

VISUAL SCANNING IN THE DESERT LOCUST
SCHISTOCERCA GREGARIA FORSKÅL

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(Received 2 April 1959)

INTRODUCTION

Locust nymphs while sitting sometimes sway the anterior part of the body from side to side. The movement was first commented on by Kennedy (1945), who observed it in the field and coined the term 'peering' to describe it, believing that it was correlated with vision. Ellis (1953) agreed with this. Chapman (1955), however, regarded its significance as 'doubtful' since he had observed that it sometimes occurred in a uniform visual field.

Peering is frequently seen when locust nymphs are in the process of orientating to objects in the visual field (i.e. turning towards them (Wallace, 1958)). This strongly suggested that it was related to vision, and a laboratory investigation was made along these lines. The present paper is an account of this work and falls into two main parts: (1) A study of the sort of peering movement observed and its relation to the position of objects in the visual field. (2) A study of peering in relation to the visual estimation of distance.

SIZE OF PEERING ANGLE AND THE POSITION OF
OBJECTS IN THE VISUAL FIELD

This experiment was designed to test whether or not peering was influenced by the position of an object in the visual field.

METHODS AND MATERIALS

The swaying of the anterior part of the body is accomplished by straightening the first and second legs on one side and bending the corresponding members on the opposite side. The hind legs are seldom involved and none of the six feet is moved. By stretching the left legs, for example, and bending the right legs the body is made to sway to the right. During the movement the head and body are not tilted, the dorso-ventral axis of the head remaining vertical. Thus in peering the insect moves the whole body except the posterior tip of the abdomen, which rests on the ground so that, in swaying, the longitudinal axis of the body moves roughly like the radius of a circle with its centre at the tip of the abdomen. In some cases the head moves with respect to the long axis of the body (see later, p. 523).

In view of the nature of the peering movement it was decided that this could best be measured as the angle between the various positions of the longitudinal body

axis taking the position of this axis before the peering as a 0° reference line and measuring peering angles to right and left of this. The instrument used was a protractor with a movable pointer. The whole was made of Perspex, the pointer being a broad sector of Perspex with a fine line etched on it. The breadth of the sector allowed the insect to be viewed through it without distortion.

During the experiments the instrument was held horizontally, approximately 1 ft. above the insect and behind it, in which position it did not disturb the insect. It could not be held directly above since with the lighting overhead this would have cast a shadow on the animal.

The longitudinal axis of the body was aligned with the 0° line on the protractor scale, the centre of the protractor being visually superimposed on the tip of the abdomen. When the insect's body moved the pointer was moved by hand to follow it, keeping the line of the pointer on the longitudinal axis of the body. The peering angle was read off in degrees.

With the instrument held as described above, trial measurements made of unknown angles drawn on paper showed that accuracy could be obtained to within one degree. The accuracy achieved in the experiments was probably less since the insect was moving, albeit very slowly.

It was found that a locust nymph placed on a narrow platform would walk along to the end of it, stop and peer. This method was therefore used to position the insects at a known distance and direction from an object in the visual field. The platform was placed inside a white-walled, white-floored arena 2 ft. in diameter and with a wall 10 in. high. Lighting was from overhead. The object was a black stripe 10 in. tall and 2 in. broad stuck on the arena wall. Nymphs of the desert locust are attracted to such objects (Wallace, 1958).

The long axis of the platform was taken as the line of bearing 0° since almost all insects settled with their bodies initially on this line.* In the statement of results the bearing of the object in degrees is therefore expressed with reference to this line.

The insects used were fifth-stage nymphs of the phase gregaria (Uvarov, 1928) since their large size facilitated measurement of the peering angles.

The experiments were performed in a constant-temperature room maintained at 28°C .

EXPERIMENT

Two groups of tests were made, one with an object placed in front of the animals and one with an object at the side.

Object in front. In this test the object was placed directly in front of the insect at a distance of 6 in. At this distance it subtended a horizontal angle of 20° and thus when placed symmetrically on the 0° line its vertical edges lay 10° to the right and left respectively (Fig. 1 a).

Object at the side. In this test the object was at the right-hand side again at a distance of 6 in. The bearings of its vertical edges were 40° and 60° respectively (Fig. 1 b).

* Insects which did not take up this position are excluded from the results.

