THE VISUAL ACUITY OF THE FIDDLER-CRAB, UCA PUGNAX*

By LEONARD B. CLARK

(From the Laboratory of Biophysics, Columbia University, New York)

(Accepted for publication, May 1, 1935)

Visual acuity in the human eye varies in a specific way with the illumination. The relation between the visual acuity and the logarithm of the intensity is described by a sigmoid curve (Koenig, 1897; Hecht, 1927–1928). Hecht and Wolf (1929) presented the first quantitative data on the relation between visual acuity and illumination in an animal with compound eyes. They used an experimental procedure involving neither conditioned reflexes nor training. Their data show that despite the morphological differences between the vertebrate and the arthropod eye a similar relation exists between visual acuity and illumination in the honey bee and man. *Drosophila* was found to show a like relation by Hecht and Wald (1934).

The importance of such results indicates the advisability of extending the study to other animals. Hecht and Wolf, starting with the common observation that most animals with eyes respond to a sudden movement in their visual field, developed a method of measuring visual acuity quantitatively.

Observation showed that movement in the visual field above a fiddler-crab elicited a response. Application of the reasoning and methods of Hecht and Wolf indicated a method by which quantitative data might be secured.

This paper reports a study of visual acuity in the fiddler-crab. It involves an investigation of monocular and binocular visual acuity, and analysis of the responses to a visual pattern in terms of the structure of the eye, and finally, field observations which attempt to confirm the laboratory findings.

---

* Investigation pursued during tenure of a National Research Fellowship.

Nature of Response

The experimental procedure with bees and *Drosophila* consists in moving a pattern made up of alternate dark and light bars in the visual field of the animal. It was found that the normal fiddler-crab, while giving uniform and consistent responses to a pattern plate made up of one dark bar on a white background, gives inconsistent, indeterminate, or no response to a pattern plate made up of alternate dark and white bars such as was used in the experiments with bees and *Drosophila*.

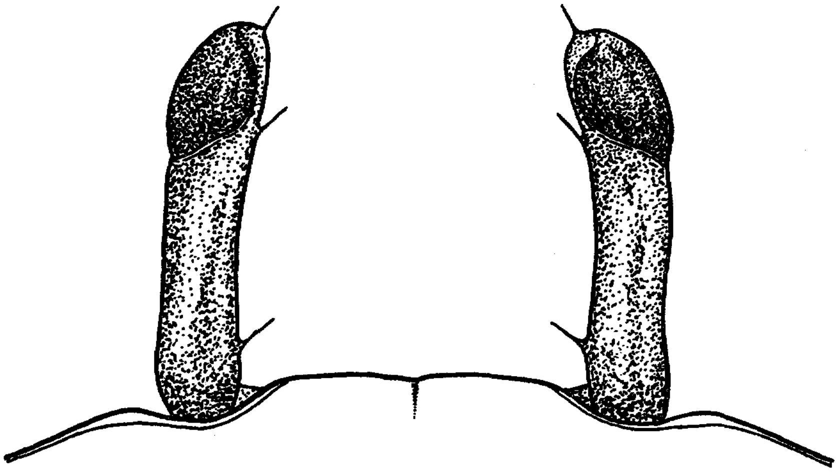

FIG. 1. View of the eye stalks and ommatidia in the fiddler-crab. Note that the ommatidia are found only on the distal outer side of each stalk.

An examination of the ommatidia on the eye stalks of the crab and an analysis of the response provides the explanation. The ommatidia are arranged only on the distal outer side of each eye stalk as shown in Fig. 1. Thus there is little or no overlapping of the visual fields of the two eyes. When a pattern plate composed of a single stripe is passed over a fiddler-crab the following reactions may occur. (*A*) If the stripe is moved slowly, the crab will move away, keeping in front of the stripe continuously. (*B*) If the stripe is moved so as to overtake and pass the crab, the crab will move ahead of the stripe until the stripe passes over it, at which time the crab will stop and move in the opposite direction. (*C*) If the stripe is moved rapidly the two movements of the crab as noted above in (*B*) occur so rapidly that the crab appears to "jump."

The three responses are not separate types, but are variations due to the speed at which the stripe is moved. If the stripe is moved from the animal's right to its left to give type (*B*) response, the crab will move first to the left then to the right. If the stripe is moved from the animal's left to its right, the direction is reversed. It seems that a moving object stimulating the right eye (irrespective of direction of movement) will cause the crab to move to the left, while stimulation of the left eye will cause the crab to move to the right. If this is true then a pattern plate made up of stripes in passing over a fiddler-crab would of necessity stimulate both eyes, and tend to cause movements in opposite directions. It may well be that under such conditions the stimuli inhibit each other with the result that little or no response appears.

