A REPETITION OF McDOUGALL'S LAMARCKIAN EXPERIMENT

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(With Eleven Text-figures and Five Pedigree Charts)

CONTENTS

I. INTRODUCTION

PROFESSOR WILLIAM McDOUGALL has been conducting, since 1920, an experiment devised to examine the validity of the Lamarckian hypothesis, and has obtained results, as revealed in the three reports that have appeared (McDougall, 1927, 1930; Rhine and McDougall, 1933), that are impressive and seem to warrant the interpretation presented. It is difficult for the critic to find flaws in the techniques that McDougall has so patiently developed, and it is impossible not to be impressed by the scientific quality of the reports themselves.

Reading the earlier reports, I found it impossible to overthrow McDougall's conclusions by argument. Yet, though I could not deny that McDougall was possibly justified in so regarding them, I could not bring myself to accept the results he had obtained as satisfying evidence of the reality of Lamarckian transmission. I formed the opinion that his conclusions would be shown, by further experimentation, to be unwarranted, for I had become more and more critical of McDougall's use of controls, of his neglect to maintain pedigrees and individual records, and of his method of presenting his data. This being so, there was nothing left for me to do save to repeat the experiment myself.

McDougall trained rats by a standardised procedure to avoid the brightly lit and electrified route out of a water tank. The rat is lowered by hand gently into the middle blind compartment of the tank out of which there are two lateral ways leading to platforms, one of these, alternately on the right and left, being illuminated and so wired that the rat, stepping on to it out of the water, receives an electric shock. The tank is such that the rat has the choice of leaving the water either by way of the dim platform and thence out of the tank without receiving a shock, or else by way of the lit platform and getting a shock.

In order to accustom the rat to the conditions of the experiment, each is given 6 runs in the tank with the light alternating but without shock as a preliminary to the actual training period, during which each rat is placed in the tank 6 times daily. On the first of these occasions the light and shock are on the right of the rat as it swims down the middle blind compartment, on the second they are on the left, on the next they are on the right, and so on, and this practice is continued until the rat has mastered the task; that is, until it has left the tank 12 times in succession by the dim, unshocked route. The training is completed when the rat "learns to discriminate between the bright and the dim gangway (in anthropomorphic terms it learns to accept the bright light as a signal warning it of a shock)".

Up to the time of the third report 34 successive generations of rats of the tank-trained stock, and a number of controls (rats whose ancestors were not so trained) have been trained, and the facility in learning has been measured by the number of errors made (shocks received) by the rat before it learns to avoid the light and shock and always to choose the dim, unshocked exit. The main conclusions to which McDougall has arrived are: (1) with the passing of the generations the average number of errors per rat made by individuals of the tank-trained stock has decreased gently and progressively; (2) the average number of errors per rat made by the individuals of the tank-trained stock has become much less than that provided by the individuals used as controls; (3) rats of the trained and control stocks respectively are to be distinguished one from the other by marked differences in the behaviour they exhibit during actual training whilst in the tank; and (4) during the preliminary 6 runs in the tank with alternating light and no shock, individuals of the two stocks are to be distinguished one from the other by their behaviour in relation to the light.

II. APPARATUS AND METHODS

In order that I might be in a position to examine these conclusions I have copied as far as possible McDougall's apparatus and methods. Since he had found that modifications and improvements in the construction of his tank had seriously influenced the scores of his rats, I tried to make a tank that, as far as I could judge from the descriptions given, was a fair copy of his latest edition. However, having seen it, McDougall tells me that our tanks do differ, and this has to be remembered when our results are compared.

My tank (Fig. 1), roughly square in outline with the corners of one side rounded off, is of sheet metal and measures 28½ in. across, and 23½ in. from the middle of the straight side to the middle of the curved one. It is 15 in. deep and is divided into three compartments by two incomplete partitions. The lateral compartments are 10½ in. wide, and the middle one 7½ in. The partitions are 14½ in. long, and their free ends are curled outwards upon themselves in order that the rat may not be able to grip the edge. The depth of the water (kept at 60–62° C.) is 9 in. In each of the lateral compartments on the straight wall of the tank there is a square hole just above the water level, and into it there juts an enclosed rocking platform. The rat, in leaving the water, clutches and tilts this platform, and in so doing completes an electric circuit. As the rat moves along the platform this returns to the level and the current is broken. In the movable roof of each lateral compartment there is a 5 candle-power electric light which is so shaded as to illuminate brightly the platform and also the whole of the lateral passage, so that the rat, about to leave the central blind compartment, can see which side is illuminated and which is dim.

My electric supply is taken from the main, 230 volts A.C., and passes through a neon lamp of 0·5 watt to be reduced to 0·002 amp. In view of the fact that McDougall had found that the number of errors made by the rats was fewer with a strong than with a weak shock, I wished particularly to ensure that my shock should be identical with his. But I could not do this, for he measures the strength of the current by its effect upon the rats: "the current is strong enough to tetanise the muscles of the rat's legs and hold him fast in as nearly as possible 50 per cent. of all contacts made by any batch of rats." He controls the duration of the shock by counting three slowly before breaking the current and releasing the rat. I tried by mechanical means to standardise

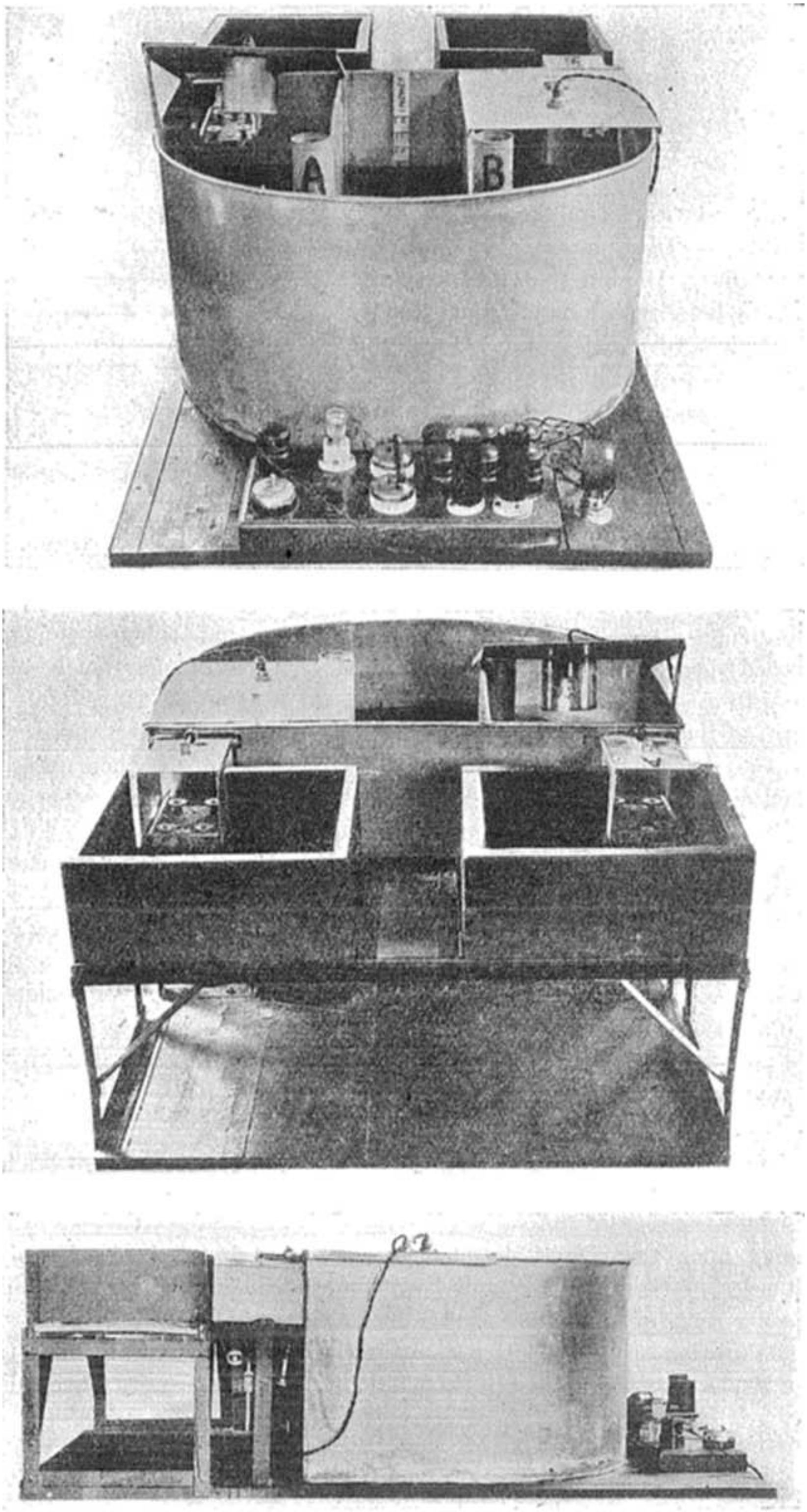


Fig. 1

the duration and at the same time preserve the strength of the shock, but after many trials and failures I decided that though I standardised the strength and duration of the shock, I could not hope to standardise the rats, for not only do individuals differ among themselves in respect of their reactions (a shock that merely tickles one being sufficient to tetanise another), but the effect of the shock is determined very largely by the age and size of the rat, and especially by the particular way in which it makes contact with the platform. My shock is sufficient to "fix" the rat that grips the platform with his hands. I hold the rat there for 3 sec. and then cut off the current and so release the rat. But should a rat bump the platform with its nose, and particularly should it grip the platform with its teeth, unless the current is cut off immediately the rat is paralysed and usually does not recover. The strength of the shock is constant, but the duration varies from rat to rat and from time to time. By manipulating a switch I accommodate the rat that rushes the platform, the rat that bumps the platform with its nose or grips it with its teeth, and the rat that is so feeble that it takes a relatively long time to hoist itself out of the water. Agar (1935), who is also repeating this experiment, and whose first report has appeared since the first draft of this paper was written, has devised mechanical means of controlling both the intensity and the duration of the shock, and has eliminated the personal element. This, of course, is much to be desired, but unfortunately I cannot adopt his plan at this stage of my own experimentation. I must remain content with the knowledge that I myself have been trained along with the rats during the last 5 years, and that, as far as is possible, my manipulation of the switch has become automatic and standardised.

Obviously, if a considerable number of rats were electrocuted, a selective mortality might be operating and affecting the end-result of the experiment. But such injury only occurs during the very early days of training, and so it is most improbable that those which are hurt are only such as would have made high scores or low scores. McDougall has lost less than 2 per cent. from this cause, and I have lost only 8 rats among 2000+, and these all during the earlier years of the experiment; and so, in discussing our results, death from electrocution can safely be disregarded.

The tank itself rests on a table of such a height that the observer, seated, can, by looking over the lip of the tank, see the rat in the middle compartment and later swimming along the lateral passage toward the exit. The experiment is carried out in a darkened room: the only lights are those above the lateral passages in the tank and another on the switchboard.

When the litter is removed from its mother, each rat is ear-marked: the first male to be withdrawn from the cage becomes male No. 1 of that litter, the first female, female No. 1, and so on. At one time I thought that perhaps the rat that thus became No. 1 differed from the rest, that it was the first to be removed because of some peculiarity that was associated with quickness in learning. But examination of my own figures has shown me that such a suggestion is unsound, and so I have no comment to make upon McDougall's method of taking certain individuals from a litter at random.

