# ON THE RELATION BETWEEN MEASUREMENTS OF INTENSITY DISCRIMINATION AND OF VISUAL ACUITY IN THE HONEY BEE

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I

A method for study of *discrimination of photic intensity* by the honey bee, and certain experimental results, have been described (Wolf, 1932–33). It was shown that the bee's discriminating power for different brightnesses varies with illumination in much the same way that this function does for the human eye (Koenig and Brodhun, 1889; Hecht, 1924–25). The discriminating power is poor at low illuminations; as the intensity of illumination increases the discrimination increases, ultimately less rapidly, until it reaches a certain level at high illuminations. The total range over which the bee can distinguish between different intensities was found to be very much smaller than for the human eye, and at an illumination where the discriminating power of the human eye and of the bee's eye are at their best, the intensity discrimination by the bee is one-twentieth as good as that by the human eye. The experiments by which these results were obtained were made under "optimal" conditions as regards the visual acuity of the bee's eye; for test object a pattern of stripes was chosen which could be easily reacted to even at the lowest illuminations used during the experiment.

The *visual acuity* of the human eye varies with illumination in such a way that at low illuminations the resolving power is poor; at higher illuminations it increases, until it finally reaches a maximum level (Koenig, 1897; Hecht, 1927–28). The same kind of relationship was found for the facetted eye of the bee (Hecht and Wolf, 1928–29). While the relation between visual acuity and illumination is the same in principle for the two organisms, there is a tremendous difference in the absolute magnitudes of the visual discrimination powers. The bee's visual acuity at its best is lower than the lowest human visual acuity. Under maximal conditions for each eye the fineness of the resolving power of the human eye is about one hundred times that of the bee.

No data have been available concerning the relation between visual acuity and intensity discrimination. Accordingly, an investigation of this relationship has been made, with the bee's eye. The procedure was in principle the same as in the previous studies (Hecht and Wolf, 1928–29; Wolf, 1932–33).

## II

### *Apparatus and Procedure*

If the visual field of a bee is made up of a pattern of alternating dark and illuminated bars, or of alternating bars of different brightnesses, the animal will respond to any displacement of this field as long as there is maintained not less than a certain minimum difference in the brightnesses of the alternate bars. In case the animal cannot "resolve" the pattern, either on account of the width of the stripes at a given illumination, or on account of a smaller difference in brightness of alternate bars than is necessary for distinction, the field will act as if uniformly illuminated and a displacement of the field will not elicit a response.

The general method for testing the visual acuity and the intensity discrimination of the bee has been described in detail in two previous papers (Hecht and Wolf, 1928–29; Wolf, 1932–33). With the help of Fig. 1 the nature of the experimental procedures can be made out. The striped pattern underneath the inclined creeping plane upon which the bee crawls can be moved sidewise. For the *visual acuity* test the pattern plates were made of stripe systems of different widths, and for each width of stripe the necessary intensity given by source B was determined for the first noticeable response of the bee. In testing *intensity discrimination*, only one wide stripe width was used, and for each given illumination $I$ furnished by source $A$ the necessary intensity of $\Delta I$ for minimal response furnished by source $B$ was determined; and thus one curve was obtained with that one width of stripe. In combining *both* visual acuity and intensity discrimination tests, the width of the stripes had to be altered and a complete curve for intensity discrimination worked out for each width of stripes. Altogether, ten different widths of stripes were used. The larger ones were made by putting opaque black paper strips on the lower surface of opal glass plates, and covering the paper stripes from underneath with a clear glass plate to press them tight against the opal glass. The finer stripes were machine-engraved on glass and have the opaque areas filled in with black printer's ink. These plates were covered with opal plates

