A QUANTITATIVE GENETIC ANALYSIS OF RUNWAY LEARNING IN MICE*

Patrick A. Tyler and Gerald E. McClearn

University of Colorado, Institute for Behavioral Genetics
Boulder, Colorado

Genetic influences on learned behaviors have been firmly established by inbred strain comparisons and selection studies (see review by McClearn and Meredith, 1965). Yet, apart from the studies which have found a pleiotropic effect of the albino gene on avoidance and escape learning in mice (Fuller, 1967; Henry and Schlesinger, 1967; Winston, Lindzey and Connor, 1967), there have been very few attempts at further genetic analysis. Learning phenomena would seem to provide an ideal set of phenotypes for analysis by the techniques of quantitative genetics, since most of their genetic variance is probably attributable to the action of large numbers of genes, each with a relatively small effect. However, with the exception of one study which found a fairly high heritability (about 0.5) for avoidance learning in young pigs (Willham, Cox and Karas, 1963), these techniques have been virtually ignored.

This study was undertaken to provide a quantitative genetic analysis of a selected learning process. The straight runway was chosen for study because it represents a simple, basic learning situation and it provides a fast, reliable testing procedure. The intent was to fit an empirical curve, the second-degree polynomial regression, to the learning function of each individual so that the parameters of the fitted curves could be used as the scores in parent-offspring comparisons. For the purpose of thinking about the meaning of the data the 3 parameters yielded by the curve were tentatively identified in psychological terms. The linear coefficient measured a change in behavior and was therefore identified as the amount of learning. The mean measured the overall activity of an animal in the runway situation and the quadratic coefficient represented the rate of change, or rate of approach to asymptote.

MATERIALS AND METHODS

Mice: The HS population was produced by crossing the following 8 strains maintained at the Cancer Research Genetics Laboratory, University of California, Berkeley: A, AKR, BALB/c, RIII, C3H/2, C57BL, DBA/2, Is/Bi. This population was subsequently maintained by 40 matings each generation, mates being selected randomly with the restriction that they could not have a single common

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grandparent. Further details of production and maintenance have been described (McClearn, Wilson and Meredith, in press). At the time that this experiment was started, the last litters were being produced from the 5th generation following the cross. The parent generation for this study therefore contained 47 mice from the 5th HS generation and 81 animals from the 6th HS generation. These animals were tested, paired at random and mated in 8 approximately equal groups. Whenever possible 2 offspring of each sex from the first litter produced by each family were tested. If for some reason an animal was unavailable or failed to complete testing it was replaced by siblings of the same sex from later litters. A total of 274 mice was tested from the offspring generation; of these 237 were from first litters, 37 from later ones.

Behavioral measures: The straight runway apparatus consisted of a continuous red plastic shell with a clear, smooth plastic liner. The inside dimensions were $36'' \times 1.75''$ deep and $1''$ wide. Six inches from each end was a gate which opened by swinging upwards toward the center of the runway. Alongside and parallel to the runway at a distance of $2.2$ inches was a 3-foot long, 40-watt fluorescent lamp. Three photocells, one placed $1''$ from each gate and one in the center, were activated by the lamp, and were connected to a clock and an event recorder.

The apparatus was designed symmetrically so that an animal could be placed in at one end and tested in one direction and then in the other, back and forth as many times as desired, without being handled. Both starting and running times were recorded on the chart and running times were also read from the clock.

Experimental procedure: Each mouse was between 55 and 66 days of age on the first day of the testing. About 5 days before testing subjects were separated from their like-sexed litter mates into individual cages and taken to the experimental room where they were housed throughout the experiment. On the following day their baseline weight was obtained and for the next 2 days they were given 10% of their bodyweight in a standard laboratory mouse food. They were then maintained at about 85% of their baseline weight by being fed between 10 and 15% of their initial bodyweight each day.

The mice were tested in groups of about 12 and the order of testing within each group was randomized each day. Each mouse was given 5 trials per day for 8 consecutive days. Reward was present on the first 5 days (25 trials of acquisition) and absent thereafter (15 trials of extinction). On each test day the mouse was taken from its cage and placed in the runway at one end; the starting end was alternated on each consecutive day of testing. The first trial started when the gate was opened and a button pushed to start the recorder. After each acquisition trial the animal received one Noyes peanut pellet weighing 45 mg. The gate was opened to start the next trial when the animal turned to face it after finishing the pellet (about 20-30 seconds for most mice). The procedure was exactly the same for the extinction trials with the exception that the food pellet was omitted. After 5 trials the animal was returned to its cage and the runway wiped clean with an alcohol solution. After testing all animals were weighed and fed.

