THE DISTRIBUTION OF STIMULATIVE EFFICIENCY IN THE ULTRA-VIOLET SPECTRUM FOR THE HONEYBEE[1]

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INTRODUCTION

During the last 50 years considerable evidence has gradually accumulated that insects and arthropods in general are sensitive to ultra-violet light. Lubbock (*1, p. 152–168*)[3] was one of the first to experiment in this field, and he found that ants carry their young out of a region illuminated by ultra-violet into one illuminated by light of longer wave lengths. Forel (*3*) confirmed this observation and convinced himself that the seat of this sensitivity is in the eyes and not in the epidermis of the ant's body.

One of the most indefatigable workers on the reactions to light and color among animals was Von Hess, who wrote voluminously of his experiments and theories between 1907 and 1922. Von Hess showed unmistakably that bees and several other arthropods are sensitive to ultra-violet light. In some of his experiments (*5, p. 928*) he confined 20 to 50 bees in a plate-glass box 20 by 10 by 8 centimeters and wrapped the box in a large piece of black paper in such a way that a tunnel about 40 centimeters long was formed, with the box placed near one end. He placed next to a window the end containing the box and made observations through the opposite end. He then put various light filters between the window and one half or the other of the side of the glass box lying next to the window. One of these filters was a Schottschen Schwerstflintglas (abbreviated Sfl.) which transmitted only the so-called visible rays of the spectrum; i. e., waves longer than 400 mμ. He says, in describing the behavior of the bees in one of these experiments,

> Bringe ich vor die eine Hälfte das Sfl., so gehen sie in wenigen Sekunden nach der anderen, ultraviolettreicheren Seite, *auch dann noch, wenn diese durch Vorhalten eines Grauglases* oder mit anderen passenden optischen Hilfsmitteln *für uns wesentlich dunkeler gemacht wird, als die ultraviolettarme.*

He went on further to find out how much more stimulative the unfiltered light was to the bees than the light filtered through the Sfl. filter. He says (*5, p. 928*):

> * * * ich konnte * * * feststellen, dass unter bestimmten Bedingungen an einem bewölkten Tage das durch Sfl. uv.arm gemachte Tageslicht auf die Bienen nicht anders wirkt als wie relativ uv.reiches Tageslicht, dessen Stärke für uns nur etwa 1/8–1/9 des uv.armen ist und unserem Auge neben dem letzteren ziemlich dunkel grau erscheint!

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[3] Reference is made by number (italic) to Literature Cited, p. 713.

He says further, parenthetically, that by the use of a mercury-vapor lamp he was able to show that for ants the light from this lamp, very rich in ultra-violet, is as stimulative as ordinary light made 200 times stronger. Of course, by "stronger" Von Hess meant only more brilliant to his own eye, which does not mean necessarily that it really contained more energy, but, nevertheless, if ordinary daylight had to be reduced to one-eighth or one-ninth of its original intensity in order to stimulate bees to the same lower degree as the same light with the ultra-violet filtered out, it is very probable that the ultra-violet is more efficient in its stimulation for bees than is the so-called visible light.

Von Hess investigated, furthermore, how far the spectrum visible to arthropods extends into the ultra-violet. He used for this purpose only certain caterpillars and crustaceans, but found (*5, p. 929*) "dass die Bewegungsrichtung von Raupen und Krebsen noch deutlich beeinflusst wird durch Strahlen von ca. 313 mμ * * *." He found this sensitivity to ultra-violet to be of general distribution among the arthropods, but concluded (*4, p. 199*) that it is due to a fluorescence of the outer parts of the ommatidia whereby the short waves are changed to longer ones, and not to true vision of the ultra-violet.

Tests of a similar nature, involving only the nontrained (instinctive) reactions of the animals in question, were made by Lutz and Richtmyer (*9*) in 1922 on Drosophila, and by Lutz (*8*) in 1923 on various insects which visit flowers, including the honeybee. All these insects reacted definitely to ultra-violet. In Lutz's experiments, for example, he made a box in each end of which was a window consisting of one or another of several light filters. The top of the box was of glass surrounded by an opaque hood within which he could put his head, drawing the free end of the hood around his neck to exclude the light but enabling him to see inside the box. The box was carried to the field, and into it were placed insects caught at flowers. In some of the experiments he used in one end of the box a very dark filter which transmitted almost no light except ultra-violet, and in the other various clear and chromed glasses which transmitted almost no ultra-violet. When he placed a worker honeybee in this box he found that it went from every one of his chromed filters to the filter transmitting ultra-violet, and when at the latter "would not leave it to go to several thicknesses of clear glass," although to the human eye the light coming through the several thicknesses of clear glass was enormously brighter than that coming through the other and was probably of considerably greater energy.

