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Genetic Analysis of Avoidance Learning by Means of Different Psychological Testing Systems with Inbred Mice as Model Organisms

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Summary. The genetic basis of active avoidance learning was investigated with mice as model organisms by means of different test systems such as the Shuttle-Box with light and sound stimulation and the Skinner-Box with light stimulation. Six inbred strains of mice and their offspring (F_1) as well as selected second and third generation progenies (F_2 and F_3 resp.) were used in this study. Furthermore we induced environmental modifications such as embryonic transplants in opposite behavioral phenotypes, crossfoster breeding as well as enriched and impoverished environment. The results enable us to postulate a monogenic inheritance of Shuttle-Box performance with codominant mode. The gene expression could not be disturbed by environmental manipulations. Therefore, the learning in the Shuttle-Box has a very simple genetic background which might underly a multiple allelic system.

Introduction

Shuttle-Boxes and Skinner-Boxes are well-known pieces of test equipment in animal psychology. For several years now Shuttle-Boxes, and to a lesser extent Skinner-Boxes have also been used in behavior genetics.

Several authors have examined genetic factors in relation to active avoidance learning in the Shuttle-Box with the diallel cross technique. A genetic basis in the manifestation of this very interesting learning behavior has been rendered likely but not yet proven by these investigations, and by investigations of sib-correlations (Williams et al. 1963) and parent-offspring regressions (Oliverio 1971). Other authors have investigated the strain specific differences by comparing different inbred strains (Royce et al. 1960).

During recent years the investigations have been extended by experiments with recombinant inbred strains and congenic lines (Oliverio et al. 1973 a, b). A comparison of the findings has afforded no clear information about the mode of inheritance. Therefore, different explanations are under discussion, some of which do not exclude major gene effects (Oliverio et al. 1973 a, b) as well as some base on an exclusively polygenic system (Royce et al. 1971).

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Up to now there has also been an insufficient comparison between different shock-avoidance systems and no detailed analysis of the nature-nurture correlation. To sum up, the mode of inheritance is not clear and it is not yet known to what extent environmental factors are able to influence the expression of this behavioral trait. The results described here represent a Mendelian analysis mainly of the speed of learning, and are concerned with the question of how far the genetic model described is able to influence learning processes at a higher level.

Methods

Animals. For the investigation described here we chose the inbred mouse strains C3H/HeJ, NMRI, C57Bl/6, Balb/c, Balb/cN, and DBA/2. The animals were bred under standardized conditions in the Institute's own animal laboratory. The humidity was kept at 75%, the temperature was 22°C, and the day-night rhythm took place at intervals of 12 h. The total air volume was changed 20 times per hour. Standardized animal cages were used . The animals were fed a standard diet. The number of animals per box was constantly seven and the animals were transferred to these boxes – separated according to sex – after a 21-day lactation period. The age of the mice at the beginning of the study was always 10 weeks ± 2 days. The animals for the experiment were chosen at random from those available. Each animal was individually marked.

Instruments

In the Shuttle-Box animals are forced to avoid electric shocks signaled by light or sound, by means of changing the compartment. In the Skinner-Box signaled electric shocks can be avoided by pressure on a lever. The extent of active avoidance during conditioning is taken here as the parameter for learning.

The Shuttle-Box was from Campden Instruments Ltd, and was originally equipped for carrying out experiments with rats. Conversion for use with mice was carried out by Heinz Albrecht GmbH & Co., Munich (Fig. 1). The internal measurements of the conditioning chambers were 48 × 22 × 21 cm. Control of the course of the experiment and the recording of data were carried out fully automatically with experiment-control apparatus from the companies Massey Dickinson and Campden Instruments Ltd. In the different experiments the animals were conditioned by two different kinds of signals, either a 10 s light flash or a 10 s sound signal (frequency 600 Hz). The intensity of the shock was 150 μA. The intertrial interval was varied by a random converter module.

The Skinner-Box (Fig. 2) is from Campden Instruments Ltd, and the program was controlled by automatic equipment from Massey Dickinson. The test chamber was varied by removal of the lever to the back of the chamber wall and of the stimulus light to the ceiling. The lever itself was constructed as a rotating cylinder and during the intertrial period the lever was outside the chamber. This was necessary to avoid a total blockage of the experimental session by a permanent pressing of the lever. The stimuli and shock times corresponded to those of the Shuttle-Box.