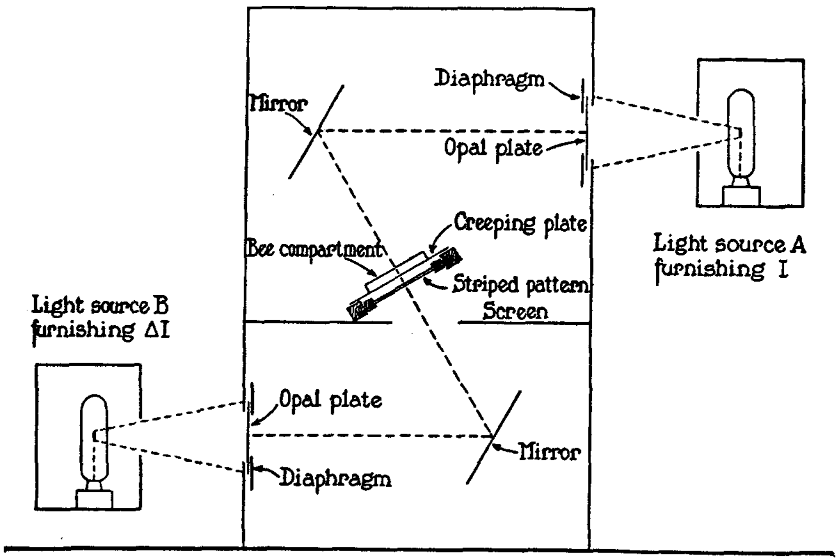


FIG. 1. Diagram of apparatus for measuring the visual intensity discrimination of the bee

in the same manner. During use they were fitted into the movable frame (Fig. 1) so that the opal plate was on top nearest to the bee. The visual acuities determined by these plates depend upon their distance from the eye of the bee. It was arranged in these experiments that the average distance of the upper surface of the opal plate from the bee's head was the same as in the visual acuity experiments carried on some years ago (Hecht and Wolf, 1928–29). The distance to be considered in the intensity discrimination tests is not the distance from the center of the bee's eye to the pattern plate, but to the upper surface of the *opal* plate, because the opal plate acts as a diffusing screen giving an image of the bars of the same width on its upper surface. The average distance, which varies slightly from plate to plate and from bee to bee, was 17.3 mm., which corresponds to the value we had in the visual acuity experiments (Hecht and Wolf, 1928–29). Consequently the values for the visual angles subtended by the bars, and the corresponding visual acuities, were in the two cases identical. In Table I the dimensions of the bars and spaces, the resulting visual angles, and the reciprocals of the visual angles representing the visual acuities, are given. As in the case of ophthalmological practice, a *visual angle* of 1 minute corresponds to a *visual acuity* of 1.

TABLE I

*Designations and Properties of Pattern Plates Used in the Experiments*

| Designation | Width of bar | Visual angle subtended by bar | Visual acuity $\times 10^4$ |
|---|---|---|---|
| | *mm.* | *min.* | |
| A | 20.0 | 2949.0 | 3.40 |
| B | 12.4 | 2136.0 | 4.68 |
| C | 9.4 | 1710.0 | 5.85 |
| D | 6.3 | 1200.0 | 8.33 |
| F | 3.2 | 630.0 | 15.87 |
| G | 1.27 | 252.0 | 39.68 |
| I | 0.635 | 126.0 | 79.37 |
| K | 0.423 | 84.0 | 119.0 |
| L | 0.363 | 72.0 | 138.9 |
| M | 0.318 | 63.0 | 158.7 |

The experiments were carried on exactly in the same manner as the previous ones. Over a desirable range of intensities ($I$), the necessary respective values for $\Delta I$ were determined, and thus intensity discrimination curves were obtained for each set of stripes. With source $A$ turned on, the upper surface of the opal plate will look evenly illuminated ($I$); with light from source $B$ in addition, the spaces in between these stripes will have a brightness $I + \Delta I$; so that by appropriately changing the intensity given by source $B$ the minimal difference in brightness between the two line systems can be determined which gives a just noticeable response of the bee to a lateral displacement of the line systems. Each point plotted on the curves (Fig. 2) represents an average of ten tests with different individuals. Besides the formerly derived intensity discrimination curve, nine new ones were obtained. Altogether 1,120 bees were tested at different intensities and widths of stripes. The results are given in 112 plotted points, to which the best fitting curves were fitted for the different visual acuity levels.

## III

## RESULTS

The experiments were carried on during the latter part of the summer and fall of 1932, with the same apparatus used during the earlier part of the year for the first determination of intensity discrimination by the bee. The light sources at their different positions and the intensity values given at different diaphragm openings were re-calibrated. Then the intensity discrimination at different visual acuities was studied in the order of the magnitudes of the bars from the largest width to the smallest, in the same order as indicated in Table I.

