SECOND REPORT ON A TEST OF McDOUGALL'S LAMARCKIAN EXPERIMENT ON THE TRAINING OF RATS

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The late Prof. McDougall's four 'Reports on a Lamarckian Experiment' are likely to become a classic of experimental biology, as being the most sustained attempt up to the present to demonstrate the reality of Lamarckian inheritance in a particular instance. Although, as will appear from this account of our own experiment, we do not believe that it will take its place in the history of biology as a successful attempt, we take this opportunity of acknowledging our appreciation of his nearly twenty years' devotion to this very laborious and exacting experiment.

Our first report (1935) on a test of McDougall's experiment dealt with the first five generations; we now offer a second report, covering twenty generations. Since the publication of our first report, McDougall published his fourth report, and Crew has published the full account of his own similar experiment, now brought to an end, of which only a preliminary report was available in 1935.

The nature of the experiment is now so well known that it is unnecessary to re-describe it in detail. Briefly, the apparatus consists of a tank full of water, divided into three parallel passages by two partitions which stop short of the far end of the tank. At that end, therefore, the passages communicate. From the near end of each of the side passages a wire ramp leads to a platform above the water level. The rat is placed in the water at the near end of the central passage. In its search for a way to escape from the water it swims down the central passage, turns right or left into one of the side passages, and swims back along this to the ramp at the end of it and climbs out. Behind a sheet of ground glass at the back of each ramp is a low-power electric lamp, which shines through the ramp down the whole length of the passage, illuminating also its communication with the central passage, so that the rat at its starting point in the central passage can see which of the two side passages is illuminated. The rat is given six trials a day (except for the first 5 days of training, when, unlike McDougall, we give only four trials) with the left and right passages illuminated alternately. The ramps are connected with an alternating current in such a way that the current is thrown into whichever ramp is illuminated, but not into the other. The rat can therefore escape from the tank by either gangway, but if it chooses the illuminated ('bright') one it does so at the expense of an electric shock. The rat has to learn always to escape by the dim gangway, irrespective of whether this is on the right or left. Facility in learning the task is measured by the number of errors, that is to say, number of escapes* by the bright

* Strictly speaking, attempted escapes. Occasionally a rat makes contact with the electrified ramp, but instead of climbing it, turns back on receiving the shock, swims to the other exit and escapes by it. This very rarely happens except during the first 4 or 5 days of training. This is recorded as an error.

gangway, made by the rat before it learns to avoid this and always chooses the dim one. The number of errors made is therefore the same as the number of shocks received. A rat is held to have learnt the task as soon as it has made twelve consecutive correct runs. Further details of the apparatus and training procedure are set out in our first report, and have not been changed since. The various factors which influence the rate of learning are also discussed in that report, especially those which appear to be responsible for the great variation in the number of errors made by individual rats even of the same litter.

The first report gave the results of two independent lines of rats; since then we have continued with only one of these lines, line A of the first report. All the rats of this line are descended from a single pair of albino rats of Wistar origin. The first generation obtained from this pair (which was not trained) was divided into two groups, one of which (five rats) was trained and became the ancestors of the trained line; the other group (four rats) was not trained and became the ancestors of the control line. The two lines have been bred parallel with each other, and under the same conditions. In each generation, the required number of rats in the trained line are trained, and mated as parents of the next generation. In the control line some of the litters produced are not trained, but are kept as parents of the next generation. Other litters of this line are trained, to provide controls to the same generation of the trained line. These trained controls are, of course, not used for breeding. In this way each generation of the trained line is tested against an approximately equal number of trained controls, differing from the trained line only in the fact that their ancestors were not trained.

Our system of mating ensures that the number of errors made by any rat in the trained line does not influence its chance of becoming a parent. As described in our first report, the few rats which have not learnt after 52 days of training (by which time they are 80 days old) are given 'special training'. These slow learners are invariably rats which, early in training, have formed the habit of using exclusively either the right- or left-hand exit passage, whether this is illuminated or not. Consequently they receive a shock on every alternate run. As the rats are given four trials a day for the first 5 days, and six a day thereafter, by the end of 52 days they have had 302 trials, and have received approximately 151 shocks. 'Special training' consists in forcing them for a few times to use the unfamiliar exit. After this they invariably learn to use the dim passage, either at once or after a very few days. Thus even the slowest learners have completed their task before any rat is mated. In fact, the reason for giving 'special training' to these rats is to ensure that slowness in learning shall not result in later age of mating (for they cannot be mated before they have learnt) and therefore in diminishing their chance of becoming parents of the next generation. The number of rats which received this 'special training' can be seen from Table 2, where they are shown by the letter S.

