

Professor Rock has given us descriptions of the ornamental trees and also of many of the larger and more showy shrubs. The trees are arranged in natural sequence beginning with cycads and pines, and ending with *Ixora* (Rubiaceæ).

Probably the most striking street trees in midsummer are two species of *Cassia*, *C. fistula*, the golden shower, and *C. nodosa*, the pink shower. The golden shower (plate 43) has long racemes of golden yellow flowers followed by cylindric woody pods, 20 to 30 inches in length, straight and smooth like a musician's baton. The pink shower (plate 44) has dense racemes of pink and white flowers, a gorgeous sight when in full bloom in June. There is a colored plate of this in Mr. Rock's book.

Another showy tree is the flame tree, *Delonix regia* (*Poinciana regia*) (plate 45). This is frequently planted in south Florida, where it is called royal poinciana. The large bright scarlet flowers are in large terminal racemes.

The visitor to the Hawaiian Islands is at once impressed with the number and beauty of the varieties and hybrids of *Hibiscus rosasinensis* (page 137). In this country the species is sometimes called rose of China. In Honolulu the hibiscus is commonly used as a hedge plant, the large red or white flowers being conspicuous throughout the summer.

Another common hedge plant is a species of the Aralia family (*Nothopanax guilfoylei*) (page 168). This does not flower in Honolulu, but the white-bordered compound leaves are attractive. The crotons (*Codiaeum variegatum*) (page 128) are common in Honolulu as they are in all warm countries. The narrow leaves are variegated with white and red, in some varieties strongly spirally twisted.

The pepper tree (*Schinus molle*) (page 132), with feathery drooping foliage and racemes of small red berries, is extensively planted. The plumeria or graveyard flower (*Plumiera acutifolia*) (page 175), with thick stubby branches, milky juice and white or yellow fragrant flowers, is commonly planted around cemeteries. The flowers are much used for the familiar Hawaiian leis or wreaths made by stringing the corollas on a thread.

One of the most beautifully shaped trees of the parks is the rain-tree or monkey-pod (*Samanea saman*) (plate 33). The crown is slightly convex and very wide spread. Another member of the Leguminosæ is the now thoroughly naturalized algaroba (*Prosopis juliflora*) (plate 36). This tropical American tree is now common in a belt along the shore of all the islands. The pods furnish an excellent feed for stock and the flowers furnish honey. It is often planted along streets.

Professor Rock has devoted considerable space to the palms, of which many species are cultivated in the parks and gardens throughout the islands. To this group 23 plates are devoted. The commonest and probably the most beautiful of the palms is the royal palm (*Oreodoxa regia*) (plate 19), the smooth white trunk being very attractive especially when the plants are growing along driveways. The date palm (*Phoenix dactylifera*) (plate 3) is frequent, and the oil palm (*Elæis guineensis*) (plate 22) is not uncommon. The fish-tail palm (*Caryota urens*) (plate 16) is conspicuous because of the great drooping masses of flowers and fruit; the betel palm, because of the tall and very slender stem. Our California fan palm (*Washingtonia filifera*) (plate 10) is rather frequent.

The visitor to the Hawaiian Islands will find the book very helpful in identifying the cultivated trees. The plates are from excellent photographs and the descriptions give just that information that one wishes to know.

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SPECIAL ARTICLES

A COMPARISON OF THE RESPONSES OF ANIMALS IN GRADIENTS OF ENVIRONMENTAL FACTORS WITH PARTICULAR REFERENCE TO THE METHOD OF REACTION OF REPRESENTATIVES OF THE VARIOUS GROUPS FROM PROTOZOA TO MAMMALS¹

THE behavior of animals in gradients of intensity of stimuli has long been studied.

¹ Contribution from the Zoological Laboratory, University of Illinois, No. 120.

Gradients of temperature, light, moisture, etc., were established by the earlier experimenters with a view to determine the conditions which the animals "preferred." Others tested the reactions of animals in gradients of food and other chemicals in connection with investigation of senses and sense organs. The earlier work was very general, but later the study of the reactions of protozoa in accurately determined temperature gradients² was undertaken. In the study of reactions to light, Yerkes³ first used the cylindrical lens and established definite and accurate light gradients. Mast⁴ developed methods of measuring light.