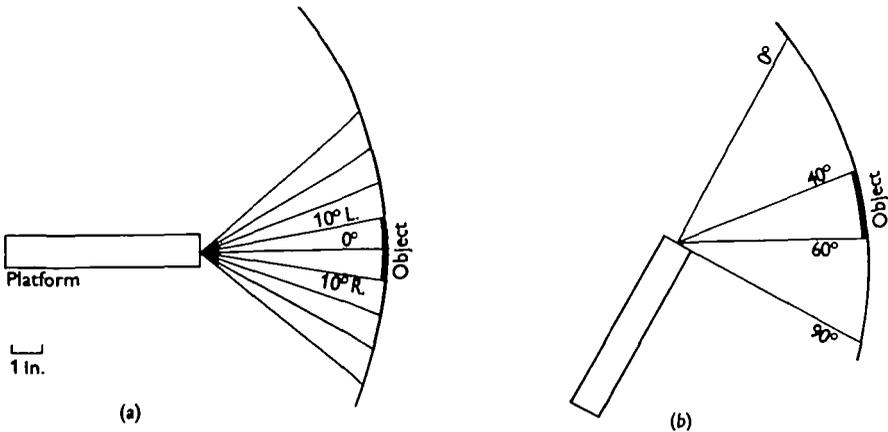


Fig. 1. Plan view showing relative positions of platform and object in an experiment to study the effect of object position in relation to the peering observed. (a) Object in front. (b) Object 40-60° to the right.

RESULTS

The distributions of the different-sized peering angles in the two situations are presented in Fig. 2*a*, *b* and *c*.

The angles of peering varied from 1 to 12°. For convenience they are divided into four categories, 1-3°, 4-6°, 7-9° and 10-12°. In Fig. 2*a* the total frequency of occurrence of angles in each group is plotted irrespective of whether they are to right or left. This is done for both situations. In Fig. 2*b* the frequency of occurrence of different-sized angles to right and left is plotted for the situation where the object is in front. In Fig. 2*c* similar values are plotted for the situation with the object at the side.

From Fig. 2*a* the following points can be made. The maximum angle recorded is 12°. In both situations angles of peering between 4 and 6° are most common. When the object is in front there is a high proportion of angles of 4-6° and angles of 7-12° are rare. When, however, the object is at the side the distribution is different. Angles of 4-6° are still most common but not significantly more so than those of 7-9°. The frequency of angles of 7-9° is significantly higher when the object is at the side than when it is in front ($P < 0.01$ by χ^2).

The two remaining histograms show the frequency with which certain sizes of peering angle lie to right or left of the mid-line. It is at once clear (Fig. 2*b*) that with the object in front the distribution to the right is the same as to the left. The distribution is different when the object is at 40-60° to the right. The smaller angles of 1-3° and 4-6° are still distributed equally to right and left, there being no significant difference between the corresponding points ($0.1 > P > 0.05$, $P > 0.99$ respectively by χ^2). The larger angles 7-9° and 10-12° show a marked difference in distribution, there being a significantly greater number to the right, i.e. to the same side as the object ($0.05 > P > 0.02$; $0.02 > P > 0.01$ respectively by χ^2).