The rats are paired without any reference to their training scores; in fact, the pairs are formed by drawing lots, brother-sister matings being, however, avoided in both lines, except in a few cases where the total number of rats available was small. Not all the rats mated become parents of the next generation, for many of the matings prove infertile, and others only produce litters after the number of young required for the next generation has been obtained. It is our usual practice to reduce large litters to six; the number of litters required to produce a generation of fifty is about ten. Although our system of mating does not discriminate between rats in regard to their training scores, it is always possible that by chance the rats which have become parents may not be a representative sample of the total population. This can only be ascertained by comparing the training scores of those rats which became parents, with those of the total population. The figures in heavy type in Table 2 are the rats which became the parents of the next generation. It will be seen that there is a total of 193 parents (trained line), and that these form a representative sample of the 702 rats in that line. The median score of these 702 rats is 24, and the percentage of rats learning with fewer than 10 or more than 100 errors is 15·2 and 6·7 respectively. The corresponding figures for the group of 193 parents are 24, 12·4 and 6·2. Thus there has been no accidental selection of rats with high or low scores.

RESULTS OF THE EXPERIMENT IN RELATION TO LAMARCKIAN INHERITANCE

McDougall measured the performance of each generation of rats by the mean number of errors made by that generation, and by the scores of the best and worst rats. Crew used the same measures, with the addition of the median.

Table 1. *Distribution of number of errors made (shocks received) by individual rats in the twenty generations; i.e. in the trained line* 107 *rats made* 0–9 *errors, etc.*

No. of errors	0–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89
Trained line	107	158	170	105	55	22	11	17	6
Control line	99	133	163	107	53	16	18	6	6
Totals	206	291	333	212	108	38	29	23	12

No. of errors	90–99	100–109	110–119	120–129	130–139	140–149	150+	Total no. of rats
Trained line	4	4	0	2	2	1	38	702
Control line	7	4	4	3	4	3	44	670
Totals	11	8	4	5	6	4	82	1372

The arithmetic mean is an unsatisfactory measure of the central tendency of a group in which the distribution is as unsymmetrical as the distribution of number of errors made by the rats in this experiment (Table 1). Indeed, the use of this measure becomes impossible in our case, for the distribution includes a final class (the rats which, having failed to learn after 302 trials, received 'special training') in which the number of errors which the members of that class would have made, if training had continued in the same way, is unknown. For this reason we have used three measures for comparison: the median (Tables 2, 3), together with the percentage of rats learning with fewer than ten shocks, and the percentage requiring more than a hundred shocks before learning (Table 3). The data for calculating any other measure of the collective performance of each generation or group are available in Table 2, which gives the individual score of every rat.

In order to obtain larger groups, Table 3 has been constructed, in which the generations have been grouped in fours. As, however, no rats were trained in the first generation of the control line, the first group contains only generations 2, 3 and 4 of this line.

An examination of the medians in Table 2 discloses no evidence of a progressive reduction in the number of errors made by the trained line as compared with the control

Table 2. *Showing the number of errors made (shocks received) by each rat, and the median number of errors in each generation. In the trained line, the rats which became the parents of the next generation are in heavy type. The total number of rats in the trained line is* 702, *in the control line* 670