In the beginning I adopted McDougall's plan and began the rat's training when it was 4 weeks old, but I was forced to the conclusion that my rats of this age could not tolerate 6 immersions in rapid succession. Moreover, with the shock that I was using, danger attended every trial. It may be that in Edinburgh the rat and its coat are not sufficiently well grown at 4 weeks. I decided to postpone the commencement of training until the rats reached 8 weeks of age. This difference in age between my rats and those of McDougall and of Agar at the beginning of training must be remembered when a comparison of our results is made. I have no reason to think that this makes any real difference to the end-result. I have trained individuals of small litters at 4 weeks and have compared their records with those of others trained at 8 weeks, and it would seem that the delay is attended by a somewhat higher average score in the case of my rats. In general, it appears that the smaller the rat the greater is its sensitiveness to the shock, and that the more severe the shock and the greater its duration, the lower is the score. In order to facilitate the rats' emergence from the water a submerged wire ladder is placed in front of each exit during the first 50 runs of the actual training period, and thereafter removed. The result of its removal is to increase the severity of the shock, for with the ladder in position, the rat is able to spring from it and pass rapidly over the electrified platform. In the absence of the ladder the rat must pull itself out of the water by gripping the platform itself. It was upon McDougall's advice that I introduced these ladders. He pointed out that in his tank the rat could rest upon a platform in front of the exit and take time to think things out. It could refuse to leave the tank by that route and re-enter the water and make its way to the alternative exit. But I have found it convenient to have movable ladders, for, after 50 runs or so, the rat that rests upon the ladder conveys no suggestion to me that it is considering whether or not to leave the tank by that particular exit. It simply sits there, apparently very content to have removed most of itself from the water.

In the case of the earlier generations of my rats I adopted McDougall's plan of giving each rat 6 preliminary runs in the tank with the light alternating but without shock. McDougall had noted that "while the members of most litters go pretty evenly to both *A* and *B* (the right and left exits) before training, all the members of some litters and some members of others showed a strong bias to one side or to the other. It seemed that what might be called a right-handed or a left-handed tendency, or a tendency toward or away from the light, was innate in some strains, quite apart from any training of their ancestry." McDougall estimates that of his rats about 50 per cent. of all leave by the right or left platform irregularly, and about equally often; about 45 per cent. acquire at an early stage the habit of always leaving the tank by one and the same route and continue in this habit up to the time of learning; and that less than 5 per cent. at some stage of their training process, after turning right or left at random, acquire the habit of turning always to the illuminated side. These estimates relate to the actual training period when light and shock are alternating.

In view of these observations it seemed to me necessary to examine each rat before the light was introduced, for evidence of this right-hand and left-hand turning habit, and again with the light alternating but without shock, for evidence of the habit of going towards or away from the light as light. So each rat of the later generations has been given 50 runs in the tank with the light equal on both sides and without shock. The roofs of the lateral passages are removed and the room light immediately central to and above the tank is switched on. Thereafter, with the room darkened the light in the tank is alternated but the current is cut out for another 50 runs. These two phases of the preliminary training being completed, the third phase (alternating light plus shock) is then commenced. It is just as well that I did adopt this plan, for Agar reports that the great majority of his rats have shown a preference for the right-hand passage, and further, that they have a slight but unmistakable initial bias to the light. Again, these observations refer to the actual training period. It is to be noted that Agar derives his conclusions relating to the behaviour of his rats in respect of right- and left-handedness and of avoidance or otherwise of the light from figures provided during the actual training period when the light is associated with shock. It seems to me now, as it did when first I adopted this plan, that in any examination of handedness the experimentation must not be complicated by the presence of an alternating light, and especially by a combination of light and shock, and that in any examination of a bias to the light, this must not be associated with any other factor.

Each day and every day, for as long as is necessary, each rat is given 6 runs in the tank, one immediately after another. Agar's plan is somewhat different: each rat of a batch is placed in turn in the water, and the whole batch goes through the tank once before the first is placed therein again, so that the interval between two trials in the case of one and the same rat is much longer with Agar than with myself. This is not an important difference really, for my rats are twice as old as his when their training begins and therefore much more able to endure 6 immersions and exits in rapid succession. I adopted this plan because I found that by it I could recognise the behaviour pattern of any given rat much more clearly. Through time my assistant at the other end of the tank has developed an unvarying routine method of holding a rat and lowering it into the water at the far end of the middle blind compartment. But it really is of no consequence which way the rat is placed therein, for each rat, after it has completed its 100 preliminary runs, invariably displays a behaviour pattern which comes to be characteristic of that particular rat before leaving the central compartment to swim towards an exit. I agree with McDougall that after two or more rats have been in actual training for a fortnight or so it is possible to put them into the tank synchronously for the reason that the time spent in the middle compartment before moving towards an exit can differ markedly from rat to rat. If rats differing one from the other in respect of this habit are placed in the tank together they come out from the central passage separately and preserve the same order of leaving. I am satisfied that in the case of rats which after weeks of training have still not learnt, this procedure in no way disturbs each rat's demonstrated preference for one or the other exit. Agar regards the practice of having several rats in the tank at the same time as unsafe, since the behaviour of one rat might influence that of another. I use it only in the case of rats which after weeks of training show no signs of learning, and as soon as I recognise that one of the rats concerned is about to learn I run it through the tank alone. With this qualification I agree entirely with McDougall on this point.

Sooner or later, after a number of immersions and escapes, and after receiving a number of shocks (a number which, according to my own records, ranges from 0 to 307) every rat leaves the tank 12 times in succession by the dim unshocked exit. Unlike McDougall, who has encountered rats "that would rather drown than leave the tank", I have never had a rat that did not ultimately complete its 6 daily runs and finally leave 12 times in succession by the safe route. No rat can learn in a day: this is important, for experience has shown that a rat about to learn is much more likely to make a mistake on the first than on subsequent immersions of a day's training.

Though, for purposes of comparison with McDougall's figures, it is necessary to carry on with the training of a rat, no matter how slow, until it has finally learnt, I am quite sure that by increasing the severity of the shock or by blocking up the lateral passage with a sheet of glass or metal it is possible to reduce very considerably the time required by the rat to learn.

My rats, like McDougall's and Agar's, were Wistar derivatives. They had their origin in 2 pairs imported directly from the Wistar Institute by my colleague, Dr Wiesner. The experiment started with 124 rats: 24 destined to become the ancestors of the experimental line, and 100 to form the first generation of controls. The experimental group was derived from 4 litters out of full sisters by the same male, their father. The controls consisted partly of the litter mates of these, but mainly of youngsters out of females related to the mothers of the experimental group and by the same sire. A further 100 related controls were set aside to form a breeding stock in order to provide control batches to be trained contemporaneously with each successive generation of the experimental line. After having satisfied myself that any possibility of communicability between parent and offspring and between trained and untrained could be disregarded, which I did by keeping the stocks in separate animal houses and by fostering controls on experimentals and *vice versa*, I kept both lines in the same house under identical conditions of husbandry which have never varied. The records of these stocks, when compared with those of the Institutional rat colony, permit me to hold the view that no nutritional deficiency and no disease of environmental origin is in any way responsible for the results I have obtained. This statement gains meaning perhaps in view of the unconfirmed observation of Tsai and Maurer (1930) that a vitamin-B depletion results in an increase in the incidence of left-handedness in the rat. During the course of the experiment microphthalmia made its appearance in the later generations of the experimentals and controls. One whole litter of 5 animals in the experimental line, every one of which was either completely eyeless or else had one blind or exceedingly small eye, was not trained. Four other individuals in the experimental line, and 3 in the control, were discarded for the same reason. Three experimental animals with the signs of "middle ear disease" and one with only one hindleg were likewise discarded. 19 rats (7 experimental and 12 control) have died from causes unknown shortly after having completed their training and without having reproduced.

It is quite impracticable to mate up all the individuals of a litter and of a generation; yet it is essential that any suggestion of selection should be avoided. I soon became aware that I must limit the number of rats in each generation, and that I must ensure that the slow learners of one generation, as well as the quick learners, should make their contribution in the form of offspring in the next. Since those which learn quickly are available for mating long before those of the same litter which learn slowly, nothing would have been easier than to have allowed a generation to be provided solely by the "quicks" of the previous generation. An examination of my pedigrees will show that at the beginning of this experiment one generation was being produced by one or two pairs of "quicks" of the previous generation, and that later, though few individuals of one generation are represented by progeny in the next, these include rats with low, median and high scores.

Since it seemed to me that the most serious defects in McDougall's procedures have been the neglect to maintain the records of the performance of every individual, to record all his animals on pedigree charts, and to use systematically an adequate number of controls, I arranged my own experimentation in ways which would remove from my own results flaws due to such deficiencies. The plan I devised happens to be that which in his third report McDougall states to be the most desirable, and that which, in the cases of his own rats, is now about to be adopted.

III. RESULTS

McDougall presents his results in the form of a table showing the average number of errors per rat and the number of errors made by the best and by the worst rat in each generation (Table I). The table relates to generations 13–34 only, for at the time when the first 12 generations were being trained the procedures had not been standardised and several modifications of the tank had been made, so that the results obtained could not be harmonised with those yielded by the 13th and subsequent generations. McDougall is of the opinion that the average error of the 1st generation, had it been recorded, would not have been less than 150 and that in all probability it would have been about 165+. The table shows that the highest arithmetical means representing the average number of errors are to be found at the top of the table, and the lowest at the bottom. It may well be that the differences in the arithmetical means do possess a real significance, but as they stand I do not think that they can support the superstructure of hypothesis that has been built upon them. The figures given in the table for the average score and for the scores of the best and worst rat of each batch cannot be accepted as a true measure of the distribution of these errors. Obviously, the average for any batch must be unduly affected by variation in the number of rats with scores of 100–300. In order to obtain a figure for the controls which McDougall used, since he himself has shown that in respect of the quality which was being examined strain differs from strain, it is permissible to select from his records such batches of rats as were related to his tank-trained stocks, and to neglect the rest (some 31 animals) which belonged to various and unrelated stocks. The controls then consist of 140 animals which give an average score of 122+ + with a range of 14–352.

TABLE I

Generation	No. of rats	Average no. of errors per rat	No. of errors made by	
			Best rat	Worst rat
1	—	165+	—	—
13	23	68+	30 (1)	90+
14	10	80	42 (1)	102
15	10	70	39 (1)	96
16	5	73	39 (1)	88
17	11	46	9 (1)	147
18	22	62	15 (1)	142
19	15	47	12 (1)	100
21	34	37	9 (3)	74
22	16	36	6 (3)	89
23	26	25	3 (2)	71
24	14	33	10 (1)	62
25	18	38	14 (1)	78
26	23	43	9 (1)	75
27	32	54	12 (1)	96
28	17	44	13 (1)	90
29	20	50	18 (1)	105
30	11	20	3 (2)	56
31	38	40	3 (2)	100
32	42	17	3 (5)	70
33	24	33	2 (3)	73
34	34	36	2 (3)	88
Controls	140	122+ +	14	352

Although in my opinion this method of presentation cannot convey all that is of significance, it will be convenient for purposes of comparison if I give my results after the manner of McDougall. The actual figures for the experimental animals will be found in the pedigree charts and those for the controls in Table VII. In each generation the control and experimental batches are of the same age (within 7 days), and each control batch, consisting of more or less equal numbers of males and females, was trained contemporaneously with its own experimental batch and was derived from untrained litter mates of the animals used as controls in the preceding generation. The figures in black type indicate that the animal is a male.