Meanwhile Kühn and Pohl (*7*) in 1921 reported the results of their experiments on the honeybee involving training. These investigators first trained bees to come for food to a narrow trough illuminated by the light of the ultra-violet line 365 mμ of the mercury-vapor spectrum, and then, after the bees were trained, they removed the food and allowed the image of the entire spectrum to fall on a piece of white paper. The bees that now came for food congregated almost exclusively on the region illuminated by the light of the line at 365 mμ. Various checks seemed to show that the distinction was not based on the relative position of this line with respect to the others, nor on its relative brilliance; and Kühn and Pohl conclude, therefore, that light of wave lengths near 365 mμ is not only visible to bees but is qualitatively distinguished by them from that of other wave lengths of the mercury-vapor spectrum. This fact indicates that the ultraviolet probably appears to the bee as a color distinct from any other color in the mercury-vapor spectrum, and not, as Von Hess postulates, merely as a fluorescence. A continuation of this set of experiments by Kühn (*6*) led to the further conclusion that the spectrum for the bee extends at least to wave length 313 mμ (as Von Hess had found for "Raupen und Krebsen"), and that this wave length is also distinguished from those longer than 400 mμ, but not from wave length 365 mμ.

Furthermore, the experiments of the present writer (*2*) on the relative efficiency for the bee of regions in the so-called visible spectrum showed that at 431 mμ, the lowest wave length attainable with his apparatus at that time, the efficiency is still one-tenth as great as at its maximum in the yellowish-green region at about 553 mμ. The efficiency at 431 mμ is thus relatively considerably greater for the bee than for the human eye—a fact which tends to confirm the evidence that the spectrum visible to the bee extends to considerably shorter wave lengths than does that visible to man.

The results of these various researches show clearly that bees are sensitive to ultra-violet light down to at least wave length 313 mμ, and indicate that the efficiency of this light is fairly high. The next step is to find how efficient various regions in the ultra-violet are in stimulating the bee, and to ascertain more accurately, if possible, how far into this portion of the spectrum the vision of the bee extends. If the efficiency at wave length 431 mμ is 10 per cent as great as at 553 mμ, one wonders if it gradually drops off until the limit of perception is reached or if it again rises to another maximum. It was to throw further light on these questions that the experiments now to be described were performed.

METHOD

The procedure necessary to find the relative stimulative efficiency of different regions of the spectrum by the method chosen in this investigation involves three steps: (1) To find the relative stimulative effect of each region studied, in terms of the intensity of white light necessary to equal the effect of that region in stimulating the bee; (2) to find the relative physical energy emitted by each of these regions; and (3), in each case, to divide the value for the relative effect by the corresponding value for its relative energy, obtaining as a result a series of values representing the relative efficiency (i. e., effect per unit of energy) of the several regions.

The apparatus for carrying out the first step of this procedure is shown in Figure 1. The main box, *a*, was shallow and rectangular, 67 by 26 by 4 centimeters inside, and provided with a hinged lid covered with screen wire. In the ends of the box were three openings, one, *b*, in what will be designated as the left-hand end, and two, *c* and *d*, in the right-hand end. Openings *b* and *c* were each covered by a piece of ground glass, opening *d* by a piece of ground quartz. Opposite opening *b* was a small lamp house, *e*, containing a 15-watt lamp the light from which passed through a small aperture and illuminated the ground-glass screen behind that opening. Opposite opening *c* was a long lamp house, *f*, having a total length of 140 centimeters and containing a lamp mounted on a support sliding on a track, so that within the limits of the apparatus the lamp could be placed at any desired distance from the opening. The light from this lamp went through a rectangular aperture and illuminated an area 6.5 by 13.0 millimeters on the ground-glass screen covering opening *c*. By the use of a 10-watt lamp for the lower intensities and a 75-watt lamp for the higher, and by placing the lamp at stated distances ranging from 40 to 126.5 centimeters from the ground-glass screen, the screen could be illuminated with light having relative intensities in the proportion of 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 129, 258, 387, 516, 645, 774, 903, 1,032, 1,161, and 1,290. (The minimum intensity 10 equals approximately 3.5 meter-candles.) A glass cell, *g*, 3 centimeters thick inside the glass walls, containing a solution of copper sulphate in the proportion of 19 grams per liter, screened out the infra-red and heat rays.