Corroboration is given to the above explanation by the behavior of fiddler-crabs with one eye extirpated or removed. If the right eye is blinded and the pattern plate is moved from the left to the right, the animal will move to the right until the stripe passes over it, whereupon it will stop. If the pattern plate is moved from the right, no response is elicited until the stripe passes over the animal, which then moves to the right. If the left eye is blinded the response is similar but opposite in sign. In other words if one eye is blinded part of the normal response to the pattern plate disappears as would be expected.

Apparatus and Procedure

A thousand watt lamp (Fig. 2) enclosed in a double lamp-box was used to radiate light through a water cell and a neutral tint wedge on to a mirror placed at an angle of 45° to the beam of light. The light was reflected downward by the mirror on to an opal glass plate. Immediately beneath was the pattern plate, made by inserting a strip of black paper between two plates of glass, thus giving a pattern of a single black bar on a transparent field. Fifteen pattern plates with stripes of different size were made. A frame which would move freely in a pair of grooves held the pattern plate. The movement of the frame with the plate constituted a moving visual pattern.

The fiddler-crab was confined in a glass bottomed compartment, 10 × 10 cm. in area, directly below the pattern plate. A mirror placed below the animal compartment gave a view of the crab and the visual field.

The intensity of the illumination of the visual field was varied by movement of a calibrated neutral tint wedge. By addition of neutral filters the intensity could be varied over a range of 1:100,000.

The procedure for making a measurement was as follows: A pattern plate was inserted in the movable frame. A fiddler-crab which had been adapted overnight was placed in the animal compartment under a low illumination and left until it became quiet. Then the pattern plate was moved with a sharp but not rapid movement. If no response was elicited it was assumed that the animal could not distinguish the components of the visual pattern and the illumination was increased. If the displacement of the pattern did cause a response the intensity was lowered.

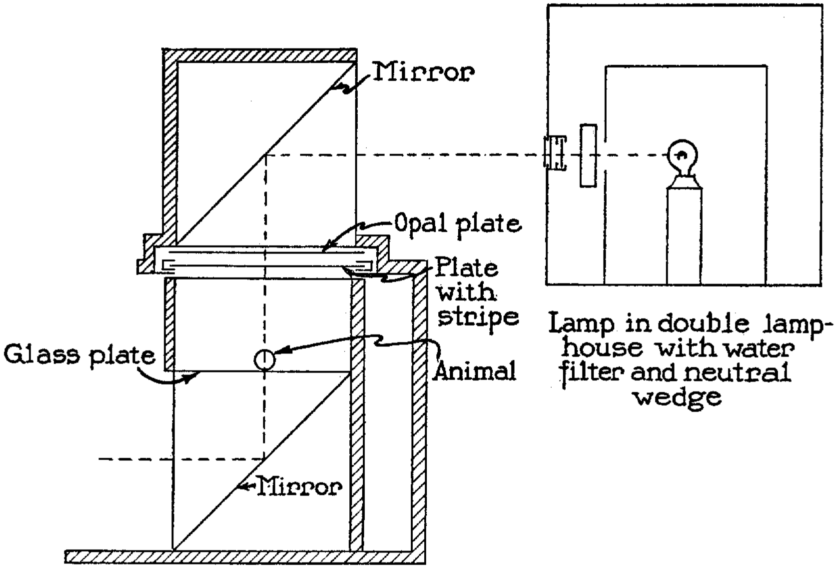

FIG. 2. Apparatus for measuring the visual acuity of the fiddler-crab.

This procedure was repeated until the minimum illumination was found at which the crab would react to a displacement of the field. The visual acuities secured by the use of the plates depend on the width of the stripes and their distance from the eye of the crab. The distance was measured for each crab, because of the difference in size of the crabs; the size of the bar being known, the resulting angle in minutes and its reciprocal—the visual acuity—could then be computed.

RESULTS

Measurements for each of eighteen normal crabs were made with most of the fifteen pattern plates. It is a simple matter to cover or extirpate one eye of the fiddler-crab. Measurements of monocular visual acuity were made in the same apparatus with seven crabs using six pattern plates.

