

a large chart presenting the results, and write a paper. Could some of these earlier workers but have foreseen the gold mine of facts underlying each appearance of acid in his culture tubes, the history of much scientific progress in the last twenty years might have been quite different. Even now, decomposition of glucose to alcohol and CO₂ by yeast appears to be the best understood of these fermentative processes, resembling in many ways the oxidation of sugar in the animal body and involving the recognition of both the nature and function of certain "vitamins." Before these chapters can be extended to describe the detailed mechanisms of all the various types of bacterial fermentation and respiration, other equally important substances will have to be sought and their actions clarified.

The chapter on "Enzyme Variation and Adaptation" also bears directly on this problem, as well as on other matters of very broad biological interest. The purposeful production of strains of bacteria showing abnormal sugar fermentation, the development of an enzyme specifically decomposing the polysaccharide of the Type III pneumococcus or of one which oxidizes thiocyanates of gas-waste liquors may seem to be unrelated phenomena. One may well inquire, however, what further practical applications will develop from this ability of unicellular organisms to produce specific enzymes in response to particular stimuli and how far an understanding of the principles underlying it will go toward explaining, for example, antibody formation in the animal body.

The chapter on "Nutrition and Growth" provides a further example of the recent advances which characterize the entire subject-matter of the book. It is stated in the preface that "this subject (bacterial growth) now attracts mathematicians and statisticians less than formerly, but has passed into the hands of biochemists interested in problems of nutrition." The new type of investigations began to bear fruit not more than five or six years ago, and a rich harvest of new facts is appearing annually. Miss Stephenson's chap-

ter admirably summarizes the situation at the moment of publication. The discovery by the L'Woffs that the V factor for the growth of the Pfeiffer bacillus was identical with cozymase, and that of Knight that vitamin B was essential to the growth of the staphylococcus, attracted the immediate attention of investigators of animal nutrition to the possibility of using bacterial growth as a tool in their own field. The recognition that nicotinic acid was essential to the staphylococcus and the nearly simultaneous isolation of this material from liver extract in connection with studies on growth of the diphtheria bacillus were followed in a matter of weeks by the demonstration that the same substance cured black tongue in dogs and pellagra in man. With the continued extension of the subject-matter of this chapter will come many further contributions of the greatest importance to both biochemists and bacteriologists.

Other chapters merit equally favorable comment. Those dealing with nitrogen fixation and photosynthesis are particularly stimulating. In short, it is not too much to say that the biochemist or bacteriologist who reads this book will not fail to derive profit from the variety of facts now available in this borderline field, and to see many applications of possible new methods to his own particular problem.

The book is well printed and singularly free from typographical and editorial mistakes. Miss Stephenson recently told the reviewer that it was full of errors of omission and commission, but to the casual reader, at any rate, this would appear to be an over-statement. It is replete with excellent charts and tables, which illustrate many of the actual experiments of those workers who have contributed to the establishment of bacterial metabolism on a basis where it may now perhaps be considered to represent a science in its own right.

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SPECIAL ARTICLES

A KINESTHETICALLY CONTROLLED MAZE HABIT IN THE RAT

THE problem of the role of kinesthesia in the control of such serial responses as are present in the maze habit has been investigated for thirty-odd years without a clear-cut proof that kinesthesia can control maze behavior. Watson believed that kinesthesia was the only necessary type of stimulus control, but later investigators were prompt in indicating the functioning of other types of stimulation both from within and without the maze. Lashley and Ball,¹ who used a simple alternation maze that was not rotated and whose units

¹ K. S. Lashley and J. Ball, *Jour. Comp. Psychol.*, 9: 71-106, 1929.

were not interchanged, severed practically all tracts in the spinal cords of rats, some tracts in one rat and other tracts in other rats, and found that the ability to perform the maze habit survived the operation irrespective of the locus of injury. The authors concluded that "the maze habit can not be interpreted as a series of kinesthetic-motor reflexes but must be referred to some intraneural mechanism capable of producing an integrated sequence of movements in the absence of directive sensory cues" (p. 100). These results were extended by Ingebritsen² to show that rats could acquire the maze habit after extensive cord lesions.

² O. C. Ingebritsen, *Jour. Comp. Psychol.*, 14: 279-294, 1932.

