INHERITANCE OF EDUCABILITY

A FIRST REPORT ON AN ATTEMPT TO EXAMINE PROFESSOR MCDOUGALL'S CONCLUSIONS RELATING TO HIS EXPERIMENT FOR THE TESTING OF THE HYPOTHESIS OF LAMARCK

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It will be well known to all here assembled that in 1927 there appeared the first report of WILLIAM MCDOUGALL'S *Experiment for the testing of the hypothesis of Lamarck* and that his second report was published in 1930. These reports have attracted considerable attention, as was to be expected, since they deal with a subject that always arouses controversy and provides ample opportunity for the clashing of opinions and prejudices. It has to be agreed, however, that of all the experiments on which the neo-Lamarckian case is based these of MCDOUGALL stand in a class by themselves for the reasons that he used as his experimental material an animal stock which can be regarded more or less as pure line and that he took very considerable precautions to avoid selection.

You will remember that his experiment took the form of dropping rats 3 to 4 weeks old in the middle blind compartment of a water tank out of which there were two ways which led to platforms, one of these (alternately on the right and left) being illuminated and so wired that a rat stepping out of the water on to it received an electric shock. The rat had the choice of going either to the dim platform and thus out of the tank without receiving a shock or to the lighted platform and getting a shock. Each rat was dropped in the tank 6 times daily until it learned to avoid the illuminated and live platform. The rat had learned when 12 times in succession it had taken the dim, safe platform. As the experiment proceeded the technique employed underwent several modifications, but after 12 generations of rats had been trained the procedure was finally standardized. In 9 generations thereafter the average number of errors fell from 80 to 25 and the number made by the best from 42 to 3. In the case of another related group the number of errors fell from about 170 in the first generation to 114 in the fifth. Finally, the worst performers were selected during 2 generations, but in spite of this adverse selection the time needed for training fell. To obviate the possibility of tradition, mothers of a slightly trained stock were mated first with slow-learning and subsequently with quick-learning males. The first mating gave an average number of 164 errors, the second of 62.

MCDOUGALL'S tentative conclusions are as follows:

"Twenty-three generations of rats have been trained in the tank to the

performance of a specific task. The rats of the successive generations have displayed increasing facility in mastering this task. Whereas rats of the control stocks make on the average 165 errors (and receive the same number of shocks) before learning to avoid the shock, rats of the twenty-third generation of trained stock make on the average only 25 errors, the latter having acquired a greatly increased facility in mastering the task, the increase being measured by the difference between 165 and 25 shocks required for learning."

"The average degree of facility shown by any group of rats is in the main a function of their genetic constitution."

"In the light of our present knowledge there would seem to be only two ways in which such change of constitution as is shown by the rats of the trained stock can be brought about; first, by steady selection of such variations and mutations as may occur in the direction of such change; secondly, by transmission of modifications acquired by the rats in the course of training."

"It seems to me very improbable that the first process, selection, can have played any appreciable part in producing the change of constitution and still more improbable that selection can have been the main or the sole process."

"It begins to look to me as though Lamarckian transmission were a real process in nature and I submit for criticism the proposition, if continuance of the experiment, combining training with strongly adverse selection should result in steadily increasing facility, the reality of Lamarckian transmission will have been demonstrated."

Now it so happened that I was sufficiently misguided as to consent to review McDOUGALL's second report, and while doing this I became intrigued, puzzled, worried, impressed, and shortly nothing would satisfy me until I had built a tank, collected some rats and had chosen my career—that of bathroom attendant to a rat colony—a pleasant enough billet even though the hours are long and the vacations few. The not unreasonable conclusions to which McDOUGALL is arriving as a result of careful experimentation possess such importance that they cannot be washed away by a flow of words. His attitude, save perhaps when he seems to assume that biologists generally must necessarily be hostile to his views, commands respect and makes it most necessary to examine with the greatest fairness and care the strong *prima facie* case that he has made out. He himself, as I myself know from many conversations with him, would be the last to deny that it is reasonable to suspend judgment for a while until certain legitimate criticisms have been answered.