In 1932 I presented a preliminary account of this experiment to the 6th International Congress of Genetics, and in so doing made a silly mistake that demands correction. I stated therein that the original 11 pairs of rats with which the experiment started (the remaining pair was electrocuted) gave an average score of 77·8 errors per rat. Actually, the figures I gave represented the average number of immersions and not the average number of shocks. I thought then that perhaps the length of time taken to learn might prove to be a more useful measure than the numbers of errors made. The average number of errors of generation I of the experimental line was 31·31, and not 77·8. It is seen that whereas McDougall's arithmetical means fell between 80 and 17, those of my experimental group range between 61·64 and 20·51, and those of the controls between 72·46 and 18·08. But whereas his highest

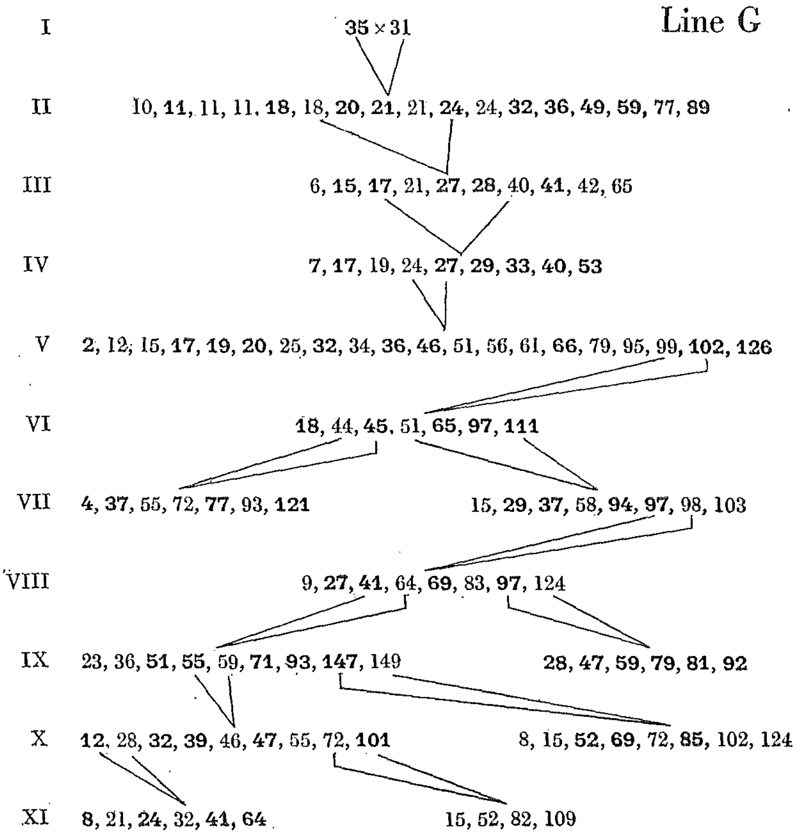
TABLE II

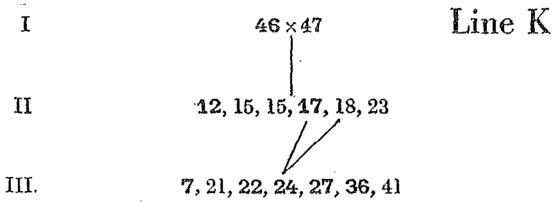
	Experimental				Control			
Generation	No. of animals	Average score	Median	Range	No. of animals	Average score	Median	Range
I	22	31·31	32	5– 47	100	18·08	16	0– 81
II	39	23·86	18	0– 89	50	42·74	19	0–194
III	80	20·51	17	1– 92	50	61·24	38	0–291
IV	133	33·91	19	0–244	50	34·66	19	1–179
V	88	30·27	20	0–126	50	50·04	36	5–275
VI	43	52·34	49	4–152	50	48·44	34	4–123
VII	52	59·30	53	4–172	50	59·80	45	8–194
VIII	51	55·17	53	0–124	50	21·70	16	2– 94
IX	67	61·64	55	0–181	50	32·50	16	2–162
X	60	43·85	39	0–152	50	69·12	58	4–201
XI	55	59·63	47	1–291	50	25·38	11	0–111
XII	65	50·38	42	0–283	50	23·22	13	2–101
XIII	133	41·36	23	0–212	50	34·90	19	0–121
XIV	160	52·75	36	0–307	50	52·86	26	4–291
XV	136	43·99	26	0–200	50	72·46	33	1–298
XVI	137	38·70	27	0–148	50	47·96	32	2–173
XVII	90	54·20	43	0–233	50	50·04	41	2–216
XVIII	38	22·23	15	0– 97	114	26·39	12	0–144
	1449	43·39	—	0–307	1014	40·50	—	0–298

mean was given by his 14th generation and his lowest by his 32nd, *this fact permitting him to conclude that the later generations displayed a greater facility in learning than did the earlier*, the figures that I have so far obtained do not arrange themselves in any such order. In the experimental line my highest figure is in the middle of the table and the lowest is that given by the 3rd generation, whilst among the controls the lowest figure is that given by the very first batch. There is no suggestion of a gentle progressive decrease in the arithmetical mean in the case of my rats. There has been no marked decline in the average number of errors made by the best rat of each generation, in fact there could not be since one rat in my second generation of experimental rats and another in the first generation of controls had scores of 0. Neither has there been any decline in the number of errors made by the worst rat. Since McDougall's figures are not given in full I cannot carry a comparison between them and my own any further. I incline to the view that now that he has adopted methods of pedigreeing and recording similar to or identical with mine it is not improbable that in the figures that he will obtain during the next five years, these being exposed to the same methods of examination as are mine, there will be revealed the explanation of the disagreement that now exists between our results.

My figures further show that as far as my rats are concerned the average number of errors per rat made by the trained stock is not essentially different from that of the control. The average score of 1445 experimental rats is 43·39, that of 1014 controls 40·50. The range of the experimental group is 0–307, that of the control 0–298. It is of interest to compare these figures with those of McDougall (generations 13–34): best 2, worst 147; and of Agar: trained stock best 0, worst 142; control best 5, worst 143. But Agar's figure for the worst cannot really be compared with the others for the reason that he gives such rats as take a long time to learn special training which reduces their total number of errors.

Since in respect of arithmetical mean and range the two stocks and the later and earlier generations respectively are essentially similar, it follows that my figures do not suggest that there has been any unsuspected change in the conditions of the experiment or in the constitution of the stock during the period of the investigation. It is impossible for McDougall to make such a statement for the reason that he has not used adequate controls. This being so he is not justified, in my opinion, in relating the results he has obtained to any particular cause. Had he used controls properly and had observed this increased facility only in the trained stock his case would have indeed been strong. As it is, manifestly any unsuspected variation in the intensity of the shock, any progressive decline in general vigour consequent upon inbreeding (and he indicates that the reproductive rate of his present stock is causing anxiety), could possibly account for the improvement that he has observed. Further, in the absence of complete pedigrees, it is impossible





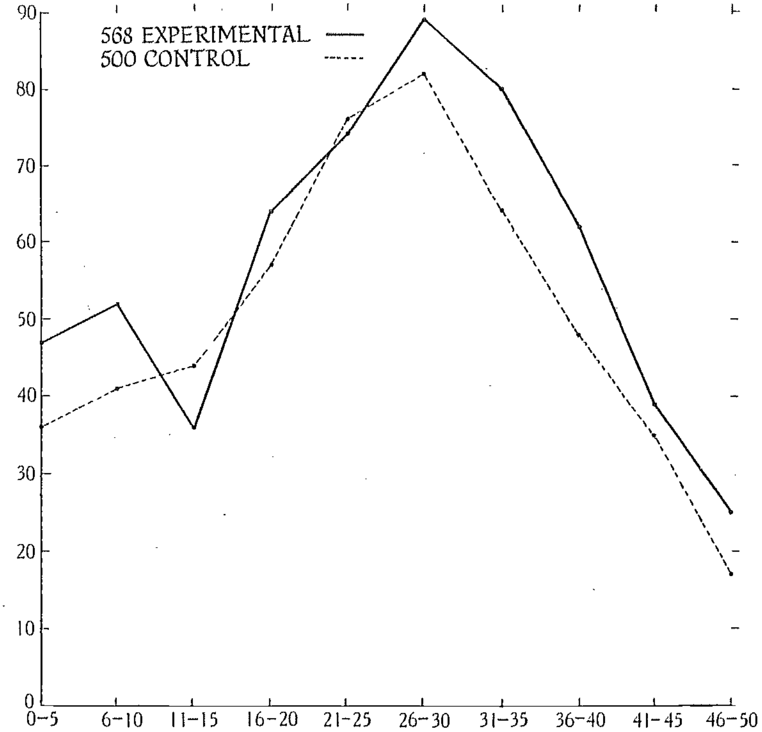
to know which of the animals comprising the earlier generations are represented in the later. Agar, in maintaining pedigrees, is in a position to know that 30 of the 34 parents of his 3rd generation are represented by progeny in the 5th generation. In my own case only 5 of the original 11 pairs are represented in generation II. Line K contributed nothing beyond generation III; Lines C and G came to an end in generation XI; so that generations XII–XVIII inclusive, for the time being at least, are composed of descendants of only 4 of the original 24 rats with which the experiment started, and these were the 4 with the lowest scores. I confess I have been surprised to see this state of affairs evolving, for the 12 original rats were out of an intensely inbred stock and, according to current genetical thought, ought to have been exceedingly similar one to the other in respect of genetic constitution. They were out of a stock that had undergone prolonged gene purgation, and yet the history of my stock reads like an experiment in inbreeding. There is a broad base of family lines and a narrow apex of two remaining lines. The reproductive rate falls, and line after line becomes extinct. Agar is wise in avoiding such close inbreeding as I have practised. However, the figures I have secured are of value in that they reveal the kind and degree of variability among the descendants of one or two pairs.

IV. HANDEDNESS

Before attempting to interpret further my own records relating to the number of errors, I propose to deal with the 3rd and 4th of McDougall's main conclusions: (3) that rats of the control and trained stocks respectively are to be distinguished readily one from the other by marked differences in the behaviour they exhibit in the tank during the actual training period, and (4) that during the preliminary period of the training individuals of the two stocks are to be distinguished one from the other in respect of their behaviour in relation to the light.

McDougall groups his rats into three classes in respect of their behaviour during the prediscriminatory period of their actual training. He estimates that about 50 per cent. of all his rats leave the tank by the right or left exit irregularly and about equally often; about 45 per cent. acquire at an early stage the habit of always leaving the tank by one and the same route, and continue in this habit up to the time of learning; and that less than 5 per cent. at some stage of the training process, after turning right or left at random, acquire the habit of turning always to the illuminated side.

As I have already stated, because it seemed possible that a particular behaviour pattern of this kind might affect the score, I decided to test for handedness and for movement towards or away from the light before the shock was introduced. The graph (Fig. 2) gives the records of 568 rats of the experimental batch and of 500 controls in respect of handedness (light equal on both sides and constant, and no shock). It is seen that there is no difference between the two groups, and that the graph does not even remotely resemble a chance distribution. There is a great excess of rats which tend to go habitually out of the tank by one route, the right or else the left, and there is a majority in favour of the right-hand turn. According to my records there are three easily distinguishable categories of rats; those that habitually make the right-hand turn (40 or more times to the right out of 50 runs), those that make the left-hand turn (10 and less times to the right), and those that turn



Number of times to the right out of 50 runs

Fig. 2

equally often to right and left (20–30 times to the right). In order to examine the effect of these habits upon the score I compiled Table III from the graph (Fig. 2). It will be seen that, of 1068 rats, 456 could not be accommodated by this classification and fell into the disregarded 11–20 and 31–40 times to the right groups. Of the remaining 612, 321 favoured the right- and left-hand turn equally often, whilst of the rest (291), 175 displayed the left-hand turn and 116 the right-hand turn habit. (The preponderance of the right-hand turn habit in the graph is due to the fact that the 31–40 group is much larger than the 11–20.) This table indicates that handedness in the first and preliminary phase of the training cannot be related to score. I certainly expected to reach a very different conclusion, for it seemed reasonable to assume that the rat with a "one-way habit" would encounter more difficulty in learning than the rat that turned one way as easily as the other, for the reason that his habit would have to be broken down. I still think that handedness is a factor which influences the score, but that its action is overshadowed by others which refer to the various types of reactions on the part of the rats to the light, and especially to the shock.