In 1911⁵ the writer and Dr. Allee devised a gradient tank in which a definite permanent gradient of substances dissolved in water can be obtained. This was later improved and some of the sources of irregularity eliminated. A figure of the improved tank is shown by Wells.⁶ He tested the gradient fully with a conductivity cell and established the general character of the gradient for salts.⁷ The writer⁸ also devised a gradient cage for air work, air of different character being driven across the respective thirds of a cage so as to give three kinds of air with a slight mixing at the meeting points.

In connection with the study of fishes the writer devised a method of graphing the movements of animals in gradients. This is illustrated on the accompanying chart, graph 1. Here the distance from right to left represents the length of the gradient tank or the distance at right angles to the iso-lines such as isotherms, that might be drawn across it. In making the graphs, movements along the iso-lines are ignored and only movements which change the position of the animal in the stimulus are represented. Thus in graph 1

the distance from right to left represents the length of the cage. The scales at the sides represent time in minutes, each of the larger units being two minutes. The movements of the animal are drawn to the time and cage length scale. The animal shown in graph 1 (a white-footed wood mouse) remained in the still air (left third) 45 seconds, spent fifteen seconds going the middle of the high velocity third (right third), turned back and returned twice, and was headed toward the still air end at the end of one minute and thirty seconds after the beginning, etc. These graphs can not be made with mechanical exactitude but a high degree of accuracy can be attained. With a watch adjacent to the cage and a little practise there is no difficulty in making such records.

The gradient as encountered by the animal is usually a uniform increase or decrease in the intensity of stimulation except in the air work where there are three steps with two steep gradients between them. In all the experiments cited here one end of the container is near to the optimum for the species. In experiments where the optimum is near the center animals turn back from both ends. There is nothing to cause the animals to move. They do so spontaneously or because of the unusual surroundings. In the narrow tank they must go lengthwise; in so doing they encounter the stimulus. No marked adaptation appears to take place. Goldfish were observed to behave in the manner described below for six hours. Controls in which the animal encounters no change in going the length of the tank are not shown here. In the work cited controls accompany all experiments and have been considered in the case of all work here discussed. A number of psychological points arising in this connection such as learning, Weber's⁹ law, etc. are discussed in the papers cited. The purpose of this account is to compare animals of different groups.

In watching the behavior of mammals, reptiles, amphibians, fishes, insects, myriopods, annelids, flatworms and protozoa in gradients of temperature, light, moisture, air velocity,

² Davenport, *Expt. Morphology*, Vol. I., pp. 260-262.

³ Yerkes, Mark Anniversary Volume, p. 361.

⁴ Mast, "Light and the Behavior of Organisms," Philadelphia.

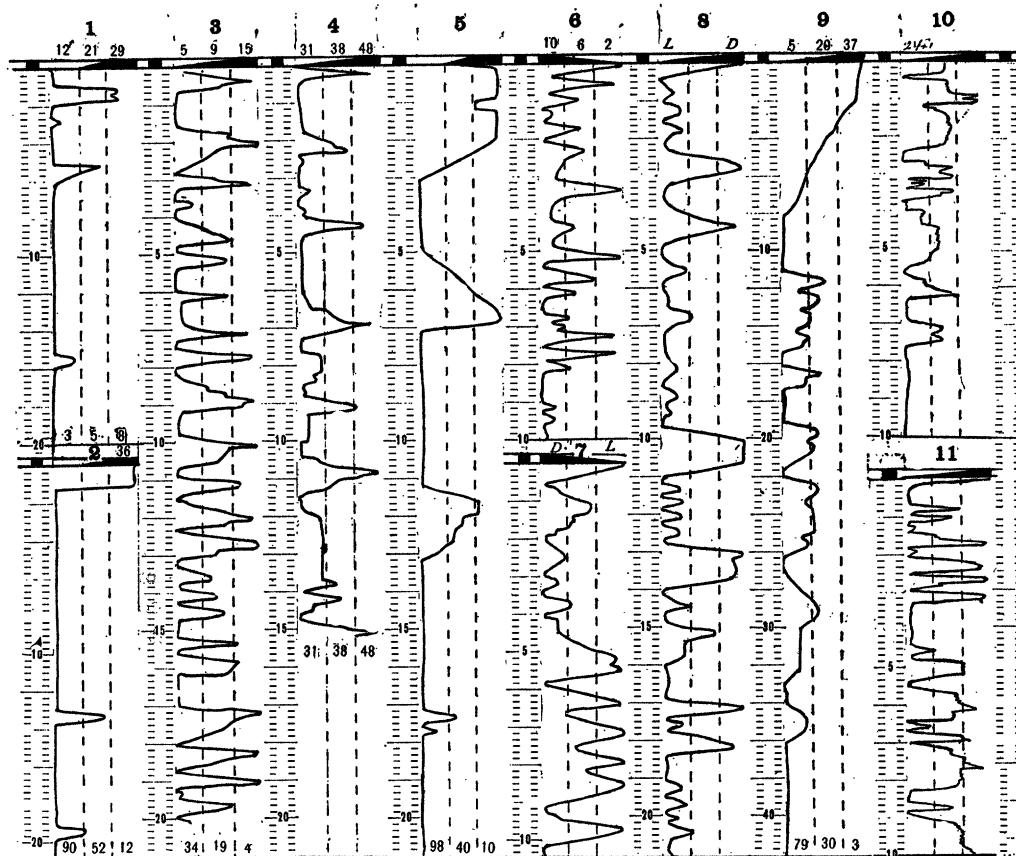
⁵ Shelford & Allee, *Jour. Expt. Zool.*, Vol. XIV., p. 226.