Analysis: The raw data consisted of 2 latency measures for each animal on each of the 40 test trials. The distribution of latencies tends to be highly skewed and
produces a strong correlation between means and variances. Since this is corrected by a logarithmic transformation of raw scores, this transformation was normally used in analyses. Starting and running times were recorded to the nearest 0.1 second. When this resulted in a value of 0 seconds for the starting time a constant value of 0.05 was added. All time scores were multiplied by 10 before the logarithmic transformation was made to ensure that all means would be positive.

The values used as the basic data for most of the analyses were the 8 means of the 5 daily transformed scores, calculated for each individual animal. To these values a second degree polynomial regression curve was fitted \(Y = a + bX + cX^2\). The genetic analysis consisted of estimating the heritabilities of the means of the transformed latencies and of the parameters of the fitted curve using the regression of the offspring means on mid-parent scores (see Falconer, 1960). Phenotypic, genetic and environmental correlations among these variables were also calculated.

**RESULTS**

The means and standard deviations of the transformed running time scores for the two generations on each of the days of testing are presented in Table 1. Table 2 shows similar data for the starting times. Informal observation during testing suggested that animals performed more variably during extinction and

**TABLE 1**

<table>
<thead>
<tr>
<th>Day</th>
<th>Parents Mean</th>
<th>S.D.</th>
<th>Offspring Mean</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acquisition</td>
<td>1</td>
<td>1.944</td>
<td>0.168</td>
<td>1.915</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1.655</td>
<td>0.158</td>
<td>1.614</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1.541</td>
<td>0.149</td>
<td>1.540</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>1.436</td>
<td>0.164</td>
<td>1.468</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>1.375</td>
<td>0.172</td>
<td>1.415</td>
</tr>
<tr>
<td>Extinction</td>
<td>1</td>
<td>1.439</td>
<td>0.207</td>
<td>1.443</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1.574</td>
<td>0.193</td>
<td>1.567</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1.629</td>
<td>0.200</td>
<td>1.629</td>
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**TABLE 2**

<table>
<thead>
<tr>
<th>Day</th>
<th>Parents Mean</th>
<th>S.D.</th>
<th>Offspring Mean</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
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<td>1.250</td>
<td>0.359</td>
<td>1.155</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.927</td>
<td>0.291</td>
<td>0.842</td>
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<tr>
<td></td>
<td>3</td>
<td>0.796</td>
<td>0.263</td>
<td>0.787</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0.778</td>
<td>0.259</td>
<td>0.771</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.706</td>
<td>0.260</td>
<td>0.712</td>
</tr>
<tr>
<td>Extinction</td>
<td>1</td>
<td>0.774</td>
<td>0.305</td>
<td>0.800</td>
</tr>
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<td>0.915</td>
<td>0.257</td>
<td>0.958</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.951</td>
<td>0.317</td>
<td>0.989</td>
</tr>
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</table>
this is confirmed by slightly higher standard deviations in extinction. More striking, however, is the difference in the standard deviations of the starting and running times. As is commonly found in such situations the starting time data were much more variable. There is a slight difference in the means of the two generations especially toward the end of acquisition. Such fluctuations over time are frequently encountered and usually ascribed to uncontrollable environmental variations. Finally, behavior in the runway apparatus resulted in a classical learning curve which could be subjected to genetic analysis (Figures 1 and 2).

**Heritabilities:**

Unless otherwise noted all heritability estimates were calculated using the regression of the mean of all offspring in each family on the mean of the parents. Each point was weighted by the number of offspring in each family. This regression directly estimates the heritability; thus, the standard error of $h^2$ is the standard error of a regression calculated in the usual way. The heritabilities and standard errors of the daily means for running and starting times are shown in Table 3. For the running time acquisition data the heritabilities fluctuate between a low of .21 on day 3 and a high of .41 on day 5. There is then a sharp drop during extinction. The starting time estimates also fluctuate with the highest occurring on day 1. A test for trend on the running time acquisition estimates

![Figure 1](image-url)
found no evidence for a consistent increase. Moreover, because of the size of the standard errors, the differences between the highest (day 5) and the lowest (day 3) estimates were not significant.