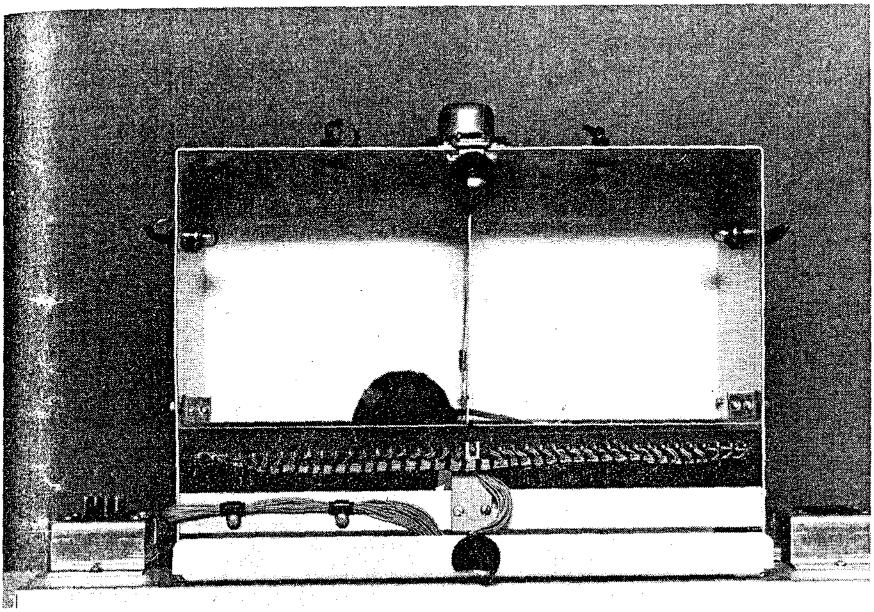

Fig. 1. Shuttle-Box experimental set-up

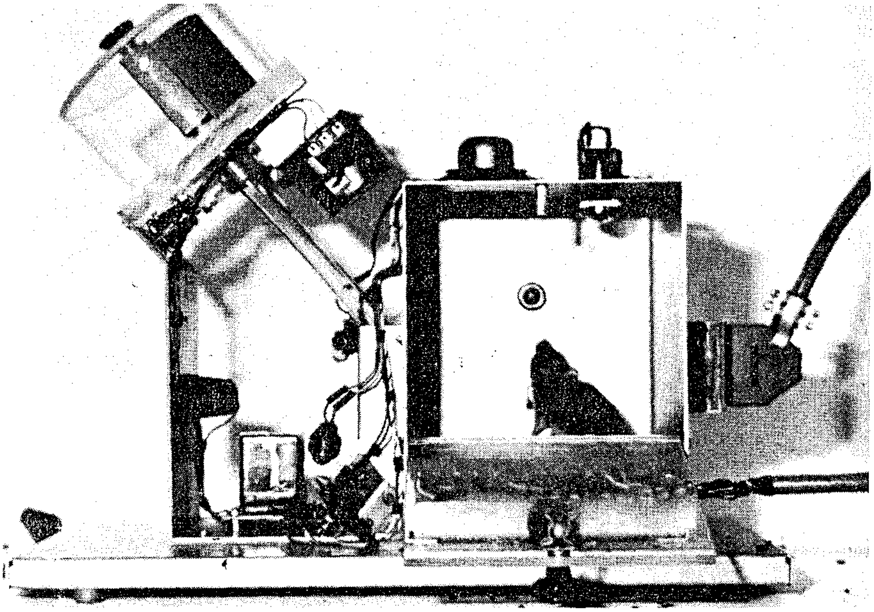

Fig. 2. Skinner-Box experimental set-up

Experimental Set-up

The shock-avoidance programme was equipped with three modifications:

1. light — shock — intertrial period	Shuttle-Box: shock avoidance by changing the compartment
2. sound — shock — intertrial period	
3. light — shock — intertrial period	Skinner-Box: shock avoidance by pressing the lever

Twenty-four animals (12 male and 12 female) of each inbred strain were tested in the Shuttle-Box with light conditioning in the parental and first hybrid generation. A total of 140 animals of both sexes were tested in F_2 crosses of ♀♀ C3H/HeJ x♂♂ DBA/2; the F_3 generation of this cross consisted of 160 animals. A total of 160 animals of both sexes were tested from an F_2 generation of ♀♀Balb/cx♂♂DBA/2.

To recognize early environmental influences we tested crossfoster breedings of C3H/HeJ and DBA/2. In order to examine an intra-uterine environmental influence we transplanted C3H/HeJ embryos in NMRI foster mothers. We obtained 12 animals from this experiment that reached the adult stage and thus the testing age. A detailed description of the transplant techniques is shown in Buselmaier et al. (1981, in preparation). As additional environmental modifications between the post-lactation phase and puberty, 20 animals of DBA/2, C3H/HeJ, C57Bl/6, and Balb/c were socially and visually isolated. A second group of animals was handled. These animals too were conditioned at the usual testing age.

All inbred strains described — crosses and animals which had been environmentally manipulated — were conditioned at five daily sessions of one h (beween 90 and 100 trials/h). Furthermore, we conditioned 12 animals of DBA/2 and C3H/HeJ over a period of 10 days in order to study the effect of long-term conditioning.

According to the second modification of our experimental setup (sound -- shock – intertrial) we trained all the inbred strains (16 animals of both sexes) according to the schedule of sessions described above. Their F_1 generations were examined in the same manner.

In the Skinner-Box experiments we studied the inbred lines C3H/HeJ, NMRI, and DBA/2. The conditioning was carried out with 16 animals per strain. We tested the animals for 1 h in the afternoon and 1 h in the morning for a five-day period.

Statistical analysis

In order to obtain a statistical analysis of the increase of learning behavior of the inbred strains and the hybrids, we used the Friedman two-way analysis of variance combined with the Wilcoxon matched-pairs signed-ranks test. The Friedman two-way analysis tested the general conditioning effects without regard to whether a decrease or increase in learning behavior occurred. The second test systematically examined the day-to-day increase of learning behavior over a period of five conditioning days. The one-way analysis of variance combined with the Duncan multiple range test was used in order to judge the differences occurring between the strains as well as the differences between the differently treated groups of one strain at a specific time during the conditioning. Once again the first test examined overall differences (heterogeneity) between the strains and the second test examined which strain differences formed the basis of this heterogeneity. This means that the inbred strains as well as the F_1 crosses can be divided into groups which have significant differences. Significances at the 5% level are interpreted as weakly significant and on the 1% level as significant.

Results

We interpreted the changes of compartments during the light phase or the sound phase respectively as indicators for operant learning behavior in the Shuttle-Box. Shock avoidance during the shock phase was not taken into account because in our opinion this is only a doubtful indicator for operant learning behavior. Therefore, in the Skinner-Box too we interpreted only the reactions during the stimulus period as positive reactions. The results of the various inbred strains (P-generations) after a conditioning with light and sound stimuli are shown in Fig. 3.