It is the case, for instance, that since McDOUGALL's records have never

been published in full it has been quite impossible for anyone to glean from them whether or not there is ground for thinking that capacity for learning is inherited in some particular fashion. It is doubtful indeed that the plan of experimentation adopted by McDOUGALL could adequately examine this matter. If capacity for learning were inherited, then of course any process of change would have been greatly accelerated if selection had unwittingly taken place. Secondly, as noted by SONNEBORN, the intensity of the shock varied considerably and was not measured. McDOUGALL found that rats subjected to light shocks took nearly three times as long to learn as when the shocks were relatively heavy. It follows therefore that a steady and progressive increase in the shock intensity could account for the results obtained. SONNEBORN further points out that if the method of choosing two rats "at random" from a litter was to take the first two available in the cage this could tend to the selection of rats of a peculiar psychological disposition. Then again it is found that in one of his experiments, broken off after 4 generations, McDOUGALL found that the times needed for training actually increased generation after generation. Various other criticisms can be made, but debate alone can not satisfy: actual experimentation is demanded. Commonly, it is impossible accurately to repeat the experiment of another owing to differences in the genetic constitutions of different animal stocks and to differences in environments, but at least it is possible to devise an experiment to yield results that can profitably be compared with those of a previous experiment conducted elsewhere by another investigator. This I have tried to do.

Perhaps I am ill advised to communicate to a meeting of this kind a story that must necessarily be so incomplete. I have arrived at no conclusions other than that the inherent difficulties of such experimentation are varied and profound. Perhaps caution should have determined that I should have waited for 10 or 20 years when I might have exhausted the experimental approach to the problems that are involved and then announced that the riddle was solved or beyond solution by me. But I have gone far enough to realize very clearly that I need the advice of many colleagues if I am to continue the work hopefully and really intelligently. You will understand me when I say that there can never be the same joy in repeating someone else's work, however important this may be, as in prosecuting one's own. There is no real lasting satisfaction in proving that someone else is right or wrong. Yet this motive has been the mainspring of much endeavor.

In planning this work I decided that as far as possible I would imitate McDOUGALL, but that I would so arrange matters that the data that emerged could be expected to illuminate the action of any genetic factors that might

be operating. I built a tank that as far as I was able to judge was a fair copy of the latest edition of McDOUGALL's. McDOUGALL has visited me and agrees that save in one respect my tank is to all intents and purposes similar to his own. The difference lies in the fact that the intensity of the light on the illuminated side is greater and more widely spread than in his tank. His light is situated beyond the platform; mine (5 candle power) is in the roof of the lateral passage and illuminates both the platform and the whole of the surface of the water on that side.

My electric contraption differs from his. He uses a secondary coil. My supply is taken from the main which is 230 volts A.C. The current passes through a neon lamp (0.5 watt) to be reduced to 0.002 amp. In addition, an anode resistance, which usually is cut out, of 500,000 ohms is inserted in order that I can, when occasion requires it, temper the shock to the weakling. The rat with part of his body in the water and part on the platform closes the circuit. When he is entirely on the platform and moving on along the tunnel, the platform tips and the circuit is broken. Though I have no exact knowledge of the quantity of electricity that passes through the rat, I am allowed to think that it is fairly constant. It should be remarked, however, that special manipulation of the switch is required in order to accommodate, on the one hand, the rat that rushes the platform and, on the other, the rat that is so feeble that it takes a relatively long time to crawl out of the water. I recognize that this system is far from satisfactory since by it I cannot hope to attain absolute uniformity. However, it works, and moreover I cannot afford to get an equipment such as is regarded by KNIGHT DUNLAP as the most desirable. He found that to obtain exactly the same current in each application and the minimum current necessary to evoke the response desired, it was necessary to employ higher voltage and higher external resistance than were available to me. He standardizes his shock at 0.00015 amp., and this has no deleterious effect upon the rat. The shock used by me, like that used by McDOUGALL, is such as will tetanize a rat which grips the platform with its teeth and will cause paralysis of the hind limbs, bladder and rectum in such as hold on to the platform for more than 3 seconds. This refers to the rats as a group; it is not necessarily true of any given individual, for rat differs from rat in the most remarkable fashion: a shock that merely tickles one rat will tetanize another, and danger attends every trial in the case of the rats during the first week of their training; for at this time they are younger and smaller. Even though one standardized the shock, one could not hope to standardize the rats, so far as I can see. Therefore in the table that I shall show, the number of shocks is not an exact measure of the total amount of current that has passed through the

rat, since the time during which the circuit is closed by the rat varies from rat to rat and from trial to trial.