The data obtained for the different widths of stripes are given in Tables II to X. The values of $\Delta I$ and of $\Delta I/I$ in the tables are *mean* values for the total numbers of individuals tested at each $I$, with the probable errors of $\Delta I/I$ and of $\Delta I$ computed according to Peter's formula.

The values for $\Delta I/I$ at each level of visual acuity vary in a significant manner with illumination. For each case, at low intensities $\Delta I/I$ is greatest; it decreases smoothly as the illumination is increased. At the highest illuminations the values for intensity discrimination at different visual acuities are about identical. At lower illuminations they differ significantly according to the dimensions of the striped pattern used and to the visual angles subtended by the different stripe systems. The probable error of $\Delta I/I$ decreases with increasing $I$ for each visual acuity in the same way as does $\Delta I/I$ itself; and as $\Delta I$ increases with increasing $I$, the probable error of $\Delta I$ increases.

In Fig. 2 the data are set out graphically. The points plotted are the mean values for all individuals tested at the respective intensities.

TABLES OF DATA

Mean values for intensity discrimination at different visual acuities and at different intensities measured in millilamberts with their P.E. (number of observations = 10 in each case).

| I Millilamberts | ΔI Millilamberts | ΔI/I |
|---|---|---|
| **TABLE II** | | |
| Stripes B, 12.4 mm. wide. Visual acuity × $10^4$ = 4.68 | | |
| 0.107 | 0.528 ±0.021 | 4.924 ±0.192 |
| 0.134 | 0.451 ±0.010 | 3.374 ±0.076 |
| 0.166 | 0.501 ±0.012 | 3.010 ±0.080 |
| 0.302 | 0.594 ±0.011 | 1.968 ±0.038 |
| 0.417 | 0.784 ±0.015 | 1.880 ±0.035 |
| 0.695 | 1.056 ±0.019 | 1.245 ±0.027 |
| 1.031 | 0.951 ±0.048 | 0.922 ±0.035 |
| 1.439 | 1.199 ±0.044 | 0.833 ±0.028 |
| 2.711 | 1.581 ±0.023 | 0.583 ±0.0088 |
| 3.900 | 1.630 ±0.020 | 0.418 ±0.0052 |
| 6.792 | 2.821 ±0.083 | 0.415 ±0.0129 |
| 13.87 | 3.430 ±0.221 | 0.247 ±0.0136 |
| 34.68 | 8.445 ±0.298 | 0.243 ±0.0088 |
| 110.02 | 21.490 ±0.353 | 0.195 ±0.0032 |
| **TABLE III** | | |
| Stripes C, 9.4 mm. wide. Visual acuity × $10^4$ = 5.85 | | |
| 0.166 | 0.760 ±0.018 | 4.567 ±0.113 |
| 0.214 | 0.710 ±0.017 | 3.319 ±0.075 |
| 0.302 | 0.763 ±0.030 | 2.527 ±0.094 |
| 0.695 | 1.175 ±0.029 | 1.690 ±0.042 |
| 1.439 | 1.447 ±0.019 | 1.005 ±0.014 |
| 2.711 | 1.675 ±0.035 | 0.617 ±0.013 |
| 5.261 | 3.068 ±0.093 | 0.583 ±0.018 |
| 9.572 | 3.732 ±0.098 | 0.391 ±0.0099 |
| 19.96 | 6.305 ±0.116 | 0.316 ±0.0057 |
| 34.68 | 8.630 ±0.119 | 0.249 ±0.0035 |
| 55.04 | 13.400 ±0.234 | 0.243 ±0.0042 |
| **TABLE IV** | | |
| Stripes D, 6.3 mm. wide. Visual acuity × $10^4$ = 8.33 | | |
| 0.214 | 0.948 ±0.025 | 4.433 ±0.106 |
| 0.417 | 0.992 ±0.019 | 2.381 ±0.052 |
| 0.695 | 1.169 ±0.015 | 1.681 ±0.034 |
| 1.439 | 1.663 ±0.026 | 1.155 ±0.019 |
| 2.711 | 1.878 ±0.033 | 0.693 ±0.0099 |
| 5.261 | 3.356 ±0.123 | 0.638 ±0.0238 |
| 19.960 | 6.292 ±0.206 | 0.315 ±0.0117 |
| 81.460 | 20.670 ±0.310 | 0.254 ±0.0039 |