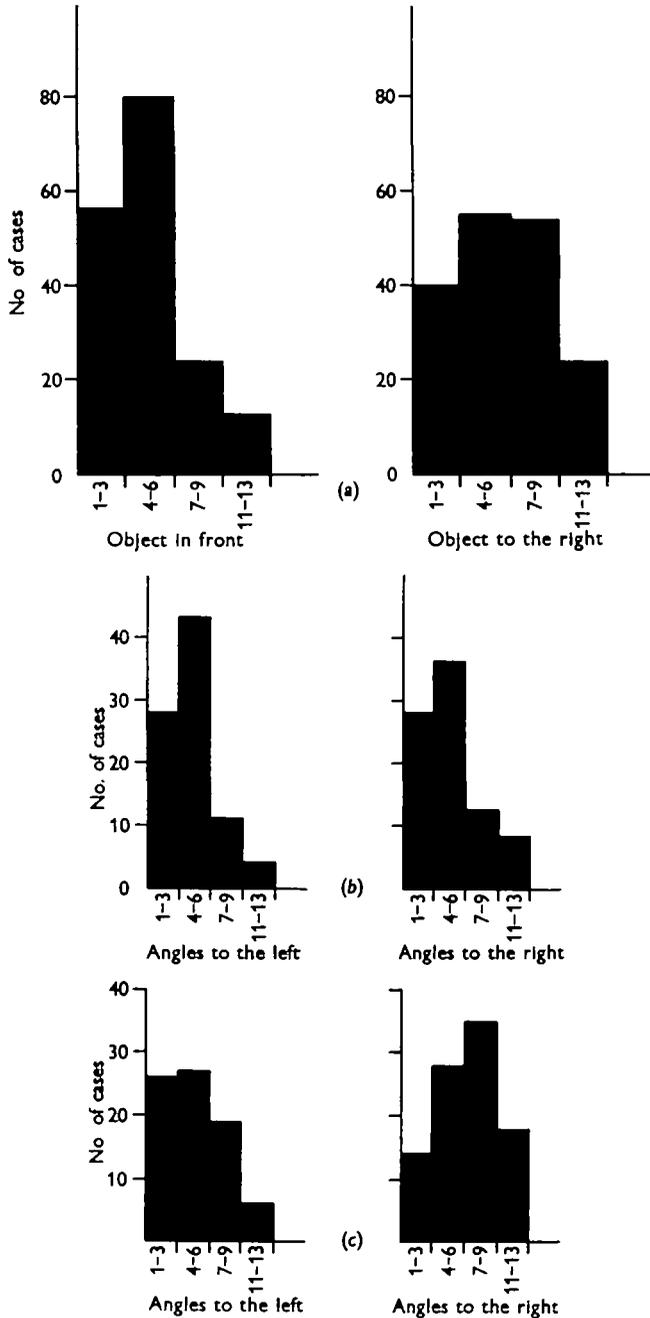


Fig. 2 (a-c) Histograms representing the various distributions of peering angles in the two situations shown in Fig. 1. The x-axis represents four categories of peering angle: 1-3°, 4-6°, 7-9° and 11-13°. The frequencies of occurrence of these categories are plotted on the y-axis as number of cases. The total number of angles recorded for the two situations (object in front, object at the side) is 173 in each case. (a) This shows the distribution of peering angles in both situations irrespective of whether the angles are to the right or left. (b) This shows the distribution of peering angles to right and left when the object is in front. (c) This shows the distribution of peering angles to right and left when the object is to the right.

DISCUSSION

The complete results may be stated as follows. The frequency of small peering angles is not affected by the position of an object in the visual field. When an object lies in front of the animal most peering angles are small and all angles occur equally to right and left. When, however, the object is at the side, there is a significant increase in the number of large peering angles and most of these lie to the same side as the object. The smaller angles are still equally represented to right and left.

Since, then, the position of an object in the visual field influences peering in this way, it can be concluded that the movement is correlated with the visual sense. The fact that the distribution of the smaller angles is unaffected does not of course mean that these are not correlated with vision. As will be mentioned later it is possible that this is a preliminary scanning.

Peering and distance estimation

The above experiment had shown that peering was related to vision but had provided no information as to the function of the movement. Both Kennedy (1945) and Ellis (1953) suggest that it 'sharpens' vision, presumably in the sense of increasing visual acuity. This hypothesis would be difficult to verify.

There was, however, a second possibility, namely, that it was a means of estimating distance. Observation had shown that the nymphs often jumped accurately on to objects and that in all cases (except when the insects were frightened) such jumping was preceded by peering. This ability to jump on to objects was therefore studied with respect to the peering observed.

FIRST EXPERIMENTAL SERIES

This series was designed to test whether or not nymphs discriminated between objects at different distances, to study the importance of certain distance cues and to observe the occurrence of peering in the behavioural sequence preceding jumping.

Apparatus

The narrow platform already described was placed inside the arena with overhead lighting. The long axis of the platform was taken as the 0° line and corresponding reference lines were drawn on the floor at intervals of 5° from 0° to 90° to right and left. The direction of the insect's body could be noted by visually aligning the longitudinal body axis with one of the floor lines. A plain white barrier 2.5 in. high was placed right across the arena between the platform and the objects. The platform itself was 2 in. high and therefore when an insect was sitting at the end of it the barrier cut off all lines of sight below the horizontal, thus preventing any estimation of distance using the positions of the objects' bases.

Since fourth-instar nymphs jump more readily than fifth instars and since they have a sufficiently large body size to make observation easy, nymphs of this instar were used in all the remaining tests.

