ommatidia. Here the manner of communication of impressions between ommatidia comes into question. When a stripe corresponding in width to a single ommatidium moves in consecutive slits of  $8^\circ$  cut out from the sector of  $9^\circ$  (3 ommatidia), the stripe stimulates successively 3 ommatidia which are in a row. Moreover, before complete disappearance from the preceding slit, the stripe stimulates ommatidium of the next sector adjoining at the distance of  $1^\circ$ . Therefore, impressions of the stimulus obtained are continuously transmitted from sector to sector like their communication between ommatidia within a single sector; thus, perception of movement arises. The increase of width between slits disturbs the transmission of the impression, and according to the degree of disturbance, the responses become less in number. This assumption also explains the difference in responses between the experiments carried out by the use of slits equal in width but different in number. Responses to move-

ment of an object seen through the consecutive slits of  $2^\circ$  clipped out from the sector of  $3^\circ$  (single ommatidium) numerically exceeded responses to movement of an object appearing from the slits of  $2^\circ$  in the sector of  $9^\circ$  (3 ommatidia). Impression of the moving object in the former case may be communicated between ommatidia before it entirely fades out. But in the latter case, the impression of the moving stripe disappears without being transmitted between ommatidia within the sector because the distance between slits is remarkably wide in this case. Thus, sequential stimulation of adjoining ommatidia is one of the most fundamental mechanisms of evoking the perception of movement in the compound eyes of the mosquitoes.

In cases of continuous exposure of every two adjacent ommatidia to stimuli of different strengths, responses profoundly differ according to the presentation of the stimuli. Responses to the repetition of stimuli which are being reduced in strength are numerically superior to responses to stimuli of increasing strength (Fig. 15, a, b and Fig. 16, a, b, f, g). This is closely related with summation of impression left in the stimulated ommatidia. Impression of a strong stimulus in a given ommatidium is kept during a comparatively long interval and readily joins with the impression of a weak stimulus coming in succession in the neighbouring ommatidium, the latter being strengthened by the former by summation. In this manner, a sharp impression of movement arises in the eyes. On the other hand, the impression of a preceding weak stimulus fades rapidly with the progression of time, so the impression has little chance to be followed and to connect with the impression of a succeeding strong stimulus arriving in the contiguous ommatidium; accordingly, the link of impression is not built up. To the eyes of mosquitoes, thus, perception of change from the weak to strong stimulus became more difficult than perception based upon the reverse order of stimuli.

When every two an ommatidial row was stimulated, combination of two modes of stimulation, i.e., a direct change from a stimulus degree III to I without passing through degree II and the inverse stimulation brought about responses more inactive than did the single application of each mode of stimulation. As seen clearly in Figure 16, when these two modes of stimulation are connected each other at distance equal to the ommatidial angle, the real distance between two stimulation modes is somewhat wider than the corresponding distance in the independent arrangement of each stimulation mode (Fig. 16, a, b, c). Therefore, the transmission of impression may be more difficult in the combination of two modes than in independent application of each mode. In both experiments in which either two modes of stimulation mentioned above were given in combination without placing the intermediate distance equal to the ommatidial angle or the adjacent ommatidia were continuously stimulated by means of alternation of stimuli of degree III and I, responses again became active (Fig. 16, d, e). In this way, mutual communication without a pause between ommatidia is seen to play a cardinal role in the perception of movement by the compound eyes.

Considering the results of the experiments hitherto detailed, the mode of

stimulation of every two ommatidia quite resembled the manner of stimulation of every three ommatidia in tendency to release responses, but in the frequency of responses, the former mode of stimulation surpassed the latter one to a great degree (Figs. 15 and 16, a, b, c, d, e). This probably means that the mosquitoes are capable of perceiving rapid variation in strength of stimuli much more easily than gradual change.