⁶ Wells, *Biol. Bull.*, Vol. XXIX., p. 223.

⁷ Wells, *Jour. Exp. Zool.*, Vol. XIX., p. 246.

⁸ Shelford, *Biol. Bull.*, Vol. XXV., p. 81.

⁹ Powers, *Biol. Bull.*, Vol. XXVI., pp. 177-200.



Description of Chart. For further details see citations in text.

Graph 1. A white-footed wood mouse (*Peromyscus leucopus noveboracensis* Fischer) in an evaporation gradient due to differences in air velocity. The figures at the beginning of the graph indicate the evaporation for the experimental period in tenths cubic centimeters of water; those at the end indicate air velocity in meters per second. (After Chenoweth.)

Graph 2. A white-footed wood mouse in an air humidity gradient. The figures at the beginning of the graph indicate evaporation and at the end relative humidity in per cent. of saturation. (After Chenoweth.)

Graph 3. A horned lizard (*Phrynosoma modestum* Gir.) in air humidity gradient; figures as in 2. (After Weese.)

Graph 4. A horned lizard in a substratum temperature gradient; the figures indicate temperature in degrees centigrade. (From Weese, unpublished.)

Graph 5. A common toad (*Bufo lentiginosus* Shaw) in an air humidity gradient. Figures as in 2 and 3.

Graph 6. A small sunfish (*Lepomis humilis* Gir.) in an ammonia gradient in alkaline water. Maximum concentration of ammonia at left, 7-10 pt. per million.

Graph 7. A ground beetle (*Platynus cupripennis* Say) in a light intensity gradient.

Graph 8. The same individual ground beetle in an oblique cage intensity-direction gradient.

Graph 9. An earthworm (*Helodrilus caliginosus*) in an air moisture gradient. Figures as in 2, 3 and 5. (From Heimbürger, unpublished.)

Graph 10. A single *Paramœcium* in a temperature gradient in which the cool end was near the optimum.

Graph 11. A single *Paramœcium* in a temperature gradient which resulted in death at the end of 12 minutes.

dissolved chemicals, lack of oxygen, etc., and in examining several hundred graphs made of their movements one is impressed with certain almost universal features of the reactions. ✓ In nearly all cases the animal becomes more sensitive to the stimulus after encountering its maximum intensity in the tank. It turns back from a weaker stimulus after encountering a stronger one; the threshold of stimulation is lowered. In the case of some animals the increased irritability persists for an hour or more while in others it lasts only a few minutes. In the latter case a few turnings in the lower intensity or a brief stay in the lower intensity permits a return to the original sensibility and the animal enters the highest intensity again, a rhythm of increased and decreased irritability thus occurs.

The graphs shown on the accompanying chart are selected to illustrate several stimuli and the reactions of several animal groups. Graph 1¹⁰ shows the reaction of a white-footed wood mouse in a gradient of air velocity producing evaporation as shown at the head of the graph in tenths cubic centimeters. It will be noted that after entering the high velocity air at the right once the subsequent movements in that direction were each shorter than the preceding. Graph 2¹⁰ shows the reaction of a mouse to air of different humidities. The method of reaction is similar to that to moving air. The relative humidity in the thirds is shown at the end of the graph and the evaporation at the beginning.