Although Lashley and Ball's conclusion can be shown to be untenable on the evidence submitted, numerous experiments exist which show that kinesthetic sensitivity is so crude that it alone could not guide the pathway followed by the rat, that it can be greatly altered and the maze habit still persist, and that it can be eliminated as a differential factor by means of the double alternation technique and yet maze habits can be acquired.³

The whole drift of the interpretation of maze learning has been characterized by a tendency to deny the role of kinesthesia either in the acquisition of the habit or in its execution after acquisition. The extent to which such views can be carried is indicated by Honzik,⁴ who worked with a complicated maze pattern and who wrote as follows: "The conclusion that is forced upon us by the results with blind-deaf-anosmic rats is not that kinesthesia has no function in learning but that an act can not be learned by kinesthesia alone. . . . Thus among the various senses kinesthesia holds the unique position that by itself it is powerless but can, when operating with other senses, assume a share in the management of acts initially learned through them" (p. 56).

There are essentially but two methods by which one can attempt to set up a habit which would be controlled by kinesthesia. The first method involves surgical interference with the animal in an attempt to eliminate all sensory avenues other than the kinesthetic and then find the animal able to learn the maze. The difficulty with this method is the impossibility of completely eliminating non-kinesthetic avenues of stimulation. The second method is to plan the maze and the method of experimentation in such a manner that, with a minimum of surgical interference, only kinesthesia can operate to determine which turns the animal shall make. If then the maze habit is established, the conclusion can be drawn that it is kinesthetically controlled. It is this second method which has been followed in the present experiment where I have had the assistance of Miss Beatrice Hall, a graduate student at Brown University.

The maze utilized was a block type elevated maze containing 8 culs-de-sac as diagramed in Fig. 1. Each individual block was 30 inches long, 1½ inches wide and 12 inches high, so arranged that each cul was 9 inches long. The maze stood on a platform, mounted on castors, and could be easily rotated about its center. The sequence of correct turns was *lrlrlrlr*.

Five blinded untrained male white rats 90 days old were first trained to run 90 inches on a straight elevated path to food, 3 trials daily for 8 days. They were then transferred to the maze and given one trial

daily, retracing not prevented, under the following conditions which were first used in the Clark University Laboratory by Casper:⁵ (1) Between trials the maze

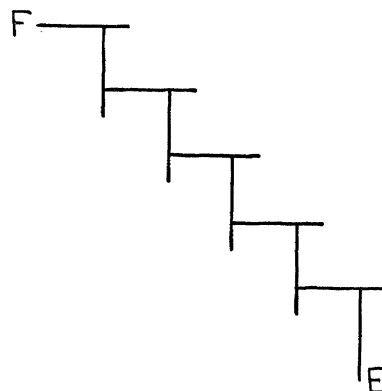


FIG. 1. The ground plan of the maze. E is the entrance; F is the exit where food was placed.

as a whole was rotated 45° clockwise, so that it never occupied the same position relative to stimuli from outside the platform for any two successive trials. Vision had been surgically excluded, and the changing orientation of the maze made it impossible for the rat to use extra-maze and extra-platform stimuli as directive cues for the correct responses. (2) Between trials all units of the maze were interchanged in one of 15 predetermined orders, leaving only the *lrlrlrlr* constant. Under these conditions no stimuli from the maze could afford differential cues controlling the direction which the rat should turn at the choice points.

All five rats learned the maze to a criterion of 3 perfect trials in succession in 9, 10, 9, 16 and 15 trials, respectively, not counting the criterial trials. However, as early as the second trial one rat made but two errors, and brief sequences of simple alternation were common in all rats. The first completely perfect runs were made after 6, 4, 5, 3 and 2 trials by the respective rats.⁶ The learning curves for time and errors per trial show no peculiarities, and hence they are not reproduced here. The distribution of the total errors of all rats per cul was as follows, taken in the order first cul to eighth cul: 36, 16, 6, 3, 2, 11, 7. It is thus clear that the greater difficulty lay at the two ends of the maze and the lesser difficulty in the middle culs. This was true for each rat, and it raises interesting questions about goal gradients. The last response learned by each rat was the correct (left) turn at the first choice point.

An explanation of this completed maze habit may be formulated in the following terms: When the rat

⁵ B. Casper, *op. cit.*, p. 271 ff.

³ W. S. Hunter, *Jour. Genet. Psychol.*, 36: 505-537, 1929. B. Casper, *Jour. Genet. Psychol.*, 43: 239-292, 1933.

⁴ C. H. Honzik, *Comp. Psychol. Monog.*, 13: No. 4, 1936.