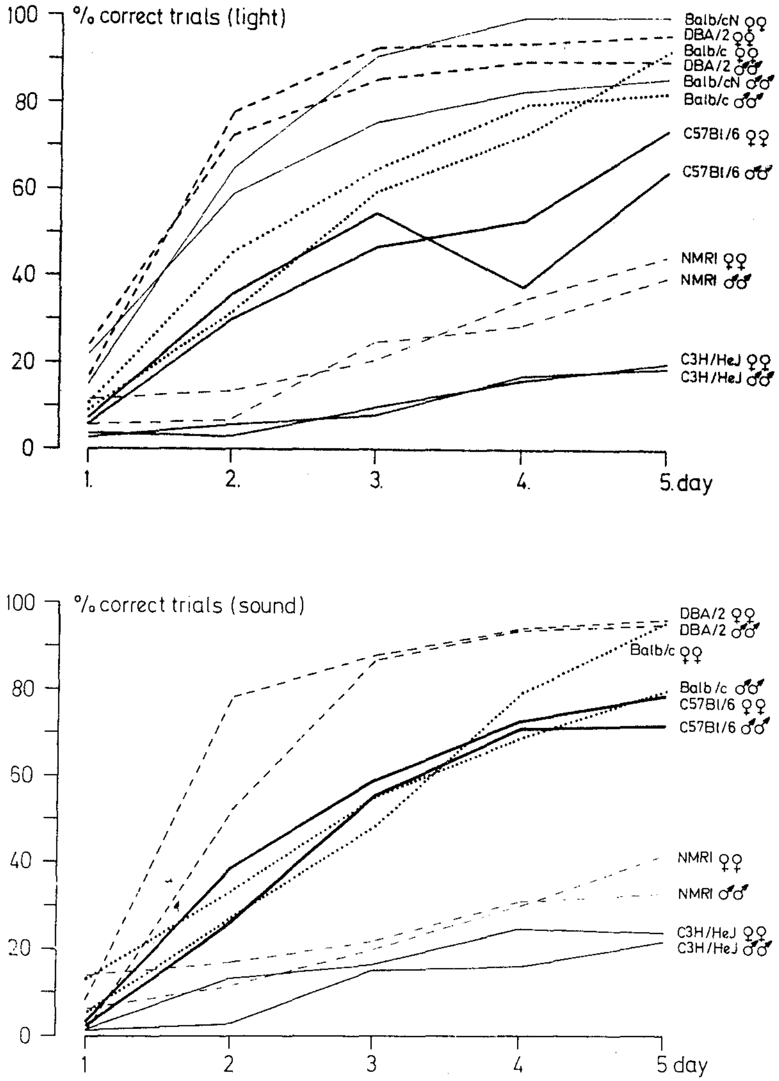

Fig. 3. Shuttle-Box performance of six inbred strains of mice during sessions day 1 – 5

The Friedman two-way analysis of variance showed a significant conditioning effect, based on the percentage rate of active avoidance, for all the tested inbred strains over the total conditioning period. Examination of the increase of learning behavior from day to day by means of the Wilcoxon matched-pairs signed-ranked test revealed that the increase after light conditioning for C3H/HeJ was significant from day 2 to 3 and from day 3 to day 4. NMRI showed significances from days 2 to 3, 3 to 4, and 4 to 5, and C57Bl/6 from days 1 to 2, 2 to 3, and 4 to 5. The significant increases for Balb/c, Balb/cN, and DBA/2 occurred between days 1 and 2, and 2 and 3. The described significances apply not only to the separate analysis of males and females, but also to the analysis of the pooled sexes. After sound conditioning we found a significant increase in C3H/HeJ from the 2nd and 3rd day for both males and females and, in addition, for females alone from the 1st to the 2nd day. The pooled sexes showed significances from the 2nd to the 3rd day. NMRI was significant from the 2nd to the 3rd and the 3rd to the 4th day and C57Bl/6 from days 1 to 2, 2 to 3, and 3 to 4. In the case of the Balb/c strain the increase of learning was significant over the total period. DBA/2 showed significances from days 1 to 2 and 2 to 3. This is valid for the separate analysis of both sexes and for the pooled sexes.

The one-way analysis of variance revealed that the interstrain differences were significantly higher than the intrastrain after both types of conditioning.

Duncan's multiple range test enabled us to prove differences from strain to strain. After light conditioning we found the following groups which differed significantly at the 1% level: C3H/HeJ – NMRI – C57Bl/6 – Balb/c, Balb/cN, and DBA/2.

After sound conditioning we found weak significances at a 5% level between the groups: C3H/HeJ, NMRI – C57Bl/6 – Balb/c, DBA/2. At the 1% level two main groups differ significantly: C3H/HeJ, NMRI, and C57Bl/6 – Balb/c, DBA/2.

These biometrical differences are a first clear indication of a different genetic background. Of course a detailed genetic analysis is only possible after some special Mendelian crosses. Further results of the F_1 support the genetic background discussed; all F_1 crosses (after light conditioning) are situated between the parental strains.

Neither an age-dependent distribution (we tested 4- and 50-week-old animals in additional experiments) nor a heterosis effect nor differences between light and sound stimuli at the F_1 level (Fig. 4) could be found. The Duncan multiple range test showed that most of the F_1 crosses formed groups with the better learning parental strains. In the case of great differences between the parental strains (DBA/2 and C3H/HeJ, C3H/HeJ and Balb/c) both parental strains and the hybrids differed significantly.

For further investigations of the mode of inheritance, F_2 crosses were tested from the most interesting parental strains C3H/HeJ, DBA/2, and Balb/c. On the 3rd, 4th, and 5th test days one could assume that a segregation of the different phenotypes according to the genes involved had taken place. Of course this could not happen at the hybrid level (C3H/HeJ × DBA/2 and DBA/2 × Balb/c) because hybrids of inbred strains are heterozygous for all loci and phenotypically and genotypically identical. Theoretically, and this is well known, with a multifactorial mode of inheritance (participation of many genes), a distribution curve of the behavioral patterns with one main reaction peak is to be expected in F_2 generations. Contrary to this, the F_2 of the most extreme strains C3H/HeJ × DBA/2 show a bimodal distribution with the two peaks at the extreme points of the distribution (Fig. 5). On the ordinate one can find the number of animals with a specific reaction; on the abscissa, the segregation into individual percentage groups of correct reactions. The data are summarized from the 3rd to the 5th day of conditioning. The 1st and 2nd conditioning days were necessary in order to divide the animals with different learning abilities into their individual reaction groups and are