Graph 3¹¹ shows the reaction of a horned lizard to air of high evaporating power, the humidity being shown at the bottom and the evaporation in tenths cubic centimeters at the beginning. The invasions of the dry air during the first three minutes were followed by invasion only into the medium air. These are followed by six invasions of the dry air but with very short stays. Following this, from the thirteenth to sixteenth minute, the invasions reached only just through the medium air. The rest of the graph shows similar modifications and illustrates the rhythmic raising

and lowering of the threshold of stimulation. Graph 4 (from Weese—unpublished) shows the reaction of a horned lizard in a temperature of substratum gradient; the temperature in centigrade at the ends and center is shown by the figures at the beginning of the graph. Each excursion in to the higher temperature is followed by shorter invasions reaching only to medium temperatures.

Graph 5 shows the reaction of a common toad in a gradient of air moisture and evaporation, the evaporation is given at the beginning of the graph and the humidity at the end. In this case each invasion of the dry air is shorter than the preceding ones. Graph 6 shows the reaction of a sun fish (*Lepomis humilis*) in a gradient of ammonia in alkaline water. The fish was positive to the ammonia, and made excursions only into the low concentration of ammonia, following each invasion into the water nearly free from ammonia.

Graph 7 shows first graph of the reaction of a ground beetle taken at random, in light intensity gradient (Yerkes grader with Nernst lamp; triangular aperture). During the first five minutes the beetle avoided the stronger light in a lower intensity with each invasion, until it reversed and repeated the same rapid modification in invading the darker portions. After a five minute interval following the end of the first observation, the animal was transferred to a grader in a horizontal position with an oblique cage, cylindrical lens,¹² and triangular aperture. The oblique cage was turned so that in moving away from the source of light the animal came rapidly into lower intensities. Graph 8 shows the reaction of the same beetle in this gradient. Each invasion of the darkest part of the cage is followed by turning back a number of times in a comparatively high light intensity. The rhythmic change in sensibility is well illustrated here also.

Graph 9 (from Heimburger) shows the reaction of an earthworm (*Helodrilus caliginosus*) in a gradient of air moisture. The first twenty minutes which were spent in the dry

¹⁰ Chenoweth, *Biol. Bull.*, Vol. XXXII., p. 192.

¹¹ Weese, *Biol. Bull.*, Vol. XXXVII., p. 115.

¹² Shelford, *Biol. Bull.*, Vol. XXVI., p. 309.

air where the worm was placed, are not shown. After entering the moist air the worm turned back in progressively higher moisture contents, until the end of fifteen minutes of the scale; another somewhat longer invasion is followed by the same repeated decrease in invasion between 16 and 26 minutes and between 29 and 36 minutes.

A series of preliminary experiments were performed on *Paramæcium*. After a number of trials in which chambers of different sizes were used, a chamber was cut out of a large drop of beeswax darkened with graphite, on a slide. This chamber was 2 mm. wide, 9 mm. long, and 1 mm. deep. The slide was laid over the edges of two Petri dishes. Water at 36° C. was run into one of these and water at 16° C. into the other. The optimum of the culture was 23° C. as shown by the point of aggregation of the greatest number of individuals in a box 5 mm. deep, 20 mm. wide, and 170 mm. long. The apparatus at hand did not permit measurements of temperature in the 2 mm. x 9 mm. chamber. The position of the slide over the hot and cold water was so adjusted with a considerable number of individuals in the cell, that they aggregated at the cold end rather than at any point in the long axis of the cell. Movements were observed with a binocular. A single individual was then introduced from a diluted infusion.

It is not possible for one person to observe and graph the movements. The writer accordingly observed the animals and stated their position according to a scale, etc., while another person with watch at hand drew the graphs. Graph 10 is typical of what was observed repeatedly. Several invasions of the high temperature occurred before the graph began. This is due to the fact that when water was removed from the cell and another drop added it was necessary to allow two or three minutes for the drop to attain the temperature which accorded with the temperature of the slide beneath it. After the graphing began, an invasion of the high temperature at the end of the first minute was followed by turning in lower temperature. An invasion which did not reach the highest temperature

at the end of the third minute was followed by two turnings in much lower temperature. An inspection of the rest of the graph shows that each invasion of the high temperature is followed by two or three turnings in lower temperature; this was the rule in the ungraphed observations.