TABLES OF DATA—*Continued*

| I Millilamberts | ΔI Millilamberts | ΔI/I |
|---|---|---|
| **TABLE V** | | |
| Stripes F, 3.2 mm. wide. Visual acuity × 10⁴ = 15.87 | | |
| 0.302 | 1.229 ±0.017 | 4.068 ±0.055 |
| 0.417 | 1.247 ±0.038 | 2.991 ±0.080 |
| 0.695 | 1.244 ±0.023 | 1.790 ±0.033 |
| 1.031 | 1.573 ±0.043 | 1.506 ±0.042 |
| 2.711 | 2.609 ±0.083 | 0.962 ±0.036 |
| 6.792 | 3.732 ±0.166 | 0.549 ±0.024 |
| 19.960 | 6.831 ±0.151 | 0.342 ±0.0075 |
| 34.680 | 10.310 ±0.178 | 0.297 ±0.0054 |
| 81.460 | 18.920 ±0.296 | 0.232 ±0.0037 |
| **TABLE VI** | | |
| Stripes G, 1.27 mm. wide. Visual acuity × 10⁴ = 39.68 | | |
| 0.417 | 2.272 ±0.020 | 5.451 ±0.047 |
| 0.695 | 2.214 ±0.028 | 3.186 ±0.040 |
| 1.031 | 2.527 ±0.087 | 2.451 ±0.045 |
| 2.153 | 3.966 ±0.090 | 1.331 ±0.043 |
| 3.900 | 3.989 ±0.137 | 1.023 ±0.037 |
| 9.572 | 6.266 ±0.118 | 0.654 ±0.012 |
| 13.870 | 5.958 ±0.214 | 0.430 ±0.015 |
| 34.680 | 10.650 ±0.257 | 0.307 ±0.0083 |
| 70.270 | 17.380 ±0.293 | 0.247 ±0.0041 |
| **TABLE VII** | | |
| Stripes I, 0.635 mm. wide. Visual acuity × 10⁴ = 79.37 | | |
| 1.031 | 5.719 ±0.200 | 5.547 ±0.138 |
| 1.439 | 5.691 ±0.186 | 3.955 ±0.129 |
| 2.711 | 6.426 ±0.120 | 2.370 ±0.060 |
| 3.900 | 6.869 ±0.254 | 1.761 ±0.079 |
| 6.792 | 10.860 ±0.375 | 1.465 ±0.058 |
| 9.572 | 10.910 ±0.200 | 1.140 ±0.020 |
| 19.960 | 13.630 ±0.203 | 0.683 ±0.010 |
| 34.680 | 15.150 ±0.189 | 0.437 ±0.0052 |
| 61.720 | 18.630 ±0.361 | 0.302 ±0.0059 |
| 110.020 | 29.570 ±0.299 | 0.270 ±0.0025 |

TABLES OF DATA—*Concluded*

TABLE VIII

Stripes K, 0.423 mm. wide. Visual acuity × 10⁴ = 119.0

| I Millilamberts | ΔI Millilamberts | ΔI/I |
|---|---|---|
| 2.711 | 11.600 ±0.296 | 4.280 ±0.111 |
| 3.900 | 13.700 ±0.197 | 3.514 ±0.047 |
| 5.261 | 15.590 ±0.313 | 2.394 ±0.060 |
| 9.572 | 16.030 ±0.279 | 1.675 ±0.030 |
| 13.870 | 16.630 ±0.271 | 1.199 ±0.019 |
| 19.960 | 19.190 ±0.273 | 0.962 ±0.014 |
| 34.640 | 23.100 ±0.313 | 0.666 ±0.0091 |
| 55.040 | 27.110 ±0.477 | 0.493 ±0.0087 |
| 110.020 | 30.340 ±0.350 | 0.276 ±0.0032 |

