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FOURTH (FINAL) REPORT ON A TEST OF McDOUGALL'S LAMARCKIAN EXPERIMENT ON THE TRAINING OF RATS

BY THE LATE W. E. AGAR AND
F. H. DRUMMOND, O. W. TIEGS AND M. M. GUNSON
The Zoology Department, University of Melbourne

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INTRODUCTION

This is the final report on the experiment, begun by us in 1932, and of which three interim reports have already been published (1935, 1942, 1948). It was essentially an examination of the well-known experiment of McDougall, purporting to have demonstrated a Lamarckian effect in the inheritance of an induced light phobia in rats.

Our experiment consisted in placing the rats into a tank of water from which they emerged by the choice of one of two exits. Of these one was illuminated, the other not; and a preference for the non-illuminated (dim) exit was induced in the rats by electrifying the illuminated exit. With this apparently simple problem of learning to avoid the lighted exit, the rats were daily confronted until they learnt to solve it. The number of errors made by the rats was recorded and a sustained diminution in the number of these errors in successive generations, measured against a control series of generations, is the criterion for the operation of a Lamarckian factor.

Over the thirty-two generations of McDougall's experiment, for which records are available, there was such a progressive decline in the number of errors. McDougall attributed this improvement in facility in learning to the inheritance of the effects of ancestral training. At the time, this conclusion was justified to the extent that no alternative explanation could be advanced to account for it. It was this that led us, and Crew, to repeat the experiment. Crew (1936) found no evidence of increased facility in learning during the eighteen generations of his experiment.

TRAINING PROCEDURE

We will give a brief description of the methods we have used; fuller details are to be found in our First Report. The apparatus was essentially as designed by McDougall (1930). It consisted (Fig. 1) of a tank of water divided into three parallel passages communicating with one another at the far curved end of the tank. At the near end of each side-passage was a sloping wire ramp up which the rats could scramble from the water. Behind a sheet of ground glass at the back of each ramp was an electric lamp which shone down the passage and illuminated its communication with the central passage. The circuit was arranged so that one or the other lamp could be lit alternately. Coupled with the lighting circuit was a second circuit that electrified the ramp on the illuminated side; a current of 230 V., 1·2 mA. was used, with a duration of 3 sec.

A rat placed in the water at the near end of the central passage swam along it and then had a choice of two escape routes. If it chose the bright ramp it escaped at the expense of a 3 sec. electric shock. The rat had to learn to escape always by the dim exit, irrespective of whether this was on the right side or the left. Facility in learning was measured by the number of errors made, i.e. the number of escapes by the bright exit, before it learnt to use the dim one always. A rat was held to have learnt the task as soon as it made twelve consecutive correct runs.

Our routine procedure has been to wean the rats when 26 days old. To acquaint

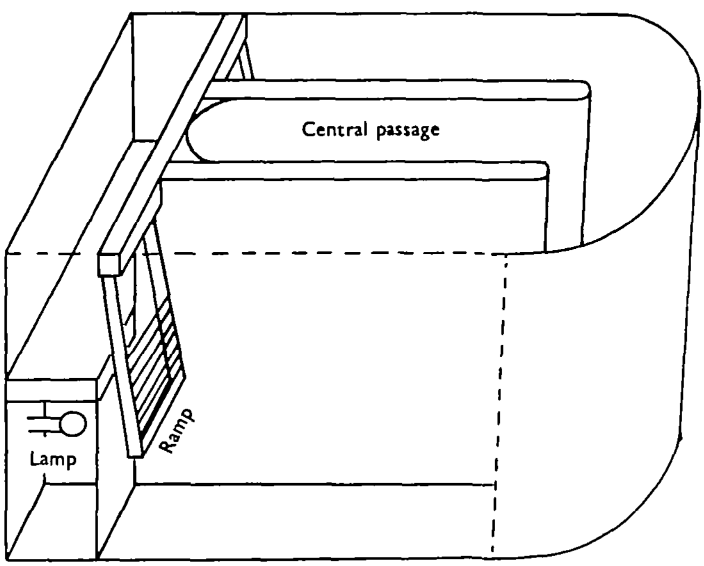

Fig. 1. Diagram of training tank.

them with the training apparatus, they were given, on the following day, six 'runs' without illuminated ramps, after which normal training began. This consisted of four runs per day for 5 days (the animals still being rather small) and thereafter six per day until the task was learnt. A small proportion of rats, that had failed to solve the problem by the 52nd day of training, were given 'special training'. They were, almost without exception, rats that had developed the habit of going exclusively to one ramp and were quite unable to solve the problem because of unawareness of the alternative exit. 'Special training' consisted in forcing the animals, usually against strong resistance, to take the correct pathway. Training of all rats was continued after learning was complete, and until the time of mating, but was limited to two runs per day.

CONTROLS

A fundamental weakness in McDougall's experiment was his failure to maintain a control line of rats for comparison with his trained line. In our experiment we instituted a proper control line, bred parallel with the trained line and under the same conditions. All the rats were descendants of a single pair of Wistar origin. The first generation obtained from this pair (which was not trained) was divided into two groups, one of which was trained and became the ancestors of the trained line (*T*). The other group was not trained and became the ancestors of the control line (*C*). In each generation the required number of rats of the trained line was trained and mated as parents of the next generation. In the control line some litters were not trained but were kept as parents of the next generation; other litters of this line were trained to provide controls to the same generation of the trained line. These trained controls were, of course, not used for breeding. In this way each generation of the trained line was tested against an approximately equal number of controls, differing from the trained line only in the fact that their ancestors were not trained.

In our Third Report we stated that genetic differences in colour pattern and body size between the trained and control lines had appeared, and suggested that mutations could have been responsible for the consistent superiority of the trained line over the control between about generations 12–28. This raised the possibility that further mutations, having a direct effect on the rate of learning, might occur. If such mutations accumulated in the trained line their effect would simulate that of Lamarckian inheritance. To meet this possibility we took the precaution of maintaining from generation 41 onwards, two trained sublines (*TA* and *TB*) and two control sublines (*CA* and *CB*). The offspring of generation 40 of the trained line were divided into two groups. One became the ancestors of subline *TA*, the other, the ancestors of subline *TB*. The controls were treated in a similar manner. The two control sublines were thus joint controls to the two trained sublines; there was no special relationship between *TA* and *CA*, or between *TB* and *CB*. It may be stated at once that there was no evidence of divergence, in respect of facility in learning, between the sublines during the ten generations, 41–50.