Graph 11 shows the reaction of an individual, beginning within five to ten seconds after the drop was introduced into the chamber. No time was allowed for the temperature of the drop of water to become adjusted. Accordingly the temperature at the warm end rose while the observations were going on. The slide has also been shifted too far over the hot water. When the graph began the animal was in the hot end; it moved to the cool end and on its return, turned back twice in lower temperatures. Then one long invasion of high temperature was followed by a very short one; three long ones, by a period of rest. During this period avoiding reactions had increased in violence until they began to dominate over other movements and the temperature had risen to a point where normal reaction did not occur. The animal darted rapidly, giving the avoiding reaction in the higher temperatures, so violently that none of the courses were followed up and after a number of rather long stays in the high temperature it died. One striking feature of the behavior is the orientation of the individuals in the long axis of the gradient. This is however apparently trial and error and, as Jennings has noted, when headed toward the optimum temperature they swim ahead without giving the avoiding reaction. The graphs bring out the fact that they give the avoiding reaction at different temperatures in accord with their preceding experience. It is however evidently not correct to assume that the *Paramæcium* distinguishes the difference between the temperature of the water in contact with the two ends of the body as shown by dividing the total distance necessary to give a degree difference by the length of the animal. On this basis Mendelssohn¹³ decided that they can distinguish one one hundredth of a degree centigrade.

¹³ Davenport, *loc. cit.*

They appear from these observations to distinguish the difference between the temperature of the water where they assume the normal forward course and the point where they give the avoiding reaction. This difference within the range of temperatures compatible with the life of the animal is probably some tenths of a degree, varying with the immediate antecedent experience of the individual.

The method of graphing has been found very useful in making accurate determinations of reaction where modification by environment has been attempted and where accurate determination of sensibility is necessary. One has only to take readings from a graph like number 3, make statistical records, and compute percentages in the thirds, repeating the readings, at $\frac{1}{2}$ min., 1-min. and 2-min., intervals, beginning after $\frac{1}{2}$, 1, 2 minutes, etc., after the graph began to demonstrate that percentage in the thirds, with short intervals at least, is a very unreliable method of making records, unless the reading is done with absolute precision.

The occurrence of the rapid modification of behavior described in practically all the great groups of the animal kingdom leads one to attempt to explain the phenomenon on the basis of some physiological characteristic common to all. In connection with the study of fishes the writer and Allen¹⁴ suggested that in both the case of carbondioxide and lack of oxygen in water the increased irritability is due to increased acidity. In support of this we cited Waller who found that a small amount of carbondioxide increases irritability of nerves.

A similar explanation of the shorter invasions of light in a light gradient in which the Daphnias turn back in a lower intensity as described by Davenport and Cannon, was offered by Loeb¹⁵ who anticipated our conclusion, independently derived, and cited Waller though he attributed the development of

acidity to the increased metabolism of the organism due to the stimulation.

Since the phenomenon of modification under consideration takes place in gradients of ammonia in alkaline water, and the fishes concerned are positive to the ammonia, and since such behavior has been noted in the avoidance of cold, darkness, etc., which depress metabolism, thus the hypothesis of increased irritability due to acidity can be maintained only on the assumption that all changes in the environment stimulate the metabolism temporarily. This is not out of accord with the effects of depressing drugs which nearly all stimulate first, for a short time, and then depress.

✓ Whatever may be the correct physiological explanation of the phenomenon, we have noted that the process is similar in the mammal and in the Protozoan. The reactions of both are such as to suggest learning, that is, the possible association of increasing stimulation with stronger stimulation farther on in the course being pursued, though it is hardly to be expected in the Protozoan. If the most intelligent animal behaves like the simplest Protozoan and if pleasure and pain are the basis for intelligence, an analysis of this type of modification may yield data showing that the modification is not essentially different from associative memory. The graphs appear to be but a general statement of the gagging of the chick at the sight of a distasteful species of caterpillar which it has tried on an earlier occasion.

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SCIENCE

A Weekly Journal devoted to the Advancement of Science, publishing the official notices and proceedings of the American Association for the Advancement of Science

Published every Friday by

THE SCIENCE PRESS

LANCASTER, PA.

GARRISON, N. Y.

NEW YORK, N. Y.

Entered in the post-office at Lancaster, Pa., as second class matter

¹⁴ Shelford and Allee, *Jour. An. Beh.*, Vol. IV., p. 7. Shelford, *Jour. An. Beh.*, Vol. IV., p. 31.

¹⁵ Loeb, "Mechanistic Conception of Life," p. 222.