Responses to a continual stimulation of every two ommatidia by stimuli of degrees III and II are different from those to the stimulation by degrees III and I: when the mode of stimulation changing from stimuli III to II was connected with the inverse mode of stimulation at distance of  $3^\circ$ , responses were activated more strongly than in the independent application of one mode (Fig. 16, f, g, h). These three modes of stimulation are fully similar to each other both in width and in number of corresponding distances between slits; for this reason, the increase of responses in the combination of the two stimulation modes different in direction of change is not explainable on the basis of variation in chances to catch the movement. In this case, whether the reinforcement of impression different from the case of independent application of each mode exists or not is still not clarified from the present experiments.

The writer's opinion as to the channel for communication of impression is as follows: There is at least a single translator between neighbouring two ommatidia which mediates impression of the preceding stimulus to that of the next stimulus. This is easily surmised from the results of experiments which used various slits. Responses to movement of black stripes which travel in a wide slit and stimulate successively neighbouring ommatidia are conspicuous. In proportion to the enlargement of distance between slits resultant from narrowing the width of the slits, responses to the movement of the stripes become diminished (Fig. 17). As stated already, it is indubitable that communication of stimuli between contiguous ommatidia plays the principal role in the perception of movement in compound eyes. The translator administers the transmission of stimuli between ommatidia. Consecutive stimulation of adjoining ommatidia by stimuli of different strengths gives rise to a summation of excitation of various degrees within the translator. The field of impression which corresponds to the degrees of summation of excitation within the translator is constructed in the center of perception. In connection with the experimental results about the spatial arrangement of black stripes, it was known in detail that responses to the simultaneous stimulation of different areas of eyes are introduced by means of the mutual relationship of summation between the fields of impression. The perception of movement in the compound eyes of mosquitoes is thus carried out by the multiple structure of communication channels of stimuli.

*Acknowledgement:* The writer wishes to express his sincere thanks to Professor Tohru Uchida for his instructive guidance in the course of this research and his kindness in reading through the manuscript.

### Summary

1. The optomotor reaction of mosquitoes varied with the species and velocities of rotation of a pattern consisting of black stripes which were placed quadrantly on a white ground. Males of *Aedes vexans nipponii* most actively responded to the pattern revolving at the speed of 5 rotations per minute; both males and females of *Culex pipiens pallens* made a peak of responses at the revolving speed of the pattern of about 11 rotations per minute.

2. *C. pipiens pallens* females responded by turning the head to the direction of movement of the pattern, whilst the males of both *C. pipiens pallens* and *A. vexans nipponii* responded mainly by walking. Velocity of motion of the mosquitoes did not always accord with the rotatory speed of the alternate pattern of black and white stripes; therefore, it was inferred that the reaction of the mosquitoes to the moving pattern is a response to "movement" of object, namely, to an alternate change of light rather than a response aimed at fixation of object at the same place in the eyes.

3. The optomotor reaction of *C. pipiens pallens* females to the patterns of black and white stripes is affected by the width of the stripes. The mosquitoes can perceive movement of black stripes wider than  $2^\circ$  on white ground, but seem to find it very difficult to catch movement of black stripes less than  $1.5^\circ$  wide. This almost accords with the fact that the minimum visual angle of an ommatidium is  $3^\circ$  and suggests that the ommatidium is a functional unit in the vision of mosquitoes. In general, responses to movement of black stripes on white ground were inferior to responses to movement of white stripes on black ground. But when placed at extremely wide distance, black stripes on white ground surpassed white stripes on black ground in releasing the responses. These facts indicate that the relative relationship between stripes and distances, i.e., the degree of contrast participates in arousing the responses.

4. The optomotor reaction of *C. pipiens pallens* females to black stripes on white background depends upon the arrangement of the stripes. Frequency of responses increased with the increase of number of stripes when they were arranged at the same distances, while in the case of uniform number of stripes, frequency became large with the increase of width of distance between stripes. From these results, it was surmised that there is an effect of summation between the expanse of impression in the perception center.

5. In the experiments using a cylinder with slits, it was observed that the optomotor reaction is dependent upon number and width of slits. The frequency of responses is proportionate to the width of slits when the number of slits is uniform, and in response to movement of stripes seen from slits of similar width, the frequency became higher with the increase in number of slits. Furthermore, responses varied with the mode of stimulation which was given to neighbouring ommatidia. The mosquitoes were able to perceive movement of an object when stimulus was changed from strong to weak better than movement of

the stimulus offered in the reverse succession. Consequently, it was inferred that between adjoining ommatidia there exists a translator which mediates the previous impression to the newly approaching impression, and that mutual communication of impression between ommatidia is the most essential condition in the perception of movement in compound eyes.