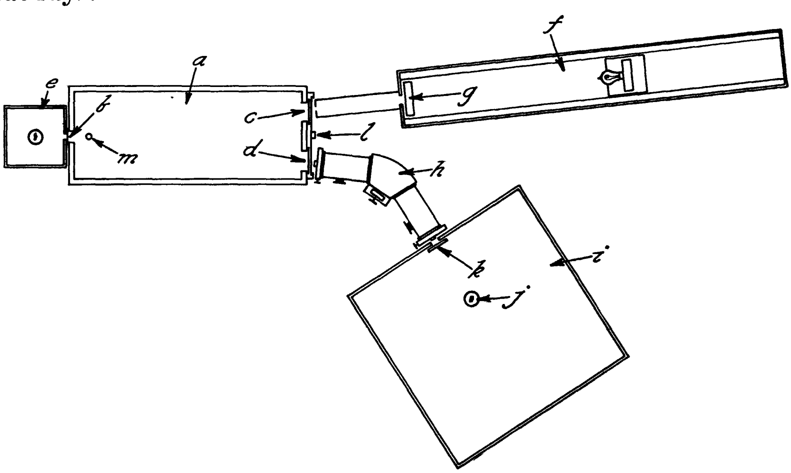

FIGURE 1.—Diagram (plan) of apparatus used to ascertain the intensity of white light necessary to produce stimulative effects upon bees equal to those of the light from selected lines of the mercury-vapor spectrum. (For explanation, see text.)

Opposite opening *d* was placed the telescope end of a spectroscope (Monochromator), *h*, of the constant-deviation type; all its lenses and prisms were of quartz, and opposite the collimator end of this spectroscope was placed a lamp house, *i*, containing a 220-volt, quartz mercury-vapor lamp, *j*, of the horizontal type, run with a current of about 5 amperes (the Cooper-Hewitt "Uviarc"). Light from this lamp passed through the spectroscope *h*, by which any desired line of the mercury-vapor spectrum could be selected and made to illuminate the screen of ground quartz covering opening *d*, forming there an illuminated area of the same size and shape as that formed on the screen covering opening *c*. Lines of the wave lengths 280 mμ, 297 mμ, 302 mμ, 313 mμ, 334 mμ, 365 mμ, 405 mμ, and 436 mμ were used. A glass filter, *k* (Corning Glass Works', "Corex A, red purple"), was placed between the mercury-vapor lamp and the spectroscope in all experiments in which a line of wave length shorter than 405 mμ was used, since this filter cuts off all visible light above wave length

405 mμ, thus excluding any stray visible light that otherwise often finds its way through a spectroscope by reflection from the inside wall of the tube of the instrument.[4]

The lamp in house *e* was turned on or off as desired by means of a small switch, but the lamp in house *f* and the mercury-vapor lamp *j* in house *i* were left on continuously during the course of an experiment, the light coming from them being cut off at will from opening *c* and *d* by means of a shutter, *l*, sliding vertically in a track.

A hole, *m*, in the floor of the large box *a*, permitted the entrance of the bee used in an experiment. The whole apparatus was placed in a dark room maintained constantly at a temperature of about 12° C.

In performing an experiment with this apparatus, a bee at a feeder outside was captured in a small screen-wire cylinder about the size of an ordinary test tube, taken inside the dark room, and fed with sugar sirup (by inverting over the cylinder a small vial containing this liquid, the mouth being covered with a layer of cheesecloth) until it was satiated, then released into the large box *a*, through the hole in the floor near the left-hand end. The feeding of the bee, together with a temperature in the dark room lower than that outside, tended to quiet the bee and prevent it from racing wildly about the box when released into it, and the time taken for feeding allowed the eyes of both the bee and the observer to become somewhat adapted to the darkness.