MATING AND MORTALITY

The minimum age at which the rats were mated was 85 days. By this time even the rats which required 'special training' had learnt the task. In order that every rat, whether it had learnt quickly or slowly, should have an equal chance of becoming a parent, all the rats of a generation were mated at the same time.

The rats were mated without reference to their training scores. Except for a short period, brother-sister matings were avoided as far as possible. Not all the mated rats became parents of the next generation, for many of the matings proved infertile, and others did not produce litters till after the number of young required had been obtained. This, of course, applied to both the trained and control lines.

Of the 4654 rats which started training forty-three died before they had learnt the task. These forty-three rats have been excluded from our figures. Throughout the whole of the experiment there were no injuries of any kind attributable to the electric shock.

MEASURE OF PERFORMANCE

In previous reports we have discussed the problem of finding a satisfactory measure of the performance of a group of rats as a whole. The use of the arithmetic mean number of errors made by the rats is unsatisfactory owing to the extreme skewness of the distribution (Second Report, Table 1) and, in any case, is invalidated by our practice of giving 'special training' to the very slow learners. In this report, and for the analyses of the results of the experiment, we have used the measure adopted in our Third Report: 'The scores of the first thousand control rats were arranged in order of magnitude, and the whole group divided into ten classes, each containing as nearly as possible an equal number of rats, having regard to the fact that the number of errors are necessarily whole numbers.'

The resulting distribution is shown in Table 1.

Table 1. *The first 1000 controls classified according to the number of errors made*

Class ...	1	2	3	4	5	6	7	8	9	10
No. of errors	0–5	6–10	11–15	16–19	20–23	24–27	28–32	33–40	41–67	68–
No. of rats	93	110	102	105	93	96	106	95	99	101

Thus all the rats with training scores 0–5 errors inclusive are placed in class 1, and so on. The arithmetic mean of the classes so obtained will be referred to as the *mean class* of the group of rats concerned.

BODY SIZE IN THE TRAINED AND CONTROL LINES

In our Third Report we discussed a genetic difference in body size between the trained line and the control. Weighings made in generations 25–28, and also in generations 34–36, showed that the rats of the trained line were substantially heavier than the controls. At 26 days old the difference in mean weights was approximately 13 g. (Table 2).

Further series of weighings at 26 days old were made in generations 49 and 50. These showed (Table 2) that there was no difference in weight between the two trained sublines, but that the mean weights, by comparison with those of generations previously weighed, had fallen by about 9 g. The mean weights were: females (85) 43·6 g., males (70) 45·2 g. Only 6% of the rats in these two generations weighed more than 50 g.; in generations 25–28 and 34–36, 60% exceeded this weight.

In the controls, the mean weights of the two sublines in generation 49 were much the same. They conformed to those of earlier generations of controls and this was also true of subline *CA* of generation 50. However, in subline *CB* of this generation the mean weights were: females (23) 43·2 g., males (23) 43·8 g. These are practically the same as those of the trained sublines.

Greenman & Duhring (1931) have recorded the weights of a large number of rats from the Wistar Institute colony. Over a period of 4 years, eight groups of males and females were weighed. At 25 days old, the mean weights of the groups varied from 34·3 to 48·6 g. If 2·5 g. is added to the figures of Greenman & Duhring to allow for the fact that they refer to rats 1 day younger than ours, the total mean weights become: females (423) 43·2 g., males (455) 43·8 g.

Thus, at the end of our experiment there was no evidence of the genetic difference in body size which previously had distinguished the rats of the trained line from the controls and also from Wistar Institute stocks.

Table 2. *Mean weight in grams, with standard errors, of rats at 26 days. The figures in brackets are the number of rats weighed*

Generation	Trained line	Control line
25–28	♀ (73) 50·5 ± 0·5 ♂ (72) 50·4 ± 0·6	(153) 38·0 ± 0·4 (139) 38·7 ± 0·4
34–36	♀ (50) 53·0 ± 0·7 ♂ (50) 54·8 ± 0·7	(50) 38·0 ± 0·7 (50) 40·3 ± 0·7
49*A*	♀ (17) 42·6 ± 0·7 ♂ (12) 44·5 ± 1·4	(40) 36·1 ± 0·6 (29) 37·9 ± 0·6
49*B*	♀ (21) 43·0 ± 0·6 ♂ (14) 43·6 ± 0·8	(30) 36·4 ± 0·7 (23) 38·3 ± 0·7
50*A*	♀ (21) 43·3 ± 1·0 ♂ (20) 43·6 ± 1·0	(21) 38·0 ± 1·0 (24) 39·8 ± 0·9
50*B*	♀ (26) 45·2 ± 0·8 ♂ (24) 47·9 ± 1·0	(23) 43·2 ± 0·6 (23) 43·8 ± 0·5

GENERAL RESULTS OF EXPERIMENT

Data covering generations 1–36 are given in our earlier reports. Tables 3 and 4 of the present report give the data for generations 37–50 which conclude the experiment. The results are summarized in two graphs (Figs. 2, 3). Fig. 2 shows the annual performances over the 20 years of the experiment; Fig. 3 gives the performances of successive generations. In the latter figure, we have arranged the generations as nearly as possible in groups of 4 (see Table 4), in order to minimize chance fluctuations.*

The general result is that periods of progressively decreasing scores have alternated with periods of progressively increasing scores, and in this the controls have participated. Thus there was a fairly regular decrease in the number of errors during the first sixteen generations, a slight increase in the following four and then a further decrease until the twenty-eighth. Over the next eight generations there was a marked increase in the number of errors, and high scores were maintained until the 40th generation after which a further decrease occurred. Thus in spite of the great improvement during the first half of the experiment the scores of the

* The last group necessarily contains only two generations (49 and 50) and in the first group of controls only generations 2–4 are, of course, included.

Table 3. *The number of errors made (shocks received) by each rat, the median number of errors, and the mean class, in each of generations* 37–50

(*T*, trained line; *C*, control line. *S* indicates that the rat qualified for special training. In the trained line the rats which became parents of the next generation are in heavy type.)