Behaviour

When placed on the platform an insect would usually walk along to the end of it, stop, peer, then after a pause change the body position and peer again. Changes of orientation always accompanied by peering might occur several times. Finally the insect would usually jump on to one of the two objects present.

Readings

The body position at every orientation was noted and the final choice of object recorded. The actual peering angles were not noted. Each insect was tested five times. A summary of the test situations and the results is given in Table 1.

Table 1. Summarized conditions and results of jumping tests with two stationary objects

(The columns N and D show the number of jumps made on to the near and distant objects respectively. Numbers in parentheses represent jumps not aimed at either object. The objects were black rectangles of the dimensions stated.)

Test	Experimental conditions		Choice		Total	P by χ^2
	Near object	Distant object	N	D		
1	6 x 1 at 3 in. and 45° L	12 x 2 at 6 in. and 45° R	23	2	25	< 0.01
2	4 x 1 at 3 in. and 45° R	12 x 2 at 6 in. and 45° L	23	2	25	< 0.01
3a, partially blinded	6 x 1 at 3 in. and 45° L	12 x 2 at 6 in. and 45° R	14	1	15	< 0.01
3b	6 x 1 at 3 in. and 45° L	12 x 2 at 6 in. and 45° R	20 (3)	2	25	< 0.01
4, partially blinded	4 x 1 at 3 in. and 45° L	8 x 2 at 6 in. and 45° R	14 (1)	5	20	0.05-0.02
5, one eye blind completely	4 x 1 at 3 in. and 80° R	8 x 2 at 6 in. and 30° L	12 (1)	2	15	< 0.01
6a, partially blinded	4 x 1 at 3 in. and 80° R	8 x 2 at 6 in. and 30° L	15	5	20	0.05-0.02
6b	4 x 1 at 3 in. and 30° L	8 x 2 at 6 in. and 80° R	19	1	20	< 0.01

Test 1

The purpose of this test was to see if the insect could distinguish between two objects at different distances but subtending the same vertical and horizontal angles from the insect's position (so that their retinal images were the same size) and with their images appearing on corresponding parts of the two eyes.

The objects were two black rectangles. One was 6 in. tall and 1 in. broad at a distance of 3 in. from the insect and at a bearing of 45° to the left. The other was 12 in. tall and 2 in. broad and at a distance of 6 in. from the insect and 45° to the right.

Test 2

This was similar to test 1 except that the nearer object was reduced to a height of 4 in. and placed at 45° to the right. The distant object was now on the left. By thus reversing the positions of the objects, this tested the probability of the insects orientating to some positional cue in the environment. Reducing the size of the nearer object ensured that the image of the further object was always slightly larger than that of the nearer one, irrespective of the position of the insect on the runway.

Tests 3-6

These tests were to test the importance of binocular vision in the estimation of distance. The insects were blinded wholly or partly in one eye. Since locusts are photopositive they might tend to turn to the unblinded side, and for this reason in the first few tests, where the objects were on either side, the nearer object was placed on the blinded side. If there were any bias due to blinding it would be towards the side of the distant object.

Under a dissecting microscope the insects were blinded by application of three coats of cellulose acetate paint. They were examined at the beginning and end of each experiment and in any case where the blinding was faulty as seen by holes or thin places in the cover the insect was rejected. In a preliminary test the insects were tested 3 hr. after blinding but this did not appear to be a sufficient length of time to allow recovery. They showed little inclination to jump. They walked to the end of the platform and then walked all round the end, down the side, often turning several times and moving sideways over the edge. In some cases the animals which jumped somersaulted and missed the object, or jumped, banged into the object and dropped. After 24 hr. they jumped more readily. In all cases therefore the insects were kept for 1 day before testing.

The extent of blinding was checked by observation of the pseudopupil. This is seen apparently on the surface of the compound eye when the eye is viewed under incident illumination. It arises from a group of ommatidia whose optical axes are parallel, or nearly so, to the line of sight. The dark effect is due to total absorption of the incident light by the pigment lying around the reticular cells. The centre of the pseudopupil thus represents a line of sight which is directed along the optical axis of the underlying ommatidium (after Burt & Catton, 1954). Binocular vision in insects arises as a result of the intersection of the lines of sight of ommatidia in the two eyes. It is therefore clear that binocular vision exists at any point of the visual field from which the pseudopupils of both eyes can be seen simultaneously. The blinded insects were therefore scrutinized under a low-power dissecting microscope and the regions of binocular vision which remained after blinding were ascertained by the above method. An attempt was made to allow for the fact that the ommatidial visual field is greater than that subtended by the ommatidial angle (Burt & Catton, 1954). This was done by painting out more than the minimum region indicated as necessary from observation of the pseudopupil.