When the bee entered the box all was dark except the two illuminated areas in openings *c* and *d*. On seeing these the usual reaction of the bee was to walk rapidly toward the right-hand end of the box, and as it approached this end to veer toward one or the other illuminated area, depending, presumably, on which was the more stimulative to it. As soon as it could be ascertained toward which illuminated area the bee was going, the opaque shutter *l* was drawn up, cutting off the light from these areas, and at the same time the lamp in box *e* was turned on. At this, the bee turned around and walked rapidly toward the left-hand end of the box. As soon as it had come back near the starting point the lamp in box *e* was turned off and at the same time the shutter *l* dropped down, at which the bee turned and walked again toward the right-hand end of the box, veering often toward the same illuminated area as before, sometimes toward the other area. This marching and countermarching was continued until the bee had made five trips toward the right-hand end of the box, a record being kept as to which illuminated area it approached on each trip. Then it was recaptured in the wire cylinder, taken into the open and released, and a new bee brought in and treated in the same way. For comparing the stimulative effect of the light of any given line of the mercury-vapor spectrum with any given intensity of white light, from 5 to 20 bees were used, giving a total of from 25 to 100 reactions.

Usually a very low intensity of white light was used in the first test with any spectral line. If the reactions of the bees indicated that this intensity of white light was less stimulative than the spectral light—that is, if less than 50 per cent of the reactions were toward the white—it was raised to a slightly higher intensity, and another

[4] The advisability of using such a filter was suggested to the writer by Prof. A. H. Pfund, of the Johns Hopkins University.

test made. If this showed that the white light was still less stimulative than the spectral light, the intensity of the former was raised again and another test made. This procedure was continued until an intensity of white light was found which definitely induced more responses than did the spectral light.

By finding in this way some intensities of the white light which produced less than 50 per cent of the total responses and some which produced more than 50 per cent, and then by plotting these values and interpolating, an intensity was computed which, theoretically, would have produced exactly 50 per cent of the total responses. The intensity thus computed was regarded as the value of the stimulative effect of the particular spectral line under consideration. In a similar way values were obtained for all the spectral lines used. This procedure accomplished the first step mentioned at the beginning of this section as being necessary in the method here chosen.

The second step, the finding of the relative energy emitted by each spectral line used, was done in the radiometry laboratory of the United States Bureau of Standards by W. W. Coblentz and R. Stair.

There remained then only the third step, the dividing of the value representing each relative effect by that representing each corresponding relative energy, in order to obtain values representing the relative efficiency of each spectral line.

RESULTS

The results of the experiments to find the relative intensities of white light necessary to produce upon the bees the effects of the several spectral lines used are presented in Table 1. It will be observed that for wave length 280 mμ all the reactions of the bees were toward the white light, even at the lowest intensity producible with the apparatus; that is, the bees entirely ignored the spectral light of wave length 280 mμ, and the probability is that they did not see it at all. When light of wave length 297 mμ was compared with white light at an intensity of 10, in the scale of intensities named on page 706, 88 per cent of the reactions were toward the white light, indicating that the bees saw this spectral line, but that it was much less brilliant to them than was the white light even at that very low intensity. For all other wave lengths used, however, intensities of white light were found some of which elicited fewer responses than did the spectral line (less than 50 per cent of the total), same more.

The intensity of white light which would elicit exactly as many responses as the given spectral line is, of course, what is needed. This can easily be ascertained by plotting the percentage going to the white light as an ordinate, with the intensity of that white light as an abscissa, and connecting the points by a curve, as is done in Figure 2 for each wave length used. In making these curves only intensitites were considered for which as many as 50 responses had been observed, since the larger numbers of observations presumably gave the more reliable results, and these intensities furnished sufficient points to establish the curves desired. By examining the graphs, the point at which each of the curves crosses the line representing 50 per cent of the total responses toward the white light can be easily ascertained, and this point for each spectral line gives the relative stimulative effect of that line in terms of the intensity of white necessary to produce its effect on the bees. These values are given in the second column of Table 2.