The rats I have used are, like McDOUGALL's, Wistar derivatives, taken from the Institutional rat colony in which 1,000 breeders are regularly maintained and recorded. I began by taking the rats for training at 4 weeks old but I was forced to relinquish this practice for the reason that at this age my rats, unlike McDOUGALL's apparently and possibly because of poor coat development, could not endure 6 immersions in water at 60° to 62°. After 2 or 3 trials the majority became water-logged and exhausted and were then not in a fit condition to make any considered choice, and moreover quite slight shocks (that is, of minimum duration) either killed or crippled. I decided to begin training at 7 weeks. On the day before training commenced, the individuals of the litter, previously weaned and thereafter kept away from their parents, were taken one by one from the cage between 10 and 12 midday and earmarked with serial numbers, No. 1 male being the first male to be taken, No. 1 female the first female to come to hand.

McDOUGALL tested and discusses the relative performances of generations. From the litters provided by one generation he took some individuals from each to be tested in their turn and to become the parents of the next generation. The performances of offspring and parent respectively are not given. The plan adopted by myself was to take twelve pairs of pedigreed rats from the Institutional rat colony and to train these, to take the pair with the lowest scores, the pair with the next lowest scores and so on, and thereafter to train every individual produced by these pairs, to take from among the individuals of first litters the pair with the best records, or with the worst records, and to continue this practice generation after generation. My methods will become clearer as the story unfolds.

The original twelve pairs of rats were of exactly the same age and were taken straight from the rat colony when 3 weeks old. They were from 4 different litters out of parents closely related to each other. Their training commenced when they were 7 weeks old. They registered the following scores (one male and one female were paralyzed and discarded):

Pair	1	2	3	4	5	6	7	8	9	10	11	
♂ ♂	19	44	58	67	72	73	73	76	78	84	95	errors
♀ ♀	69	75	78	81	82	86	93	97	101	104	107	errors

An average of 77.8 errors.

Their training being completed, certain pairs were placed in separate cages to become the progenitors of the following lines:

Line A	*Line B*	*Line C*	*Line G*	*Line J*	*Line K*
♂ 1 and ♀ 1	♂ 2 and ♀ 2	♂ 3 and ♀ 3	♂ 7 and ♀ 7	♂ 10 and ♀ 10	♂ 11 and ♀ 11

Line J has not produced a single litter. Line K has produced 1. The rest when compared with the general colony stock not exposed to the experimental procedures involved have produced relatively few litters. But there are in the colony plentiful instances of low reproductivity, and I cannot be certain that the training is responsible for the infertility that characterized this first generation of the experiment. On the other hand I am not yet sure that it will not be shown, as the experiment proceeds, that a considerable number of shocks and a low reproductive rate are associated. This remains an impression and nothing more for the present, but it is certainly the case that as yet my task is being complicated by the fact that on the whole my slowest learners are the poorest reproducers. If this proves to be a verifiable fact it will throw considerable light upon the question as to how it is that one generation can give better scores than its predecessor.

