THE INHERITANCE OF MAZE LEARNING ABILITY IN RATS

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I. INTRODUCTION

Several years ago we started on the problem of selective breeding for maze learning ability. The immediate aim is to develop two lines—one of bright animals and the other of dull animals.[1]

This paper is a presentation of the material to and including the F4 generation.

Before presenting the results, however, we would like to point out some of the reasons why we believe that a problem of this sort should prove profitable. We believe that this approach will be a valuable avenue of attack upon the following general problems:

1. It is quite obvious that the question of hereditary factors in maze learning is one problem that can be attacked by the process of selective breeding. If maze learning depends upon hereditary factors to the extent that such factors have an influence greater than the magnitude of the errors of measurement, then to that extent, it should be possible ultimately to separate two lines of animals. Furthermore, if the process of selective breeding is continued for a sufficient length of time it should be possible to purify these two lines. Then the geneticist may cross-breed them and arrive at some generalization concerning the methods of transmission of the hereditary factors underlying maze learning.

2. Should it be possible to produce two pure lines, then we will

[1] These terms are used because they are short and convenient. Throughout the paper "dull" will mean animals coming from relatively slow maze learning parents, and "bright" will mean those coming from relatively quick maze learning parents. No other connotation of the terms is meant or desired.

have a situation in which we can experiment adequately upon the problem of nature versus nurture. It seems to the writer that experimentation upon this problem with human subjects can never be entirely adequate because, with one exception, such experimentation cannot adhere to one of the fundamental rules of scientific procedure—namely, to vary only one factor at a time, or, at least, if more than one factor is varied, to know the extent to which each is varied. Nature and nurture are two factors. To find adequately the influence of the former, the latter should be held constant and *vice versa*. This is not and cannot be done with human subjects with the exception of work upon identical twins in which the two members of each pair have identical heredity.

We are not implying that the data secured on human subjects is valueless, because some generalizations can be drawn in so far as the various lines of evidence converge toward a common position. However, the numerous discussions and arguments concerning the relative influence of nature versus nurture indicate that the evidence at hand is ambiguous and open to various interpretations.

It would seem, therefore, that it might be well to settle the question for one species even though we cannot make broad generalizations from the rat to the human being.

If the two pure lines are obtained then we will know what to expect of the offspring under standard environmental conditions. In other words, we can keep the hereditary factor constant and vary the environmental factor as desired.

3. If two lines of animals are obtained which differ from each other in respect to their hereditary ability to learn the maze, it follows that these two strains must differ in some physiological, neurological, or biochemical respect or respects, or in a combination of all. If the animals are examined by techniques belonging to these various fields, it may be possible to determine the existence of such differences. We may, therefore, be able to determine the somatic variations underlying different degrees of maze learning ability.

This problem may be and has been attacked by the correlation technique in a random sampling of the population. However, errors of measurement may destroy the possibility of obtaining a correlation if the existent relationship is not relatively larger. The relative importance of errors of measurement is reduced when using the method of selective breeding since one is dealing with two groups, the respective averages of which are widely separated. One may, therefore, be able to establish relationships which would otherwise appear to be non-existent.

It seems to the writer that we are too prone to be content in saying that the degree to which an individual possesses an ability is a hereditary characteristic and to allow the matter to rest. We seem to forget that many characteristics which are determined by hereditary factors may be changed by the application of proper agents within the lifetime of the individual. Is it too optimistic to say that we may some day be able to treat an individual of low hereditary ability along some line in such a way as to increase that ability? Failing a happy stroke of extreme good luck, we will never be able to do this until we know what is somatically wrong with the individual. Once having secured this knowledge with reference to the human being, it eventually may be possible to reduce greatly the number of inmates in our institutions for the feebleminded. To some that statement may seem too optimistic. But, on the basis of available knowledge, can they prove that it is?

4. The method of selective breeding also opens a method of attack upon the overlap or lack of overlap of psychological abilities. Are the bright animals also more proficient in learning a brightness discrimination, or problem box, or delayed reaction problem as compared with the dull animals? Here again the correlation technique with random samplings may be used, but as was pointed out above, a real relationship may be obscured by errors of measurements.

No doubt other problems could be stated which would be subject to attack by this method. We believe, however, that we have mentioned sufficient to justify the undertaking of the long and arduous task which lies before one who starts the problem of selective breeding.

II. PROCEDURE

The maze which is being used is the Minnesota automatic maze described by Heron (1). There are twelve units in this maze which involve the following sequence of turns by the animals L R L L R R L R L R R L.