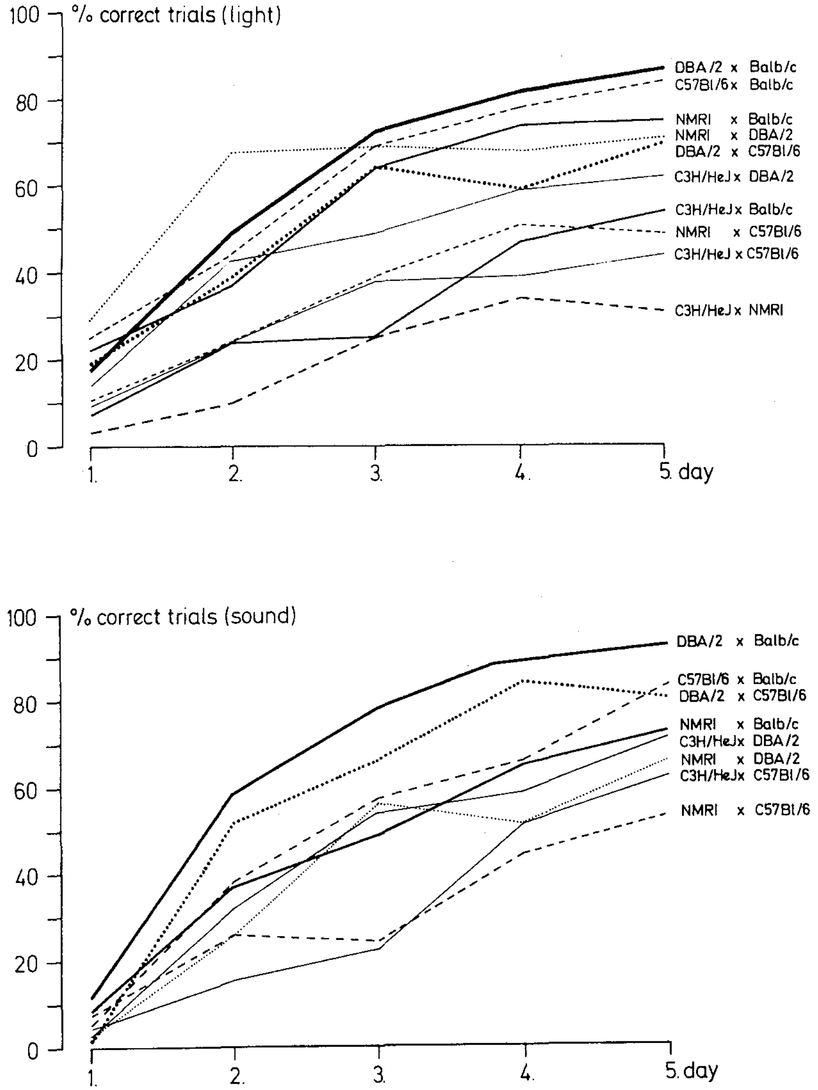

Fig. 4. Shuttle-Box performance of the F_1 generations during sessions day 1 - 5

therefore not integrated into the analysis. Furthermore, the figure allows a comparison of the distribution pattern of P and F_1 generations. Both P generations are separated very clearly – C3H/HeJ at the beginning of the segregation curve and DBA/2 at the end. The F_1 occupies a central position between both parental strains with a slight shift to the better learning P strain. According to this shifting, the F_2 patterns show a slight tendency to better learning parameters. The peaks of the bimodal F_2 distribution are identical with the main reaction pool of both P generations and the section between the extreme data is identical to the distribution of the F_1 hybrids. If one only considers one

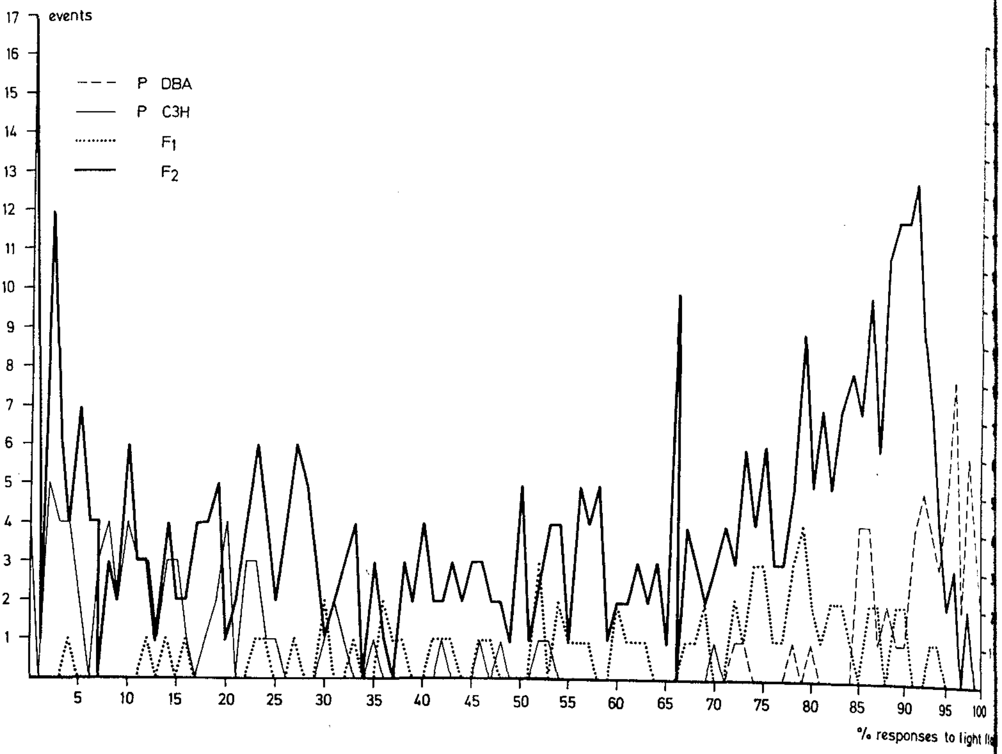

Fig. 5. Distribution patterns of the F_2 generation compared with F_1 hybrids and both P generations (events = number of animal reactions summarized from day 3 to day 5)

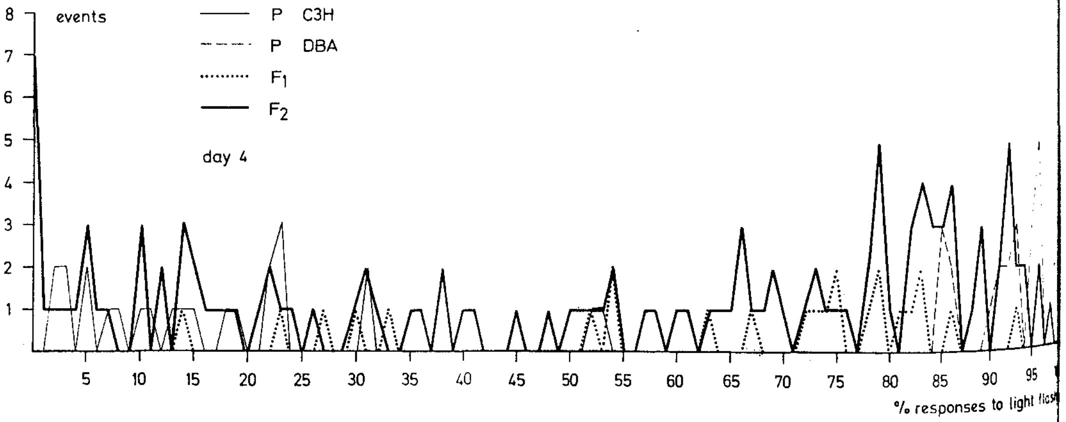

Fig. 6. Distribution patterns of the F_2 generation compared with F_1 hybrids and both P generations (events = number of animal reactions summarized from day 4)

day of the conditioning period, for example day 4 (Fig. 6), the distribution is similar to the summarized days 3 – 5. This unusual observation of a bimodal distribution in the F_2 generation and segregation in the position of the parental phenotypes enables us to postulate a monogenic mode of inheritance. This conclusion is supported by the fact that quantitatively about half of the animals separate themselves according to the F_1 hybrids and the others according to their grandparents. This is in accordance with the classic Mendelian inheritance of single genes. To prove the hypothesis of a monogenic mode of inheritance, it is necessary to study a further Mendelian cross – the F_3 generation of C3H/HeJ x DBA/2.