As time passed litters appeared, to be trained in their turn, and soon it became very obvious that the scores of the individuals of this generation were to be infinitely better than those of their parents. When 39 individuals had been trained the best among them had a score of 0 and the worst one of 80, while the average of the whole was 23.8. This drop from an average score of 78 to one of 24 in one step was most disturbing and demanded prompt explanation. Naturally I jumped to the conclusion that it was my own capacity for learning and not that of the rats that had been weighed and not found wanting. So I obtained, over a limited period of time, a total of 100 more colony rats, 50 males and 50 females, and put them through the tank. The results I obtained were startling. The best performer, as was the case in the F_1, made not a single error. Six times a day for 30 days in succession this rat was dropped into the tank and on each of the 180 occasions it emerged from the dim tunnel. It invariably avoided the light and therefore the shock. Here then was my first really serious complication. Was I dealing with a stock which, in spite of a hundred generations of inbreeding, included within it individuals differing from the majority in that they were photophobic? Now it so happened that I had decided to put all the rats 6 times through the tank with the lights working but with the shock current cut out before the real training began. I did this in order to accustom the rats to the water, the lighted channel alternately right and left, the platform and the tunnel and the handling. Referring to this rat's "pre-shock" record I found that it had been twice to the light at the beginning. The F_1 rat with a score of 0 had been to the light 4 times. In the case of these rats it seemed to be true that, though they went to the light to begin with, when once they had become accustomed to the water and to the intricacies of the tank they thereafter always chose the dim side.

The worst record scored by an individual of this 100, known to me as the Repeat P_1 (RP_1) was 81 and the average of the whole was 18.09, a figure very near that of the so-called F_1 group. (These symbols, P and F,

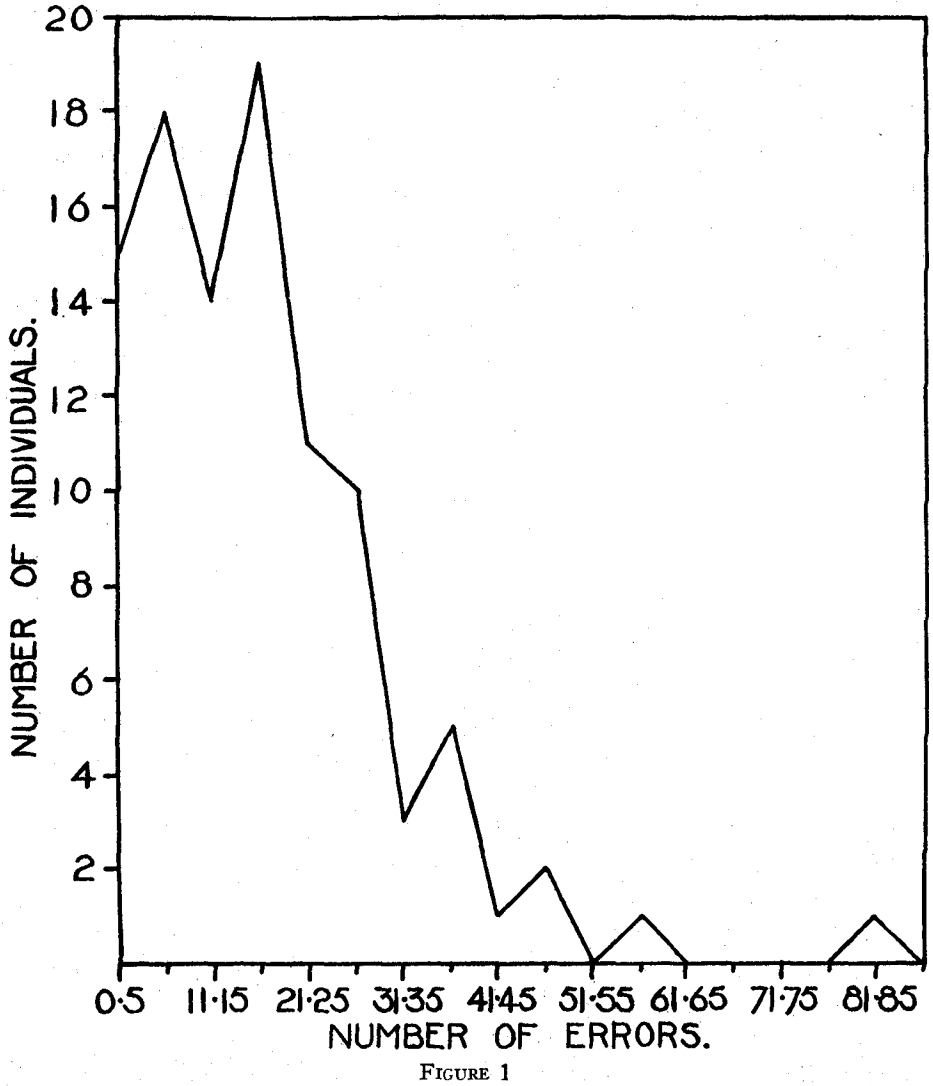

FIGURE 1

have no genetical significance of course but they came readily to my tongue.) I show you a distribution of errors and individuals in RP_1. It is extraordinary and surely significant of something though of what I confess I do not know.