When the problem was first started it was the intention to run all animals for 27 trials and count the total errors for each animal in the last 25. However, the results from the F2 generation indicated that 17 trials, counting the total errors for each animal in the last 15, would be sufficient. From that time on, therefore, we used a training period of only 17 trials.

The age at which the succeeding generations have been run has varied to some extent owing to various exigencies. However, no generation has been run at an age, at the beginning of training, of less than sixty-five days and none at an age of over one hundred days with the exception of the parents, the age of which was unknown, but, all were within the prime of life. The age variation within a generation has not been more than ten days.

The basis of selection of breeding animals from each generation to produce the succeeding generation has been primarily the record made by the animals in the maze in terms of total errors for the number of trials run. However, we have always mated within the line even though an animal from dull parents might have made fewer errors than the animals from the bright parents or *vice versa*.

If the maze record permitted, we have used as a supplementary basis of selection for breeding the size of the litter from which the animal came. We always breed the animal from the larger litter under these circumstances. This will help possibly to maintain the virility of the two lines.

Another selective factor is involved in the fact that we secure in each generation more animals than we can train in the maze. We make 30 matings in each generation, this is done by mating each of 15 males with two females. As far as possible one female is a sister of the male and the other female is of no immediate relationship.[2] The matings of the F3 gave us over 200 offspring. Of these we could use only approximately half. In making this selection we consider the following factors: (*a*) The date of birth of the litter as compared with date of mating; other things being equal, we choose the litters of those animals which bred the quickest; (*b*) the size of the litter; and (*c*) whether the litter is from the inbred or the outbred female—other factors allowing we choose the inbred litter. Up to the present, however, no attempt at continuous inbreeding from generation to generation has been made for fear that we might introduce some lethal factors which would cause us to lose our lines.

All animals are given preliminary training for about ten days before they are allowed to traverse the maze in order to accustom them to the doors and to get them on the proper rhythm of feeding.

After the animals are started in the maze, they traverse it in the same order each day. The animals from each strain are mixed in a random order but the males and females are kept separate. There is no particular reason for this except that it is easier to introduce the animals to the maze situation if the males and females are not mixed.

Up until the F4 generation we did not take the time records in the maze. This was not done for two reasons: *1*, we had not yet attached a synchronous motor to the maze recorder, and *2*, we did not anticipate that time records would be of any great value to us. However, the time records for the F4 generation were taken and are presented under results.

Our control of motivation up to the present has perhaps not been as good as we would like. The use of the automatic maze introduces certain difficulties in this respect. Since the animals are never handled from the time they are started in the maze until they have finished the complete training period, it is impossible

[2] Our parent rats were taken from the stock of rats which has been maintained in this laboratory for probably a period of 15 years. This stock is a mixture of hooded and albino animals. Since the stock has been maintained for such a long period it is no doubt highly inter-bred although in no systematic manner.

to weigh the animals each day. However, it is difficult to see how there could be a differential influence upon the two lines in this respect unless the selective breeding itself is introducing certain factors which would account for it. That there may be a possibility in this direction is indicated by the apparent tendency for the animals from the bright parents to have a higher basal metabolic rate than those from the dull parents (2). This may mean that the bright animals are hungrier each day than are the dull. If this is true and all animals are given the same amount of food in proportion to their weight then the bright animals should gain weight at a slower rate than the dull. This would, of course, be apparent in daily weight records. For that reason we are now planning the construction of an apparatus which will, we hope, automatically record the weight of each animal at the conclusion of each day's trial. In the F5 generation we plan to determine by this means whether there is a differential weight increase between the two lines during training period. If there is, then in the next generation we shall endeavor to feed in such a manner as to reduce or entirely eliminate this differential.

In concluding this section on procedure it remains to be pointed out that since our animals do not receive any water during the training period except that which is mixed in their food, they are probably motivated by a combination of hunger and thirst. It would, of course, be possible to keep water before the animals but since we have been very fortunate in maintaining, at a very high level, the health of the animals it has not seemed necessary to change this procedure. We have been very careful, however, to give the animals a weekly ration of cabbage and codliver oil which, together with the otherwise balanced diet (a commercial chick-growing mash), maintains their health in a very satisfactory manner.