TABLE 1.—*A summary of the reactions of bees to different intensities of white light when these intensities were exposed to them simultaneously with light from selected lines of the mercury-vapor spectrum*

Wave length (in millimicrons)	Relative intensity of white	Number of reactions observed	Percentage going to the white
280	0.10	25	100
	1.29	25	100
297	.10	50	88
302	.10	100	48
	.30	100	62
	.50	100	65
313	.10	25	24
	.50	50	48
	.60	25	20
	.70	25	80
	.80	25	32
	.90	25	32
	1.00	50	28
	1.29	100	39
	2.58	100	53
	3.87	100	63
	4.40	25	36
	5.16	25	40
	6.45	100	55
	7.74	25	48
	9.03	100	58
	10.32	25	72
	12.90	50	74
334	.20	100	38
	.40	100	50
334	0.60	100	60
	1.00	100	70
	3.87	25	100
	6.45	25	80
	9.03	25	88
	11.62	25	96
365	.20	25	0
	.30	25	16
	1.00	25	4
	1.29	25	20
	2.58	25	16
	3.87	100	27
	5.16	25	44
	6.45	100	40
	7.74	25	48
	9.03	100	52
	10.32	25	68
	11.62	100	58
	12.90	25	88
405	.10	100	21
	.20	100	60
	.40	100	59
436	.10	100	40
	.20	100	56
	.40	50	68

TABLE 2.—*The relative stimulative effect of the light from each spectral line used, as obtained from Figure 2, together with the measured energy of each spectral line (where measurable), and the calculated efficiency of each*

Wave length (in millimicrons)	Relative stimulative effect (=S)	Relative energy (=E)	Relative stimulative efficiency (=S/E×5,206.7)
280	None.		0
297	([a])	1.3	?
302	0.1	7.6	68.5
313	2.3	55.9	214.2
334	.4	5.3	393.0
365	8.6	100.0	447.8
405	.2	51.8	20.1
436	.15	78.1	10.0

[a] Less than 0.1.

The relative energy emitted by each of the spectral lines used (except by the line at 280 mμ, which was too small to be measured) was, as has been stated, measured by a thermopile and galvanometer at the United States Bureau of Standards. The results of these measurements are given in the third column of Table 2.

When the values for relative stimulative effect are divided by the corresponding values for relative energy and the dividend multiplied by 5,206.7 (in order to bring the value for 436 mμ to 10.0) the resulting values for stimulative efficiency are those presented in the last column of Table 2. It will be observed that the efficiency is low at 302 mμ, the shortest wave length for which complete data were obtained, and

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that it rises gradually through 313 mμ and 334 mμ to a maximum at 365 mμ, from which it decreases suddenly again toward 405 mμ and 436 mμ.

The relation of these values to each other and to those previously found (*2*) for the longer wave lengths, as well as to those for the human eye, are strikingly shown in Figure 3. In the previous work, just referred to, the efficiency at wave length 431 mμ, the lowest attainable with the apparatus used at that time, was found to be 10.11 per cent as high as the maximum at 553 mμ. In order to join the curve formed by the values obtained in the present investigation as closely as practicable to that formed by the values found for the longer wave lengths, the efficiency at 436 mμ was given an arbitrary value of 10.0 and the