⁶ W. Dennis and R. H. Henneman, *Jour. Genet. Psychol.*, 40: 396-404, 1932, used normal (non-blinded) rats on a simple alternation maze of the present type and found that some rats made no errors on the first trial.

is placed on the maze at the entrance, it is stimulated by the maze and the experimenter. Call this total stimulation S_E . S_E causes a response of running left at the first cul. Call this response R_L . This turn to the left and the approach to the next choice point produce more stimulation from inside and outside the maze as well as kinesthetic stimuli within the rat. We shall call all these sensory consequences of R_L by the symbol S_L . S_L causes the rat to turn right (R_R) at the next choice point; and R_R has S_R as its sensory consequences. S_R is then followed by a left turn, etc., through the maze. What the animal has had to learn, then, is to turn left for S_E and for S_R and to turn right after being stimulated by S_L . We shall leave aside the question whether the rat responds to S_L and S_R as individual stimuli or as interrelated patterns, since our major concern is with the sensory modality which is controlling the behavior.

If the maze were not rotated and the units were not interchanged, there would be cutaneous and olfactory stimuli from the various maze units as well as kinesthetic stimuli from the animal's own activity which, with stimuli from outside the maze, would enter as components of S_L and S_R as has been shown in the work of Hunter, Honzik and Wolfe. If, however, as under the present conditions, the maze is rotated and the units are interchanged, S_L and S_R reduce solely to the kinesthetic stimuli resulting from the rat's own activity in making left and right turns, in so far as differential stimuli are concerned. To be sure, the edges of the paths stimulate the rat and "show" him when a turn is to be made, but such stimuli can not determine the difference between a left and a right turn.

It is theoretically possible that some symbolic process, some symbolic equivalent of "go left-right-left-etc.," may be present to control a habit set up under the above conditions, as indeed it would be were the sequence of turns in double alternation *lrrllrr*.⁷ However, the presence of adequate differential kinesthetic stimulation makes such a hypothesis untenable on the basis of parsimony; and the great difficulty which the rat has with double alternation temporal problems as compared with the great ease with which the present maze habit was established renders the hypothesis of symbolic control still less tenable in the present case.

The significance of the present experiment lies not only in its demonstration of a habit built up and controlled by kinesthesia but also in the basis which is now laid for an extension of the neurological study of such intelligent acts. A repetition of Lashley and Ball's experiment on rats trained as here described (but in alley mazes because of the rat's motor inco-

ordinations) should show an interference with the habit if kinesthetic impulses are carried in definite tracts of the cord and if they can not shift to other tracts when their own are destroyed. Furthermore, cortical extirpations of the kinesthetic projection areas should reveal a localization of function in some rats as opposed to the equipotentiality which Lashley's work on the neural control of maze habits has hitherto supported. The expression "in some rats" is used advisedly because some rats can, with difficulty, develop the equivalent of symbolic controls. It remains to be determined whether or not localized brain lesions destroy the rat's capacity to perform the responses so controlled. (Jacobsen's⁸ work indicates that monkeys are unable to relearn the delayed reaction, which is also symbolically controlled, after bilateral frontal lobectomy.)

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A RADIOACTIVE ISOTOPE STUDY OF THE ABSORPTION OF PHOSPHORUS AND SODIUM BY CORN SEEDLINGS

THE artificial radioactive method is readily adapted to studies of the factors influencing the absorption of mineral matter by plants. The design of Geiger counter developed in this laboratory¹ is suited to studies of this type, since it has a low background of only two counts per minute, since it will detect rays with energies as soft as 50,000 volts and since it yields quantitative results when calibrated against known solutions.

The technique involved in a quantitative study of the absorption of phosphorus and sodium by corn seedlings is simple. The plants tested were germinated in sand and the seedlings transferred to water or culture solution; at the time of the experiment they were about 12 inches high. In making the tests a measured quantity of radioactive phosphorus in the form of tripotassium phosphate or of radioactive sodium as sodium chloride was added to the culture solution. At regular intervals thereafter the plant was placed so that the leaf to be examined was directly below the counter window and the number of counts per minute were recorded.

Effects of various factors influencing the assimilation of phosphorus and sodium are illustrated in Figs. 1, 2 and 3. Fig. 1 shows the total number of disintegrations counted per minute per unit area of leaf as a function of time for different total phosphorus concentrations in the solution. Total phosphorus (radioactive and non-radioactive) taken up

⁸ C. F. Jacobsen, *Comp. Psychol. Monog.*, 13: No. 63, 1936.

¹ A. K. Brewer and A. Bramley, *Jour. Applied Physics*, 9: 778, 1938; *Jour. Ind. Eng. Chem.*, 30: 893, 1938.

⁷ W. S. Hunter, *Jour. Genet. Psychol.*, 36: 512, 1929.