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Evidence from the rat for a general factor that underlies cognitive performance and that relates to brain size: intelligence?

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The data on a group of 22 rats, each measured for their speed of reasoning, accuracy of reasoning, response flexibility, and attention for novelty, were subjected to two different methods of factor analysis. By both methods, the correlation matrix of their performance was consistent with a single-factor model. In a second cohort of rats, where brain size was known, the score for this 'general factor' was computed. The regression for brain weight and the general factor was significant.

Can research on rats determine the biological basis of the observed correlation between brain size and intelligence [21]? Animal research allows adequate behavioral and anatomical definition of subjects, but do animals possess 'intelligence' of some qualitative similarity to human intelligence?

Factor analysis is a statistical tool which has proven useful in understanding the nature of individual differences. For example, used to explain the invariable tendency of intelligence tests to correlate positively among themselves, the method has suggested an underlying general, or 'g' factor (for review see ref. 6). If certain animal tests are to be considered as measuring intelligence, then the tests' intercorrelations should be positive and it would be expected that factor analysis should show a general factor. Further, animal intelligence as defined by these tests should correlate with brain size, as shown for humans.

In constructing a battery of intelligence tests for animals, reliability and construct validity should be considered in the selection process. We can select tests that assess either learning or insight [13]. Learning is the acquiring of knowledge whereas insight is the creating of new knowledge. There are practical and theoretical reasons for selecting animal measures that assess abilities related to insight. Practically, Lashley [13] and others [18] have failed to find significant correlations among normal rats submitted to test batteries comprised predominantly of learning measures (although not all similar attempts have met with failure [19]). Theoretically, it appears the essence of human intelligence is not learning but problem solving, not recall but reasoning [9, 16].

The measures selected for this initial investigation included a measure of accuracy on a 'reasoning' problem, a measure of speed of solving a reasoning problem, a measure of response flexibility, and a measure of attention for novelty. None of these measures is an assessment of learning.

The reasoning test assessed speed and accuracy of solving a problem which relied on non-contiguously learned experiences [14, 15]. The response flexibility test determined the rat's capacity to find a new route to the goal box when the prior route was blocked (i.e. an 'Umweg' problem). The attention for novelty test measured how much a rat preferred novel items. In human infants, preference for novelty correlates with I.Q. measured by standard assessments later in life [5, 8, 20].

This report has two components. First, the data on a small group of normal rats from two separate experiments were subjected to factor analysis to see if the correlation matrix was consistent with a 'general' factor. Second, rats, some of whom had been exposed to methylazoxymethanol acetate, a chemical that induces micrencephaly [7], were evaluated to see if their performance on the behavioral measures, when collapsed to a

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single score for the general factor, would correlate with brain size.

The details of the rat subjects and the testing procedures have been described previously [1, 3] and will be recounted here briefly.

All subjects were male Long–Evans rats. Some rats were exposed to methylazoxymethanol acetate 14 mg/kg on gestational day 15, and a subset of these received 50 mg/kg of naltrexone on postnatal days 1–21. All subjects were part of two experiments reported previously. The first study assessed the reliability of a reasoning test [3] and the second study assessed the pattern of behavioral deficiencies associated with mild micrencephaly [1].

Attention for novelty. This basic procedure for this test has been described elsewhere [3]. The test used an open field chamber. The floor was divided into 9 equal sized squares. Each animal was placed in the enclosure for 3 min per session. Beginning on the 4th or 7th day (depending on which of the 2 studies) the amount of time spent in the center square was recorded. On the next 2 days, a red magic marker was taped to the center square. On the following 2 days a soda pop can was affixed to the center square. For each animal the time spent in the center square (in seconds) on the first 2 exposures to the novel objects was summed to provide the preference for novelty measure.

Reasoning test. The test procedure has been described [3]. An 8-arm radial maze was used. Rats were started on this task at 80–85% of their initial weight.

Experience 1: exploration of the maze. Groups of 5 or 6 animals were placed in the center platform and allowed to explore the unbaited maze for 10 min.

Experience 2: demonstration of the goal arm. Next, the arm selected as the goal arm was baited at its distal end with 1/2 a Froot Loop in a recessed cup. A rat, individually, was placed near the food and allowed to eat. Access to the rest of the maze was prevented.

Reasoning test – training. After eating for 30 s, the animal was picked up and carried to the start arm and placed facing out at the distal end. The rat was allowed to acquire the rebaited goal arm. There were two trials per session and a session was conducted daily for 8 days. Each day used a new combination of start and goal arms. Each arm served as the start arm once and as the goal arm once across the 8 session block. The purpose of the training phase was to familiarize the animals with the components of the procedure before analyzing performance.