III. RESULTS

We will present our results in both numerical and graphical form. In table 1 we show the results for the successive generations from the standpoint of a comparison of the sexes. A word of explanation is necessary at this point. The F2 generations were divided into two groups, one which was started in the maze a week after the other. For some reason which is not apparent the animals in the second group to start did better in the maze than the animals of the first group. A reference to the table will show that this is particularly true of the dull animals. We have, therefore, listed these two groups separately in table 1. Also, in the case of the F4 generation, we reversed the maze after the animals had had their regular training period on the pattern which had been used for the preceding generation. This reversal of the maze meant that in each unit what had been the true path became the blind alley.[3]

It was thought that this reversal should penalize the bright animals on the average more than it would the dull animals, since the former had more nearly learned the original pattern. We desired to know if the bright animals could overcome this handicap and still out-distance the dull animals in the learning.

This will explain the data in both tables 1 and 2 under the title of maze reversed. Likewise, time is shown for the F4 generation only since it was not taken, as explained above, for the other generations.

To return to the question of sex differences, only one comparison shows a statistically significant difference, namely for the bright line of the F2 generation in the first group run. This difference is in favor of the males as shown by the minus sign in front of the difference in table 1. However, of the 17 comparisons, 13 show differences in favor of the males. In some cases these differences are very small.

Since we are not primarily interested in sex differences we will not dwell further upon this point. If one were interested in this question it would be wise to alternate male and female in the maze as it is possible that the fact that all of one sex group is run each day after all of the other, may have some influence.

The data in table 2 are designed to bring out the differences between the two lines in the successive generations. In this

[3] If the reader has difficulty in understanding how it is possible to do this, he should refer to the article mentioned above by Heron (1) in which the maze is described. We do not wish to take space to repeat that description here.

TABLE 1

Bright versus dull (sexes separate)

	Males		Females		Difference	σd
	Average error	σ	Average error	σ		
P	79.26	4.58	90.10	2.19	−10.84	5.08
F1						
B	62.77	4.31	51.17	4.11	11.6	5.96
D	68.45	3.55	57.21	5.11	11.24	6.22
F2. First group run						
B	58.27	2.87	78.86	3.66	−20.59	4.65
D	88.8	2.9	92.25	6.57	−3.45	7.18
F2. Second group run						
B	55.75	5.14	65.50	3.51	−9.75	6.22
D	66.17	2.47	74.38	4.31	−8.21	4.97
F3						
B	42.85	2.77	43.50	3.25	−0.65	4.27
D	63.90	2.98	61.82	2.23	2.08	3.64
F4						
B	57.19	3.26	60.88	2.6	−3.69	4.17
D	84.18	3.08	89.25	2.49	−5.07	3.96
F4. Average seconds						
B	992.95	54.46	878.92	40.9	114.03	68.1
D	1319.68	71.90	1570.22	105.82	−250.54	128.0
F4. Maze reversed (average error)						
B	46.14	1.46	48.55	1.09	−2.41	1.82
D	59.59	4.16	62.70	2.78	−3.11	3.88
F4. Maze reversed (average seconds)						
B	583.38	52.23	599.48	26.94	−16.10	58.8
D	996.40	169.7	1129.44	118.28	−133.04	207.0

table we have combined the data for the sexes and also have brought together the two groups of F2.

Table 2 shows that since the F1 generations, the two lines show significant difference with the magnitude of the differences growing progressively greater. It shows also that the bright

TABLE 2

Bright versus dull (sexes combined)

	BRIGHT	DULL	DIFFERENCE	σd
	F1			
Average error.................	56.26 (41)*	62.97 (39)	6.71	4.38
Standard Deviation...........	3.06	3.14		
	F2			
Average error.................	66.36 (50)	77.16 (53)	10.80	3.25
Standard Deviation...........	2.21	2.39		
	F3			
Average error.................	43.12 (48)	62.73 (51)	19.61	2.71
Standard Deviation...........	2.06	1.76		
	F4			
Average error.................	59.27 (48)	86.97 (49)	27.70	2.82
Standard Deviation...........	2.02	1.96		
	F4. Time in seconds			
Average seconds..............	933.0 (48)	1458.00 (49)	525.0	75.86
Standard Deviation...........	33.47	67.57		
	F4 maze reversed (errors)			
Average error.................	47.5 (48)	61.3 (49)	13.8	2.53
Standard Deviation...........	88	2.37		
	F4 maze reversed (time in seconds)			
Average seconds..............	292.5 (48)	1068.0 (49)	775.5	100.28
Standard Deviation...........	18.51	98.56		

* Numbers in parentheses are the number of cases.

animals made significantly fewer errors than the dull during the course of their 10 trials in the reversed maze. Therefore, if the reversal of the maze did handicap them they were able to overcome that handicap even in a space of only 10 trials.