Details of the blinding in each case and the positions of the objects are given in Fig. 3.

In all the tests the aim was to remove the field of binocular vision with the minimum upset to the rest of the visual field. When positive results were obtained in the initial tests, the extent of blinding was increased in the later ones (with both objects on one side) in an attempt to preclude even the remotest possibility of binocular vision.

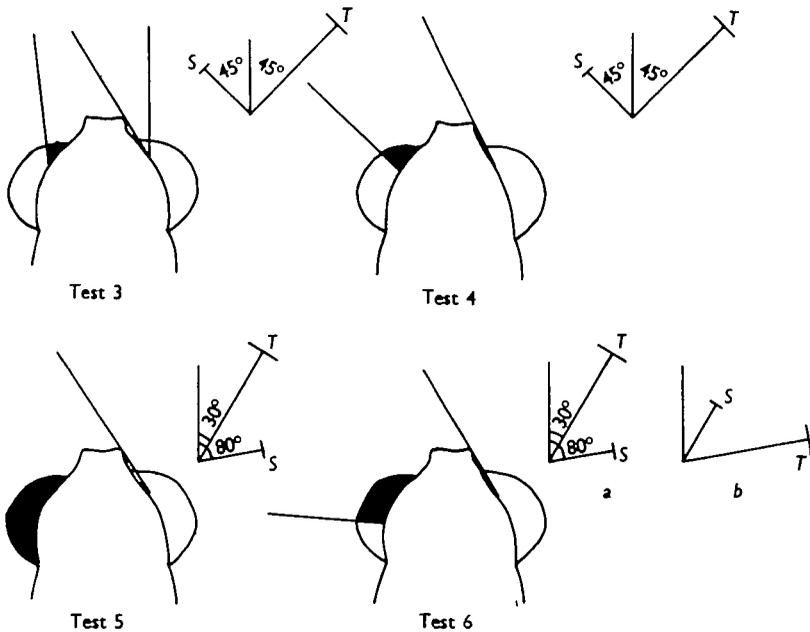


Fig. 3. Diagram showing the area of the eye blinded and fractions of the object in the jumping tests. The head and eye are seen in plan view. For method of estimating the extent of blinding see text. The angles are given with respect to the long axis of the platform (see text). *S* = short object, *T* = tall object. Details of object size are given in Table 1.

Results of the first experimental series (tests 1-6)

The tests in this series showed that when presented with the two objects described, one at half the distance of the other, the majority of the insects in all cases chose the nearer object. The results indicated that, within the limits imposed by the tests, this choice is not based on the angle subtended by the objects nor is binocular vision necessary. The judging of distance therefore appeared to be made on other criteria than these. A closer study of the orientation behaviour prior to jumping suggested that distance might be estimated during the peering movement.

Table 2 shows the orientations observed in test 1 and is typical of the readings taken in the other tests. The figures for the other tests are therefore not given. The point to note is that before jumping the insects orientated fairly accurately towards the chosen object. From this kind of data a further analysis can be made in terms of the sequence of the orientations and whether or not they are towards the side of the chosen object. The actual angle of orientation is not used. The results of such an analysis for tests 1 and 2 are given in Table 3.

Table 2. *Body orientation while insect peered in a situation with two objects 45 degrees to left and right*

(For further description see text. The orientations were measured with respect to a 0° line midway between both objects. Orientations marked N and D represent orientation to the side of the nearer and more distant object respectively. N and D in the jumping column indicate the object on to which the insect finally jumped.)