Generation		No. of rats	Median	No. of errors made by each rat
1	T.	5	58	32, 50, 58, 70, S
	C.	—	—	—
2	T.	15	40	21, 24, 28, 28, 34, 38, 40, 40, 42, 46, 54, 71, 88, S, S
	C.	7	36	24, 30, 35, 36, 36, 37, 56
3	T.	25	41	11, 14, 20, 25, 26, 30, 32, 32, 35, 36, 38, 38, 41, 42, 42, 51, 54, 54, 54, 58, 69, 98, 121, S, S
	C.	24	46	17, 20, 22, 27, 28, 29, 32, 33, 34, 39, 42, 45, 47, 53, 65, 67, S, S, S, S, S, S, S, S
4	T.	19	31	18, 18, 19, 20, 23, 24, 24, 25, 27, 31, 36, 51, 62, 65, 81, 123, 136, S, S
	C.	23	34	12, 15, 18, 18, 21, 27, 28, 29, 29, 30, 31, 34, 36, 42, 45, 56, 72, 78, 80, 94, 134, 143, S
5	T.	22	44·5	2, 21, 24, 25, 27, 31, 31, 34, 35, 39, 44, 45, 48, 60, 60, 67, 79, 87, 99, 142, S, S
	C.	20	36·5	17, 23, 28, 29, 29, 32, 32, 35, 35, 35, 38, 40, 43, 45, 48, 49, 50, 52, 122, S
6	T.	22	32·5	18, 19, 20, 20, 24, 26, 29, 29, 29, 30, 32, 33, 37, 41, 43, 43, 45, 56, 70, S, S, S
	C.	22	24	3, 5, 8, 9, 13, 13, 17, 19, 20, 22, 23, 25, 27, 27, 28, 30, 31, 33, 47, 66, 97, S
7	T.	31	29	0, 3, 16, 16, 18, 18, 19, 19, 19, 23, 24, 26, 27, 28, 28, 29, 29, 32, 38, 39, 41, 41, 42, 44, 56, 84, 94, 105, S, S, S
	C.	33	30	8, 9, 11, 15, 16, 21, 21, 21, 24, 24, 25, 27, 28, 28, 29, 30, 30, 31, 31, 31, 32, 35, 40, 44, 50, 63, 63, 65, 90, 94, 100, 102, S
8	T.	41	34	1, 6, 8, 10, 17, 18, 19, 19, 20, 22, 24, 26, 26, 30, 30, 30, 31, 33, 33, 34, 34, 35, 38, 41, 42, 42, 47, 51, 55, 64, 74, 75, 76, 78, 81, S, S, S, S, S, S
	C.	16	24	3, 4, 6, 13, 17, 18, 21, 24, 24, 27, 28, 31, 32, 38, 46, S
9	T.	12	14	1, 2, 2, 5, 6, 12, 16, 20, 21, 25, 28, 65
	C.	47	28	4, 12, 14, 15, 17, 18, 19, 20, 21, 21, 22, 22, 23, 23, 23, 24, 25, 25, 25, 26, 26, 27, 27, 28, 28, 29, 31, 31, 31, 34, 36, 36, 39, 40, 40, 41, 42, 44, 47, 59, 60, 65, 69, 76, 124, S, S
10	T.	13	19	2, 16, 18, 18, 19, 19, 19, 21, 26, 27, 37, 44, 131
	C.	37	43	12, 14, 15, 17, 19, 20, 21, 22, 25, 25, 27, 28, 32, 33, 34, 36, 41, 42, 43, 44, 47, 47, 47, 49, 50, 50, 59, 61, 67, 68, 85, 89, 113, 138, S, S, S
11	T.	44	28	5, 8, 8, 10, 12, 15, 16, 16, 16, 17, 20, 20, 21, 22, 22, 24, 24, 24, 25, 25, 25, 28, 28, 28, 28, 29, 29, 30, 30, 30, 33, 34, 34, 36, 37, 38, 38, 38, 41, 42, 45, 46, 53, 68
	C.	60	25·5	5, 6, 6, 6, 8, 10, 10, 11, 13, 16, 16, 18, 18, 18, 18, 19, 19, 20, 20, 20, 21, 22, 22, 23, 23, 23, 23, 23, 25, 25, 26, 26, 27, 27, 27, 27, 27, 29, 29, 31, 32, 32, 33, 33, 34, 37 38, 40, 40, 41, 44, 44, 47, 59, 59, 72, 73, S, S, S
12	T.	36	32·5	3, 14, 20, 20, 20, 21, 21, 23, 24, 24, 26, 28, 28, 29, 30, 31, 32, 32, 33, 35, 39, 42, 43, 43, 45, 57, 60, 70, 72, 75, 76, 77, 108, S, S, S
	C.	33	22	3, 3, 3, 4, 5, 6, 6, 7, 13, 13, 13, 17, 19, 20, 21, 21, 22, 22, 24, 25, 25, 26, 27, 27, 28, 35, 35, 36, 43, 63, S, S, S
13	T.	38	24·5	2, 3, 4, 5, 8, 9, 10, 10, 10, 10, 12, 14, 17, 17, 18, 19, 19, 19, 24, 25, 27, 27, 28, 30, 31, 33, 35, 37, 39, 42, 43, 79, S, S, S, S, S, S
	C.	11	31	10, 10, 24, 26, 30, 31, 36, 38, 40, 141, S