TABLE III

	No. of rats		Average no. of errors		Range	
Times to the right	Experimental	Control	Experimental	Control	Experimental	Control
(1) 0–10	98	77	46·7	42·7	0–203	0–195
(2) 21–30	163	158	46·6	51·6	0–307	4–132
(3) 41–50	64	52	45·3	52·8	0–133	0–116

These figures are to some extent in harmony with the conclusion of Peterson (1934) that right- and left-handedness, as demonstrated in his case by the method of holding food, occurs in about equal numbers in a rat population, that ambidexterity occurs much less frequently than either of the other conditions, and that handedness itself is an enduring and stable characteristic. I concur in his statement that it is not dependent upon the dominance of one eye over the other, for I have occluded each eye in turn without in any way affecting the habit. Peterson assumed that if one hand was favoured for eating it would be stronger than the other and would thus influence the route taken by the swimming rat. He therefore made use of McDougall's water tank to test this assumption only to find that the animals could not be classified into definite right- and left-handed groups, apparently for the reason that the procedure aroused emotional conditions which complicated his own investigation. However, his figures show that 6 rats given 6 trials a day for 7 days gave a total of 128 times to the right and 124 times to the left, and that one of the rats went only once to the right and 41 times to the left, another 37 times to the right and only 5 times to the left. I am sure that had he used more animals he would have found that they could in fact be classified in the same way as mine.

This right- and left-hand turn habit revealed in the first phase of the training which my rats have received (light equal on both sides and no shock) is not to be confused with the right- and left-hand turn habit displayed by the rat during the third phase (alternating light and shock). An examination of my records makes it abundantly clear that in about 90 per cent. of all cases, unless a rat learns within the first 4 or 5 days of its training, even though up to this point it has been going to right and left equally often, it settles down to a one-way habit, going continually either to the right or else to the left, and, having settled down so, it will continue to leave the tank by this one route for a period of time that may be anything from 2 days to 2 months, and will then with apparent abruptness, that at first surprises the observer, swim down the middle compartment and take the alternative route out of the tank. Of my rats which display this one-way habit in phase 3, approximately 60 per cent. take the right-hand turn and 40 per cent. the left. The behaviour of the rat is such as to permit one to think that after a few days of trying both exits and getting shocks at both, it concludes that it may as well stick to one route. Thereafter it seems completely to have forgotten the existence of the other. But if one has been noting the time spent by the rat in the middle compartment before making for the chosen exit, it becomes clear that a day or two before the rat is to begin to learn, this time is longer when the chosen exit is lit (and shocked) than when it is dark. A difference of 2–5 sec. is not uncommon, and when looked for is easily recognised. At this time, too, if as the rat is turning into the lateral passage the light is switched off and on rapidly, it will often turn away and leave the tank by the alternative exit, a procedure which has no effect unless the rat is on the point of learning. If that lateral passage down which, according to its habit, a rat will inevitably pass is blocked, the rat can be taught that there is an alternative route out of the water long before, under the ordinary conditions of the experiment, this would have been realised. Also, if a rat has been taking the right-hand turn, for example, for 150 or 200 times without a break, it can, with practice, be shaken off the electrified platform by manipulation of the switch, and if each time the rat approaches the platform the current is switched on and off rapidly and the exit thus denied to it, sooner or later the rat will turn away and swim to the alternative exit. A few treatments will result in the rat learning after having made some 3–6 additional errors. Undoubtedly fatigue and irritation on my part have reduced in this way several scores of 250+ to scores of about 120–150. Agar has deliberately adopted a similar plan of giving special training to all his rats that have not learnt after 302 trials. It seems to me, therefore, that when McDougall states that about 50 per cent. of his rats turn right and left equally often, and that 45 per cent. persist in going either to the right or else to the left, he is merely stating in other words that about half of his rats learn quickly and the other half learn slowly, for it is the rat that learns slowly that exhibits the one-way habit during the actual training period.

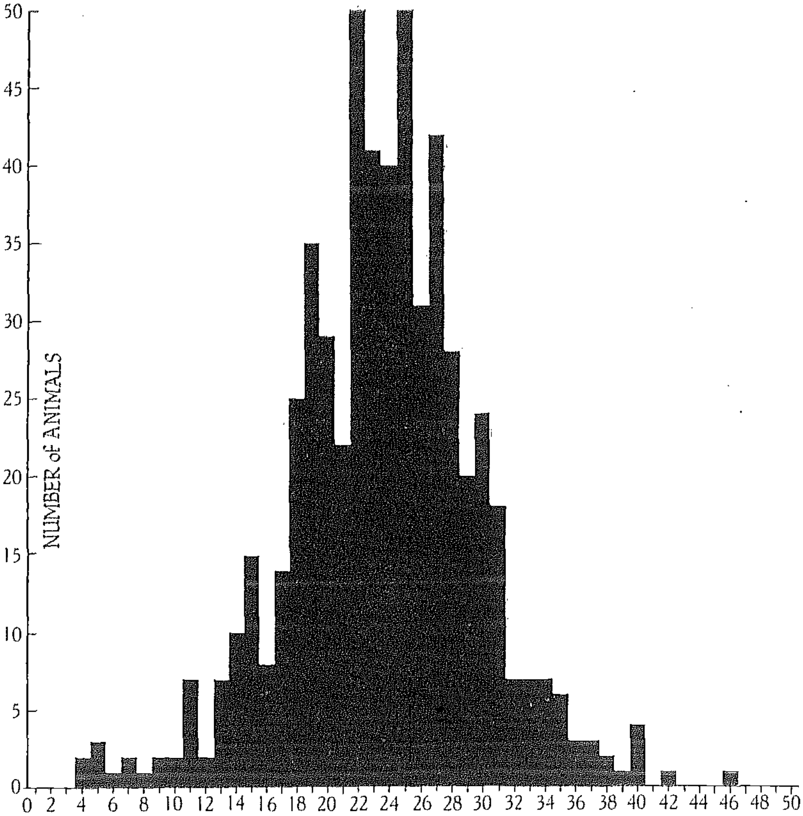
Agar has observed that out of 323 rats of his generations 2–5, 212 formed a right-hand habit and 44 a left-hand habit, whilst 67 failed to do so. He states that the latter were mostly rats that learnt quickly, and quite rightly argues that early learning and failure to form the habit are undoubtedly causally connected. But he concludes that rats which do not quickly form the right-hand or left-hand habit tend to learn much sooner than those that do. My interpretation is exactly the opposite one: I hold the view that it is because a rat does not learn quickly that it develops the one-way habit. The situation as I see it is as follows: the rat is set the task of forming an association between light and shock but fails to do so so long as it must take into account both exits. It settles down to leaving the tank by one route. Later there comes into being an appreciation of the difference in experience when the chosen exit is illuminated and when it is not. The time spent in the middle compartment before leaving becomes prolonged when the light is on the chosen side, and shortened when it is not. Later still the memory of the alternative exit is rekindled or perhaps the rat begins to observe that when one exit is illuminated the other is dim, and then hesitation is shown at the entrance of the illuminated passage and the rat will swerve away toward the opposite exit. I agree with Agar that the extent of the swerve may make all the difference to the ultimate score, for a wide swerve can carry the rat right round the tank into the dark lateral passage, whereas a narrower swerve can find the rat once more back in the central compartment so that nothing really has been learnt.

But dozens of my record cards offer evidence which makes it difficult for me to agree with Agar's view that it is because a rat does not display during the earliest days of its training the one-way habit that it learns quickly. These records relate to rats which do not display the one-way habit until they have been irregularly alternating for 100–150 and more trials, exhibiting a behaviour pattern that forces me to the conclusion that thought is in no way determining their choice. My view is that as a general rule every rat that does not learn quickly (with a score of 20 or under for example) sooner or later develops the habit of persistently going either to the right or else to the left, and that the actual score in these cases is determined by the length of time this one-way habit persists. It is to be noted that though it is common for a one-way habit displayed during phase 1 of the preliminary training to be prolonged into phase 3, this is not always so, for if a rat with such a habit in phase 1 is to learn with a score of 2–5, obviously there will be no opportunity for such a habit to be displayed. If the rat is to make a score of 150, on the other hand, it will sooner or later display the one-way habit in phase 3, and in the majority of such cases, though not in all, the chosen side in phase 3 is the same as that in phase 1.

I agree with Agar that McDougall is mistaken in assuming that in the case of these animals with a one-way habit in phase 3 the rat is required to discriminate between a lit exit on one side and a dim exit on the other. It is quite clear that the first discrimination in these cases is between the occasion when the chosen side is illuminated and shocked and when it is not. But this refers only to rats which are slow learners and display the one-way habit; these first discriminate between light and no light on one and the same side, and only then achieve the discrimination between the one side that is illuminated and the other side which is dark. It does not apply to those rats that learn quickly with scores of 10 and under, for their behaviour indicates clearly that they are aware that there are two ways out of the tank.

V. REACTIONS TO THE LIGHT

Because McDougall had estimated that some 5 per cent. of his rats acquired the habit of turning always to the illuminated side, because he had concluded that during the preliminary 6 runs with alternating light and no shock, individuals of the trained stock tended on the whole to show a slight preference for the dim route whereas the controls showed a slight but decided preference for the bright route, because he had had rats in his first experiment which learnt without making a single error, though he regarded it as a happy chance that the rats had done so, and especially because in my own first batch of controls I had had one rat which made a score of 0, I decided that I must test every one of my rats for photophobia. Phase 2 of my preliminary training consists of 50 runs with alternating light and no shock. Agar also has encountered one rat that made not a single error, but because not one of its ancestors or descendants in the next generation had a similar score, he decided that this avoidance of the light was not due to genetic factors.



Number of times to the light out of 50 runs

Fig. 3

The diagram (Fig. 3) depicts the records of a group of 573 experimental animals. Since those of 500 controls give an exact replica of this, I do not show it. Experimental and control lines are not to be distinguished. Clearly the distribution here is not determined by chance. That this is so is shown even more clearly in Table IV. Assuming that it is a matter of chance whether a rat goes towards the light or away from it, from the binomial distribution, the points beyond which 5 per cent., 10 per cent., or any other proportion of the observations should lie, can readily be calculated. The table has been constructed to show the portions of the range within which each succeeding 10 per cent. of the observations should lie (except that the end classes have been divided into two).

TABLE IV

Range	Expected number	Observed number	χ^2
0 –19·18	29	125	317·8
19·18–20·47	29	39	3·4
20·47–22·02	57	49	1·1
22·02–23·14	57	51	0·6
23·14–24·10	57	38	6·3
24·10–25·00	57	41	4·5
25·00–25·90	57	37	7·0
25·90–26·85	57	34	9·3
26·85–27·97	57	40	5·1
27·97–29·53	57	36	7·7
29·53–30·81	29	29	0·0
30·81–upwards	29	54	21·6
	—	573	384·4

Manifestly, this distribution is not one governed by chance. There is a significant discrepancy in the first and last of the classes, especially in the first, whilst the second is also similarly affected. There are very many more rats going to the light less than 20 times out of the 50 runs than would be expected. The chance of getting a rat that goes 12 times or less to the light is only 1 in 1000; yet out of 573 rats I have no less than 22 which went to the light 12 times or less. There are in my stock rats which avoid the light as light. It follows that such rats must be greatly advantaged under the conditions of the experiment since in avoiding the light they also avoid the shock.