We selected and bred F_2 animals belonging to the extreme phenotypes to F_3. As an example for this, the offspring of the poorer learning F_2 phenotypes are described (Fig. 7). In selecting the extreme parental F_2 animals for the F_3 generation, we took all animals that showed less than 15% and more than 85% positive reactions. In the figure, 82% of the animals show avoidance reactions of between zero and 50%, thus resembling the C3H/HeJ inbred strain. Of the tested animals 18% reached better learning positions. We believe these animals to have parents of the hybrid type because of the difficulty of completely error-free selection based only on phenotypic traits.

The hypothetically heterozygous animals were separated in this way (animals showing between 15% and 85% avoidance reactions). We retested these animals after a four week interval for one further conditioning of one hour. The results are shown in Fig. 8 in comparison to test day 5 of the first conditioning. Only one animal which showed 17% positive reactions on day 5 now reached 14%, and only two animals with 82% and 84% positive reactions respectively now showed 92% and 97% respectively. This slight

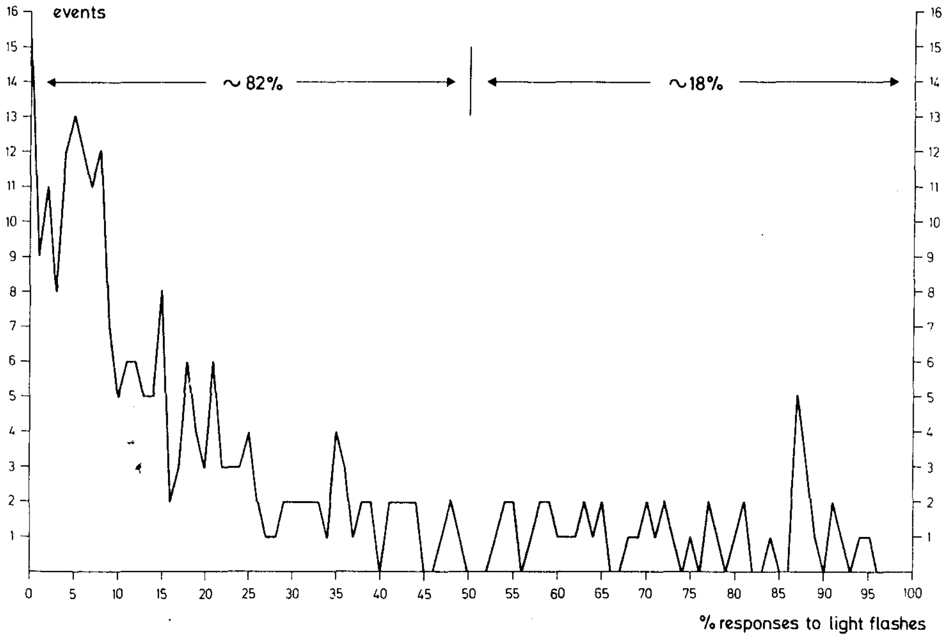

Fig. 7. Distribution pattern of the F_3 generation (poorer learning phenotype)

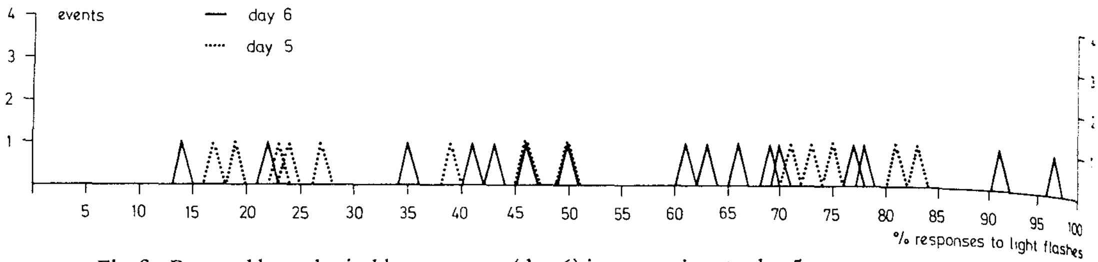

Fig. 8. Retested hypothetical heterozygots (day 6) in comparison to day 5

shift on the cutting points can easily be explained by a misinterpretation of the genetic background of these few animals. All other animals showed the expected reactions of more than 15% and less than 85% of positive reactions. This is a clear demonstration of the possibility of selecting the genetic background by phenomenological criteria.

A further cross analysis after pairing these hybrids with each other simulated the previous F_2 and again showed the expected segregation into three phenotypes, interpreted – according to our hypothesis – as two homozygous and one heterozygous line.

Provided that the monogenic model has a real background, a cross of two fast-learning strains (DBA/2 and Balb/c) to F_2 should show, in contradiction to the previous segregation, a congregation of all three phenotypes to one single peak on the upper part of the distribution curve. Figure 9 shows the data obtained and is interpreted as follows: The inbred strain DBA/2 has a relatively small range between 71% and 100% positive reactions. Balb/c, on the other hand, shows a relatively wide range lying between 30% and 100%, with a maximum between 73% and 100%. This wide range recurs in the F_1 hybrids, but nevertheless the maximum peak could be found in the area of very good learning performance. As expected, the F_2 showed its main reaction pool between 50% and 100%, but here we found a slight shift towards a poorer learning performance. This situation, which is in part difficult to explain, is in our opinion the result of the genetic background of the parental strain Balb/c, whose learning ability is slightly poorer and of greater variance within the animals. The only relevant facts are however, the disappearance of the bimodal distribution and the impossibility of a division into three phenotypes.

The whole discussion about the results up to now has been based on the idea of the total learning ability of animals. The success of the learning processes, however, is always dependent upon a clear time parameter. We tested therefore the animal behavior of C3H/HeJ and DBA/2 with considerably enriched learning possibilities in a long-term experiment covering a conditioning period of 10 days. According to our hypothesis one can show that the monogenic situation described is only valid for learning speed and not for learning ability (Fig. 10), because after 10 days C3H/HeJ reached avoidance reactions of about 80%.