Animal	Body orientation to nearest 5°				Jump	
					N	D
1	0°	5° D	90° N	45° N	+	-
	0°	60° N	.	.	+	-
	0°	60° N	45° N	.	+	-
	5° N	10° D	45° N	.	+	-
	45° N	30° D	20° N	45° N	+	-
2	0°	20° N	.	.	+	-
	0°	10° N	30° N	.	+	-
	0°	45° N	.	.	+	-
	5° D	20° N	30° N	.	+	-
	0°	30° N	.	.	+	-
3	0°	45° N	.	.	+	-
	10° D	0°	20° N	.	+	-
	5° N	25° N	.	.	+	-
	0°	10° D	.	.	-	+
	10° N	20° N	.	.	+	-
4	0°	45° N	.	.	+	-
	10° D	90° N	20° N	45° N	+	-
	0°	45° N	.	.	+	-
	0°	45° N	.	.	+	-
	10° N	45° N	.	.	+	-
5	10° D	90° N	45° N	.	+	-
	0°	45° N	.	.	+	-
	5° N	45° N	.	.	+	-
	10° D	40° D	.	.	-	+
	5° N	45° N	.	.	+	-
			Total	23	2	

Table 3. *The frequency and order of orientations made prior to jumping on to one of two objects at different distances and at 45° to right and left (tests 1 and 2, Table 1)*

(Orientations: O = along line of 0°; N = to one side of the 0° line, the side of the nearer object, D = to one side of the 0° line, the side of the more distant object. Choice N or D indicates final jump on to near or distant object respectively. 1-5 indicates temporal sequence of orientations.)

Test	Order of orientations					Final choice											
	1			2					3		4		5				
	O	N	D	O	N	D	O	N	D	O	N	D					
1	13	7	5	1	19	5	.	9	.	.	3	23	2
Totals	25			25		9		3		0							
2	14	7	4	.	18	2	.	7	23	2
Totals	25			20		7		0		0							

There is no significant difference between the numbers of first and second positions (columns 1 and 2), but there is a highly significant difference between the numbers of the second and third positions (columns 2 and 3) (test 1, $P < 0.01$, test 2, $0.02 > P > 0.01$ by χ^2). In other words, the majority of the insects only peer in two positions. Few show a third orientation and fourth orientations are very rare. Approximately half the insects peer first in an unbiased position midway between the two objects. The insects, therefore, 'decide' during the first peering, then turn towards the chosen object, peer in that position and jump.

This behaviour strongly suggested that the insects were measuring the distance to the object by the peering movement.

SECOND EXPERIMENTAL SERIES

Exner (1891), in discussing distance estimation, suggested, among other methods, that for crabs with movable eyes the rate of movement of the image of the object over the eye might be used as a measure of its distance from the animal. The closer the object the faster its image would move over the retina as the eye moved from side to side. Now a locust nymph could achieve exactly the same result by peering. The second series of tests on peering and distance estimation was designed to test this hypothesis directly. The principle was to present the insects with a single object which was moved slightly when they peered at it. By this means it was hoped to confuse the insects as to the distance of the object by increasing or decreasing the relative movement of the image over the retina.

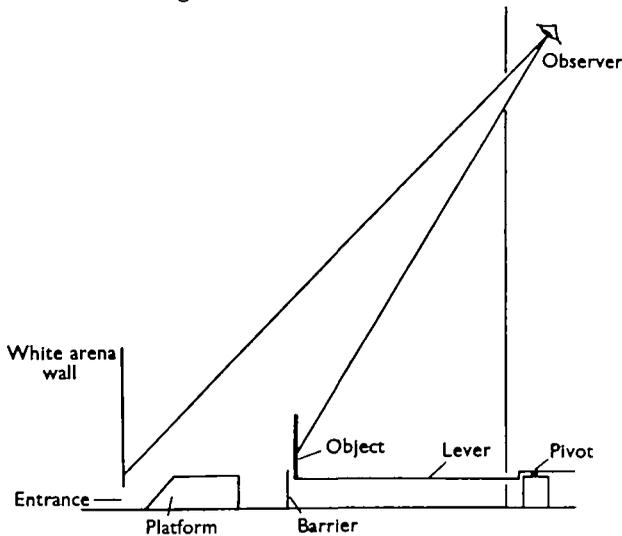


Fig. 4. Elevation of apparatus used in the jumping test with moving object (see text).

Apparatus and method

The apparatus is shown in Fig. 4.

The object was a black rectangle 4 in. tall and 1 in. broad at a distance of 3.5 in. There were two experimental conditions—'moving against' and 'moving with'.

In the former, every time the insect swayed to one side the object was moved slightly in the opposite direction. In the latter the object was moved in the same direction as the animal. Controls were run with the object stationary.