For further analysis of the change in heritability of the running and starting time data, the components of variance are shown in Figures 3 and 4. During acquisition the change in $h^2$ is chiefly attributable to the fluctuations in the additive genetic component ($V_A$), since the environmental component ($V_E$), which
appears in the figures as the difference between $V_A$ and $V_P$, remains fairly constant. The decline in $h^2$ from acquisition to extinction appears to be caused both by a decrease in $V_A$ and an increase in $V_E$. 

FIGURE 3. The change in components of variance during learning: running times.
The polynomial regression curve, \( \hat{Y} = \bar{Y} + b (X - \bar{X}) + c (X^2 - \bar{X}^2) \) was fitted to the acquisition data and the mean and a linear coefficient were also calculated for the extinction data. The heritabilities of the means and the linear and qua-
### TABLE 4

Heritabilities and genetic and environmental correlations among components of learning curves. Heritabilities are shown with their standard errors on the main diagonal. Above them are the genetic correlations (± standard error) and below them are the environmental correlations.

<table>
<thead>
<tr>
<th></th>
<th>Running Times</th>
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<th></th>
<th></th>
<th>Starting Times</th>
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<th></th>
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</tr>
</thead>
<tbody>
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<td>7</td>
<td>8</td>
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<td></td>
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</tr>
<tr>
<td>Acq. Mean</td>
<td>1.41 ± .12</td>
<td>.27 ± .18</td>
<td>.12 ± .20</td>
<td>1.11 ± .08</td>
<td>−.11 ± .29</td>
<td>.92 ± .05</td>
<td>−.29 ± .20</td>
<td>.06 ± .20</td>
<td>.82 ± .11</td>
<td>−.31 ± .34</td>
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</tr>
<tr>
<td>B</td>
<td>2</td>
<td>0.00</td>
<td>−.10 ± .21</td>
<td>−.08 ± .25</td>
<td>−1.29 ± .26</td>
<td>.31 ± .19</td>
<td>.65 ± .15</td>
<td>.11 ± .22</td>
<td>.32 ± .21</td>
<td>−1.69 ± .48</td>
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<tr>
<td>Ext. Mean</td>
<td>4</td>
<td>.24</td>
<td>.61</td>
<td>.14</td>
<td>.07</td>
<td>.11 ± .10</td>
<td>.41 ± .29</td>
<td>−.08 ± .35</td>
<td>−1.03 ± .28</td>
<td>−.55 ± .31</td>
<td>.66 ± .43</td>
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<td>.11</td>
<td>−.10</td>
<td>.14</td>
<td>.07</td>
<td>.11 ± .10</td>
<td>.41 ± .29</td>
<td>−.08 ± .35</td>
<td>−1.03 ± .28</td>
<td>−.55 ± .31</td>
<td>.66 ± .43</td>
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<tr>
<td>Starting Times</td>
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<td>−.06</td>
<td>−.02</td>
<td>−.05</td>
<td>.36 ± .11</td>
<td>−.29 ± .21</td>
<td>.03 ± .21</td>
<td>.91 ± .08</td>
<td>−.48 ± .37</td>
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<tr>
<td>B</td>
<td>7</td>
<td>−.68</td>
<td>.44</td>
<td>−.16</td>
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<td>−.19</td>
<td>.19 ± .12</td>
<td>−.71 ± .17</td>
<td>.25 ± .24</td>
<td>−.59 ± .36</td>
</tr>
<tr>
<td>C</td>
<td>8</td>
<td>.04</td>
<td>−.06</td>
<td>.08</td>
<td>.15</td>
<td>−.02</td>
<td>.02</td>
<td>−.21</td>
<td>.25 ± .10</td>
<td>.09 ± .28</td>
<td>−1.28 ± .44</td>
</tr>
<tr>
<td>Ext. Mean</td>
<td>9</td>
<td>.20</td>
<td>.06</td>
<td>−.02</td>
<td>.48</td>
<td>−.18</td>
<td>.46</td>
<td>.18</td>
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<td>.25 ± .10</td>
<td>−1.05 ± .45</td>
</tr>
<tr>
<td>B</td>
<td>10</td>
<td>.06</td>
<td>−.20</td>
<td>.09</td>
<td>.09</td>
<td>.28</td>
<td>.21</td>
<td>−.21</td>
<td>.04</td>
<td>.15</td>
<td>.06 ± .10</td>
</tr>
</tbody>
</table>
A Quantitative Genetic Analysis of Runway Learning in Mice

The quadratic coefficients are presented on the main diagonal of the matrix in Table 4. These data indicate that for both traits the acquisition mean was the most heritable component. For each trait too the heritabilities of the other two components of the acquisition curve were similar in magnitude. Heritabilities for extinction data were generally low and the means were again the more heritable components.