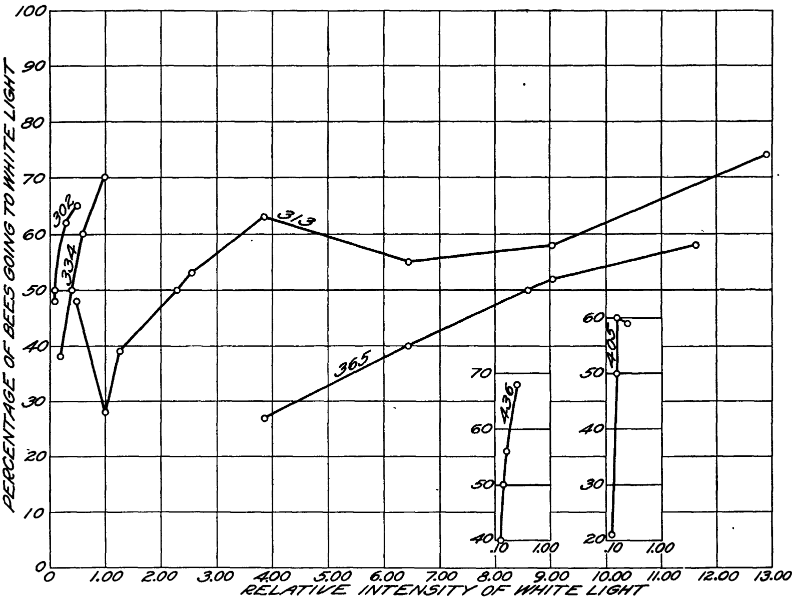

FIGURE 2.—Curves plotted from data given in Table 1, in order to find by graphic interpolation the relative intensities of white light needed to produce stimulative effects upon bees equal to those of the light from selected lines in the ultra-violet portion of the mercury-vapor spectrum. The point at which each curve crosses the line representing 50 per cent of the responses toward the white locates the relative intensity of light which should be required to produce a magnitude of response equal to that produced by the light from the spectral lines indicated

others were related to it. The complete curve shows that the efficiency at 365 mμ, the maximum for the ultra-violet, is nearly four and one-half times as great as that for 553 mμ, the maximum in the so-called visible portion of the spectrum. The relative values derived for efficiency of the two maxima, expressed for comparison on the same scale, are 447.8 and 100.0.

DISCUSSION

The results of this investigation, while somewhat to be expected from the work of Von Hess and Kühn, are nevertheless a little startling. For no other animal has it been shown, so far as the writer has found, that the curve of the distribution of stimulative efficiency has more than one maximum. Furthermore, the fact that the maximum in the ultra-violet is so much greater than that in the so-called visible spectrum again raises the old question as to the significance of floral colors in attracting insects. It is not the writer's purpose to review the various controversies on this question, but simply to indicate the possible contribution of this investigation.

The nature of the visual stimulation which a bee receives from looking at a flower in sunlight obviously depends on three factors: (1) The nature of the sunlight, i. e., the length of its spectrum and the distribution of energy therein; (2) the nature of the reflection by the flower, i. e., the wave lengths reflected and the intensity of

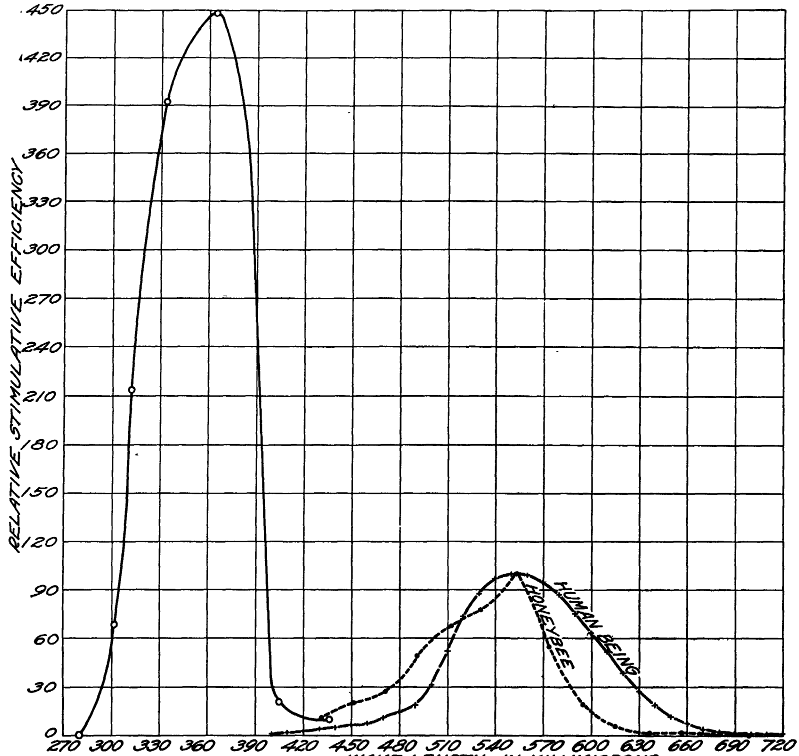

FIGURE 3.—Distribution of stimulative efficiency in the ultra-violet spectrum for honeybees (solid line), together with a reproduction of the corresponding curve for the visual spectrum as found in a previous investigation (dotted line) and with the corresponding curve for the human being

light of each wave length relative to the intensity of each present in the sunlight; and (3) the nature of the bee's photoreceptors, i. e., the lengths of waves to which it is sensitive and the relative sensitivity for the different wave lengths.