The great difference between the average scores of my original P_1 and

of the Repeat P_1 demanded an explanation. I was quite willing to think that improvements in technique were possibly responsible, since unquestionably many small improvements had become incorporated as time passed. But I was not, and still am not, sure that this is the case, particularly in view of the fact that recently I have been getting scores even higher than those of the original P_1. There is this to be said. When I got the original P_1 individuals from the colony, rats of the right age were not plentiful and there was strong competition for such as there were. I certainly received rats that were not wanted for other purposes by my colleagues. But I only borrowed the Repeat P_1 and this at a time when rats were plentiful. I then got the best, according to the judgment of those whose first charge is to select among young stock for future breeders. This may seem to be a matter of no importance, but I am not inclined to disregard it for on the whole it seems that such rats as are physically the most vigorous, that is, such as would be retained as breeders, put up the better scores.

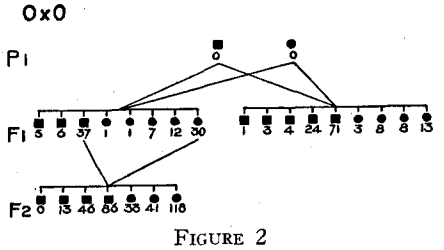

FIGURE 2

I now possessed two individuals each with a score of 0. Fortunately one was a male, the other a female. I mated these to found a separate line, for it seemed to me that if I had photophobia in my stock I must demonstrate the relation of this to rapidity of learning. There was no reason for not assuming that two factors, photophobia and speed of learning, were involved in the experiment and that a photophobic rat might still be a stupid rat. If, perchance, a photophobic rat is a rat of relatively poor constitution then I might find myself first selecting for photophobia and then later against it. Furthermore, a complication might arise if photophobia proved to be genetically simple and speed of learning polygenic and greatly affected by environmental agencies. Again, since McDOUGALL's light is less intense than mine, it might well be that in his case photophobics are not identified.

These two rats have so far produced 2 litters which have been trained. The scores of their offspring were as follows: The best was 1, the worst 71, and the average 13.7. From the first litter I took the two best and the two worst males and females and mated them, best to best and worst to worst. So far only the latter couple have given me a litter which has been

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trained. The best record among these generations was 0, the worst 118, and the average 48.1. The male with 0 never went to the light, not even during his pre-shock career. I shall mate him to his grandmother. It is too early for me to discuss this particular aspect of the problem further.

I have examined the pre-shock career of my trained rats in order to see whether or not the number of times a rat went to the light and to the right or left had any relation to its subsequent record.

The following table gives the relevant figures:

	To A				*To Light*		
Times	*No. of Animals*	*No. Expected*	*Average No. of Errors*	*Times*	*No. of Animals*	*No. Expected*	*Average No. of Errors*
0	35	5.47	34.66	0	7	5.47	20.71
1	40	32.81	19.88	1	30	32.81	21.67
2	51	82.03	27.14	2	63	82.03	21.08
3	59	109.38	23.41	3	140	109 38	26.65
4	72	82.03	19.82	4	76	82.03	20.49
5	53	32.81	18.85	5	31	32.81	19.55
6	40	5.47	22.25	6	3	5.47	24.00

It is clear that the way a rat habitually goes during the pre-shock period is not determined by chance. Many of the rats exhibit the tendency to be strongly right- or left-handed. The slight asymmetry of distribution shows that there are rather more right-handed than left-handed rats. It would seem, perhaps, that the strongly left-handed rats learn somewhat less quickly, but, of course, greater numbers are required before this point can be settled.