**Correlations:**

Product-moment correlations ($r_p$) were obtained between all pairs of variables for both parent and offspring generations. Genetic correlations ($r_A$) were estimated using the formula

$$r_A = \frac{\text{Cov}_{A}}{(\text{Var}_A \times \text{Var}_A)^{0.5}}$$  

(Falconer, 1960).

Two estimates of the genetic covariance, Cov$_A$, were available from the covariance of the parents on one trait with the offspring on the other trait. These estimates were averaged as recommended by Reeve (1955) and the formula derived by Reeve for estimating the standard error of the genetic correlation was also used. Environmental correlations ($r_E$) could then be obtained by substituting in the formula $r_p = h_Xh_Yr_A + e_Xe_Yr_E$ where $h = \sqrt{h^2}$ and $e = \sqrt{1-h^2}$.

The correlations among the daily means for starting and running times were highest between successive days (see Table 5) and decreased as the days were more widely separated (see Tyler, 1969, for more complete data summaries).

**TABLE 5**

<table>
<thead>
<tr>
<th>Var 1</th>
<th>Var 2</th>
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<th>SE</th>
<th>r_A</th>
<th>r_H</th>
<th>Par</th>
<th>Off</th>
<th>SE</th>
<th>r_A</th>
<th>r_H</th>
<th>r_E</th>
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<tbody>
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<td>0.67</td>
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<td>0.07</td>
<td>0.54</td>
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<td>Acq. 5</td>
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<td>0.74</td>
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<td>0.73</td>
<td>0.98</td>
<td>0.06</td>
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<td>Acq. 5</td>
<td>Ext. 1</td>
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</tbody>
</table>

**TABLE 6**

<table>
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<tr>
<th>R.T.</th>
<th>S.T.</th>
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<th>SE</th>
<th>r_A</th>
<th>SE</th>
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<td>0.78</td>
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<td>2</td>
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<td>0.56</td>
<td>0.93</td>
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<td>0.45</td>
<td>0.95</td>
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<td>0.50</td>
<td>0.83</td>
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<tr>
<td>5</td>
<td>5</td>
<td>0.51</td>
<td>0.52</td>
<td>1.05</td>
<td>0.07</td>
<td>0.31</td>
</tr>
</tbody>
</table>

Both genetic and environmental factors appeared to change as learning progressed and both contributed to a decrease in the phenotypic correlation. While this decrease was predictable from what is known about correlations among repeated measures, the increase in the correlation between the early days of
acquisition and the later days of extinction was not (see Figure 5 for an example of this trend). As extinction progressed control over behavior in the runway apparently returned to some of the factors influencing earlier acquisition performance including, perhaps, individual activity level or exploratory behavior. In Table 6 the correlations between corresponding days for running and starting time data can be seen. The phenotypic correlations were only moderate, the genetic ones considerably higher.

The correlations among the components of the curves and between acquisition and extinction are shown in Table 4. For both running time and starting time data the most interesting correlations are those between acquisition and extinction. Animals which ran faster over all trials during the former also ran faster during the latter, and this was largely determined by genetic factors. Moreover, mice which had a steeper acquisition slope also tended to have a steeper extinction slope, and again genetic factors appeared to play a more important part than environmental ones in producing this tendency especially in the running time data.

As with the heritabilities the patterns of correlations in the starting time and running time data were strikingly similar. The largest difference between the two lay in the correlation between the acquisition curve coefficients b and c. These were unrelated in the running time data whereas they had a moderate phenotypic and high genetic correlation in the starting time data. It was reasonable
to expect that the highest values, when the components of the learning curves for starting and running times were correlated, would be those between the comparable parameters and this proved to be the case. It is noteworthy that in all these cases the genetic correlation was higher than the environmental. Despite the high standard errors of the genetic correlations which caused some of these correlations to exceed 1.0, the consistency of this phenomenon is remarkable.