A mode of behavior allowing such a clear phenomenological distribution in different phenotypes should be only slightly subject to environmental influences. If different environmental modifications – we chose extreme ones – have no important effects, the given genetic hypothesis can be postulated as proven.

The life of an individual in his environment can be divided into three main phases:

1. the intrauterine phase where maternal influences provide the only environment for the embryo;

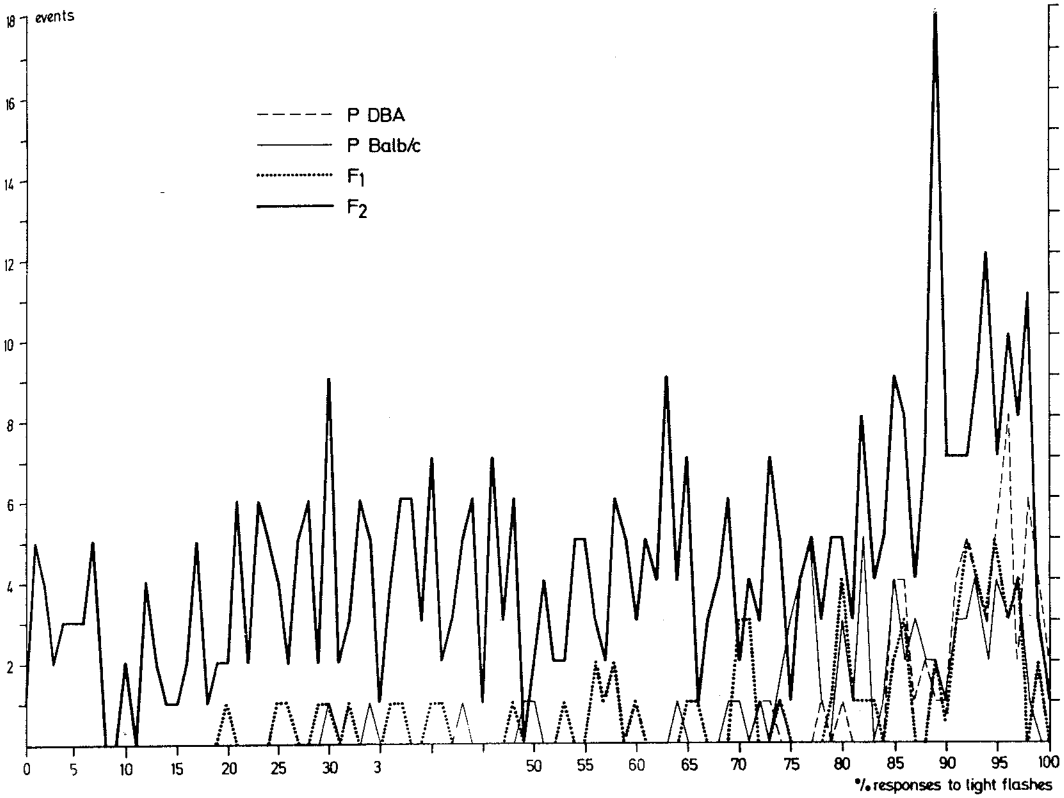

Fig. 9. Distribution patterns of the F_2 generation (DBA/2 X Balb/c) compared with F_1 hybrids and both P generations (events = number of animal reactions summarized from day 3 to day 5)

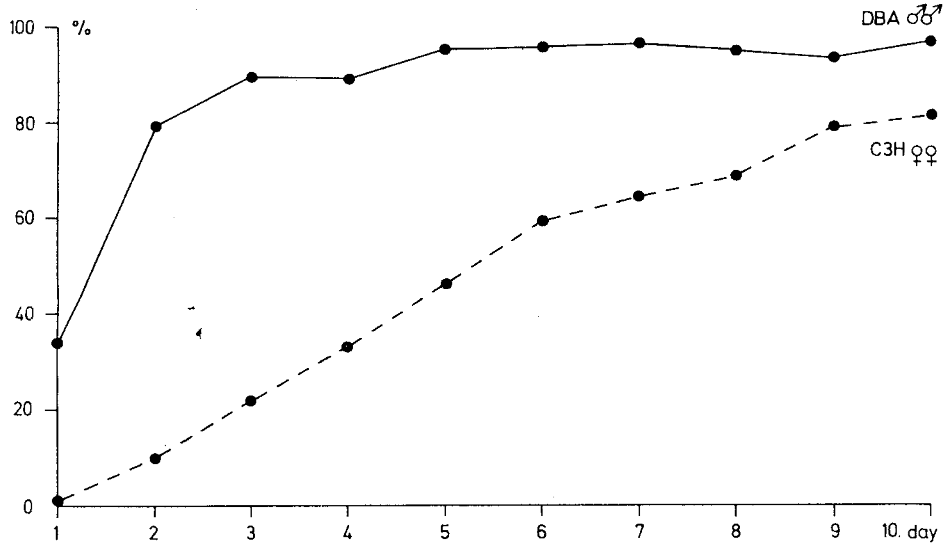

Fig. 10. Long-term conditioning over a period of 10 days of the extreme P generations

2. the early childhood phase where the most significant influences come from the parents but also to a certain degree from the abiotic environment;
3. the post-lactation phase which can be divided into the pre- and post-pubertal phase.

The influence of cross-foster breeding during the lactation period was proven by the inbred lines C3H/HeJ and DBA/2, which both have extreme phenotypes (Fig. 11). These curves show that the induced manipulations do not have any effect on the expres-

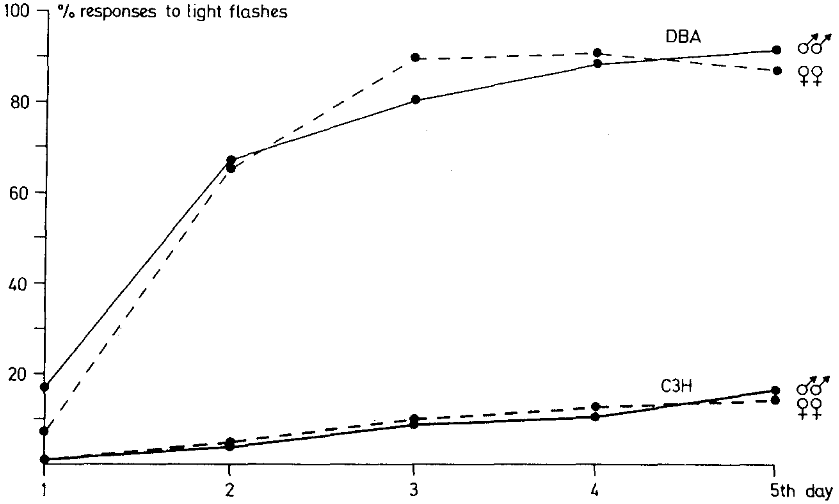

Fig. 11. Shuttle-Box performance after cross-foster breeding of the extreme P generations