The figures for the number of times the rats go to the light during the pre-shock period have to be related to those of right- and left-handedness. For the first of the six trials the light is at the right-hand and thereafter is alternated from side to side. The two classifications are not independent as is shown in the following table:

A rat going to the right 0 times will go to the light 3 times
A rat going to the right 1 time will go to the light 2 or 4 times
A rat going to the right 2 times will go to the light 1, 3 or 5 times
A rat going to the right 3 times will go to the light 0, 2, 4 or 6 times
A rat going to the right 4 times will go to the light 1, 3 or 5 times
A rat going to the right 5 times will go to the light 2 or 4 times
A rat going to the right 6 times will go to the light 3 times

The fact that there is a large excess of totally right- or left-handed rats necessarily means that there must be an excess of rats that go to the light 3 times. This is the case. The completely left-handed rats make lower scores: this is reflected in the higher scores made by rats that went 3 times to the light. It will be noted, however, that the dependence of the light classification on the direction classification does not affect the symmetry of the

former, and, actually, the light distribution is symmetrical. There is no reason to suppose from the figures given that the rats tend to avoid the light or *vice versa*. This makes the suggestion of photophobia very unlikely. It is clear that right- and left-handedness are much more important in relation to the score made by a rat than is reaction to light.

Now let me turn to such results as I have so far obtained and consider them as a whole. The following table presents them in a concise form:

Generation	*No. of Animals*	*Mean*	*SD*	*SE*	*Coefficient of Variation*
P_1	22	77.8	19.7	4.20	25.3
P_1	10	71.1	24 6	7.77	34.5
F_1	39	23.9	18.8	3.01	78.7
F_2	77	20.4	15.7	1.78	76.7
F_3	76	27.9	81.3	9.33	291.6
F_4	15	54.9	37.3	9.63	68.0
RP_1	100	18.1	13.1	1.31	72.4

I confess I do not know what to make of these figures. The large coefficient of variation in F_3 and F_4 is due to the appallingly bad scores of one litter in each, and even in these some individuals have exceptionally good scores. Apart from the F_3 the variability of all the generations is slight. If I explain the drop from P_1 to F_1 as a reflection of refinements in technique how am I to explain the worsening seen in F_2 — F_4? It cannot be technique when some individuals in a litter give me scores of 4 while others give 140. I have tried to think that a seasonal influence is operating, but I cannot satisfy myself that this is so.

My numbers are not yet sufficient for genetical treatment, and all that I can hope to do for the present is to explore such as I have in order to gain ideas that later can guide experimentation.

As I have said, the P_1 animals with the higher scores have given the fewest offspring, and so it is that the parents as a group are more rapid learners than are the offspring as a group. The mean of 63 parents (that is, of the parents of each of all the litters) is 13.1; that of 168 offspring is 26.9. There is no help here.

I then divided the rats according to their scores into 6 classes as follows. The classification is an arbitrary one, being based on my own impressions that there were significant differences between rats falling into the different groups and that the divisions were roughly equal.

Score		*Class*
0— 5	=	1
6—10	=	2
11—16	=	3
17—30	=	4
31—50	=	5
51+	=	6

I considered the performances of offspring in relation to those of the parents:

Matings	*Classes Of Offspring*					
	1	2	3	4	5	6
1 × 1	7	4	2	2	1	1
1 × 2	5	3	2	5	4	1
1 × 3	1	6	1	0	1	0
1 × 4	1	2	0	1	4	4
2 × 4	2	5	4	1	0	0
3 × 3	0	0	3	11	5	2
4 × 4	4	6	6	14	9	6
4 × 5	1	1	1	5	5	3
6 × 6	0	0	1	0	3	3

It is seen that I am getting more high scorers out of low by low than low scorers out of high by high.

The mid-parent-offspring correlation is 0.38 ± 0.071.

The fraternal correlations (only litter mates are regarded as brothers and sisters) are as follows:

Brother: brother	0.31
Sister: sister	0.54
Brother: sister	0.33

It is seen that sisters are more like each other than brothers are like each other, or than brothers are like sisters. Perhaps sex-linked factors would possibly account for the differences observed.

In an attempt to examine the question as to whether selection was playing a rôle in McDOUGALL's experiment, in view of the fact that he was taking two individuals from a litter and leaving the rest, I compared the performances of my own number ones with those of the rest. (The individual first taken from the cage becomes number 1.) There is no difference between them.