Time also shows a significant difference for the two lines. It would be expected of course, that the dull animals would have higher time records inasmuch as they made more errors. However, the difference in the average time scores would appear to be

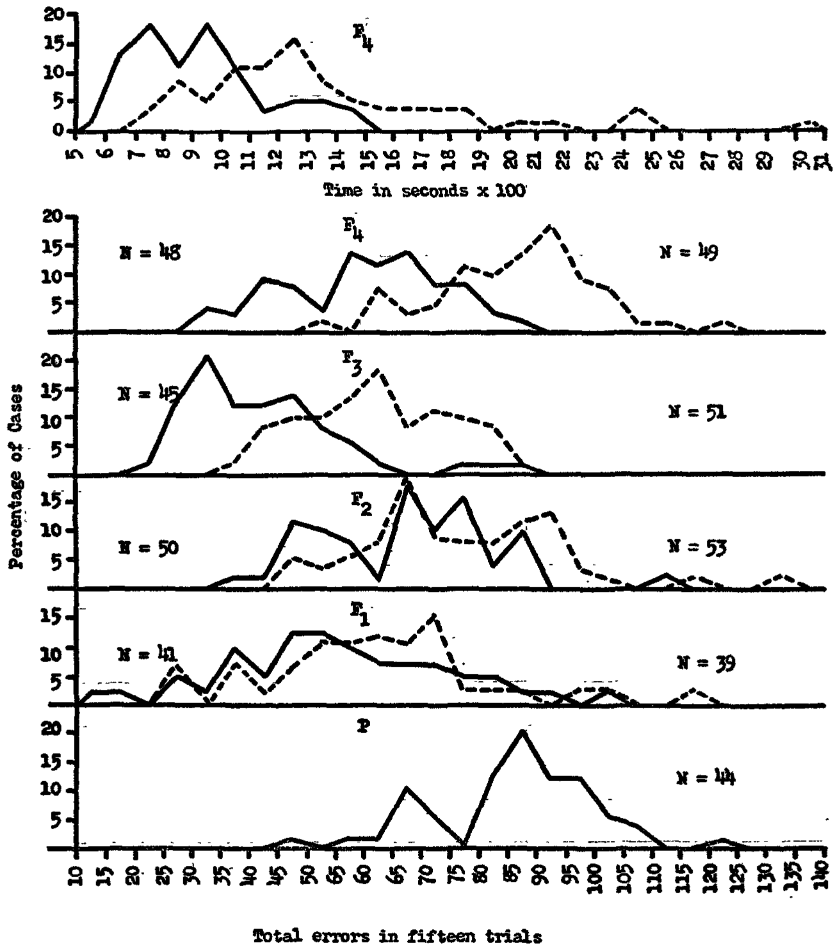

FIG. 1. THE DISTRIBUTION OF ERRORS FOR THE PARENTS AND THE FOUR SUCCEEDING GENERATIONS, AND OF TIME FOR THE F4 GENERATION

The parent distribution is at the bottom of the figure in solid line. The distributions for the bright animals of the succeeding generations are also in solid lines. Those for the dull are in broken lines. The time distribution for the F4 generation is at the top of the figure. The data on the ordinate are in terms of percentage of cases. The distribution show, therefore, the percentage of each group of animals lying in each time or error class interval.

greater than expectation on this basis. This is an unexpected finding and it will need further experimentation in an endeavor to find the cause of it.