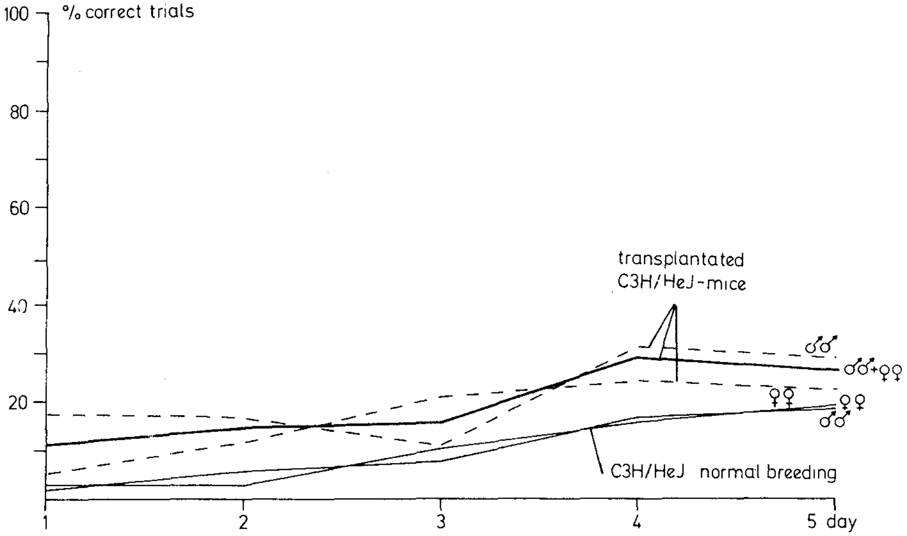

Fig. 12. Shuttle-Box performance of transplanted C3H/HeJ in comparison to normally bred ones

sion of the phenotype. The Duncan multiple range test was used to form statistical groups out of the animals of the unmanipulated original strains and, within the cross-foster animals, a division of groups occurred between C3H/HeJ and DBA/2 at the 1% level. We obtained similar results with transplantation experiments. C3H/HeJ mice do not change their original phenotype after being transplanted into animals of opposite behavior (Fig. 12), as could be shown with Duncan's multiple range test and the one way analysis of variance.

The first results of experiments with DBA/2 animals after being transplanted into NMRI seem to correspond with our original DBA/2 data. However these last data have to be extended to a larger number of animals in future experiments.

In the pre-pubertal phase after the lactation period, we carried out two experimental modifications:

1. isolation stress with complete visual isolation from events outside the cages;
2. animal handling twice a day.

The results can be seen in Figs. 13 and 14.

It was not possible to change the phenotypical expression by all environmental modifications. This was proved by means of one-way analysis of variance. As expected, no significant differences could be found between animals bred under normal conditions and the experimental variations. At a 1% level with Duncan's multiple range test the manipulated animals formed a statistical unit with normal bred ones within each strain.

As described in 'Methods' we added Skinner-Box experiments with some of the inbred lines to the various Shuttle-Box experiments. We chose the DBA/2 line because it had the best learning performance in the Shuttle-Box. Furthermore we chose C3H/HeJ, the strain with the lowest learning speed, and NMRI, the strain with a medium learning performance. The results, shown in Fig. 15, should be compared with those shown in Fig 3. The statistical analysis showed strain differences comparable to those obtained in the Shuttle-Box with the Friedman two-way analysis of variance and the Wilcoxon matched-pairs signed-ranks test. The differences in learning performance between the strains are identical in the sequence of the strains as well as in the increasing rate. After a one-way analysis of variance we found no significant differences

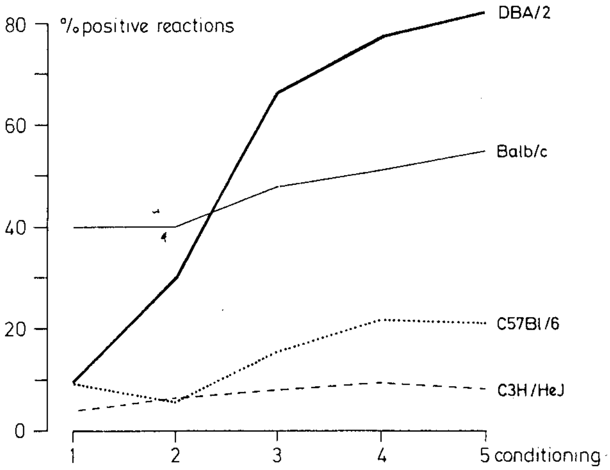

Fig. 13. Shuttle-Box performance of four inbred strains after induced isolation stress

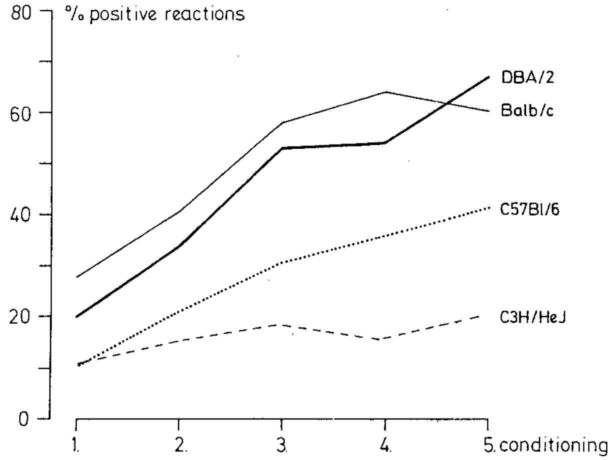

Fig. 14. Shuttle-Box performance of four inbred strains after handling

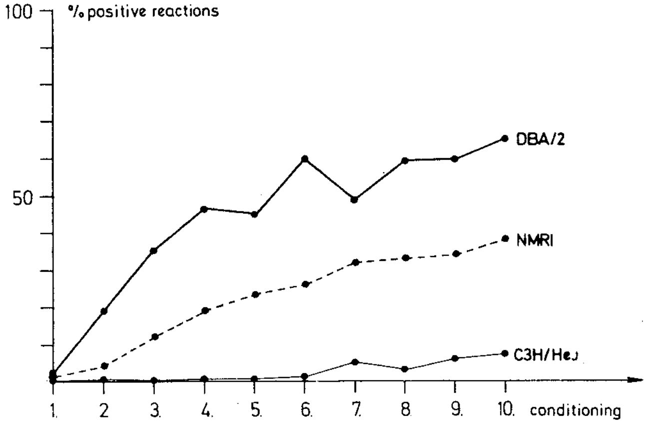

Fig. 15. Learning performance in the Skinner-Box of three inbred strains with two conditionings per day over a period of five days