14	T.	50	9·5	1, 1, 2, 2, 2, 2, 3, 3, 3, 4, 4, 4, 4, 5, 5, 6, 6, 6, 7, 7, 7, 8, 8, 8, 9, 10, 11, 12, 13, 13, 13, 14, 14, 15, 16, 20, 22, 22, 23, 25, 25, 26, 26, 26, 30, 38, 39, 46, 47, 47
	C.	37	19	3, 3, 4, 5, 5, 5, 5, 6, 6, 7, 7, 9, 11, 13, 14, 15, 15, 18, 19, 20, 21, 22, 25, 25, 26, 26, 29, 30, 31, 32, 32, 33, 34, 34, 38, 41, 47
15	T.	49	17	1, 3, 4, 5, 6, 7, 8, 8, 8, 8, 10, 10, 11, 11, 12, 12, 12, 14, 15, 15, 15, 16, 16, 17, 17, 17, 18, 18, 20, 20, 20, 21, 24, 24, 24, 28, 28, 28, 28, 29, 30, 31, 32, 37, 44, 49, 62, 79, S
	C.	50	26·5	4, 5, 5, 6, 6, 7, 8, 9, 11, 11, 13, 13, 13, 16, 16, 17, 18, 19, 21, 22, 23, 25, 25, 25, 26, 27, 28, 29, 29, 30, 30, 30, 32, 32, 32, 36, 37, 37, 37, 38, 39, 41, 44, 46, 49, 54, 65, 78, 87, S
16	T.	50	19	3, 3, 4, 4, 5, 5, 6, 9, 10, 11, 12, 12, 13, 13, 13, 13, 13, 14, 14, 15, 17, 17, 17, 18, 19, 19, 19, 19, 19, 19, 21, 22, 22, 22, 22, 23, 24, 25, 27, 27, 31, 32, 36, 36, 39, 41, 44, 70, S, S
	C.	50	17	2, 2, 2, 4, 5, 5, 6, 6, 6, 7, 7, 9, 9, 9, 9, 10, 10, 10, 12, 12, 13, 13, 14, 15, 17, 17, 17, 18, 18, 19, 21, 21, 23, 25, 25, 26, 26, 26, 28, 30, 30, 33, 34, 38, 61, 67, 95, 106, 131
17	T.	80	19	0, 0, 1, 1, 2, 2, 2, 2, 3, 3, 4, 4, 4, 5, 6, 7, 7, 7, 8, 9, 10, 10, 10, 11, 11, 11, 12, 13, 14, 14, 15, 15, 16, 16, 16, 17, 18, 18, 19, 19, 19, 20, 20, 21, 21, 21, 22, 22, 22, 22, 23, 23, 24, 27, 28, 28, 28, 29, 30, 30, 30, 31, 31, 32, 34, 34, 34, 35, 37, 38, 39, 44, 46, 51, 52, 53, 57, 86, 107, S
	C.	50	18	1, 2, 2, 3, 4, 4, 4, 4, 7, 8, 8, 9, 10, 10, 11, 11, 12, 14, 14, 14, 15, 15, 17, 17, 18, 18, 20, 23, 24, 24, 25, 26, 28, 29, 29, 34, 34, 36, 36, 40, 40, 41, 42, 42, 102, 152, S, S, S, S
18	T.	50	27·5	0, 6, 8, 9, 12, 14, 15, 15, 16, 17, 17, 18, 19, 20, 20, 21, 21, 22, 23, 23, 24, 26, 27, 27, 27, 28, 28, 29, 30, 30, 33, 33, 34, 34, 36, 36, 37, 39, 40, 40, 41, 41, 42, 42, 46, 51, 54, 94, S, S
	C.	50	29·5	3, 4, 6, 8, 9, 9, 10, 14, 14, 16, 16, 17, 18, 18, 19, 20, 21, 22, 24, 25, 25, 25, 25, 28, 29, 30, 33, 34, 34, 34, 35, 37, 39, 40, 43, 51, 60, 80, 90, 111, 125, S, S, S, S, S, S, S, S, S
19	T.	50	21	0, 1, 1, 2, 2, 3, 5, 5, 5, 7, 8, 9, 10, 13, 13, 13, 16, 17, 17, 18, 18, 19, 19, 20, 21, 21, 21, 22, 23, 23, 23, 23, 24, 24, 26, 26, 27, 28, 28, 28, 29, 29, 31, 31, 35, 40, 43, 44, 51, S
	C.	50	18·5	1, 2, 2, 2, 5, 6, 6, 6, 6, 7, 8, 9, 10, 10, 10, 11, 11, 11, 13, 13, 15, 16, 17, 18, 18, 19, 19, 20, 22, 22, 23, 23, 24, 24, 25, 25, 25, 29, 30, 32, 35, 36, 37, 40, 44, 45, 56, 57, 61, S
20	T.	50	18·5	0, 5, 6, 6, 7, 8, 12, 12, 12, 13, 13, 14, 15, 15, 15, 15, 16, 16, 16, 17, 17, 17, 17, 17, 18, 19, 20, 21, 21, 22, 22, 24, 25, 26, 26, 29, 30, 31, 31, 32, 32, 35, 36, 39, 41, 41, 43, 70, 105, S
	C.	50	18·5	0, 0, 1, 2, 3, 3, 3, 5, 7, 7, 8, 10, 11, 12, 12, 12, 12, 15, 15, 15, 17, 17, 17, 18, 18, 19, 19, 19, 20, 21, 22, 26, 28, 29, 30, 30, 34, 36, 36, 38, 40, 85, 91, 113, 138, S, S, S, S, S