Generations		No. of rats	Median	Mean class	No. of errors made by each rat
37	*T*	50	29	6·48	5, 5, 8, 9, **15**, 16, 17, 18, **19**, **19**, **21**, 21, **23**, 23, 25, 25, **27**, 27, 27, 27, 28, **29**, **29**, 29, 29, 29, **30**, **30**, 30, 30, **31**, **32**, **34**, 34, 34, 35, 37, 38, 38, **40**, **40**, 40, 43, **47**, 52, 54, **58**, 91, **99**, *S*
	C	50	27·5	6·48	2, 6, 10, 11, 12, 13, 14, 14, 17, 17, 18, 18, 19, 19, 19, 21, 22, 23, 23, 24, 25, 25, 25, 27, 27, 28, 28, 29, 33, 34, 36, 38, 38, 40, 41, 44, 44, 51, 53, 56, 59, 65, 67, 84, *S*, *S*, *S*, *S*, *S*, *S*
38	*T*	50	27·5	6·16	9, 10, 11, 11, **12**, **14**, 14, 15, **16**, **18**, **19**, 19, 19, 20, 20, **21**, 22, 23, 23, 24, 25, 25, 26, 26, 27, 28, 29, **30**, 30, 31, **31**, **32**, 32, 32, 32, 33, 34, 36, 36, 38, 39, 41, **42**, 45, 47, 49, 50, 53, 56, 124
	C	50	26·5	6·32	4, 5, 7, 8, 8, 9, 10, 12, 12, 16, 18, 20, 21, 21, 22, 22, 22, 22, 23, 24, 24, 25, 25, 26, 26, 27, 28, 30, 31, 32, 32, 33, 35, 38, 39, 41, 41, 42, 44, 46, 47, 49, 53, 59, 97, 126, *S*, *S*, *S*, *S*
39	*T*	50	21	5·00	**2**, 2, 2, 2, 3, 4, **5**, 7, 8, **9**, 9, 9, 10, 11, 11, 12, 12, **14**, 15, 17, 17, 17, 20, **21**, 21, 21, **22**, 22, **27**, 27, **28**, 30, **31**, 31, 32, 32, 34, 34, 35, 36, 36, 38, 38, 38, 39, 40, **46**, 54, 60, 93
	C	50	22	5·88	6, 8, 9, 11, 13, 14, 14, 15, 15, 16, 16, 16, 16, 17, 17, 17, 18, 18, 18, 19, 19, 21, 21, 21, 22, 22, 23, 25, 25, 29, 29, 30, 31, 32, 33, 34, 34, 36, 41, 41, 42, 46, 48, 57, 67, 74, 76, 93, 108, 118
40	*T*	49	25	5·69	7, 8, **11**, 11, 11, 11, 13, **14**, 14, 15, 15, 16, 17, **18**, 19, 19, 19, 20, **21**, 21, 22, 23, 24, 25, 25, 26, 27, 28, 28, 28, **30**, 30, 30, 30, 30, **31**, **31**, **31**, **32**, **33**, **35**, 37, 39, 39, 40, 44, 48, **55**, 75
	C	33	22	5·24	6, 6, 8, 8, 9, 10, 11, 12, 12, 13, 13, 14, 15, 16, 20, 20, 22, 23, 23, 25, 26, 29, 31, 31, 32, 33, 36, 38, 47, 54, 55, 69, *S*
41	*TA*	35	23	5·46	2, 5, 6, 9, 10, 11, 11, 11, **12**, 12, 13, 14, 16, 18, **20**, 20, 21, 23, 24, 25, 25, 26, **27**, **29**, 29, 32, **34**, **49**, 52, 53, **54**, 54, **68**, 75, **119**
	TB	36	16·5	4·14	1, **3**, 3, 4, 4, 5, 6, 6, 8, **9**, **9**, 9, 9, 14, 15, 15, **16**, 16, **17**, 17, 18, 18, **19**, 19, 20, **21**, 26, **27**, 27, **32**, 32, **43**, **46**, 46, 48, 97
	CA	30	20	4·63	4, 11, 11, 12, 13, 13, 13, 14, 14, 14, 14, 15, 16, 17, 19, 21, 21, 21, 21, 22, 22, 23, 25, 26, 26, 29, 32, 40, 48, 49
	CB	30	22	5·53	2, 10, 12, 13, 14, 14, 15, 15, 15, 15, 17, 17, 19, 20, 22, 22, 26, 27, 28, 29, 30, 32, 34, 39, 41, 44, 52, 57, 82, 105
42	*TA*	34	15·5	3·94	**3**, **5**, **5**, 6, **7**, 7, **8**, 8, 8, 10, 12, 12, 14, 15, 15, 15, 15, **16**, 16, 17, 18, 18, 19, 21, 21, 22, **23**, **24**, 24, 25, **26**, 55, 60, **74**
	TB	32	18·5	4·75	**4**, 5, 6, 6, 7, 7, 8, 11, **12**, 12, 12, **13**, 13, 16, 16, 18, **20**, 20, 21, **22**, 22, 22, 23, 25, 27, **32**, 41, 42, **52**, 61, 96, **101**
	CA	29	25	6·21	0, 5, 6, 9, 11, 13, 15, 16, 19, 23, 23, 23, 24, 24, 25, 32, 35, 37, 37, 39, 39, 42, 42, 44, 81, 103, 105, *S*, *S*
	CB	28	21·5	5·03	4, 4, 6, 10, 12, 12, 15, 15, 15, 17, 17, 18, 20, 21, 22, 22, 23, 25, 26, 28, 29, 30, 32, 37, 39, 40, 57, *S*
43	*TA*	36	15·5	3·92	2, **5**, 5, 6, **7**, 7, 7, 8, 9, **10**, 10, 10, 11, **12**, 12, 12, 13, **15**, 16, 16, 17, **19**, 19, **20**, 20, 23, 23, **24**, 25, 26, 26, 29, **31**, **31**, 33, 53
	TB	34	24	5·88	7, 8, 10, 12, 12, **14**, **15**, 15, 17, **19**, 20, 21, 22, 22, 22, **24**, **24**, 24, **25**, 25, **26**, 27, 27, 28, 32, 34, **35**, 43, 44, 45, 46, **47**, 63, **65**
	CA	43	21	4·93	0, 2, 4, 6, 6, 7, 8, 8, 9, 9, 10, 10, 11, 11, 14, 15, 15, 18, 20, 20, 20, 21, 21, 21, 22, 23, 23, 24, 24, 24, 24, 24, 24, 34, 35, 39, 39, 41, 119, 128, *S*, *S*, *S*
	CB	8	—	6·62	15, 17, 24, 25, 36, 36, 37, *S*
44	*TA*	37	17	4·43	3, 3, 4, 6, 6, 6, 6, **8**, **8**, 8, 9, 10, 11, **12**, **13**, 13, 15, 16, 17, 18, 18, 18, **20**, **20**, 23, **24**, 24, 26, **28**, 28, **33**, 38, 39, **40**, 55, *S*, *S*
	TB	36	15	3·83	**4**, **7**, 7, **9**, 9, **10**, **10**, 10, 10, **11**, 11, 11, **12**, 12, 12, 12, 13, 14, 16, 16, **17**, 17, **18**, 19, 20, 20, **21**, 21, 21, **22**, 23, **25**, 27, 29, **35**, 37
	CA	29	20	5·27	3, 5, 7, 8, 9, 9, 10, 11, 12, 14, 16, 17, 19, 19, 20, 22, 23, 24, 24, 28, 33, 39, 48, 61, 62, 64, 87, *S*, *S*
	CB	30	11	3·30	5, 5, 5, 6, 6, 6, 6, 7, 7, 7, 9, 9, 10, 10, 10, 12, 12, 13, 13, 14, 14, 15, 15, 16, 17, 17, 28, 43, 92, *S*