The averaged data are given in Table I and are represented graphically in Fig. 3, where each point is an individual reading showing the actual visual acuity and minimum intensity to secure a reaction. It is immediately evident that the results are similar for both monocular and binocular vision. The data present a relation between visual acuity and intensity which is very similar to the sigmoid curve for the human eye and the honey bee. The curve drawn through the data is the stationary state equation, $0.16\, I = (x-3)/(42-x)$, where x is the visual acuity multiplied by 10,000. This gives a maximum visual acuity of 42×10^{-4} for the fiddler-crab.

TABLE I

Relation between Visual Acuity and Intensity of Illumination for Fiddler-Crabs

With both eyes		With one eye	
Intensity	Visual acuity $\times 10^4$	Intensity	Visual acuity $\times 10^4$
foot candles		*foot candles*	
0.124	3.91		
0.283	5.07	0.269	4.90
0.676	6.76		
0.723	9.87	1.32	9.73
1.70	12.62		
2.80	15.42		
3.41	19.59	4.30	19.60
4.49	23.32		
6.93	26.20		
13.8	29.25		
27.5	34.05	19.5	33.69
138.0	38.90	51.3	38.51
263.0	42.03	208.9	42.31

Field Observations

An attempt was made to verify in the field the laboratory results on maximum visual acuity. It is commonly observed that when a person passes over a flat terrain on which there are numerous fiddler-crabs, they will quickly vacate a zone around the intruder. This zone remains fairly constant in radius and moves as the intruder moves; the fiddler-crabs either seek holes or move away. This phenomenon has been variously explained as the result of vibrations set up in the ground, as a visual response, or even as being chemical in nature. It seems most probable that the response is visual, and if so, it should be possible to test the maximum visual acuity in terms of the following considerations:

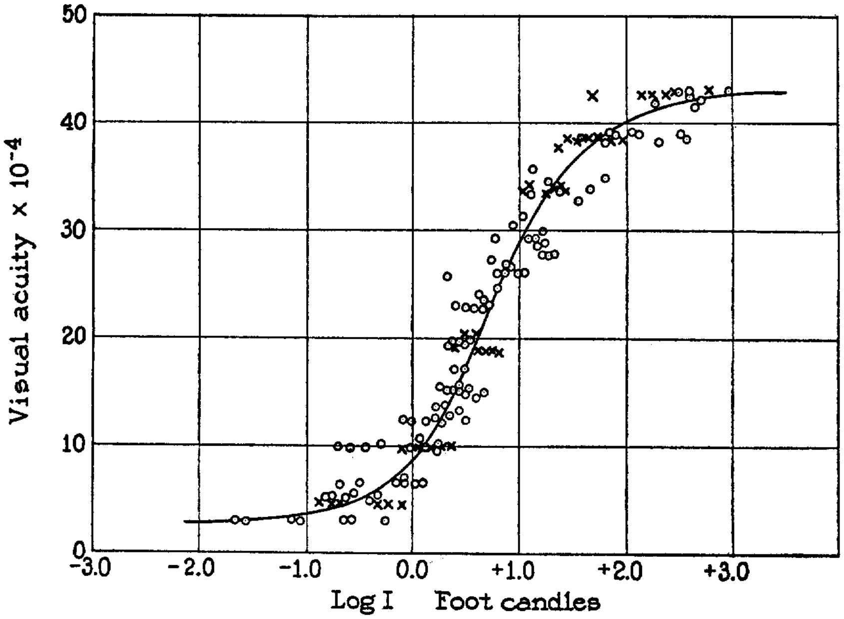

FIG. 3. Relation between visual acuity and illumination in fiddler-crabs. Circles are readings secured from normal crabs; and crosses are readings from crabs with one eye covered or extirpated. The points are individual readings.

Fiddler-crabs will retire from a moving object until they can no longer see it, *i.e.* until such time as the angle subtended by the object is smaller than the smallest effective visual angle; then the crabs will stop or move at random. Therefore the radius of the observed clear zone is a measure of the maximum distance at which the crabs can see a particular moving object. If the size of the object and the distance of the nearest crabs are known the minimum visual angle and thus the maximum visual acuity can be determined.

One of the mud flats near Hillview, Staten Island, proved satisfactory for the experiment. In the early spring the vegetation had been burned off, fiddler-crabs were numerous and well distributed, and the terrain was flat with no large obstructions.