T. trained line; C. control line. S indicates that the rat has had 'special training'. having failed to learn after 302 trials (and therefore with about 150 errors).

line, as should be the case if Lamarckian inheritance were operating. In nine generations the median of the trained line is higher, and in nine generations lower, than that of the corresponding control generations, and in the last generation the medians of the two lines are the same.

Table 3 brings out, however, the significant fact that there are periodic changes in facility of learning (as measured by number of errors made) which run roughly parallel in the trained and control lines. In the first four groups of generations there is a progressive decrease in the number of errors made by both lines, which is more or less stabilized in the fifth group (generations 17–20). Within each group there is also considerable fluctuation, showing a parallelism between the two lines, though, with the smaller numbers concerned, there is less regularity. In the last five generations, however, the parallelism is particularly close; the medians for generations 16–20 for trained and control lines are, in order of generations: 19 and 17, 19 and 18, 27·5 and 29·5, 21 and 18·5, 18·5 and 18·5.

Table 3. *Summary of the results of the first twenty generations in groups of four generations*

Generations	No. of rats		Median		% learnt with less than 10 shocks		% learnt after more than 100 shocks	
	T.	C.	T.	C.	T.	C.	T.	C.
1– 4	64	54	40·5	36·5	0·00	0·00	15·62	20·37
5– 8	116	91	34	29	5·17	9·89	13·79	6·59
9–12	105	177	28	27	9·52	7·91	4·76	7·91
13–16	187	148	17	22	26·20	23·65	4·81	3·38
17–20	230	200	21	21·5	18·26	20·50	3·04	12·00

T. trained line; C. control line.

These parallel changes in quickness of learning in the line with trained ancestry and the line without any trained ancestry is important for an interpretation of the positive Lamarckian effect claimed by McDougall. In fact, it may provide the clue to the discrepancy between his results and the generally negative results of Lamarckian experiments, including the result of Crew's test of McDougall's experiment. If, like McDougall, we had not maintained a control line, our experiment would have appeared to provide strong evidence, in spite of occasional irregularities, in favour of the theory that accumulation of trained ancestry progressively increases facility of learning in the descendants. Such an explanation is, however, invalidated by the fact that parallel changes in quickness of learning take place in the control line, without any trained ancestry. The cause of these changes is still obscure, but there are grounds for relating them to the general hygienic condition of our stock.

For a long period, from about generation 7–17, we were troubled with low fertility in our rat colony. Indeed, in some generations fertility was so low (only a small minority of rats producing any offspring at all) that we had to be content with many fewer rats in both lines than we wished. The extreme instance of this was generation 9, the trained line of which consisted of two litters only, from a single pair of rats. McDougall mentions that he also encountered periods of low fertility, and as his sixteenth generation consisted of five rats only, it is probable that it was descended from a single pair of parents. This low fertility in our stock was accompanied by obvious signs of bad condition, such as rough and scanty coats and the prevalence of 'rat pneumonia'. Finally, in generation 15 the colony became infested with mites, and in spite of efforts to keep the infestation in check, the experiment was in danger of coming to an end by the loss of the rats. Consequently, in generation 17 we decided to take radical measures to improve the condition of the stock. Up to that period, the rats had been kept in rather elaborate cages, with sleeping and feeding compartments and exercising turn-tables. For these we substituted a very simple type of metal cage which is easily sterilized by flaming. These cages were temporarily set up in another room, and before being transferred to them, every rat was anaesthetized and sponged with tincture of larkspur seed in 90% alcohol to destroy the mites, as recommended by Greenman & Duhring (1931). After all the rats had been transferred to the new cages, the original rat room was fumigated and the new cages returned. By this means the mites were entirely eradicated. The diet was also altered, chiefly by including more fresh milk and raw meat. An extraordinary improvement in both the general health and the fertility of the rats immediately followed this treatment.