TABLE IX

Stripes L, 0.363 mm. wide. Visual acuity × 10⁴ = 138.9

| I Millilamberts | ΔI Millilamberts | ΔI/I |
|---|---|---|
| 3.900 | 21.190 ±0.558 | 5.432 ±0.139 |
| 5.261 | 21.550 ±0.454 | 4.095 ±0.085 |
| 9.572 | 22.950 ±0.443 | 2.397 ±0.043 |
| 13.870 | 22.900 ±0.378 | 1.651 ±0.025 |
| 19.960 | 23.520 ±0.465 | 1.178 ±0.026 |
| 27.420 | 30.640 ±0.355 | 1.117 ±0.013 |
| 34.680 | 32.510 ±0.355 | 0.937 ±0.010 |
| 55.040 | 35.610 ±0.744 | 0.647 ±0.011 |
| 110.020 | 55.500 ±0.795 | 0.504 ±0.010 |

TABLE X

Stripes M, 0.318 mm. wide. Visual acuity × 10⁴ = 158.7

| I Millilamberts | ΔI Millilamberts | ΔI/I |
|---|---|---|
| 13.87 | 58.020 ±0.998 | 4.183 ±0.071 |
| 19.96 | 60.400 ±1.156 | 3.026 ±0.058 |
| 27.42 | 61.730 ±0.900 | 2.251 ±0.039 |
| 34.68 | 67.210 ±1.238 | 1.938 ±0.030 |
| 81.46 | 94.730 ±0.383 | 1.163 ±0.0047 |
| 110.02 | 93.980 ±0.840 | 0.854 ±0.0076 |

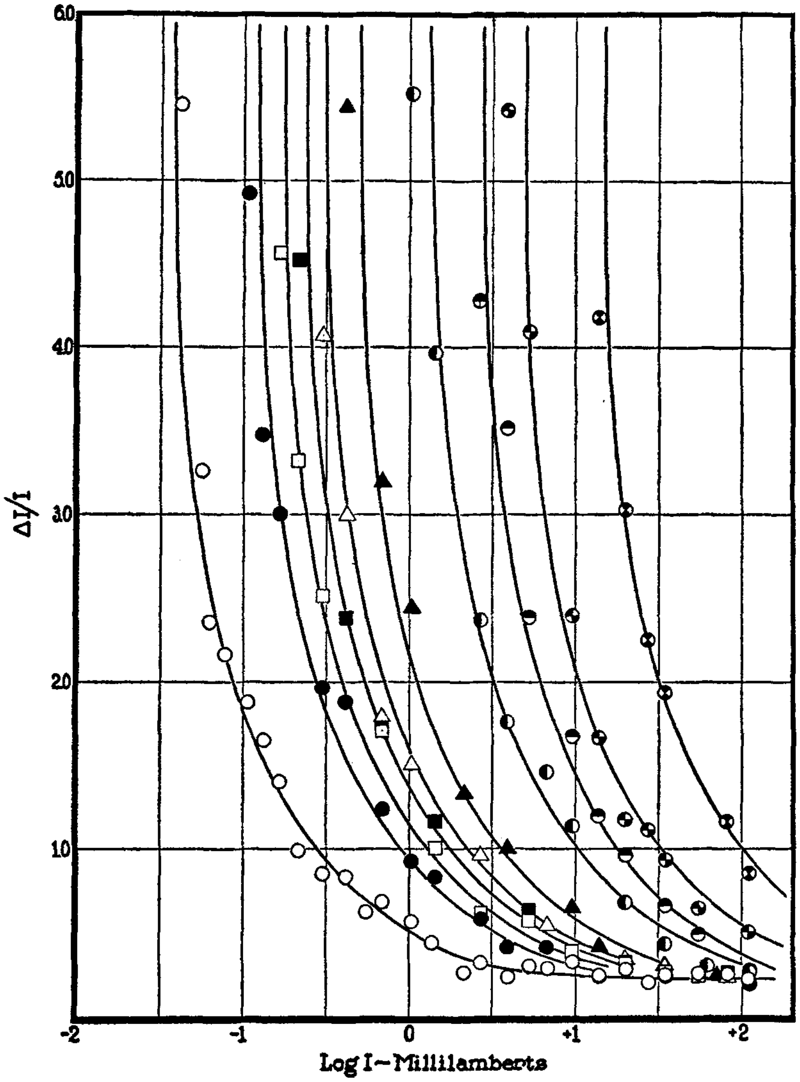


FIG. 2. Relation between intensity discrimination and illumination at different visual acuities. Each curve represents an intensity discrimination curve for a different visual acuity; the points represent averages of ten bees tested at each illumination.