between the scores obtained in the Shuttle-Box and in Skinner-Box respectively within a single strain. Duncan's multiple range test showed no significant differences in comparison to the single strains conditioned in the Shuttle-Box and Skinner Box, but significant group differences on the 1% level between C3H/HeJ, NMRI, and DBA/2. Compared with the data observed in the Shuttle-Box the rate of increase of DBA/2 was nevertheless slightly lower. This can be explained by the fact that the body weight of DBA/2 is less than that of NMRI, thus leading to anatomical difficulties in pressing the lever. By taking into account the provisional character of the last data – until now we have had no results from the F_1 generations – these results point to a controlling function of the gene under discussion as being the only responsible factor in this test-system as well.

Altogether, the results clearly show that avoidance performances resulting from the different tasks in shock avoidance programs are all controlled by one and the same gene. This gene seems to be present in the different inbred strains in a slightly different form. Genetically this is called a multiple allelic system which develops during evolution by small mutations at an intragenic level. These mutations are responsible for the differences in avoidance of the inbred strains that were used. Environmental modifications during various periods in the animals' individual life do not have a measurable influence on the behavior expression.

Discussion

During recent decades human genetics has succeeded in detecting simple modes of inheritance of many morphological and physiological traits. According to McKusick (1978) 1,364 of them are subject to such simple hereditary mechanisms. In the case of additional 1,447 diseases, this clear mode of inheritance is probable. However, it is still under discussion. In clear contradiction to these findings it has been impossible up to now to demonstrate controlling mechanisms of a corresponding simplicity for behavioral traits; the exception to this being one Mendelian mode of inheritance in the normal EEG (Vogel 1970).

The same can be stated for animal models, preferred for experiments in human genetics which are impossible for man himself. Thus, following the last review of Green (1967), 318 monogenic variants in laboratory mice are known, and in the meantime quite a few can be added to this amount. Among these, however, not a single variant can be found that exclusively controls the area of behavior.

As far as behavior defects are involved in such syndromes or variances of the normal phenotype, they are probably the results of a pleiotropic gene effect. Examples of this come from studies investigating influences of color genes in the expression of behavior (Tyler 1970) or studies concerning differences in behavior in albino mice (Winston et al. 1967; Henry and Schlesinger 1967). In our opinion, investigations concerning loci reserved for the expression of morphological phenomena have as little chance of success as those in humans suffering from clinical genetic diseases. For the study of basic genetic differences in the field of behavior aiming at detecting biological mechanisms, the most interesting area is without a doubt one that allows results of basic genetic mechanisms in mental performances, in the broader sense of the word. Controversial opinions and prejudices in this area will be able to be discussed in a new and, in our opinion, better way only when a continued demonstration of Mendelian modes of inheritance becomes possible, and also when it is possible to describe polygenic models with a clear calculation of the nature-nurture factors. This paper has aimed at investigating the genetic basis of avoidance learning in genetically normal inbred mice which is, as mentioned above, a controversial topic. In addition, we have aimed at separating the influences of nature-nurture factors – that is, the degree to which each participates in the control of this learning and memory storage phenomenon, in the case of a clear genetic basis. Considering this we felt it necessary to vary the mode of conditioning in the stimuli (light, sound) as well as the mode of shock avoidance (changing compartments, pressing the lever). In this way, a clear analysis of the quality and the inducibility of the genetic background was made possible as well as a calculation of the learning strategy. The results demonstrate a clear genetic background concerning avoidance learning, which cannot be changed, manipulated, or prevented even by radical environmental modifications. Furthermore, the genetic background can be quantified phenomenologically. The avoidance learning in the Shuttle-Box as well as in the Skinner-Box is controlled by one and the same single gene. The mode of inheritance is defined as codominant, and qualitatively different genes can be found in the various inbred strains that form a multiple allelic system, as the distribution of the P and F_1 generations show. Furthermore, it was revealed that the gene under discussion does not control the learning ability as such, but rather the speed of learning, since differences in learning cannot be discussed without due consideration of the time factor. On the whole, the data give a clear indication that even in the area of relatively complex behavioral patterns, simple genetic backgrounds acting as controlling principles can be found. In regard to all this, the function of the gene under discussion in its evolutionary concept for normal behavior is at the moment merely of secondary importance. There is no doubt that such a function does exist and is used for performing mental tasks in the broader sense of the word.

The clear starting position of modern behavior genetics as a scientific discipline does not at present allow a genetic analysis of complex ethological structures. Just as the verification of genetic principles has been accepted as biologically incontestable for many decades in the morphological and physiological areas, so genetic principles must be accepted in behavioral patterns in the future.

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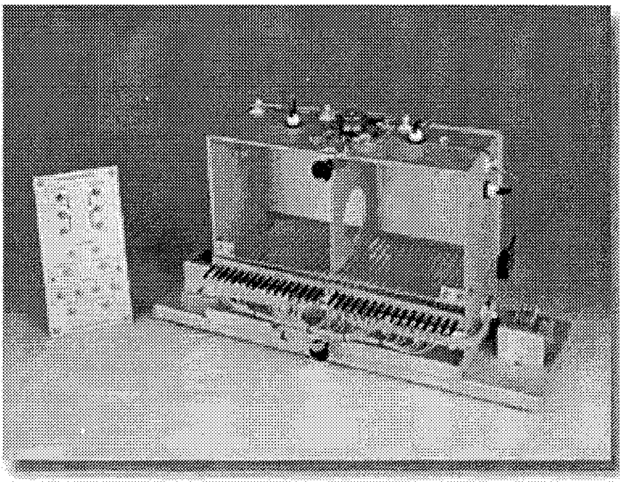

Photograph shows extra shuttle control and master shocker for use with two avoidance chambers.

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