McDougall and Crew have both expressed the view that weakly rats tend to learn more quickly than strong rats. In our first report we gave some statistical evidence supporting this conclusion; subsequent experience however has suggested that this factor is not very important. Nevertheless, this seemed at the time to give the explanation of the rise in the number of errors in generation 18, which coincided with the improvement in vigour of the colony. Moreover, this explanation seemed to be even more applicable to generation 17, the generation in which the change in housing and feeding the rats was made. In Table 2 the median of the eighty rats of the trained line is shown as 19. The generation can, however, be divided into two groups. The first forty-five rats were born and reared in the old mite-infested cages; the median of this group is 11. The median of the second group of thirty-five rats, born and reared under the new conditions, was 30. (In the control line of this generation all but six rats were born and bred under the old conditions.) The return to low training scores in generations 19 and 20, during which the rats continued in good condition, shows however that if there is a relation between health and rate of learning, it is not such a simple relation as generations 17 and 18 suggest.

A possible cause of fluctuation in rate of learning might be changes in the training procedure. There has been no change that we are aware of; indeed, the only factor in the procedure which appears likely to influence the number of errors made by the rats is the severity of the punishment for choosing the illuminated exit. So far as the severity is controllable, it depends upon the intensity and duration of the shock. These have been kept constant throughout the experiment by the methods described in our first report.

Selection may be suspected as a cause of a progressive change in the character of a population. We have already shown that, as judged by their training scores, the rats which became parents in the trained line were a representative group of the line as a whole. As we discussed in our first report, however, many accidental factors influence the number of errors made by a rat before it learns, and consequently differences in scores probably do not correspond closely with innate differences in learning ability, if indeed such exist among our rats. Consequently the fact that there was no selection of rats with high or low scores does not completely exclude the possibility that there may have been an accidental and concealed selection of potentially quick or slow learners, which, owing to the many chance factors influencing the number of errors made, did not reveal their true nature. If genotypic diversity is present in a population, and phenotypic diversity is not perfectly correlated with it, it is always possible that accidental genetic selection has taken place although there has been no phenotypic selection. It is therefore theoretically possible that the improvement both in the trained and control lines in the earlier generations was due to concealed selection of genetically quick learners. However, the fact that changes in rate of learning have occurred in both trained and control lines, and, moreover, that these run roughly parallel with each other, makes it very improbable that they have been caused by accidentally selecting for parentage genetically quick learners at some periods and of slow learners at others, which in the trained line did not reveal their true nature by their training scores. Moreover, McDougall obtained a progressive improvement in a line bred exclusively from the slowest learners in each generation, requiring on the selection hypothesis a series of coincidences between genetically quick and phenotypically slow learners too unlikely to be considered seriously.

For the present, therefore, it is not possible to state confidently the reason for the fluctuations in the rate of learning which have taken place during the course of the experiment. The all-important conclusion is, however, that since changes in rate of learning are roughly parallel in the trained and control lines, the progressive decrease in the number of errors over a long series of generations cannot be ascribed, in the trained line, to the cumulative effect of their trained ancestry.

THE PRESENT POSITION OF McDOUGALL'S 'LAMARCKIAN EXPERIMENT'