Actually in the whole 2459 rats so far trained there have been 29 experimental and 10 control which never received a single shock for the reason that on each run of the first 12 of phase 3 they went to the dim and safe exit. 11 of these are included among the 573 rats in Table IV. When their records are examined it is found that the rat which makes a score of 0 in phase 3 has, during the later part of phase 2 of its training, been consistently avoiding the light. It is because they carry over this habit into phase 3 that such rats "learn" without getting a single shock. One rat of my control stock did not go to the light even once during phase 2, and ended its training with a zero score. Usually, however, such rats only begin habitually to avoid the light in the latter part of phase 2, the last half or third. As I have stated, the change from phase 1 to phase 2 of the preliminary training is usually attended by a disturbance in the behaviour of the rat. This lasts over 1–4 days usually, and thereafter the rat settles down again to its old habit or else to a new one. If a rat makes a score of 10 times or less to the light in phase 2 (and these all in the first half) the observer is justified in expecting that the rat will learn without making a single error. But this does not always happen. The rat may leave the tank 6 times in succession by the dim route on the first day of phase 3, but on the first run of the second day it may go to the light and get a shock. If the reaction is severe, for the remaining runs it may rush squealing, splashing, swimming perpendicularly in the water, spend its energy in the hopeless task of climbing the smooth walls, in fact may do everything that must make considered choice impossible. Until it behaves quietly again it continues to add to its score, and not until it does behave quietly can it learn. I have had rats with scores of 100 and more which might, I think, have learnt with 0 had they escaped the shock on the first run of the second day. Undoubtedly just as the one-way habit can be overcome by denying the chosen passage to the rat, so also can this deliberate avoidance of the light be overwhelmed by the strength of a rat's reaction to an electric shock.

The difficulty of demonstrating a habit is illustrated by the results of the following tests which I made with some of these photophobic rats. For example, in the last 29 runs of phase 2, a certain rat had repeatedly left the tank by the dim route. The light was then kept permanently at the right exit. But the rat continued to alternate. After some 12 runs, however, as if at length noticing that the conditions had changed, it began to hesitate, and then always left the tank by the dim exit on the left. This continued for 2 days and then the light was switched over and kept permanently on the left. But the rat continued to go to the left for 12–15 runs, then began to hesitate and later turned away, always to leave by the dim right exit. This behaviour is vastly intriguing. It would appear that when faced with the task of making a decision of this kind, the rat brings thought to bear upon the problem and solves it, the decision giving expression to a preference. The decision having been made, thought, no longer required, is banished and a habit is assumed. The rat having decided to alternate, alternates, and this habit carries it past the point where the conditions are changed. It carries it 2–3 days beyond this point. Then thought enters once more, and again the same series of events is launched. It becomes a matter of some difficulty to demonstrate that any given rat is definitely photophobic. Nevertheless the difference between the behaviour pattern during phase 2 of these rats and of the rest is such as to make it quite certain that they are avoiding the light as light to begin with and thereafter continue to alternate as a habit.

I am of the opinion that a rat can display this alternating habit for other (and to me unknown) reasons. It has been shown that no less than 125 out of 573 rats went to the light less than 20 times out of 50 runs and that 54 went to the light 30–81 times and over. The expected numbers in both classes is 29. I am quite sure that a considerable proportion of the 125 rats were not deliberately avoiding the light as light, and that all the 54 rats were deliberately going towards it. There are rats, undoubtedly, which quickly develop the habit of leaving the tank first by one route and then by the other. They march in step with the alternating light and shock for a time, getting shock after shock, then go twice to the same exit and thereafter alternate again, so avoiding shocks, then go twice to the same exit and get into step with the shock again. Such a rat at irregular intervals leaves the tank 7 or 8 times in succession by the dim route, but the observer is not deceived into thinking that the rat is likely to learn. But it occasionally happens that such a rat does learn in the sense that it makes 12 successive safe escapes. But it has not learnt in the sense of having achieved discrimination, as can be shown by continuing the training process. Such a rat will certainly begin to pile up another score, whereas the rat that has really learnt only rarely makes a mistake during the 3 months subsequent to its completion of training. But for the great majority of the rats McDougall's test is adequate, and the rat that learns without mastering the task is not very common. I suspect that the whole of the excess in the 30–81 upwards class and the same number in the 125 of the first class belong to this alternating category. This would still leave some 70 animals in the 0–20 times to the light class, the behaviour of which I think is to be explained by reference to an initial deliberate and conscious avoidance of light as light.

The average score of a given batch of rats must necessarily be influenced greatly by the number of such photophobic rats within it, and so in any experiment of this kind it is necessary to include a test for photophobia. It is incumbent upon McDougall to show that the explanation of his observation that his tank-trained stock tend to avoid the bright gangway whereas his controls tend to prefer it is other than that through unconscious selection there are now many more photophobic animals among his trained stock than among his controls. Such an explanation would at once accommodate the observation that this preference made a sudden appearance, so sudden indeed as to suggest to McDougall that a mutation had appeared, having been induced by the training process in some earlier generation.

I very much doubt, however, that McDougall is warranted in basing any conclusion whatsoever on the behaviour of the rats during 6 runs with alternating light and no shock, especially if these are the first runs that the rats have ever had. For myself, I am satisfied that before the rat's reactions to light are tested, it must first have been accustomed to the tank with the light equal on both sides. I have hundreds of records in which a suggestion relating to behaviour conveyed by the earlier entries of each of the phases of training is completely contradicted by the behaviour of the rat during the rest of the phase. This being so, I am unwilling to accept McDougall's fourth main conclusion.

Agar states that his rats show a slight but unmistakable initial bias to the light during the actual training (my phase 3). Frankly I do not think that his actual observations warrant such a conclusion. It is during the first few days of the actual training that a batch of rats, which does not include a great preponderance of individuals that are to learn with very few errors, will necessarily make most mistakes, and in so doing will of course go more often to the light than away from it. Those that do not learn quickly tend to develop a one-way habit and this means that they cannot make more than three mistakes and go three times to the light more than three times a day, whereas an "alternating" rat can make more and go more often. I do not think that whilst the light is associated with the shock it is possible to relate the behaviour of the rats to one of these alone, since both light and shock provoke reactions which can disturb the behaviour displayed prior to their incoming. This is demonstrated by the increase in the frequency of defaecation whilst in the tank that occurs at the beginning of each phase of training, and especially during the first week of phase 3. It is not improbable that frequency of defaecation under these conditions might form a measure of the emotional behaviour of the rat, for those that defaecate every time they approach the exit are those that can be regarded as the most excitable. Surely it would have been equally correct or incorrect for Agar to have stated that his rats showed a slight but unmistakable initial bias to the shock. In my opinion his figures which show that his rats during the first 3 days of their training went to the light 2139 times instead of the 1968 times which would have been expected, had the choice of going to the light or away from it been random, simply illustrate the fact that the majority of rats are more exploratory and make most errors per unit of time during the first week of their training. At this time and under these conditions it is the shock and not the light that is conditioning behaviour.

VI. TIME IN THE TANK

McDougall's remaining conclusion that rats of the two stocks, trained and control, are to be distinguished by characteristic differences in their behaviour in the tank is, in my opinion, insecurely based since he has not used sufficient controls and has not used them properly. He is satisfied that the rats of the trained stock tend to stay in the water for a longer period of time before making for one or other of the exits than do the controls; that the trained stock rat typically is more cautious, more hesitant; and the implication is that it is possible to state whether any given rat is a control or an experimental after having seen it in the water during the first few days of training.

Like McDougall I have kept records of the time spent in the water by groups of the two stocks. The average time per rat for a representative group of 500 controls and 500 experimentals is roughly 3 min. per rat per day of 6 runs. There is no difference between the two stocks. But this figure possesses very little meaning, save that it indicates the total number of hours the observer spends in the dark during the course of a year; actually the time spent in the water varies markedly from rat to rat, and in the case of one and the same rat, according to the stage of its training. During the first and second phases of my training it is usual for each rat to take 1½ min. for the 6 runs, but the pace is much slower during the first day of each phase than subsequently. On the first day of the third phase when the shock is introduced the majority of rats, after their first shock, will remain in the water for some 1½ min. before beginning to move towards the exit. (Quite a number react in exactly the opposite way, rushing wildly at the platform, leaping over it and coming out of the tank like a ball from a bat.) For the next 2 days the time in the water is considerably lengthened and thereafter speeds up again to slow down once more as the point of discrimination is approached. Usually a rat stays longer in the water on its first immersion of the day than subsequently. The following sequence is not uncommon: 1½ min., 1 min., 30 sec., 15 sec., 10 sec., 10 sec. But no day is complete without the rat that stays 5–10 min. on its first immersion. I have had them, both experimental and control, stay as long as 35 min. But during the last 2 years these have not caused me any distress for I just leave them to soak in the middle compartment and carry on with the training of others. Usually there is in training a rat that stays in the water whilst 6 or 8 others pass through their daily training, and their activities in no way affect the behaviour of the laggard.

It is really astonishing to observe the display of a constant and characteristic behaviour pattern in the tank. The rats exhibit amongst themselves appreciable differences in the time spent in the middle compartment; in the method of swimming, some floating, some gently paddling to produce a quiet, rhythmical scratching on the wall of the tank; in the method of turning to face the open end of the middle compartment, some always pushing off with the hindlegs from one or other partition; in the method of approaching the ladder, some directly from the front, others always from one side; in raising themselves out of the water, some using only their forelegs, others mainly with their hindlegs; in their behaviour after emergence, some quickly peering about, others obviously excited and nervous. These and many other idiosyncracies are to be observed, but none of them is characteristic of one or the other group. It is possible to identify an individual in a small batch by reference to its behaviour certainly, but I am quite unable to distinguish an experimental rat from a control in this way.

VII. EXAMPLES OF RECORD CARDS

My procedure, results and conclusions can best be demonstrated by the presentation of copies of representative record cards. Each card can accommodate the records of 500 trials (350 on the front, 150 on the back). A = the right exit, B = the left. The horizontal lines are blue, the A vertical lines are red, the B vertical lines are blue. The first row (AB) is used for the records of the 50 runs of phase 1, equal light on both sides and no shock; the second row for the 50 runs of phase 2, alternating light and no shock; whilst the remaining rows are used for phase 3, alternating light and shock. If, on its first run of phase 1, the rat goes to the right, a dot is put where the vertical red A line cuts the horizontal A line; if it goes to the left, the dot is put at the junction of the vertical red A line and the B horizontal line. On the second occasion, if the rat goes to the left, then the dot is placed at the junction of the two B lines; if it goes to A, then it is put where the vertical blue B line intersects the horizontal A line. At the end of the 6 runs the dots are joined by lines. On the 8th day 8 runs instead of 6 are given to bring the total to 50. The number of times to the right out of the 50 is then written down at the end of the line. At the end of phase 2 the total number of times to the right, and also that of the number of times to the light are recorded. In phase 3 the total number of errors in each row is recorded in the column on the left and these are added together to give the final score. The diagram provided by the record card gives an immediate appreciation of the rat's behaviour.

Fig. 4 is a copy of the record of a rat which, having no bias in respect of handedness, and being photophobic, learnt with a score of 0. It went to the right 33 times out of 50 in phase 1, and 30 times out of 50 in phase 2. But in this second phase it went to the light only 5 times out of 50, and for the last 29 times invariably went to the dim exit. This habit persisted into phase 3 and the rat learnt without receiving a single shock.