Readings

Note was taken of whether the insect jumped on to the object, overshot it, or jumped short of it.

Results

The results are given in Table 4.

Table 4. *The results of a jumping test with a single moving object*

(For description see text and Fig. 4. The experiment was performed with two groups of animals, the first group being tested under two conditions and the second group being tested under the three conditions shown. S = jumped short, O = overshot.)

Animal	Stationary object				Object moving against insect			
	Hit	Miss	S	O	Hit	Miss	S	O
1	4	1	.	.	0	5	5	.
2	8	1	.	1	1	5	5	.
3	5	0	.	.	0	5	5	.
4	5	0	.	.	0	5	5	.
5	5	0	.	.	0	5	5	.
6	4	2	2	.	0	3	3	.
7	3	2	2	.	0	3	3	.
8	8	0	.	.	0	7	7	.
	42	6	4	1	1	38	38	0

Animal	Object stationary				Object moving with insect				Object moving against insect			
	Hit	Miss	S	O	Hit	Miss	S	O	Hit	Miss	S	O
1	5	0	.	.	5	0	.	.	0	3	3	.
2	5	1	.	1	3	2	2	2	0	3	3	.
3	3	0	.	.	3	2	1	1	0	2	2	.
4	6	1	.	1	3	3	2	1	0	2	2	.
	19	2	.	2	14	7	3	4	0	10	10	.

They showed clearly that when the object was stationary the insects seldom missed it, whereas when it was moved in the opposite direction to the animals' peering motion they misjudged the distance and in almost all cases they jumped short. They never overshot. When the object was moved with the insects the insects managed to jump on to it in most cases. Occasionally they jumped short or overshot.

Second experimental series—discussion

It is to be expected that in the situation 'moving against' the relative motion of the object as perceived by the insect is much greater than it would be for a stationary object at that distance, and is equivalent to the relative motion of a stationary object at a shorter distance from the insect. This is apparently how the insects interpret the information received and would explain why they jump short. This is further

borne out by the fact that the insects were observed to beat the antennae vigorously and to stretch out the first pair of legs and 'paw' the air. This is the behaviour observed in response to a stationary object very close to the insect and probably represents an attempt to climb on to the object.

In the situation 'moving with' the reverse occurs and the object appears to be much further away than it really is. This does not, however, prevent the insects from jumping on to it, since if their direction is correct they will encounter the object during their trajectory. Hence the number of hits in this case is significantly greater than the number of misses. If the direction is not accurate they may overshoot.

By themselves the results of this experiment are not conclusive evidence for a distance-judging method based on relative movement. A binocular method might also be upset by the movement of the object, since the insect might find it difficult to fix the object. Taken in conjunction with the previous tests, however, which showed that binocular vision was not necessary for such a judgement, they appear to support the hypothesis that the image movement produced by peering is the information on which the estimation is made.

It was previously mentioned (p. 512) that when the body moves through a large peering angle the longitudinal axis of the head moves with respect to that of the body. When the experiments reported here were performed there was no available means of measuring this small movement. It was thought possible that the head position was changed so as to minimize the image movement on the retina. Recent high-speed photography has shown that the head movement does not compensate for the body displacement; it results in a lateral movement of the head rather than a radial movement. Thus despite the head movement there is still a large movement of the image on the retina.

GENERAL DISCUSSION

The peering movement which has been described in this paper has been shown to be related to the visual sense. There is evidence to support the idea that it is a method of estimating distance.

Many of the peering angles are small and unaffected by the position of objects in the visual field and it is likely that these movements represent a preliminary scanning. It was observed that they did, in fact, precede the larger biased peering angles. In other words, locusts peer either when looking at something, i.e. measuring the distance of a particular object, or when looking for something, i.e. when scanning the surroundings. On this basis the observation made by Chapman (1955) that locusts peer in a uniform visual field is understandable.