Table 3 (*continued*)

Generations		No. of rats	Median	Mean class	No. of errors made by each rat
45	*TA*	36	15	3·72	0, 2, 3, 4, 5, 5, 6, 7, 7, 8, 8, 9, 9, 10, 12, 12, 13, 15, 15, 15, 16, 17, 19, 20, 21, 22, 22, 23, 24, 25, 26, 29, 30, 33, 35, 45
	TB	37	17	4·13	3, 5, 6, 7, 7, 8, 9, 9, 10, 10, 11, 11, 11, 11, 14, 15, 16, 16, 17, 17, 17, 18, 19, 19, 21, 21, 23, 23, 23, 24, 24, 25, 28, 34, 35, 41, *S*
	CA	33	17	4·18	0, 1, 3, 4, 6, 7, 8, 9, 10, 10, 11, 11, 11, 15, 17, 17, 17, 17, 18, 21, 23, 23, 24, 24, 25, 25, 25, 25, 26, 29, 32, 53, 68
	CB	38	17	4·26	0, 0, 4, 4, 6, 8, 9, 10, 10, 10, 11, 11, 11, 12, 13, 14, 15, 16, 17, 17, 18, 18, 20, 22, 22, 23, 23, 23, 24, 25, 28, 29, 31, 33, 39, 40, 48, 52
46	*TA*	34	18	4·73	2, 4, 8, 9, 10, 10, 13, 13, 15, 15, 17, 17, 17, 17, 17, 18, 18, 18, 19, 20, 21, 23, 24, 24, 26, 26, 27, 29, 33, 36, 37, 41, 42, 64
	TB	38	26	6·34	11, 12, 13, 19, 19, 20, 20, 21, 21, 22, 22, 22, 23, 23, 23, 24, 24, 24, 26, 26, 27, 27, 28, 28, 29, 31, 32, 33, 35, 36, 37, 40, 41, 46, 47, 75, *S*, *S*
	CA	40	22·5	5·37	0, 3, 6, 6, 7, 13, 14, 15, 15, 16, 17, 17, 18, 19, 20, 20, 21, 21, 22, 22, 23, 23, 23, 23, 24, 25, 25, 26, 26, 27, 29, 34, 36, 41, 41, 45, 53, 80, 87, 110
	CB	29	22	4·90	2, 3, 4, 4, 9, 10, 11, 12, 15, 16, 16, 18, 18, 18, 22, 23, 24, 24, 27, 27, 28, 28, 31, 32, 34, 37, 40, 52, *S*
47	*TA*	34	20	4·79	1, 2, 3, 5, 6, 6, 6, 7, 11, 12, 12, 14, 16, 17, 18, 18, 20, 20, 21, 22, 24, 24, 25, 25, 26, 30, 31, 32, 33, 33, 37, 45, 50, 150
	TB	34	17·5	4·94	3, 6, 7, 7, 9, 10, 11, 11, 12, 12, 12, 13, 14, 15, 15, 15, 16, 19, 20, 22, 25, 27, 27, 28, 29, 29, 32, 33, 34, 40, 46, 81, 100, *S*
	CA	39	20	4·72	1, 5, 5, 5, 6, 8, 9, 10, 10, 11, 13, 15, 15, 16, 17, 17, 17, 18, 19, 20, 20, 21, 22, 22, 25, 26, 28, 28, 29, 29, 30, 30, 31, 32, 34, 34, 35, 37, 46
	CB	34	26	5·44	3, 3, 4, 5, 6, 6, 7, 10, 11, 13, 13, 14, 17, 20, 21, 22, 25, 28, 29, 30, 30, 30, 31, 32, 33, 33, 34, 35, 36, 50, 59, 60, 70, *S*
48	*TA*	35	21	4·88	5, 8, 9, 10, 11, 12, 12, 14, 14, 14, 15, 15, 17, 17, 19, 20, 20, 21, 22, 22, 22, 23, 24, 24, 25, 27, 28, 29, 30, 31, 32, 36, 36, 58, 65
	TB	35	22	5·31	6, 7, 7, 8, 8, 9, 11, 12, 13, 14, 15, 17, 17, 19, 21, 21, 22, 22, 23, 26, 26, 29, 31, 31, 32, 32, 33, 33, 33, 35, 36, 37, 41, 42, 44
	CA	35	15	3·83	5, 5, 5, 6, 6, 7, 8, 8, 8, 8, 9, 9, 11, 12, 12, 12, 15, 15, 15, 15, 16, 16, 18, 19, 19, 23, 23, 24, 25, 29, 30, 32, 39, 49, 50
	CB	25	20	4·32	7, 8, 8, 9, 9, 10, 12, 13, 14, 16, 17, 18, 20, 20, 21, 24, 26, 27, 27, 29, 31, 53, 91, 110, 111
49	*TA*	35	20	5·09	5, 9, 9, 9, 10, 11, 11, 12, 12, 13, 15, 15, 16, 16, 18, 19, 20, 20, 20, 21, 23, 24, 24, 24, 27, 28, 31, 31, 34, 38, 42, 47, 48, 62, *S*
	TB	35	20	4·86	7, 10, 10, 11, 11, 12, 12, 13, 13, 15, 15, 17, 17, 18, 19, 19, 19, 20, 23, 23, 23, 24, 26, 26, 26, 26, 27, 28, 29, 29, 31, 31, 38, 39, 41
	CA	34	17·5	4·62	2, 3, 7, 9, 11, 13, 13, 13, 13, 13, 14, 14, 15, 15, 16, 16, 17, 18, 19, 22, 22, 23, 24, 25, 25, 25, 25, 27, 29, 29, 30, 52, 87, *S*
	CB	35	22	5·54	2, 7, 8, 9, 11, 12, 13, 13, 15, 15, 15, 16, 18, 19, 19, 20, 21, 22, 23, 24, 25, 28, 30, 32, 33, 36, 38, 39, 40, 50, 56, 58, 76, 113, *S*
50	*TA*	50	19·5	4·74	2, 5, 6, 7, 8, 8, 8, 9, 9, 10, 10, 11, 12, 13, 15, 16, 16, 17, 17, 17, 17, 18, 19, 19, 19, 20, 20, 20, 20, 21, 22, 23, 23, 25, 25, 25, 28, 29, 30, 30, 30, 30, 30, 32, 36, 36, 37, 40, 47, *S*
	TB	50	18	4·62	7, 7, 7, 7, 8, 8, 8, 9, 9, 9, 9, 9, 10, 11, 12, 12, 12, 12, 13, 13, 14, 14, 14, 16, 17, 18, 18, 18, 19, 19, 20, 21, 22, 22, 22, 23, 23, 25, 27, 28, 32, 33, 33, 34, 36, 39, 50, 58, 68, 71, *S*
	CA	50	18·5	4·78	4, 4, 4, 5, 5, 5, 6, 7, 7, 7, 8, 8, 9, 10, 11, 12, 13, 14, 15, 15, 16, 17, 17, 18, 18, 19, 20, 20, 21, 21, 22, 24, 25, 27, 27, 28, 31, 32, 33, 34, 34, 37, 37, 39, 42, 48, 56, 138, *S*, *S*
	CB	50	13·5	3·82	2, 4, 4, 5, 6, 6, 6, 7, 7, 7, 7, 8, 9, 9, 9, 9, 10, 10, 10, 10, 10, 11, 12, 12, 12, 15, 16, 17, 19, 19, 20, 22, 22, 23, 23, 23, 24, 24, 25, 25, 25, 26, 27, 27, 28, 31, 31, 32, 33, 34