On a day on which the illumination was at least 4500 ft. candles and consequently not the limiting factor, tests were made by carrying black screens 20, 40, and 60 inches in width into the field. Five observations were made of the width of the cleared zone with each screen. The results in each series were averaged and the minimum visual angle and maximum visual acuity determined. These gave visual acuities of 0.0041 for the 20 inch screen, 0.0038 for the 40 inch screen, and 0.0032 for the 60 inch screen. Although they do not compare exactly with the laboratory maximum visual acuity of 0.0043, they are of the same order of magnitude. The low visual acuity from all screens and particularly of the large one may well be due to small obstructions preventing a clear visual field to the crabs.

TABLE II

Average Angular Distance Apart of Ommatidia in Longitudinal Section of Eye of Fiddler-Crab. (Ommatidia Numbered from Distal to Proximal End of Eye)

Ommatidial No.	Average angular distance	Ommatidial No.	Average angular distance	Ommatidial No.	Average angular distance
	degrees		*degrees*		*degrees*
1–4	18.33	25–28	3.0	49–52	4.47 (?)
5–8	11.78	29–32	2.88	53–56	4.43 (?)
9–12	7.37	33–36	2.05	57–60	4.75
13–16	6.27	37–40	2.82	61–64	5.43
17–20	5.88	41–44	2.90	65–68	5.97
21–24	4.05	45–48	2.89	69–72	6.27

Relation between Visual Acuity and the Internal Structure of the Eye

The analysis of the variation in visual acuity with illumination for man by Hecht (1927–28), for the bee (Hecht and Wolf, 1929), and *Drosophila* (Hecht and Wald, 1934) in terms of the distribution of the functional receptors is supported by the work on the fiddler-crab. In man and the bee the minimum visual angle (which determines the maximum visual acuity) is equal to the minimum angular distance between two adjacent receptors. In *Drosophila* the minimum visual angle (9.28°) is twice that of the minimum angle (4.2°) between adjacent ommatidia.

To determine the situation in the fiddler-crab longitudinal sections of the eye were made and the angular distances between the ommatidia measured. There are approximately 72 ommatidia in longitudinal section and their average angular distance apart from the distal to the proximal part of the eye is given in Table II.

Accordingly, it will be noted there is an area near the center of the eye in which the angular distance between two adjacent ommatidia is considerably smaller than over the rest of the eye. In this area the minimum angular distance between two adjacent ommatidia is 2.05°. It would be expected from Hecht's and Hecht and Wolf's analyses of acuity in man and the bee that the minimum visual angle would be the same, namely 2.05°. Actually the minimum visual angle is 3.87°, approximately twice the minimum angular distance between two adjacent ommatidia. Although experimental error might account for this discrepancy, the similar relation between minimum ommatidial angle and visual acuity found by Hecht and Wald in *Drosophila* (4.2° to 9.28°) suggests that the difference is more fundamental.

SUMMARY

The visual acuity of the fiddler-crab can be measured at various illuminations by means of its response to a moving visual pattern. The method, although similar to that used by Hecht and Wolf for the bee and Hecht and Wald for *Drosophila*, must be modified to give consistent results. An explanation of the response to a visual pattern is given in terms of the structure of the eye.

Visual acuity of the crab varies with log I as in man, the bee, and *Drosophila*. Hecht and Wolf's explanation of the varying visual acuity with illumination in terms of the distribution of functional ommatidia in the eye is supported to that extent.

In the fiddler-crab as in man, monocular and binocular visual acuity is similar with a maximum of 0.0042 for the fiddler-crab. This agrees fairly well with visual acuities of 0.0041, 0.0038, and 0.0032 as found in the field.

In man and the bee, the minimum visual angle corresponds to the minimum angle of two adjacent receptors; in *Drosophila* and the fiddler-crab the minimum visual angle corresponds to approximately twice the minimum angle between two adjacent receptors.

BIBLIOGRAPHY

Hecht, S., 1927–28, The relation between visual acuity and illumination, *J. Gen. Physiol.*, **11,** 255.

Hecht, S., and Wolf, E., 1929, The visual acuity of the honey bee, *J. Gen. Physiol.*, **12,** 727.

Hecht, S., Wolf, E., and Wald, G., 1929, The visual acuity of insects, *Am. J. Physiol.*, **90,** 381.

Hecht, S., and Wald, G., 1933, The influence of intensity on visual functions of *Drosophila*, *Proc. Nat. Acad. Sc.*, **19,** 964.

Hecht, S., and Wald, G., 1934, The visual acuity and intensity discrimination of *Drosophila*, *J. Gen. Physiol.*, **17,** 517.

Koenig, A., 1897, Die Abhängigkeit der Sehschärfe von der Beleuchtungsintensität, *Sitzungsber. k. Akad. Wissensch.*, p. 559.