McDougall's fourth report brings the results of his experiment to generation 44. The part of the experiment on which conclusions as to an increasing facility in learning the task must be based begins, however, with generation 13, the first generation shown on McDougall's table. This is partly because in the first eight generations a different training procedure was used, which proved unsuitable; not till the 9th generation was his present procedure adopted, which is also essentially that followed by Crew and ourselves. Since training in his 10th, 11th and 12th generations was too incomplete to furnish data comparable to those from later generations, the figures available for comparison with Crew's and our own results are those for his generations 13–44, from which generation 20 is omitted as it was incompletely trained. These thirty-one generations show a marked, though naturally not quite regular, decrease in the average number of errors made by each generation, in the number of errors made by the worst rat, and still more in the number of errors made by the best rats, of each generation. The statistical significance of the decrease seems indubitable. Moreover, an independent experiment carried out in the same way, except that, in each generation, only the rats making the most errors were used as parents—thus introducing adverse selection—showed an even greater improvement than the main experiment. The criticism which must be levelled against McDougall's technique is that, although he trained four small batches of controls at different times, he failed to maintain a control line, so that it is impossible to know whether there was any change in learning facility taking place, which could not be attributed to ancestral training, as in our own control line.

The results of Crew's experiment provide very strong evidence that, where other factors tending to change the facility of learning the task are not operating, no improve ment of learning facility takes place under the influence of increasing numbers of generations of trained ancestors. Crew's experiment was carried out for eighteen generations, and with a much larger number of rats per generation than used either by McDougall or ourselves. His experimental procedure differed in several respects from that of the other two experiments, notably in the fact that instead of giving six preliminary runs in the tank without shock, he gave a hundred, consisting of fifty runs with both gangways equally illuminated and no shock, followed by fifty with alternating light but no shock. This technique has made it possible for Crew to draw some interesting conclusions about the learning process, the formation of right and left habit, and so forth, about which, however, we are not here concerned. The important fact is that no evidence of increasing learning facility was obtained, either in the trained or control line. In neither line was there a progressive diminution in the mean or median number of errors, or in the scores of the best and worst rats, of each generation.

This is shown by Crew's Table 2. As, however, McDougall has stated that this table furnishes evidence 'not entirely without indications of improvement of facility in the course of the eighteen generations of training' (McDougall, 1938, p. 345), it is necessary to examine the strength of the three indications of improvement which McDougall mentions. He cites the fact that in the trained line the score of errors for the median rat of the last generation is the lowest of the series, and that the average error of the same generation is the lowest but one. When, however, the series of generations is considered as a whole, it is evident that Crew is fully justified in drawing the conclusion that there was no improvement. The eighteen generations arranged in order of descending medians are as follows: 9, 7 and 8, 6, 11, 17, 12, 10, 14, 1, 16, 15, 13, 5, 4, 2, 3, 18, and in order of descending average errors: 9, 11, 7, 8, 17, 14, 6, 12, 15, 10, 13, 16, 4, 1, 5, 2, 18, 3. McDougall's third indication, that an improvement of learning facility took place in Crew's trained line, is that twenty-nine rats in this line made no errors, and only ten in the control line. In view of the small number of these zero-error rats in both lines, this is a very slender indication, especially as the discrepancy is diminished by the fact that the total number of rats in the trained line was 1449 as against 1014 in the control line. McDougall continues: 'It would be of interest to know the distribution of the 29 errorless rats, and of others of small numbers of errors throughout the experimental series.' He seems to have overlooked the fact that this distribution is given in the pedigrees furnished by Crew. From these it can be found that the rats with zero scores do in fact occur more frequently in the later, than in the earlier generations. But this applies to the control line as well as to the trained line. In the latter, seven appear in the first nine generations, and twenty-two in the second nine, while in the control line three appear in the first nine, and seven in the second nine generations.

The suggestion that Crew's results, contrary to his own statement, do give indications of improvement of facility in mastering the task cannot therefore be substantiated. It must be accepted that Crew's experiment revealed no increasing facility in mastering the task, though he used much larger numbers of rats than McDougall did, and carried it through many more generations than was required by the latter to obtain this effect.*

McDougall, however, has also suggested two reasons why Crew's procedure may have

* This must not be interpreted as implying that we accept Crew's explanation of the decreasing number of errors obtained by McDougall.