last six generations were of the same order as those of generations 13–16. Throughout the whole experiment the parallelism between the performances of the trained and control lines was remarkable; over the last few generations the controls were generally even superior to the trained line.

Table 4. *Summary of the results of the fifty generations in groups of four generations*

Generations	No. of rats		Mean class			% in class 1		% in class 10	
	T	*C*	*T*	*C*	Ratio: *T/C*	*T*	*C*	*T*	*C*
1–4	64	54	7·89	7·89	1·00	0·00	0·00	25·00	27·78
5–8	116	91	7·34	6·49	1·13	3·45	4·40	23·28	10·99
9–12	105	177	6·23	6·33	0·98	6·67	3·95	10·48	11·86
13–16	187	148	4·41	5·01	0·88	15·51	10·81	6·42	5·41
17–20	230	200	5·07	5·29	0·96	11·30	11·50	4·35	14·00
21–24	197	183	4·46	4·75	0·94	18·78	16·39	6·09	6·01
25–28	189	197	4·11	4·66	0·88	25·40	7·61	4·23	5·58
29–32	160	150	5·00	5·03	0·99	11·88	8·67	4·38	8·00
33–36	180	199	6·12	6·02	1·02	3·89	3·52	6·67	12·06
37–40	199	183	5·83	6·05	0·96	4·52	1·64	3·01	10·93
41–44	280	227	4·50	5·03	0·89	7·14	6·22	3·21	8·44
45–48	283	273	4·87	4·71	1·03	16·61	20·51	1·76	1·83
49–50	170	169	4·80	4·65	1·03	14·71	21·89	1·77	3·55

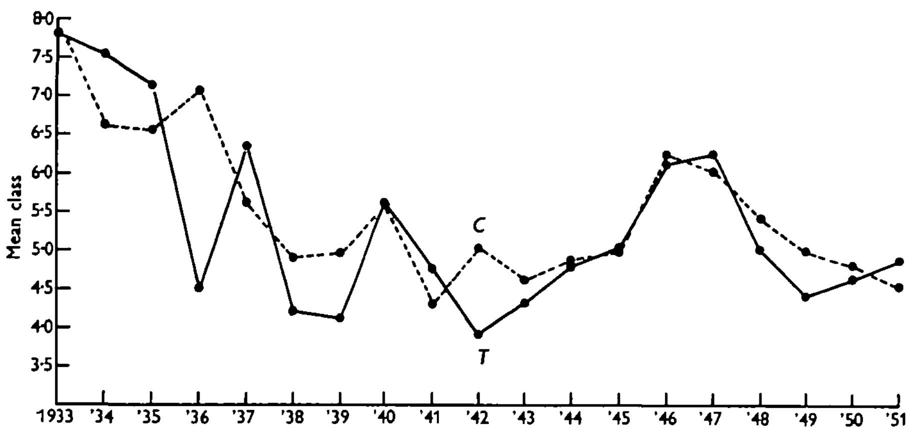

Fig. 2. Continuous line, line *T*; broken line, line *C*. The mean classes are those of all rats which began training in the year referred to. The first point, 1933, includes some rats which began training late in 1932; the last point, 1951, includes some rats which began training early in 1952.

It is unfortunate that McDougall did not publish full details of the performances of his rats; his reports give only the arithmetic mean of the scores in each generation and the scores of the best and worst rats. But although an accurate comparison of the rate, and extent, of changes in learning in the two experiments cannot be made, it is clear that the improvement which characterized our first twenty-eight generations closely parallels that of McDougall's thirty-two generations and it seems probable that the same factor, or factors, operated in the two experiments. But

McDougall's claim that the improvement was due to Lamarckian inheritance is plainly invalidated first, by the performance of our control line and secondly, by the fact that, in our experiment, the improvement was not maintained in later generations.