The first curve (open circlets) is the intensity discrimination graph published previously, where the width of the bars of the pattern was chosen great enough so that the bees were able to react to the bars at any illumination used. The nine other curves are intensity discrimination curves for increasingly greater visual acuities. These curves show that with greater visual acuities, intensity discrimination gets worse at lower illuminations, whereas at higher intensities the discrimination power is improved in practically the same course as in our first experiments—until at the highest illuminations visual acuity does not interfere with the discrimination, save for the two smallest sizes of striped patterns, for which the curves do not come down to the same level within the range of intensities used. This, however, is due only to the fact that one is practically limited in obtaining high enough intensities for $I$ and $\Delta I$, providing in the extreme case values for $\Delta I/I$ which would correspond to the minimal value found for smaller visual acuities.

## IV

The ten curves for intensity discrimination at different visual acuities are in their general course identical, with a progressive shift to greater values on the log $I$ scale in Fig. 2. This suggests a significant interrelation between visual acuity and intensity discrimination. The gradual shift of the curves to the right is not so evenly spaced in relation to the width of stripe as one might perhaps expect. The shift corresponds much more to the difference in abscissa values found for the positions of the points on a visual acuity curve for the bee. And so the question arises, whether one is able to construct a series of visual acuity curves from the intersections of the intensity discrimination curves with a given ordinate value of $\Delta I/I$.

In Fig. 3, four such reconstructions of visual acuity curves are given. The first curve (white circles) is the visual acuity curve obtained by Hecht and Wolf (1928–29). The second curve (black circles) is a visual acuity curve constructed from the intersections of the intensity curves with the ordinate $\Delta I/I = 3.0$; the third (open squares) is at $\Delta I/I = 2.0$; the fourth (black squares) at $\Delta I/I = 1.0$; and the fifth (half circles) at $\Delta I/I = 0.5$. The curves fitted to the points are the same as the original curve, only shifted to the right. The fit is reasonably good, and is sufficient to show that the curves are essentially identical. The graph shows that with $\Delta I/I$ getting smaller the fit of the curve becomes better, which is only to be expected because at higher intensities more precise settings can be made, as the bees give sharper and more definite responses.

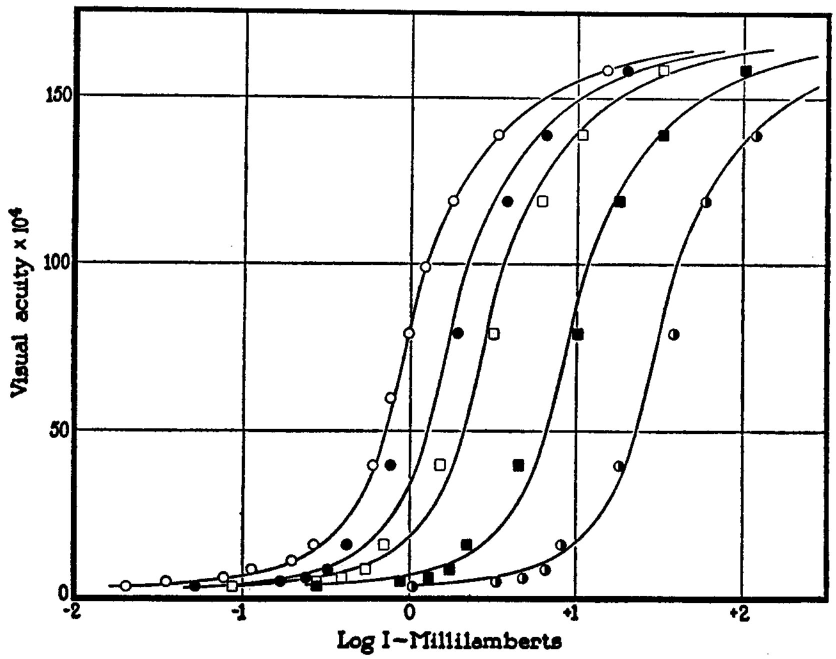


FIG. 3. Visual acuity curves reconstructed from the data given in Fig. 2. The first curve is the original visual acuity curve for the bee; the second is reconstructed for $\Delta I/I = 3.0$; the third for $\Delta I/I = 2.0$; the fourth for $\Delta I/I = 1.0$; and the fifth for $\Delta I/I = 0.5$.