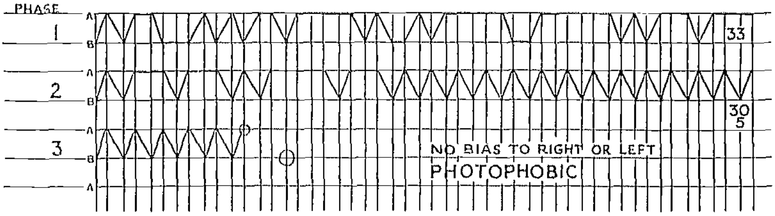


Fig. 4

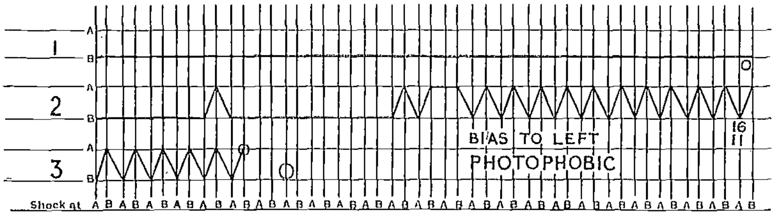


Fig. 5

Fig. 5 is the record of a rat with a strong bias to the left; it did not go once to the right in phase 1. During the first half of phase 2 this habit continued, and it went to the light 11 times. But during the second half of this phase, the rat for 23 times in succession went to the dim exit. This new habit was carried over into phase 3 and the rat learnt with a score of 0.

Fig. 6 is the record showing the astonishing persistence of habit in a photophobic rat after the conditions of the test have been changed. Shock is not involved in this case. After the rat had left the tank on 26 successive occasions by the dim route, the light alternating, the light was kept at *A*. The rat continued to alternate for a further 12 runs and thereafter settled down to leave the tank always by the dim *B* route. After it had continued to do this for 18 consecutive runs the light was kept at *B*. The rat continued to leave by the *B* route for a further 9 runs and then changed over to *A*. After it had done so for 21 runs the light was alternated again, but the rat kept to the *A* route for 7 further runs before beginning to alternate once more and to leave by the dim route.

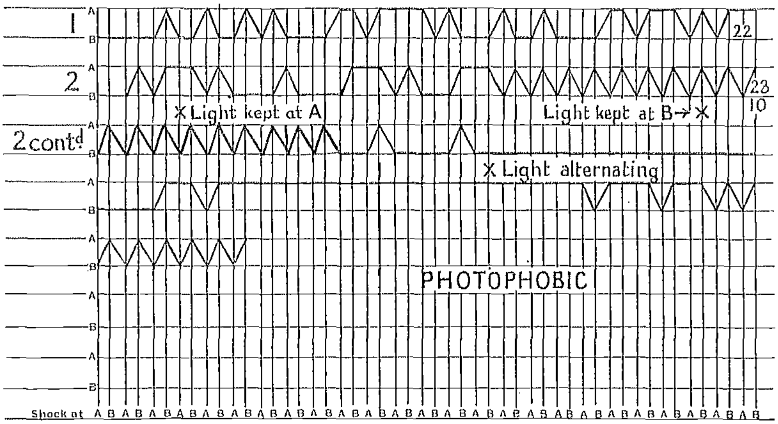


Fig. 6

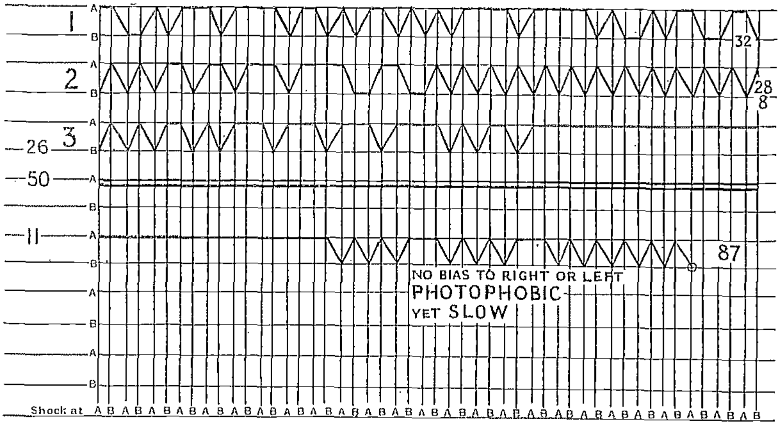


Fig. 7

Fig. 7 shows the record of a rat which according to the evidence of phase 2 is photophobic and which I expected to learn without an error. It received a shock on the first run of the second day, reacted strongly, its alternating habit was disturbed and the rat received many shocks and then settled down to the right-hand turn for 137 runs before it began to learn.

Fig. 8 shows a rat with a strong left-hand bias. It went to the right only 4 out of 50 times in phase 1, once to the right and 26 times to the light in phase 2, and continued to go to the left in phase 3 for 359 consecutive runs. The apparent abruptness of the attainment of discrimination is clearly illustrated in this record.

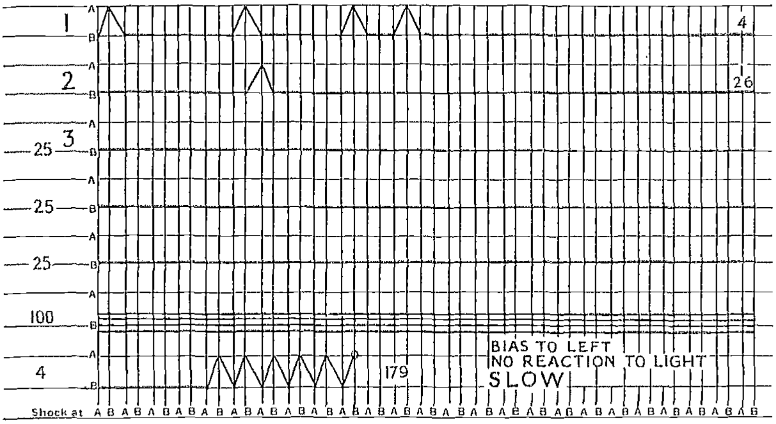


Fig. 8

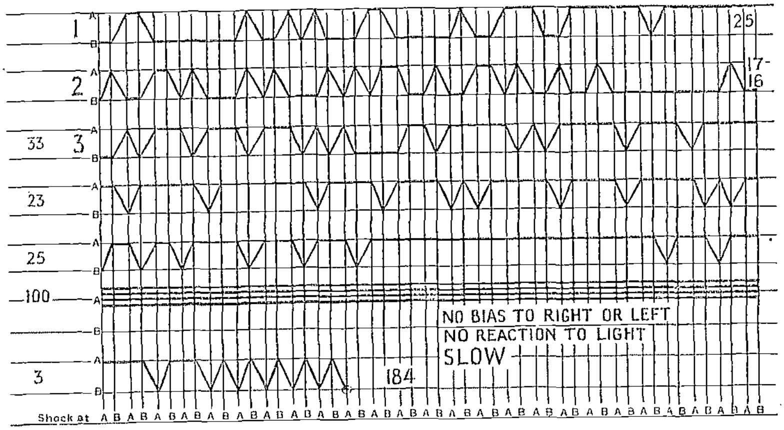


Fig. 9

Fig. 9 shows a rat which went to right and left equally in phase 1, gave no evidence of photophobia during phase 2, continued to alternate for about 150 times in phase 3 before settling down to the right-hand turn for 200 further runs. This is an instance of the records that cause me to disagree with Agar concerning the relation of handedness and quickness in learning. So also is the next.

Fig. 10 is the record of a rat which exhibited the right-hand bias strongly and this was not disturbed by the alternating light in phase 2 save in the beginning. (It is seen that the subsequent behaviour of this rat could not have been predicted from the performance during the first 6 runs.) It went to the light 26 times. In phase 3 on the first day it got

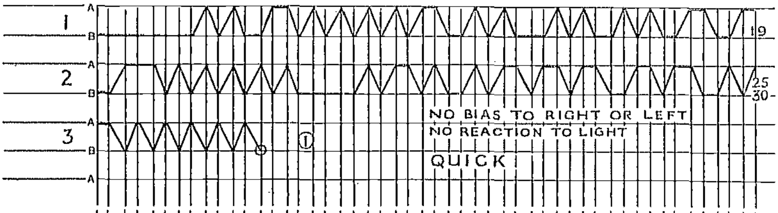


Fig. 11

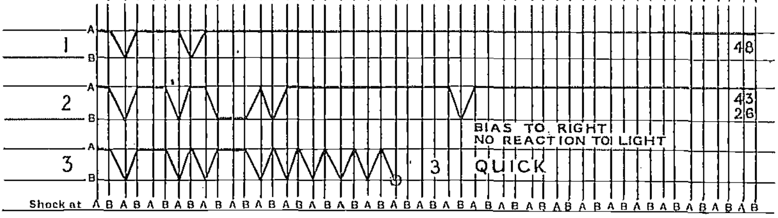


Fig. 10

a shock on the first and fifth runs, and on the second day it made a mistake on the fifth run. Thereafter it made no more. Here, then, is a rat which, though showing a definite bias to the right, yet learns with 3 shocks.

Fig. 11 shows a rat with no obvious bias and no regard for the light that is quick to achieve discrimination.

So, according to my records, there are rats with a bias to one side or to the other, and rats without this bias; there are rats that avoid the light as light and rats which do not react to it; and there are rats which are quick to achieve discrimination and rats which are slow. There are rats with a one-way bias which are quick and others which are slow. Similarly there are quick rats and slow rats without this bias. I assume that there are photophobic rats which are also quick and others which are slow, and that there are quick and slow rats which are not photophobic. These differences themselves are more than sufficient, singly and in combination, to make their analysis extremely difficult. But, in addition to these factors, which must largely determine the actual score, there are others which are to be described only vaguely. A runt, the feeble, poorly developed individual, learns quickly for the reason, I assume, that the punishment it receives is more severe. If this is so, then, as a general rule, the more vigorous the rat the higher the score may be expected to be, and so in comparing the performances of the later with the earlier generations it becomes necessary to show that in respect of general vigour there has been no steady deterioration. The members of a small litter are at a given age better grown than are those of a large litter, and so there is a tendency for the members of a large litter to give lower scores than those of small litters. (Agar wisely reduces his large litters: I have not done so.) Some rats are much more excitable than others, and these give themselves scanty opportunity for considering the problem set; they begin to swim whilst still being lowered into the tank, and immediately rush squealing down the middle compartment. They are handicapped in comparison with the quiet gentle creature that paddles about seeming to explore the tank. So that general vigour, timidity, excitability, even the habit of swimming near the outer wall of the tank, are factors which also enter and necessarily complicate the analysis.

VIII. My rats trained by McDougall

If such peculiar idiosyncracies affect the results of an experiment such as this, differing proportions of the various types must make comparison between McDougall's, Agar's and my figures somewhat difficult. I do not think for one moment that our personal preferences could in any way influence the performance of the rats in the tank, but our tanks are different, our procedures are different, as are also the intensity and duration of the shock. But such differences are not really important since each of us has rats which under the conditions which obtain learn quickly and others that learn slowly, and the problem that each of us is investigating is the same: each is studying the question as to whether or not a high average score of early generations is converted into a low average score in later generations, and, if so, by what means this is brought about. But if many constitutional factors, general vigour, excitability and so on, which have nothing to do directly with the ability to achieve discrimination but which affect the speed with which this is acquired, are concerned in the experiment, manifestly the results of the three of us can be hopefully compared only if our rat stocks are of similar constitution. If, for example, I had started with a number of photophobic runts, and if photophobia and physical feebleness "bred true", I should have got and have continued to get generation after generation of exceedingly low-scoring animals, and at the end I should not have been in a position to comment upon McDougall's conclusions. As it happens, however, all three of us have been using Wistar rats, and as the result of the genetic teaching and skilled advertisement, we, I suppose, are prepared to assume that, because each of us got our foundation stock from this same source, our rats must therefore be genetically similar if not identical. But do Wistar rats remain Wistar rats when they are born and bred in Durham, Melbourne and Edinburgh? I know that my rats no longer resemble their ancestors in respect of many of the more easily measurable qualities (Hain, 1934). I have to assume that selection of a kind has always been operating in my own rattery. I have always deliberately been selecting rats that flourished best in the conditions that obtain here, and I have inbred these most intensely. I think it would be found on examination that in respect of growth rate, litter size, age at death, incidence of abnormalities, my rats differ from those of McDougall and Agar, and certainly some of these are genetic characters. If so, then it would not be surprising, if any of the factors contributing to the achievement of discrimination in the tank were also genetic, to find that my stock is now more or less different from the other two. Obviously, there could have been no selection in respect of such factors before the experiment started, for their presence is to be recognised only by the complicated test in the tank.