DISCUSSION OF RESULTS

What is the explanation of the observed changes in the rate of learning? Selection can be ruled out. McDougall found that improvement was continued when he deliberately practised adverse selection and, in our experiment, it would be difficult to explain on any selection hypothesis, why, with a standardized system of training and mating, the direction of change in rate of learning should be periodically reversed. The parallel performance of the trained and control lines suggests that

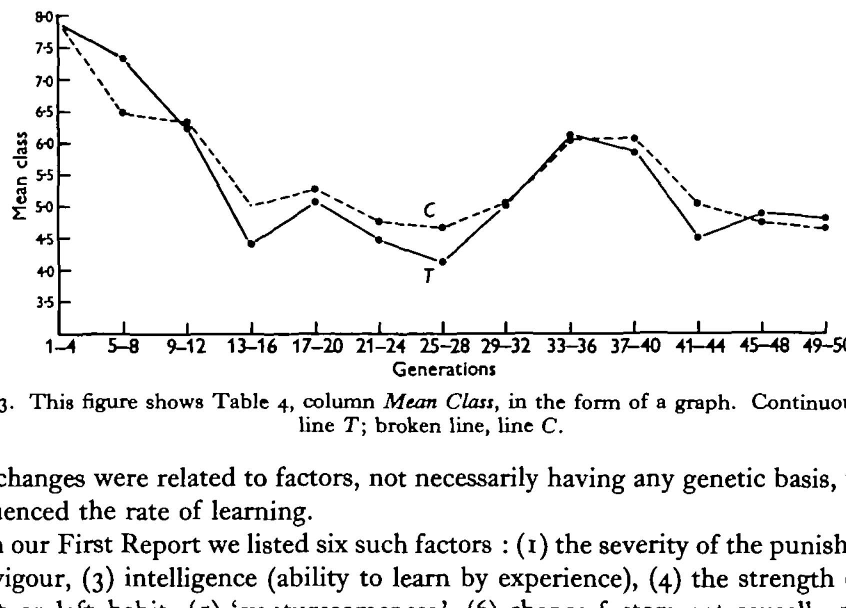

Fig. 3. This figure shows Table 4, column *Mean Class*, in the form of a graph. Continuous line, line *T*; broken line, line *C*.

the changes were related to factors, not necessarily having any genetic basis, which influenced the rate of learning.

In our First Report we listed six such factors : (1) the severity of the punishment, (2) vigour, (3) intelligence (ability to learn by experience), (4) the strength of the right or left habit, (5) 'venturesomeness', (6) chance factors not causally related to the learning process at all. Subsequent analysis of the data has shown that yet another factor needs consideration and that the performance of the rats was influenced by the season of the year in which they were trained. The separate or additive effects of these seven factors could explain the great variation in the performances of individual rats and the differences between particular generations, but only the first two, i.e. severity of punishment and vigour, seem to offer any basis for an explanation of trends of improvement or decline extending over a number of successive generations.

(*a*) *Seasonal effect*

When the rats of the whole fifty generations of the two lines are grouped according to the month in which they commenced their training and the mean class is calculated for each of the 12 months, it is found that, starting in February, the means increase regularly to reach a maximum value in July and then decrease regularly to a minimum value in November (Fig. 4, Table 5).

In order to find whether this seasonal factor had operated throughout the experiment, similar analyses were made after dividing the experiment into four 5-year periods. In the early months of the year the results were erratic, but from March–April onwards generally conformed to the pattern of the previous analysis and showed consistently that rats which commenced their training during the winter months of June, July and August were at a disadvantage by comparison with those which commenced training in November and December.*

This effect may have been due, in part, to our failure to maintain a constant temperature in the colony room and in the water in the tank. The only precautions taken were, that in winter, the room was heated and warmed water was used in the tank. In neither case, however, was the temperature raised to summer levels.

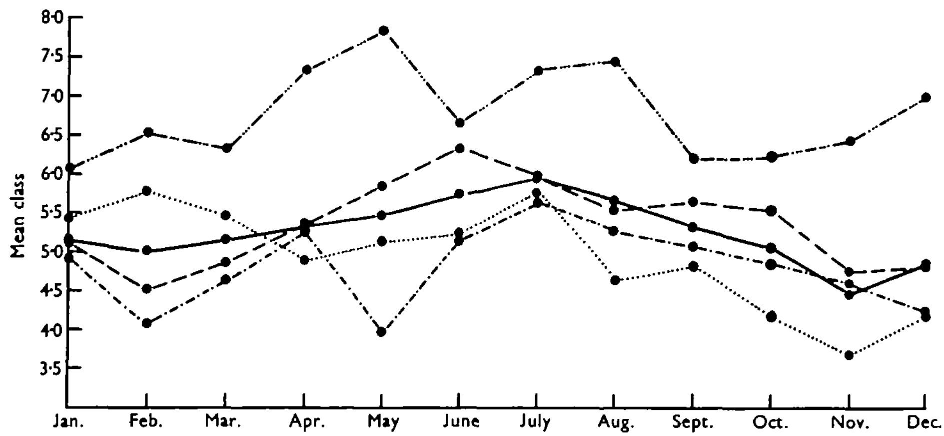

Fig. 4. The mean classes are those of the rats which began training in the month and period referred to. ——, 1932–52; —···, 1932–7; ····, 1938–42; – – –, 1943–7; –·–, 1948–52.

The lower water temperature during the winter may have had a slightly adverse effect on the performance of the rats, for Wever (1932) and Hack (1933) have found that the rat's incentive to escape from immersion varies with water temperature, being greatest at low temperatures. At lower temperatures (10–20° C.) the rats after being placed in the water swam strongly and directly to the landing platform. At temperatures from 30 to 40° C., Wever states that 'many of the animals did not head for the goal immediately but spent some time in casual exploration'. Hack describes the rats at 37·5° C. as showing an 'inquisitive attitude' with frequent reversals and re-entries into the blind alleys of the maze. This latter type of behaviour, we believe, facilitated learning in our experiment, but we are disinclined to attribute seasonal variation in performance to differences in water temperature; for the greatest range in temperature would not have exceeded 12–22° C. and the

* The main divergences from the pattern are the low values of the class mean in the May group, 1948–52, and the June group, 1932–37. In both groups the number of rats was small—considerably less than half the average number for the other months.