A visual acuity curve provides the magnitudes of $I$ corresponding to successively decreased width of stripe at a given magnitude of $\Delta I/I$; $\Delta I$ measures nearly enough, for each value of $I$, the increase of intensity which is necessary to bring into action a certain constant number of additional receptors. Consequently we should expect that, for decreasing magnitudes of $\Delta I/I$ (that is, increasing values of $I$ and $\Delta I$), the visual acuity curve must shift toward the right, that is, toward higher levels of $I$: but that its *form* should not be changed. This is evident in Fig. 3.

For visual acuity tests in which the bee reacts to a pattern of alternately black and illuminated stripes, we may say that $\Delta I/I$ equals infinity, which means $I = 0$. If we intend to obtain from our different intensity discrimination curves a curve which would be identical with the first of the five curves in Fig. 3, we have to take the values on the curves at a very large magnitude of $\Delta I/I$. It can be shown that the points of the original visual acuity curve (Hecht and Wolf, 1928–29) and the curve at $\Delta I/I = 6.0$ fall very close together, and presumably on extrapolating to still greater values for $\Delta I/I$ the two curves would actually coincide. No attempt has been made to show this graph because the intensity discriminations at even values of $\Delta I/I = 4.0$ is pretty uncertain, so that one cannot put too much emphasis on the observations made beyond that point. Some points of the desired visual acuity curve ($\Delta I/I > 6.0$) would fall onto the left of the original visual acuity curve where $\Delta I/I$ was infinite, and that would be practically impossible; consequently all such values only indicate that at such low illuminations settings of the apparatus accurate enough to be reliable cannot be made.

The reproducibility of the visual acuity curves from the intensity discrimination data, in view of the delicacy of measurement and of curve fitting, is of some special interest. The data collected in the $\Delta I/I$ curves were obtained from different animals of the same colony. Each point on the curves represents a mean value for ten different individuals. It has been emphasized previously that on account of the genetic uniformity of the members of a colony of bees, there is no special need for establishing a complete intensity discrimination curve with one single individual. It has been shown that frequent handling of the bees for repeated observations upon one worker actually interferes a good deal with the accuracy of the determinations. It is furthermore of interest to see the reproducibility of the visual acuity curve by comparison with that obtained using bees of a different colony some years ago (Hecht and Wolf, 1928–29). This indicates not only that a fairly high degree of uniformity as to reactions exists within the members of one single colony, but also among different colonies of commercial lines of bees.

The visual acuity computed from the width of the stripes and the distance of the pattern from the bee's eye is in surprisingly precise agreement with the observations. It was mentioned before that for these determinations the distance of 17.3 mm. from the center of the bee's eye to the upper surface of the opal cover-plate had to be considered, and not the distance to the actual stripes which is 18.7 mm. If one attempts to fit the original visual acuity curve to the greater visual acuity values based upon the distance to the bars, the fit of the curves at once becomes inadequate. This indicates that for one set of determinations of visual acuity values at different illuminations, only one best fitting curve can be drawn.

## SUMMARY

1. Bees respond by a characteristic reflex to a movement of their visual field. By confining the field to a series of parallel stripes of two alternating different brightnesses it is possible to determine for any width of stripe, at any brightness of one of the two sets of stripes, the brightness of the second at which the bee will first respond to a displacement of the field. Thus the relations between visual acuity and intensity discrimination can be studied.

2. For each width of stripe and visual angle subtended by the stripe the discrimination power of the bee's eye for different brightnesses was studied. For each visual acuity the intensity discrimination varies with illumination in a characteristic, consistent manner. The discrimination is poor at low illuminations; as the intensity of illumination increases the discrimination increases, and reaches a constant level at high illuminations.

3. From the intensity discrimination curves obtained at different visual acuities, visual acuity curves can be reconstructed for different values of $\Delta I/I$. The curves thus obtained are identical in form with the curve found previously by direct test for the relation between visual acuity and illumination.

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