Fortunately it is possible to examine the validity of this suggestion. In 1931 McDougall took back to Durham with him 12 of my rats whilst I kept their litter mates and trained them here. The rats that I gave him were out of my generation V, and those that I retained became the parents of my generation VI. At Durham these rats and their descendants in the hands of McDougall gave the following scores:

TABLE V

Generation	No. of animals	Average score	Range
I	11	188	16–282
II	20	78	15–315
III	14	63	10–150
IV	16	68	9–174
V	12	48	18– 75
VI	19	61	14–203
VII	21	46	4– 93

McDougall is inclined to regard these figures as supporting his own conclusions. It is seen that an arithmetical mean of 188 in the first generation is transformed into one of 46 in the seventh. But I am not willing to agree, for in the case of such small batches the average is disturbed too profoundly by the presence therein of one or more animals with very high scores. My unwillingness is reinforced by the figures I myself obtained from their litter mates. These are presented in the manner of McDougall (see generations VI–XI inclusive, Table II). It is seen that I have many more animals (328 against 113), and that the range is practically as wide (0–291 instead of 4–315). If the first two generations of my rats in Durham are disregarded, and it is surely fair to do this for the conditions there must necessarily be different from those in Edinburgh and rats undoubtedly require a little time to become acclimatised, then there is no difference whatsoever between the actual figures McDougall got and mine. This being so, I incline to the view that his own rats do not differ in any significant way from my own, and that the difference in our conclusions must refer, not to ourselves, not to our tanks or our procedures, not even to real differences in the results we have obtained, but to differences in our methods of selecting the parents of the succeeding generations and of recording, and especially in our methods of controlling the experiment.

IX. ANALYSIS OF PEDIGREES

In an attempt to determine whether or not I was justified in my strong impression that this quality that is represented by the score is in whole or part genetic, I divided my experimental rats into 9 classes with scores in geometrical progression, disregarding all rats with a score of 0, for the reason that photophobia seemed to be a quality to be examined separately, and then plotted the frequency distribution of the offspring for different parental matings. It was found that when both parental scores are low ($\leqslant$17–32, Class V) the offspring distributions are very varied and have no obvious common property save that their peaks (also their means and medians) are all $\leqslant$ 33–64 (Class VI), whereas when both parental scores are high ($\geqslant$33–64, Class VI) the distributions are all very similar in shape, having a high peak in Class VII (65–128). Consequently the collective distribution of all the offspring of parents with low scores shows a wide dispersion, whereas that of offspring of parents with high scores has a high peak and a narrow dispersion.

These observations suggest that among these rats there are two main classes, the "quick" and the "slow", and that in a general way "quickness" behaves as a dominant in relation to "slowness". If this were so, then Classes VI–IX (33–257 +) should consist largely of pure recessives, slows, and this would account for the varied pattern of the distribution of the scores of offspring of parents with low scores and for the relative constancy of the distribution of the scores of offspring of parents with high scores.

It has to be acknowledged that this suggestion of a single main factor pair (or of some system of multifactor inheritance giving similar results), though satisfactory up to a point, does not accommodate the fact that a considerable number of "quicks" appear among the offspring of slow × slow matings. It is also in conflict with the results of McDougall's subsidiary experiment in which training was combined with deliberate adverse selection (breeding consistently from the slowest in each successive generation) and with favourable selection (breeding consistently from the quickest). In the case of adverse selection McDougall got remarkable improvement after 14 generations, whereas with favourable selection no such results were obtained. He regards this ineffectiveness of adverse selection as the strongest possible corroboration of his main conclusions.

An examination of my pedigrees will show that I too have contemporaneously been practising selection in both directions, that my line *A* is now to be distinguished as a "quick" strain, being relatively fixed and yielding proportions of quick and slow offspring in matings of quick × quick, quick × slow, and slow × slow which differ significantly from the rest, and that I have failed to fix to the same degree a strain of "slows". But surely there is a very simple explanation. It is far more difficult, in my opinion, for a constitutionally "slow" rat to pass through the test with a low score than it is for a constitutionally "quick" rat to put up a high score. Quite a number of happenings, casual or accidental, can convert a potentially low score into a high one, and so the "slows" come to include a number of "quicks". For this reason I would expect the quicks to be relatively uniform and the slows heterogeneous. Thus if "quickness" and "slowness" were genetic characters, in whole or part, and polygenic in nature, and if selection of the worst implied the selection of individuals of different genotypes whilst selection of the best meant selection of a more uniform genotype, I should not expect favourable selection to be followed by a drop in the arithmetical mean, but I should expect that this might easily happen if adverse selection were practised, since in selecting "slows" one might be choosing potentially "quicks". I am quite sure that in my records there are "slow" rats entered as "quicks", and "quicks" entered as "slows", and that there are far more instances of the latter than of the former. So many factors are concerned in the establishment of the score that it is improbable that an experiment such as this could reveal individuals whose scores were commonly the direct expressions of their genotypes, uninfluenced by non-genetic factors. The average score of the 683 males of the experimental group is 45·17, that of the 762 females 41·79. That of the 586 rats of Line A is 30·8 (males 28·05; females 32·11); that of the 564 rats of Line B is 56·88 (males 61·87; female 51·90). These differences have been examined statistically; the scores of Line A rats are significantly lower on the average than are those of Line B rats: within Line A there is no significant difference due to sex, within Line B are less than 20 to 1 that the males have a higher score than the females.

Accepting the suggestion that only two main classes of rats are concerned, "quick" and "slow", and, since the median of the controls is 24, that quick rats are those with scores of $\leqslant 23$, whilst slows are those with $\geqslant 24$, it becomes possible to summarise the records of a sufficiently large group of the experimental stock. It will be noticed that there is

TABLE VI

Parents ...	Quick × Quick		Quick × Slow		Slow × Slow		Totals	
Offspring ...	Quick	Slow	Quick	Slow	Quick	Slow	Quick	Slow
Line A	271	149	15	17	12	55	298	221
,, B	35	64	6	14	77	211	118	289
,, C	32	38	8	21	6	25	46	84
,, G	—	—	9	16	24	79	33	95
,, K	3	4	—	—	6	—	9	4
Total	341	255	38	68	125	370	504	693
Percentage	57	43	36	64	25	75	42	58
Pairs of sibs:								
Quick	3926	2275	78	144	400	852	4404	3271
Slow	2275	2138	144	254	852	2518	3271	4910
Average no. of offspring per mating	$\frac{588}{55}=11$		$\frac{106}{17}=6$		$\frac{495}{63}=8$		$\frac{1189}{135}=9$	
Standard deviation	9		2		$4\frac{1}{2}$		7	

a preponderance of quick × quick matings in Line A, and of slow × slow matings in Line B. Quick × slow matings are rare; they were made only when it was not possible to mate quick with quick or slow with slow. For this reason the two lines have come to be different in respect of the proportions of quicks and slows in the three types of litter. The figures seem to suggest that quickness and fertility are connected in some way. I think they are misleading. Obviously quick by quick matings can produce more offspring during the course of an experiment limited in time than can slow by slow matings of the same generations if mating is deferred until training is completed. The quicks can have produced a litter and this can be half-way through its training before the slows of the same generation have been mated. For this reason the quicks have more entries in the records than have the slows. But it is the case that I have never had any offspring out of a rat with a score of 200+. I have no satisfying reason to offer for this.

The parent-parent correlation is 0·84, the parent-offspring 0·3, and the sib-sib 0·17. Undoubtedly the system of mating quick with quick and slow with slow is responsible for the first, and this must affect the other two coefficients. Nevertheless, the parent-offspring figure is such as to make it certain that genetic factors are largely concerned in determining the score that a given individual shall make. Since there is no difference in respect of the score between controls and experimentals and between the later and earlier generations of the experimentals, it follows that there is no need to postulate that any quality has been induced as a consequence of training, for the results obtained are interpretable in simple genetic terms. If the average score per rat of one generation differs from that of a preceding generation, then this difference merely means that in the two generations there are different proportions of genetically quicks and slows.

The hypothetical correlations occurring in a system of random mating and estimated by using the percentages instead of the actual figures are parent-parent 0, parent-offspring 0·17. On the basis of assortative mating, and neglecting all quick × slow matings, and using not the percentages but the actual figures, the parent-parent correlation is 1, parent-offspring 0·4, and the sib-sib 0·18. If the 9 class classification is used instead of the 2 class, the parent-parent correlation is 0·8, and the parent-offspring 0·3. Since these are the same whether 2 or 9 classes are considered, it can be assumed that the sib-sib correlation of the 9 class would not be far removed from 0·1.

I do not propose to carry this investigation further: I willingly bequeath its interest and labour to Agar. But I propose to carry the study of photophobia and of handedness further, and reserve a discussion of these phenomena for a future occasion. For the present I must be content with the statement that handedness is an enduring and a stable characteristic, and that if it is inherited its mode of transmission is not simple and straightforward. Neither is that of photophobia, but it is the case that this phenomenon is encountered only in certain strains.

X. SUMMARY

In order to be in a position to examine the conclusions which McDougall has reached, 18 generations of rats have been trained. The figures provided by 1445 experimentals and 1014 controls are compared with those which McDougall derived from 21 generations of rats of the same origin.

Criticism is levelled at the methods adopted by McDougall for presenting his figures, and especially at his lack of adequate control.

In the case of my rats the average number of errors per rat made by individuals of the tank-trained stock has not decreased with the passing of the generations, and there is no difference whatsoever between the scores of the experimental and control stocks. I have encountered no evidence which would suggest that rats of the trained and control stocks respectively can be distinguished one from the other by differences in behaviour. This being so I cannot accept the results which McDougall obtained as being in themselves strong enough to carry the interpretation that he has placed upon them.

Analysis of my own pedigrees shows definitely that genetic factors are heavily concerned in the establishment of the scores. Two main classes of rats are involved, quick and slow, and in a general way quickness behaves as a dominant, slowness as a recessive. The parent-offspring correlation is 0·3. A "quick" strain has been developed as the result of consistent favourable selection. To "fix" a slow strain has proved to be a much more difficult task. The reasons for this are discussed.

I submit that there is no need to postulate, in explanation of the fact that the average scores of the earlier and later generations of McDougall's rats differ, that some new quality has been acquired and is being transmitted, for the average score of a generation is determined by the proportion of quick and slow rats within it, and these proportions can, within limits, be prearranged.

Among my rats there is a great excess of those which tend to leave the tank habitually by one route during the first phase of their training when the light is constant and equal on both sides of the tank and when the platforms are not alive. A considerable number of rats reacted to light as light in the second phase of their training when the light was alternating but the platforms were not alive. Actually 29 experimental and 10 control rats "learnt" without receiving a single shock.

The relation of handedness and photophobia to the score is discussed.

I do not propose to carry the main study further. The search for the genetic basis of handedness and of photophobia is being continued.