Table 5. *The rats of lines T and C combined classified according to the month in which they began their training*

		Month in which training began											
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1932–7	No. of rats	67	40	97	36	39	15	45	83	84	38	49	66
	Mean class	6·09	6·52	6·33	7·33	7·84	6·67	7·34	7·45	6·20	6·24	6·43	7·00
1938–42	No. of rats	21	69	103	154	32	60	114	94	115	116	147	127
	Mean class	5·43	5·79	5·46	4·89	5·12	5·23	5·79	4·63	4·81	4·16	3·69	4·17
1943–7	No. of rats	90	70	151	103	80	109	90	139	115	182	41	99
	Mean class	5·13	4·51	4·89	5·35	5·86	6·36	5·98	5·55	5·65	5·56	4·75	4·82
1948–52	No. of rats	227	93	177	73	54	95	146	109	112	146	247	82
	Mean class	4·92	4·09	4·61	5·26	3·96	5·15	5·61	5·29	5·09	4·85	4·52	4·21
1932–52	No. of rats	405	272	528	366	205	279	395	425	396	482	484	374
	Mean class	5·18	5·01	5·17	5·33	5·48	5·72	5·95	5·67	5·32	5·06	4·48	4·84

maximal temperatures would have occurred in summer, not in November, which was the period of minimum scores. But in any case, seasonal effects cannot possibly account for trends, lasting over a period of some years, and it is primarily with these that we are here concerned.

As will be shown later, we do attach great importance to the effects on learning, of differences in behaviour in the tank, but we believe that these differences were largely the expression of variations in the health and vigour of the rats.

(b) *Severity of punishment*

In his preliminary experiments, McDougall found that the strength of shock had considerable effect on the rate of learning. Thus if the severity of punishment tended to wax and wane over long periods the performance of the rats would show corresponding trends. We are satisfied that this effect did not operate in our experiment. The importance of a standardized punishment was recognized from the beginning and the precautions taken to ensure this (see First Report) have been maintained. The electrical installations, as shown by periodical tests, have remained in perfect order.

(c) *Vigour*

McDougall, Crew and ourselves have all noted that less vigorous rats tended to learn more quickly. Crew attributed this to their receiving more severe punishment. We, however, agree with McDougall that it was mainly a result of their slower and more hesitant progress through the water which gave them more time to perceive the situation.

McDougall, while admitting the relationship, was inclined to minimize its effect. He wrote (1938, p. 374): 'very great vigour and liveliness is a little unfavourable to quick learning and a somewhat diminished or less-than-average vigour is probably slightly favourable'. Crew, having noted that poorly developed, feeble rats learnt quickly, suggested that 'as a general rule, the more vigorous the rat the higher the score may be expected to be'. In our First Report we produced evidence to support this view. Fifteen rats of the 3rd–5th generations which, before the 10th day of training and before learning, had been noted on the training cards as 'weak' or 'undersized' had an average score well below the general average of these generations. There was also evidence from generation 17 which was severely debilitated by a mite infestation. After this had been controlled and the diet changed there was an extraordinary improvement in the health of the colony and a striking change for the worse in training performances; forty-five rats trained prior to the eradication of the mites had a class mean of 3·29; thirty-five rats born afterwards had a class mean of 6·40. But in the following generations, although the rats remained in a good condition, there was a return to low training scores and we were then inclined to accept McDougall's conclusion that variation in health and vigour could not explain the fluctuations in the rate of learning.

Further experience led us to revise this opinion. During the course of the experiment, the general health and fertility of the rats varied considerably. At irregular intervals the colony went into a decline extending over several generations and then, for no apparent reason, regained its health and vigour. McDougall evidently had the same experience for he refers to 'waves of decline of vigour'. Greenman & Duhring (1931), working with a selected group of rats at the Wistar Institute, report large weight fluctuations over a succession of generations so that changes in the general physique of the albino rat may occur, even in colonies maintained in the most favourable environment. The occurrence of such changes in our colony, coupled with the facts set out above, justified a detailed analysis of possible relationships between health and training scores.

As the need had not been foreseen, proper records of the health of the rats were not kept and the data available are therefore few. We have, however, fairly complete fertility records, and as fertility is correlated with health these have provided us with an indirect measure of health. Since all the members of a single generation were mated at the one time, they were all therefore given an equal chance of reproducing; and it is justifiable to use, as an index of fertility, the number of fertile rats in each generation, expressed as a percentage of the number mated.*

The rats were weaned at 26 days and commenced their training on the 28th day. The great majority (about 80%) learnt during the first fortnight of training, i.e. between the ages of 31 and 42 days, when their general health would be determined, in large measure, by the nursing capacity and therefore the general health of the mother.

Thus if rate of learning were influenced by the health of the rats one would expect a correlation between *fertility, used as a measure of health, of one generation, and the training scores of the next.*

The first analysis was made in respect of generations 1–40, i.e. for the period prior to the splitting into sublines. The coefficient of correlation, for the trained line was +0·40 and for the control line +0·42. Both values are significant at the 1% level, and fertility is therefore shown to be positively correlated with high training scores.

The analysis was then extended to include the whole fifty generations, treating the trained rats and the controls each as a single population. For the trained line there was again a positive correlation significant at the 1% level. For the control line the correlation was positive but was not significant.

When the control sublines of generations 41–50 were analysed separately, it was found that there was no significant correlation between fertility and training scores in either subline, but that in subline *B*, such correlation as occurred, was negative. This latter fact was not wholly unexpected for until the 48th generation it had been obvious at the time of training that subline *B* was atypical in that, while fertility was fairly high, the rats were undersized and poor in health. Their inferiority was indicated by their small litters. In every generation from 41 to 48, the average litter

* In the trained line our records show, as fertile, only those rats whose offspring were taken into training. When fertility was high, some first litters were discarded without their parentage being recorded and the fertility index would thus give an underestimate of the true level of fertility. This situation did not often arise, and, in fact, the value of the index for the trained line was not significantly different from its value for the controls, where all first litters were required, either for breeding or training.

size in subline *B* was smaller than in subline *A*. For the eight generations combined the average for *B* was 7·3, for *A* 9·3.