The spectrum of the sunlight reaching the earth's surface extends from about wave length 290 mμ to comparatively long infra-red rays, but for our present interest we may consider only the portion from 290 mμ to 700 mμ. If this portion be divided at wave length 450 mμ into an ultra-violet and a visual section, the former will contain, roughly, about one-fifth of the total energy of this portion, and the latter about four-fifths (*11, p. 418, Table 551*).

The nature of the reflection of flowers has been taken up in late years by Richtmyer (*10*) and Lutz (*8*). Richtmyer shows the curves for ultra-violet reflection for a number of flowers, and Lutz shows photographs of flowers taken through a filter transmitting only ultra-violet. Lutz concludes (*8, p. 240*) that "* * * perhaps about 30 per cent of conspicuous flowers are distinctly ultraviolet" as compared with the fact that "perhaps about 50 per cent of the conspicuous flowers are strongly blue" and "* * * nearly 80 per cent of such flowers are spectroscopically strongly red." For an animal which can see ultra-violet as a distinct color, it appears, then, that this color must have a really significant place in the sensation which the animal gets from looking at flowers in nature.

Is the honeybee such an animal? Can it see ultra-violet as a distinct color, and do so efficiently enough to make these short waves significant at all in its vision? The answer seems to be in the affirmative. The work of Kühn (*6*) gives convincing evidence that to the bee ultra-violet is qualitatively different from other colors, and the evidence presented in the present paper leaves no reasonable doubt as to the efficiency of these short waves in stimulating the bee. In fact, if the energy in the ultra-violet section of sunlight amounts to one-fifth of the total energy in the portion of the sun's spectrum visible to the bee, and if this ultra-violet energy is four and one-half times as efficient in its stimulation as the rest of the energy, it may be concluded that the actual visual stimulation given to a bee by the ultra-violet portion of sunlight is nearly as great as that given by the so-called visual portion, and therefore that in the stimulation given by those "30 per cent of conspicuous flowers" which, according to Lutz are "distinctly ultra-violet," this color forms practically as conspicuous a part of the bee's sensation as does any other color.

SUMMARY

The results of various researches have shown clearly that honeybees are sensitive to ultra-violet light and have indicated that the efficiency of this light is fairly high.

In the present investigation of the relative efficiency, in stimulating reactions of honeybees, of the light from certain lines of the ultra-violet spectrum, a mercury-vapor lamp, of quartz, was used as the source of the radiation studied. Light from this lamp was passed through a spectroscope (Monochromator) provided with lenses and prisms of quartz, and from the resulting spectrum ultra-violet light of eight different wave lengths was tested for its effect on the bees.

The bees experimented upon were admitted, one at a time, into one end of a shallow, oblong box, in which their actions could be observed. At the opposite end of the box were two small screens alike in shape and size, one of ground quartz and the other of ground glass. Ultra-violet light, transmitted by the spectroscope, of one of the eight wave lengths chosen was thrown upon the quartz screen, at the same time that the screen of ground glass was illuminated by white light. The reaction of the bee under observation was recorded, as to which of the two screens it approached, the box being in darkness except for the two controlled illuminations. By a special light at the opposite end of the box the bee was attracted back to its starting point. After five such trips the bee was released and another was substituted.

The illuminations of the ground glass with white light were so controlled that they were always of known relative intensities, and so chosen and compared as to determine what would be the relative intensities of white light producing stimulative effects upon the bees equal to those of the several illuminations with ultra-violet light.

Finally, the relative energy of each illumination with ultra-violet light was separately determined. By dividing the values of the several stimulative effects by the corresponding relative values for energy, the relative efficiency—i. e., the relative stimulative effect per unit of energy—of the ultra-violet light of each wave length concerned was derived. These results show that the efficiency is highest at wave length 365 mμ, and that the spectrum extends at least down to wave length 297 mμ, but not to 280 mμ. When the curve representing the distribution of stimulative efficiency in the ultra-violet spectrum is joined to that for the so-called visible spectrum, as found by the writer in a previous investigation, there are shown to be two maxima, one in the yellow-green, at wave length 553 mμ, and the other in the ultra-violet, at 365 mμ, the latter being about four and one-half times as great as the former.

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