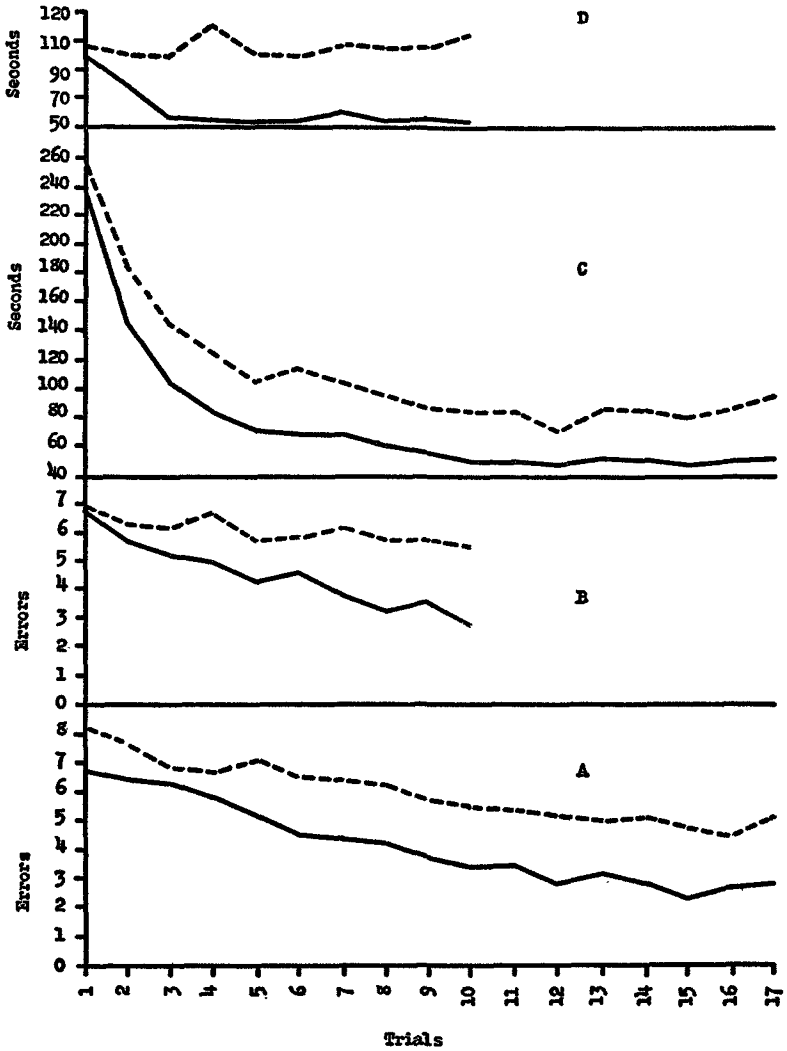

FIG. 2. LEARNING CURVES FOR THE F4 GENERATION

The bright rats are represented in the solid line and the dull rats in the broken line. Curves under *A* and *C* are the error and time curves, respectively, for the maze as used for all generations. Curves under *B* and *D* are the error and time curves, respectively, for the reversed maze.

A second way in which to present the results is by means of a distribution for the successive generations. This is done in figure 1. These distributions clearly show graphically the progress which has been made in separating the two lines. To the distributions for errors we have added the distribution for total time—15 trials—for the F4 generation. This distribution shows that the lines are separating on the basis of time also.

The reader may find it of interest to compare these distributions with those of Tryon who is doing a similar problem at the University of California. He is further advanced than we are and his distributions for seven generations plus the parents are given in the book, "Heredity and Environment," by Gladys C. Schwesinger, on pages 334–335.

Tryon's distributions show a range of errors much larger than ours. This is caused by at least two factors: *1*, he uses 19 trials as compared with our 15; and *2*, his maze has five more blind alleys than ours. There are no doubt other differences of technique as well, which affect this range of errors. In spite of these differences, however, there is a remarkable degree of similarity between the two sets of distributions.

In figure 2 are given the learning curves for the F4 generation in order to show how the two lines differ throughout the course of the learning. It is seen that the two groups are separate for the entire lengths of the curves. The only point that perhaps requires comment is why there is a separation on the first trial. The animals of the two groups are treated in exactly the same manner in the preliminary training. Therefore, it might be expected that the maze should be equally novel to both and that they should start at the same point. Our only possible explanation of why this is not true is that the bright animals profit to greater extent even by the preliminary "test breaking" period than do the dull and that, therefore, the former are better able to handle the maze situation right from the beginning.

IV. DISCUSSION AND CONCLUSION

It seems quite apparent that maze learning depends to a large extent upon hereditary factors. Just what these factors are, we do not at the present know.

We believe that if the process of selective breeding is continued for a sufficient number of generations that we will ultimately be able to secure relatively pure lines for a great many if not all of the hereditary factors involved in this activity. How long this will take we cannot predict. However, if it is ultimately accomplished, we believe, as we have pointed out in the introduction, that a valuable and stable basis will be laid from which a number of important problems of both a theoretical and practical nature can be attacked.

In the meantime while the process of selective breeding is being continued, we shall experiment in various ways upon the two groups in the hope that experimentation upon even the impure lines shall give us leads which may later be verified upon the pure lines.

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(2) Heron, W. T.: Basal metabolism and maze learning in the rat. Psychol. Bull., 1933, xxx, 723.