**DISCUSSION**

Two sets of data were of primary interest in this experiment. These were obtained by observing the time it took an animal to leave the start-box and the time it took to run to the other end-box. These sets of data were independent in the sense that one did not include the other, but inasmuch as they were collected at the same time in the same apparatus, they were clearly very closely related at least in terms of the environmental events involved. Nevertheless the starting times were much more variable than the running times and this increased variability could have produced a redistribution of the relative importance of the components of variance for the learning parameters. Thus while it was not surprising that starting times and running times showed similar patterns of inheritance, it was not a foregone conclusion.

The heritability of both traits tended to fluctuate during acquisition and decreased during extinction. The correlations between the means of consecutive days increased slightly during acquisition and decreased in extinction. This should be a reasonably good indicator of the change in reliability of the task. These changes tend to support the findings reported by Fuller and Thompson (1960) rather than those of Broadhurst and Jinks (1961). Fuller and Thompson, reanalyzing their own data with dogs, found that the reliability of their tasks increased with practice while the heritability fluctuated at about the same level. Broadhurst and Jinks reanalyzed an experiment by Vicari (1929) on maze learning in inbred mice and found that the heritability increased during acquisition. If the reliability increases it might be expected that the environmental variance would decrease due to the lessening of importance of its unreliable component. Thus the expected outcome would be that found by Broadhurst and Jinks. In fact the environmental variance was found to remain fairly constant during learning and fluctuations in heritability were chiefly caused by changes in the genetic variance.

The overall means were generally the most heritable component of the learning process. This probably reflects the specific composition of the HS population which contains genes from strains differing widely in activity level (McClearn et al., in press). The linear and quadratic components had heritabilities of about the same magnitude in both sets of data and these were a little higher for the running times. It is interesting that these coefficients were independent in the running time data but related for the starting times, suggesting that the processes were not identical. The standard errors of the fitted curves were always calculated but were not included in the results as they were not heritable and were never correlated with anything except themselves. This in itself is
worth commenting on as it was thought originally that the tendency for an individual to conform to a given fitted curve might be heritable. These results suggest that most of the genetic variance between individuals in learning was included in the variance between the components of the curve and that it would not have served much purpose to obtain higher degree coefficients such as the cubic.

In view of the similarity between the starting and running time data and of their relatedness in terms of environmental proximity and temporal contiguity, it is surprising that the correlations between the test day means were not higher. It is even more surprising that, in general, the genetic correlations between the components of the learning curves for starting and running times and for acquisition and extinction were higher than the environmental correlations. If the correlations between the variables were mainly the result of the similarity of apparatus and testing conditions, this should not be the case. These findings suggest that extra-experimental environmental factors make a more important contribution to the variances and covariances than do fluctuations in the stimuli intrinsic to the testing situation.

From the results of this experiment it appears that in the runway situation there is a large subset of genes common to each learning component (general activity, amount of learning or rate of learning) regardless of whether learning is measured by running times or starting times during acquisition or extinction. If this is true, it has significant implications for considering the mechanism of learning as involving a unitary biological process. An important further step now would be to find out the extent to which this is true for different learning situations.

**SUMMARY**

Individual differences in the acquisition and extinction of a straight runway response were studied. Sixty-four pairs of mice chosen from a heterogeneous population and motivated by hunger were given 5 massed trials a day in the runway for 5 days of acquisition and 3 days of extinction. They were then mated at random and their offspring were tested using the same procedures. A second degree polynomial function \( Y = a + bX + cX^2 \) was fitted to the learning curve of each individual. Since learning may be defined as change in behavior, \( a \), \( b \) and \( c \) may be regarded as overall activity, amount of learning and rate of learning respectively. Estimates of the heritability were made by regressing the means of the offspring on the parent means. Heritability estimates of the 3 parameters of the learning curve (the mean, \( b \) and \( c \)) were respectively \( 0.41 \pm 0.12 \), \( 0.30 \pm 0.10 \), and \( 0.26 \pm 0.14 \) for running times and \( 0.36 \pm 0.11 \), \( 0.19 \pm 0.12 \), and \( 0.25 \pm 0.10 \) for starting times. The correlations between traits were also partitioned into their genetic and environmental components. This analysis suggested that many of the same genes were contributing to individual differences in the comparable components for running and starting times for acquisition and extinction.

**REFERENCES**

A Quantitative Genetic Analysis of Runway Learning in Mice