	Total Animals	*Total Errors*	*Average*
No. 1	114	2681	23.5
Rest	201	4814	24.0

This is as far as I have traveled and already I have a feeling that I have lost my way. The reason for my doubts is that the behavior of different rats in the tank is so remarkably different. During the past two years, again and again I have thought that I could make some generalization or other and again and again I have been forced to jettison it. After the rats have been through the pre-shock stage, it is possible to group them roughly into different behavior classes—those that rush the platform and those that float—in other words those that seem to regard the shock as the lesser of two evils and those that hate the shock worse than the water. Rats of these

classes are not rapid learners. Both continue to make mistakes until, without any warning, they quite suddenly complete the task. They belong to classes 4 to 6 (17 to 51+ errors). So also do the "hopeless" rats who paddle feebly round the central compartment of the tank, who do not squeak and who have the greatest difficulty in hoisting themselves on to the platform when they decide to crawl out of the water. The best rat of all is the "eager" little fellow who dislikes both water and shock but fears neither. It is he who actively explores both lateral divisions before leaving the tank by one of the two routes. When he gets his first shock he comes through like a ball off a cricket bat. The next time he touches a platform, he screams although he is on the safe side. But he recognizes either at once or within one or two days that light is associated with pain and darkness with no pain, and he leaves his task with a score of 1 to 5 or, in exceptional cases, continues to make one or two a day to give a total score of about ten. I am of the opinion that when I have seen a rat in the water on his first or second day of training I can foretell his score fairly accurately. I have amused myself by so doing. I have seldom been grossly wrong.

McDOUGALL discarded runts and the obviously weakly members of litters. I trained every rat in every litter. I found the runt to be, in every case, better than the average of the litter to which it belonged. But the obviously weakly individuals that cropped up occasionally either gave high scores or else were paralyzed and killed. They have great difficulty in getting out of the water and hold on to the platform too firmly and too long.

McDOUGALL is of the opinion that the behavior in the tank of rats of trained stock distinctly differs from that of untrained or only slightly trained stock and that the differences can be best expressed by saying that the behavior of the rats of highly trained stock is markedly more tentative, hesitating, cautious or exploratory than that of the other rats. In his experiences the rat of untrained stock, in the early part of its training, loiters very little, hesitates very little, and rushes at a gangway; whereas the rats of the trained stock loiter, hesitate, oscillate between the two lateral passages and frequently change their minds when about to leave by a particular gangway. Even when they approach closely either the dim or the bright gangway they may turn back from it and not infrequently they approach cautiously the bright gangway, touch it lightly with nose or paw, receive a slight shock and then retreat. I agree that these two types of behavior are to be recognized but I can not agree that in this way trained can be distinguished from untrained stocks, for if a hundred rats are taken straight from the colony and trained, it is found that both types of behavior are exhibited and are equally common.

I think that I must try more accurately to classify the rats according to their behavior for I have been greatly impressed by the fact that in one and the same litter one can get two or more different behaviors exhibited and that those individuals who behave alike have scores that are very similar. On the other hand one can get litters of which all the individuals exhibit