been less likely to produce a Lamarckian effect than his own. The first is that for some reason Crew's rats were presented with a very much easier task than McDougall's. He bases this on the average number of shocks received by Crew's rats compared with the average for the various batches of rats of untrained ancestry trained by himself at various times. From this he draws the conclusion that Crew may have failed to obtain a Lamarckian effect, owing to the comparative ease with which his rats were able to learn their task, and the large number of them which received very few or even no shocks. He makes a similar criticism about our own experiment. In estimating whether the task provided by Crew and ourselves was, or was not, sufficient to produce a Lamarckian effect, the relevant comparison is not, however, solely between the number of shocks required by our rats to learn the task, and the number required by various control batches trained by McDougall. Equally relevant is a comparison between the number of shocks received by our rats, and the number received by McDougall's during that part of his experiment in which the Lamarckian factor was believed to be revealing itself, which includes the whole of the thirty-one generations of his main experiment (generations 13–44). During this period the number of rats which received no shocks was 29,* or 4·1 % of the total number of rats; in Crew's trained line the number was also 29, but owing to the larger total number of rats, this is only 2·0 % of the whole. If, therefore, the number of rats receiving no shocks is a reason for explaining the lack of a Lamarckian effect, it applies less to Crew's than to McDougall's experiment. As only eight of our 1372 rats have achieved the criterion of mastering the task with no shocks, this particular criticism does not apply to our experiment.

When we turn to the average number of shocks received, we find a similar weakness in McDougall's argument. The average number of shocks received by the 1445 rats of Crew's trained line is 43·4. Omitting McDougall's first generation (generation 13), where the average could not be given owing to some of the rats not having completed their training, we find that the mean number of shocks received by the 677 rats of his generations 14–44 is 33·3 (this figure is approximate only, as in all but one generation the average number of shocks is given in whole numbers).

Owing to our method of giving 'special training' to those of our rats which have not learnt after 302 trials (approximately 150 shocks) we cannot give an average strictly comparable with this. But even if we take 150 for the scores of the thirty-eight rats which received special training, thereby reducing the real mean by an unknown amount, the average number of shocks received by the 702 rats of our trained line is 33·9, as compared with McDougall's 33·3. Our experience with further training of rats which had exceeded 150 errors (our first report, p. 198), as well as extrapolation of the distribution of shocks in Table 1, shows, however, that even 200 is probably an underestimate of what the average score of these thirty-eight rats would have been, if their training had been completed in the usual way. Taking it as 200, the average number of shocks for the whole of our rats of the trained line is 36·6.

There is, therefore, no justification for explaining the failure to obtain the Lamarckian effect in Crew's and our own experiments on the grounds that our rats were presented with an easier task than McDougall's, if the basis of comparison is, not the isolated

* McDougall, however, does not count it an error when a rat swims up to the bright ramp, touches it with its nose, and on receiving the shock turns away, and swims out by the other passage. He says (1938, p. 329) that if these had been counted as errors (as we have done in our own experiment), then the number of cases of zero error would have been considerably reduced.

batches of controls trained by him, but the performance of his trained line during the whole period in which the Lamarckian effect was supposed to be revealing itself.

The second argument which McDougall has advanced, as a possible explanation of Crew's failure to produce any increase of facility in his trained line, is that Crew started the actual training of his rats to avoid the shock when they were 75 days old, whereas McDougall himself began it when they were about 30 days old. (This objection cannot be applied to our experiment, for we give our rats their preliminary six runs in the tank without light or shock when they are 27 days old, and start training proper on the following day.) He considers it a justifiable assumption that the earlier the age at which the training begins, the more likely is it that Lamarckian transmission of its effects may ensue. It is, of course, impossible to gauge the strength of this argument, but, if the assumption is justified, it greatly restricts the utility of the Lamarckian factor as an explanatory theory of the evolution of instincts connected with mating, nest-building, care of the young, migration, and all the other activities of organisms which are not brought into play until they are mature.

SUMMARY

This experiment, devised to test McDougall's claim that the effect of training in rats is inherited, has been carried out for twenty generations. In addition to the trained line, a control line has been maintained parallel with it, from which a number of rats have been trained in each generation, but not used for breeding. For each generation of the trained line there is therefore a corresponding group of trained control rats for comparison, differing from the rats of the trained line only in that they have no trained ancestry. During the first fifteen or sixteen generations there was a progressive, though irregular decline in the number of errors made in each generation in both lines. In generation 18 both lines showed a marked increase in the number of errors made, with fluctuations in subsequent generations running closely parallel in the two lines. This parallelism of periodic fluctuations in rate of learning in the two lines makes it impossible to attribute a progressive change in the trained line, when it happens to be in the direction of decreasing number of errors, to the inherited effects of ancestral training. Our experiment is being continued, and therefore our conclusions must be regarded as tentative only. The results of the experiment up to the present, together with those of Crew's experiment, show however, that the progressive decrease in the number of errors in successive generations of McDougall's experiment, in which no control line was maintained, cannot be held to have established the operation of Lamarckian inheritance.

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