TABLE VII

Controls

I	0, **1, 1**, 2, 3, **4, 4**, 4, 4, 4, **5, 5, 5**, 5, 5, **6**, 6, 6, **7**, 7, 7, **8, 8, 8**, 8, 8, 8, 8, **10, 10**, 10, 10, 10, **11, 11, 11**, 11, 11, **12, 13, 14**, 14, 14, **15, 15**, 15, 15, **16, 16, 16**, 16, 16, 16, 16, **17, 18**, 18, **19, 19, 19**, 19, **20, 20**, 20, 20, 20, **21**, 21, **22, 22, 22**, 22, **23**, 24, 24, **25**, 25, **26, 26**, 26, **27**, 27, 28, **29, 29**, 29, **30, 31**, 31, 32, 37, **38**, 38, **39**, 40, **45**, 46, 46, **56, 81**
II	**0**, 1, **2**, 2, **4, 6, 7, 8**, 8, 9, **10**, 10, 11, 11, **12, 13**, 13, 14, **15**, 16, 16, **17**, 17, **18, 19**, 19, 19, **20, 22, 24**, 26, **31, 33, 34**, 38, 41, 45, 52, **63**, 70, 89, **92**, 113, **115**, 117, 122, **142**, 174, **183, 194**
III	0, **4**, 7, 11, 11, 14, **17**, 18, 23, **24, 25**, 25, 25, **26**, 26, **28, 29, 29**, 29, **33**, 33, 34, **37**, 37, **38, 40**, 41, **44, 47**, 47, 48, **52**, 54, **58, 59, 73**, 75, **77, 94**, 102, **103**, 107, **111**, 116, 128, 169, **174, 182**, 187, **291**
IV	**1, 1**, 1, 2, 2, **3, 3**, 3, 3, 3, 3, 4, **5, 7**, 7, 7, **10, 11, 12**, 12, **14, 14, 16, 18, 19**, 19, 20, **22**, 22, **23**, 24, 24, **29**, 29, 33, 34, **36, 51**, 60, 64, **85, 85, 89**, 93, **101**, 102, 106, **109, 113**, 179
V	5, **7, 7**, 8, **9**, 9, 9, **13, 14**, 16, 16, 18, **21, 23**, 23, 25, **27**, 28, **29, 29, 29**, 30, 34, **36**, 36, **38**, 39, 42, **47**, 47, **48, 52**, 55, 57, 57, **59**, 64, **67**, 73, **76, 78, 85, 92**, 97, **101**, 105, **107, 111**, 129, 275
VI	**4, 6, 7**, 7, 9, 9, 9, **11**, 11, **13, 15, 17**, 17, 19, **20**, 21, **23, 23, 24**, 24, 26, 28, **31**, 33, 35, **42, 43, 43**, 52, **54, 56**, 58, 61, 61, 63, **65**, 67, 72, **84**, 88, 97, **98, 99, 103, 105**, 107, **110, 114**, 115, 123
VII	8, 10, **12, 15, 16**, 18, **19, 19, 20**, 21, 23, **24, 27**, 27, 29, 32, **36, 39**, 39, 39, 40, **41, 41, 44**, 46, 49, 52, 54, **56**, 57, **58**, 64, 66, 66, 66, **72, 81, 87**, 88, **89, 94, 97**, 103, **105, 111**, 132, 139, **152, 173**, 194
VIII	2, 4, 4, 5, **7, 7**, 7, **8, 8, 9, 9, 9, 10**, 10, 10, **11**, 11, 12, **13, 14**, 14, **15**, 15, **16, 16**, 16, 17, 17, **18**, 19, **20, 20**, 20, 21, **22**, 24, 24, **26, 26, 29**, 31, 33, 35, **39**, 42, **45, 57, 58**, 86, 94
IX	**2, 4**, 4, 4, **6**, 6, 6, **7, 7**, 7, 7, 7, **8, 9, 10, 11**, 11, 11, 13, **14, 14**, 15, 15, 15, **16**, 16, **17, 17, 18, 18, 18**, 21, 21, 22, **23**, 31, 35, 37, **44, 48**, 56, 71, **77, 89**, 102, 105, 113, **115, 120, 162**
X	4, 7, **11, 14**, 15, **21, 24, 27**, 32, 34, **35**, 35, **37, 38**, 41, 43, **44, 47**, 48, **49, 53, 54**, 57, 57, 58, **62, 63, 65, 67**, 67, 71, 71, 72, 73, 74, **76**, 78, **84, 87**, 89, 96, **104, 113**, 125, **133, 152, 174**, 181, 193, 201
XI	0, 1, 2, 2, **3, 3, 4**, 4, **5**, 6, 6, **7, 7**, 7, 7, 8, 8, 8, **9, 9**, 9, **10, 11, 11**, 11, 13, **14**, 16, **18**, 18, 19, 22, **27**, 29, 29, **32, 32**, 37, 37, 38, **40, 44**, 48, **58**, 66, **81**, 86, **87, 109, 111**
XII	**2, 3, 3, 4, 5**, 5, **6, 6**, 6, **7, 7**, 8, 8, 8, 9, 9, **10**, 10, 10, 10, **11**, 11, 11, **12, 13, 15, 17**, 17, **19**, 19, 19, 22, **24**, 24, **26**, 26, **28, 31, 34, 36, 39**, 39, 42, 44, **47, 49, 61**, 93, 95, 101
XIII	**0**, 0, **1, 2, 2**, 2, **3, 3, 4**, 4, 4, **5, 5, 5**, 6, **7, 7**, 7, 9, **10, 10**, 12, **14**, 15, **17**, 21, **24, 26, 26, 29**, 31, 33, **36**, 38, 47, **51**, 57, 62, 64, 71, 74, 83, 91, 92, 97, **99**, 99, **104**, 116, **121**
XIV	4, 7, 8, **9, 9, 11**, 12, **14**, 14, 14, **15, 15, 15**, 15, 16, 17, 17, **19**, 19, **23, 23, 25**, 25, 26, 26, **27**, 27, **29, 29**, 31, 32, **34, 47, 49, 52, 57**, 59, 67, 69, **81**, 92, **97**, 99, **107**, 113, 124, **148, 205, 279**, 291
XV	**1, 2, 4, 4**, 5, 6, **7**, 7, 7, **9, 9**, 12, 12, **14**, 15, **16, 16, 18, 21**, 23, 27, 29, **32**, 33, 35, **36, 38**, 39, **43**, 47, 49, **57, 64**, 83, 89, 97, 99, 104, **117**, 134, **162, 167**, 181, **193**, 197, 204, **231**, 259, **271, 298**
XVI	2, **3**, 4, 4, **7, 7, 9**, 11, **12**, 16, 17, **19, 19**, 19, **20**, 21, **25**, 27, 27, **28, 28, 29, 29, 29**, 31, **33**, 34, 34, **36**, 41, **45**, 46, **48**, 53, 56, 58, **67, 79**, 82, 88, **89**, 89, 93, **98, 103, 107**, 114, 137, **152**
XVII	**2, 5**, 7, 7, 8, 8, **10, 11, 11**, 11, **12, 12, 12**, 13, 15, **18**, 19, 19, **23**, 25, **28, 29**, 31, 33, **37**, 44, 46, **49**, 50, **51**, 54, 56, **61**, 63, 66, **69**, 72, **76**, 79, **83, 85, 87, 89**, 94, **97**, 104, 111, **131, 163**, 216
XVIII	**0, 0, 0**, 0, **1**, 1, 1, 1, 1, **2, 2, 2**, 2, 2, **3**, 3, 3, 3, **4, 4, 4**, 4, 4, 4, **5, 5, 5**, 5, 5, 5, 5, 5, **6**, 6, 6, **7, 7, 7, 7, 7**, 7, **8, 8**, 8, 8, **9**, 9, **10**, 11, 11, 11, 11, 11, **12, 12**, 12, 12, 12, 12, **14**, 14, 14, 14, **15, 16**, 17, **18, 19**, 19, **20**, 20, 20, **21, 21**, 22, 23, 24, **25, 26**, 26, 26, 26, 26, 28, **30, 31**, 31, **32**, 37, **39, 40, 42, 50**, 58, **59**, 59, 61, **64**, 67, 68, **76, 79, 83, 84**, 89, **90, 92**, 93, **97, 100**, 113, **116**, 133, **144**

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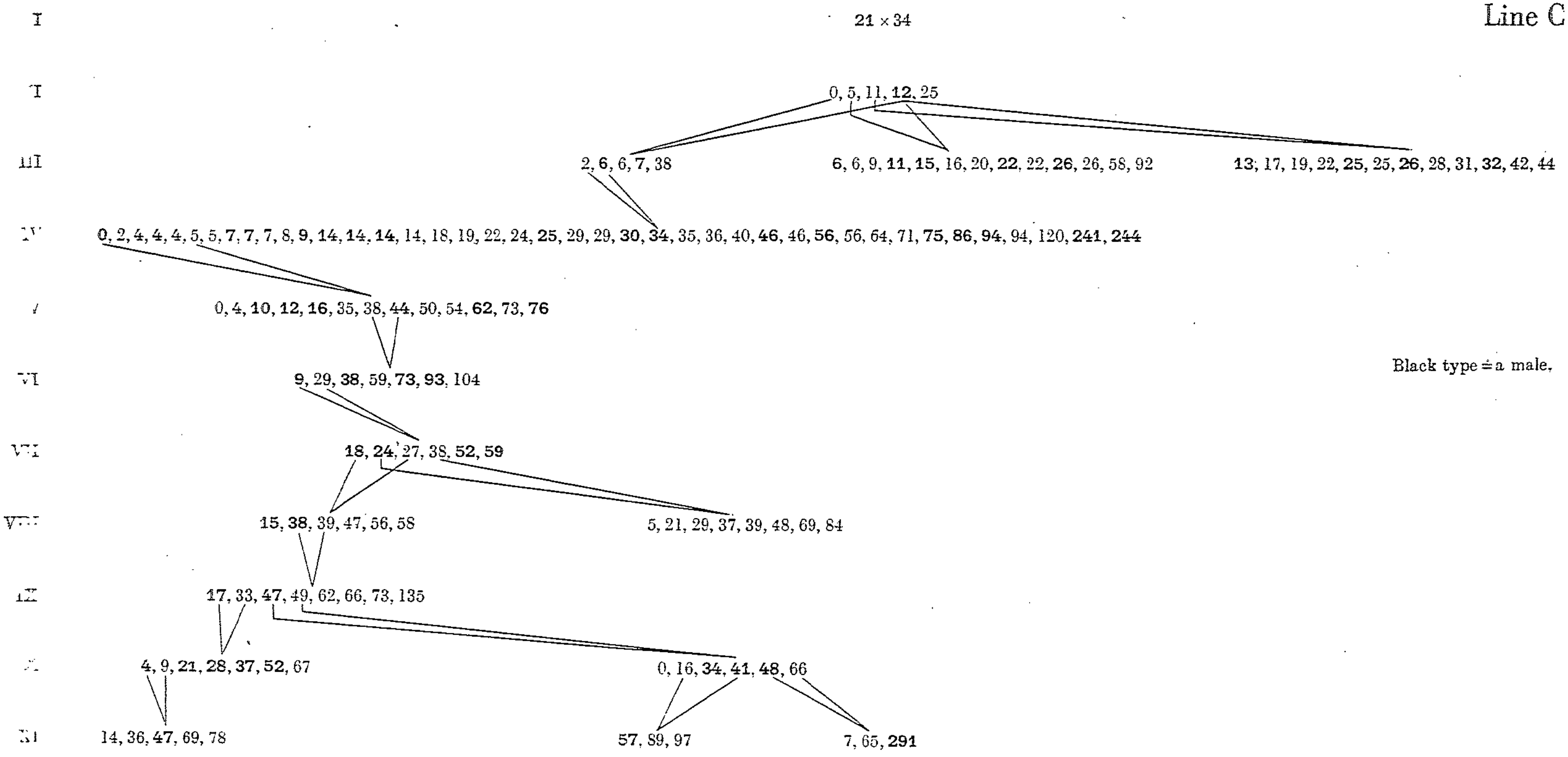
Line C



Black type ≐ a male.