It seems to be generally accepted (Wigglesworth, 1953; Roeder, 1953) that in insects possessing highly developed compound eyes with overlapping frontal fields distance estimation is accomplished by a binocular method. This is based on the work of Baldus (1926) and Friederichs (1931). It is perhaps significant that both these authors worked with predatory insects, *Aeschna* nymphs and cicindelid adults respectively. *Aeschna* nymphs catch their prey by shooting out the labial

mask and cicindelid adults use their large mandibles. In both cases extremely short distances are involved, and while it is clear that in these cases the binocular method is very accurate this accuracy will fall off with distance. In the desert locust there is a fairly large binocular field and thus at short distances the binocular method may be used. At large distances, on the other hand, such as those covered by a locust nymph when jumping, it is possible that the binocular method is no more accurate and perhaps even less accurate than one based on relative movement. It is known that the compound eye may be extremely sensitive to small movements (Burt & Catton, 1954, 1956), and it is therefore possible that even when objects are at relatively great distances and their image movements correspondingly small the locust may still measure these accurately.

Finally, distance estimation may not be the only function of peering. It is possible that it has a more general function in that the image movements may provide the insect with more information as to the finer details of the visual field.

SUMMARY

1. This paper describes a lateral swaying movement performed by desert locust nymphs. This movement is called 'peering'.
2. The angle through which the body moves is influenced by the position of objects in the visual field, showing that the movement is related to vision.
3. When given a choice of two objects at different distances the nymphs show a preference for the nearer one. The estimation of the relative distances of the two objects is not achieved by a binocular method nor is it based on the angle subtended by the objects.
4. An experiment is described in which an object is moved while the insect is peering. If the object is moved in the opposite direction to the insect's motion the insect jumps short of the object. This seems to support the hypothesis that one of the functions of peering is to estimate distance by the extent of the movement over the retina of an object's image.
5. This method of distance estimation is discussed with relation to the binocular method.
6. It is suggested that in some cases the peering observed may represent a preliminary scanning of the visual field and may provide information about the finer details of the field.

The experiments reported in this paper were performed during the tenure of grants from the Carnegie and Cross Trusts and formed part of a thesis for the degree of Ph.D. of St Andrews University. The work was carried out in the Department of Entomology, Oxford, and I wish to thank Prof. G. C. Varley for his kindness in affording me facilities. I am grateful to Dr B. P. Uvarov, F.R.S., and Dr T. H. C. Taylor of the Anti-Locust Research Centre for their encouragement at all stages. I also wish to thank Dr F. L. Waterhouse, Queen's College, Dundee, for criticism and encouragement. I am grateful to Dr D. M. Vowles, Psychology Department, Reading, and to my wife for their criticism of the manuscript.

REFERENCES

- BALDUS, K. (1926). Experimentelle Untersuchungen über die Entfernungslokalisation der Libellen (*Aeschna cynea*). *Z. vergl. Physiol.* **3**, 475-505.
- BURTT, E. T. & CATTON, W. T. (1954). Visual perception of movement in the locust. *J. Physiol.* **125**, no. 3, 566-80.
- BURTT, E. T. & CATTON, W. T. (1956). Electrical responses to visual stimulation in the optic lobes of the locust and certain other insects. *J. Physiol.* **133**, no. 1, 68-88.
- CHAPMAN, R. F. (1955). A laboratory study of roosting behaviour in hoppers of the African migratory locust. (*Locusta migratoria migratorioides* R. & F.). *Anti-Locust Bull.* no. 19, 40 pp.
- ELLIS, P. E. (1953). Social aggregation and gregarious behaviour in hoppers of *Locusta migratoria migratorioides* (R. & F.). *Behaviour*, **5**, 225-60.
- EXNER, S. (1891). *Die Physiologie der facettierten Augen von Krebsen und Insecten*, 206 pp. Leipzig and Vienna: Franz Deuticke.
- FRIEDERICH, H. F. (1931). Beiträge zur Morphologie und Physiologie der Sehorgane der Cincidellen. *Z. Morph. Ökol. Tiere*, **21**, 1-72.
- KENNEDY, J. S. (1945). Observations on the mass migration of desert locust hoppers. *Trans. R. Ent. Soc. Lond.*, **95**, 247-62.
- ROEDER, K. D. (1953). *Insect Physiology*, 1100 pp. London: Chapman and Hall.
- UVAROV, B. P. (1928). *Locusts and Grasshoppers*, 352 pp. London: The Imperial Bureau of Entomology.
- WALLACE, G. K. (1958). Some experiments on form perception in the nymphs of the desert locust *Schistocerca gregaria* Forskål. *J. Exp. Biol.* **35**, 765-75.
- WIGGLESWORTH, V. B. (1953). *The Principles of Insect Physiology*, 5th ed. 546 pp. London: Methuen.