While there are grounds for regarding control subline *B* as atypical, the occurrence of a negative correlation between fertility and scores is disconcerting. It does not, however, discredit the highly significant correlation established for the first forty generations of the control line and for the whole fifty generations of the trained line.

The possibility that there might be a correlation between fertility and rate of learning was considered by both Crew and McDougall. Crew pointed out that if there were a positive correlation between fertility and quickness, i.e. the reverse of the one established above, it could explain the progressive improvement of McDougall's rats. McDougall had been fully aware of the significance of the point made by Crew, but such evidence as he collected, supports our conclusion. In his water-maze experiments, several attempts to isolate a superior stock, by breeding from selected quick learners, failed on each occasion because of the infertility of the superior rats. He had the same experience in his first selection experiment with quick learners in the tank.

We have established a positive correlation between the fertility of one generation and the scores of the next but it is difficult to believe that there could be any direct causal relationship between them. They must have been connected by a third factor. The basic premise of the foregoing analysis is that this third factor was the general health and vigour of the rats. If it be accepted that healthy vigorous rats are more fertile than less vigorous ones, then the above correlation indicates that the more vigorous the rat the higher its expected training score.

Tryon (1929, 1932) has suggested that the reverse relationship may hold for maze-learning. By breeding rats selectively, according to their ability on a maze, he developed a strain of 'brights' and a strain of 'dulls'. Over a number of generations he found that both lines showed a progressive improvement in learning ability. Tryon was inclined to attribute this improvement to increased vigour of the rats. Were this so, it would not necessarily conflict with our conclusion on the influence of vigour on learning in the tank. Krechevsky (1932) has analysed the performances of Tryon's two strains, and has concluded that the difference between them was related specifically to maze learning. The 'brights' learned quickly because they used 'spatial hypotheses'. The 'dulls' used 'visual hypotheses'. Drew (1939) has pointed out that this, while penalizing them on a maze, would have favoured them in a light-discrimination test, and that Tryon's 'dulls' would probably have been quick learners in the tank. The two learning situations were so different that vigour could have been favourable in one, and a handicap in the other.

The training scores of individual rats were necessarily influenced by a variety of factors and all of these, no doubt, played some part in causing the changes in the average rate of learning which occurred during the course of the experiment. We believe, however, that the major changes, that is the changes involving a progressive improvement or decline extending over several generations, were due primarily to changes in the general level of health in the rat colony. The cause of these fluctuations in health of the colony is quite unknown. It may be that they result from infection, and that recovery from a decline involves a selection process, in which the enfeebled strain is eliminated through diminished fertility.

In retrospect it seems that we have been less successful than Crew in standardizing the factors that cause variation in the rate of learning. This has, however, had the positive advantage that it has enabled us to obtain the effect of a progressive improvement in learning rate that McDougall found. McDougall attributed it to the operation of Lamarckian inheritance. Our own results forbid this interpretation for the effect is not sustained, and is displayed in equal measure by the controls.

SUMMARY

This is the final report of an experiment of 20 years' duration, in which we have repeated, in its essentials, the well-known experiment of William McDougall purporting to reveal a Lamarckian inheritance of the effects of training on rats. The test is one involving light discrimination, and McDougall recorded a steady improvement in the rate of learning on a succession of 32 generations; but he omitted to check the results against a properly conducted control.

Our experiment confirms McDougall to the extent that we too have obtained long duration trends of improvement in learning-rate (Figs. 2, 3); but we find that the effect is not sustained, and that it is, moreover, shown also by a control experiment, using animals of untrained ancestry. This forbids a Lamarckian interpretation.

Statistical analysis of the data indicates that the 'condition' of the rat markedly affects its speed of learning, and that progressive changes in learning-rate, over a succession of generations, are in reality correlated with the health of the laboratory colony, which is subject to periods of decline and recovery.

REFERENCES

AGAR, W. E., DRUMMOND, F. H. & TIEGS, O. W. (1935). A first report on a test of McDougall's Lamarckian experiment on the training of rats. *J. Exp. Biol.* **12**, 191–211.

AGAR, W. E., DRUMMOND, F. H. & TIEGS, O. W. (1942). Second report on a test of McDougall's Lamarckian experiment on the training of rats. *J. Exp. Biol.* **19**, 158–67.

AGAR, W. E., DRUMMOND, F. H. & TIEGS, O. W. (1948). Third report on a test of McDougall's Lamarckian experiment on the training of rats. *J. Exp. Biol.* **25**, 103–22.

CREW, F. A. E. (1936). A repetition of McDougall's Lamarckian experiment. *J. Genet.* **33**, 61–102.

DREW, G. C. (1939). McDougall's experiment on the inheritance of acquired habits. *Nature, Lond.*, **143**, 188–91.

GREENMAN, M. J. & DUHRING, F. L. (1931). *Breeding and Care of the Albino Rat for Research Purposes*, 2nd ed. Philadelphia, U.S.A.: The Wistar Institute of Anatomy and Biology.

HACK, E. R. (1933). Learning as a function of water temperature. *J. Exp. Psychol.* **16**, 442–5.

KRECHEVSKY, I. (1932). Hereditary nature of hypotheses. *J. Comp. Psychol.* **16**, 99–116.

McDOUGALL, W. (1927). An experiment for the testing of the hypothesis of Lamarck. *Brit. J. Psychol.* **17**, 267–304.

McDOUGALL, W. (1930). Second report on a Lamarckian experiment. *Brit. J. Psychol.* **20**, 201–18.

McDOUGALL, W. (1938). Fourth report on a Lamarckian experiment. *Brit. J. Psychol.* **28**, 321–45; 365–95.

RHINE, J. B. & McDOUGALL, W. (1933). Third report on a Lamarckian experiment. *Brit. J. Psychol.* **24**, 213–35.

TRYON, R. C. (1929). The genetics of learning ability in rats. *Univ. Calif. Publ. Psychol.* **4**, 71–89.

TRYON, R. C. (1932). The inheritance of maze ability. *Rep. 40th Annual Meeting A.P.A.*

WEVER, E. G. (1932). Water temperature as an incentive to swimming activity in the rat. *J. Comp. Psychol.* **14**, 219–24.