PEDIGREES OF LINES A, B, C, G, AND K

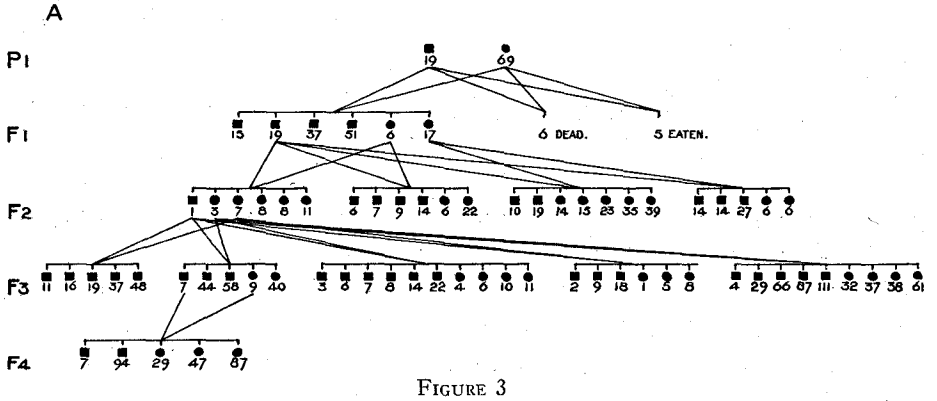

FIGURE 3

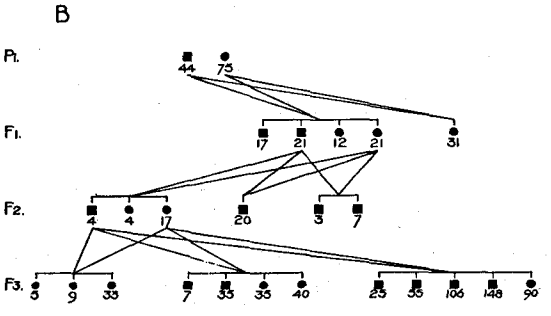

FIGURE 4

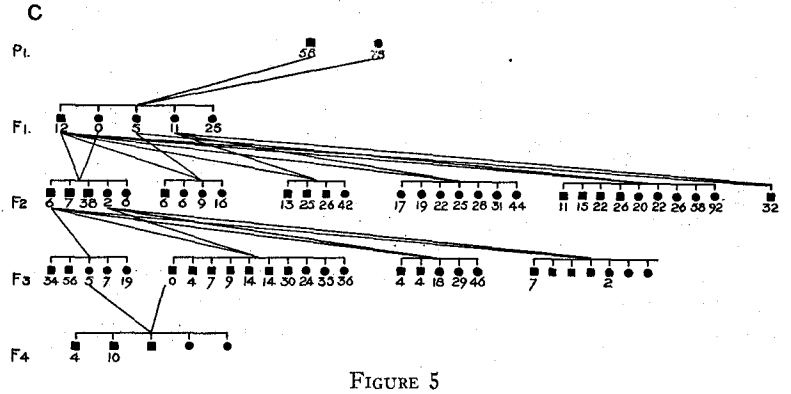

FIGURE 5

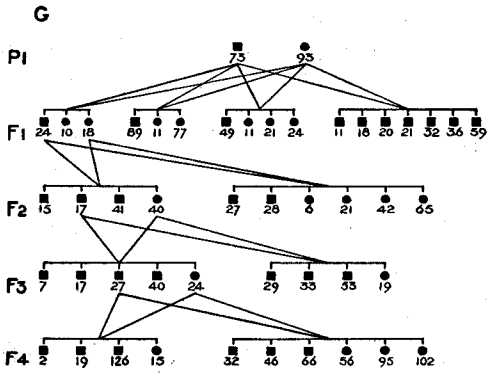

FIGURE 6

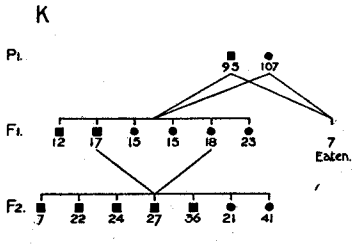

FIGURE 7

the same habit in the water, all rushing, all floating, all hopeless or all eager, and then it has been possible to identify the litter to which an individual belonged by reference to the behavior in the tank. It may well be that as this experiment proceeds I shall find myself studying the mode of inheritance not of capacity for learning but of a peculiar behavior pattern. For indeed it would seem to be the case that there are rats that persistently leave the tank by one route, rats that turn to right or left indiscriminately; rats that tend to avoid the light, rats that do not mind it; rats that are quick to associate light and shock, and rats that are slow. It must be my task to examine the possible genetic bases of these attributes which certainly distinguish rat from rat.

At the end of my story, as at the beginning, I am very aware that it is hopelessly incomplete. When I began this experiment I proposed to examine McDOUGALL'S conclusions. Now, my sole concern is to formulate conclusions of my own. And this I cannot do. Perhaps I should have remained silent but maybe I am wise in thus imitating our voluntary hospitals which habitually parade their poverty and plead for contributions.

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