### Literature cited

- Autrum, H. 1950. Die Belichtungspotentiale und das Sehen der Insekten (Untersuchungen an *Calliphora* und *Dixippus*). *Z. vergl. Physiol.* 32 : 176–227.
- Barlow, H.B. 1952. The size of ommatidia in apposition eyes. *J. exp. Biol.* 29 : 667–674.
- Bauers, C. 1953. Der Fixierbereich des Insektenauges. *Z. vergl. Physiol.* 34 : 589–605.
- von Buddenbrock, W. 1952. Vergleichende Physiologie. Bd. 1 : Sinnesphysiologie. Basel.
- und H. Friedrich 1933. Neue Beobachtungen über die kompensatorischen Augenbewegungen und die Farbensinn der Taschenkrabben (*Carcinus maenas*). *Z. vergl. Physiol.* 19 : 746–761.
- Gaffron, M. 1934. Untersuchungen über das Bewegungssehen bei Libellenlarven, Fliegen und Fischen. *Z. vergl. Physiol.* 20 : 299–337.
- von Gavel, L. 1940. Die kritische Streifenbreite als Mass der Sehschärfe bei *Drosophila melanogaster*. *Z. vergl. Physiol.* 27 : 80–137.
- Hanström, B. 1927. Über die Frage, ob funktionell verschiedene zapfen- und stäbchenartige Sehzellen im Komplexauge der Arthropoden vorkommen. *Z. vergl. Physiol.* 6 : 566–597.
- Hassenstein, B. 1951. Ommatidienraster und afferent Bewegungsintegration. *Z. vergl. Physiol.* 33 : 301–326.
- 1958. Über der Wahrnehmung von Figuren und unregelmässigen Helligkeitsmustern. *Z. vergl. Physiol.* 40 : 556–592.
- 1959. Optokinetische Wirksamkeit bewegter periodischer Muster (Nach Messungen am Russelkäfer, *Chlorophanus viridis*). *Z. Naturforsch.* 14(10): 659–674.
- Hecht, S. and E. Wolf 1929. The visual acuity of the honey-bee. *J. gen. Physiol.* 12 : 727–790.
- Hertz, M. 1934. Zur Physiologie des Formen- und Bewegungssehens. I. Optomotorische Versuche an Fliegen. *Z. vergl. Physiol.* 20 : 430–449.
- del Portillo, J. 1936. Beziehungen zwischen den Öffnungswinkeln der Ommatidien, Krümmung und Gestalt der Insektenaugen und ihrer funktionellen Aufgabe. *Z. vergl. Physiol.* 23 : 100–145.
- Power, M.E. 1943. The brain of *Drosophila melanogaster*. *J. Morph.* 72 : 517–560.
- Sakagami, F.S. 1956. Zur Wahrnehmungspsychologie der optischen Dressur bei der Honigbiene. Beitrag II. Reizäquivalenzreaktionen. *Jap. Jour. Zool.* 11 : 579–591.
- Sälzle, K. 1932. Untersuchungen an Libellenlarven über das Sehen bewegter Objekt. *Z. vergl. Physiol.* 18 : 347–368.
- Schlieper, C. 1927. Farbensinn der Tiere und optomotorische Reaktion. *Z. vergl. Physiol.* 6 : 453–472.
- Shima, T. 1942. Die optomotorischen Reaktionen des Taumerkäfers. *Annot. Zool. Japan.* 21 : 125–135.
- Tonner, F. 1938. Halsflexe und Bewegungssehen bei Arthropoden. *Z. vergl. Physiol.* 25 : 425–454.
- Waterman, H. and C.A.G. Wiersma 1954. The functional relation between retinal cells and optic nerve in *Limulus*. *J. exp. Zool.* 126 : 59–85.
- Wigglesworth, V.B. 1950. The principles of insect physiology. 4th ed. Revised, London.