Reasoning test – testing. The test procedure was the same as that described above for training. Two test trials were administered in a single daily session over 8 consecutive days. The combination of start and goal arms varied between the training and testing blocks. The results were recorded in two ways. First, as the number of test runs out of 8 on which the rat was perfect, that is the rat did not enter any arms other than the correct arm on a day's first trial. Second, as the sum of the reciprocals of the times for each of the 8 days first run. The times were used as reciprocals to minimize the effect of rare large values. This is an appropriate method of transformation for data where most values are small, and there are occasional large outlying values [4]. The results of the second run for each day are not used here since this run is contaminated by learning and not appropriate for a reasoning measure [3].

Response flexibility. This measure was tested in a 3-chamber box similar to one previously described [2]. For training, there was simply a flat floor in the choice chamber at the level of the exit from the start box and the entrance to the goal chamber. For testing, there was the same flat floor with another board placed as an inclined plane slanting with the low end toward the goal box entrance.

Training consisted of teaching the rat to run across the box to get a Froot Loop reward in the goal box without the inclined plane. After the rat had reached a baseline level of performance, the inclined plane was inserted and the rat was scored on the number of errors made until he got the Froot Loop reward. An error was placing the head and forepaws under the inclined plane.

Brain weight. At 123 days of age, the rats to be examined for brain weight were sacrificed. The brains were dissected from the skull and weighed.

A principal factor analysis and a maximum likelihood analysis were done using the SAS program. No rotation was applied in either method. Prior communalities were set equal to the squared multiple correlations. Kaiser's measure of sampling adequacy was computed. Factor scores were computed for the one-factor model of the principal factor analysis and the standardized results were converted to a single 'factor' score.

Factor analysis was performed on the 22 male rats who had completed testing on all 4 measures and who had not received any drug treatment. Thirteen animals were reported as part of reference [3] and 9 from reference [1]. Kaiser's measure of sampling adequacy was 0.63, which is adequate [11]. Only one potential factor revealed an eigenvalue > 1 (1.29), with the other 3 eigenvalues ranging from 0.2 to −0.24. The factor loading and factor score coefficients are shown in Table 1.

Additionally, a maximum likelihood analysis was performed to assess the robustness of a 'general' factor result with a different method of factor selection. One eigenvalue was 1.84 with the others ranging from 0.26 to −0.36. χ^2-analysis of the one-factor solution yielded a $\chi^2 = 13.026$, with $df = 6$; the null hypothesis, that

TABLE I

TEST CORRELATION MATRIX PLUS FACTOR LOADINGS AND SCORING COEFFICIENTS*

*PN, preference for novelty (in seconds); RT, reasoning time (the reciprocal of each day's time on the reasoning test, in seconds, summed); Perf, the number of perfect trials on the reasoning test; Rflx, the number of errors on the response flexibility problem; Fctr Ld, the factor loadings from the principal analysis; and Fctr Scr, the factor scoring coefficients computed from this analysis. The subjects were 22 normal adult male rats.

	PN	RT	Perf	Rflx	Fctr Ld	Fctr Scr
PN	–				0.43	0.18
RT	0.39	–			0.58	0.28
Perf	0.27	0.43	–		0.70	0.41
Rflx	0.13	0.23	0.51	–	0.53	0.24

there were no common factors, was therefore rejected ($P = 0.04$). In evaluating the two-factor result, the null hypothesis that one-factor was sufficient ($\xi^2 = 1.603$ with 2 df for a $P = 0.45$) was accepted. By both a principal axis factor analysis and a maximum likelihood factor analysis, the data appeared adequate and consistent with models that contained a single general factor, both by the eigenvalue > 1 criteria and the comparison to a χ^2 distribution.

Comparison to brain weight. Twenty-five rats were part of an experiment to assess the behavioral effects of methylazoxymethanol and naltrexone on behavior [1]. Twenty rats completed all the behavioral measures and had a known brain weight. Nine rats received no drug treatment and were also part of the factor analysis above. Five rats had received MAM 14 mg/kg on gestational day 15, and 6 rats had received this plus naltrexone 50 mg/kg on postnatal day 1–21.

Using the factor scoring coefficients reported above for the principal axis factor analysis, the standardized scores on the behavioral measures for each animal were converted to a total 'factor' score. This result was standardized to a mean of 100 and a standard deviation of 15 to yield a familiar scale. This result was compared to brain weight (independent variable) by linear regression. The F ratio (1/18) was 5.30 with $P = 0.03$. The graphic presentation of the relationship is shown in Fig. 1

Comparing the anatomic measures to the individual behavioral tasks showed significant regressions for both the number of errors on the response flexibility apparatus (F ratio (1/22) = 6.31, $P < 0.05$) and the preference for novelty measure (F ratio (1/19) = 4.41, $P < 0.05$). Degrees of freedom vary because the number of rats completing any one test was greater than the number completing all 4.

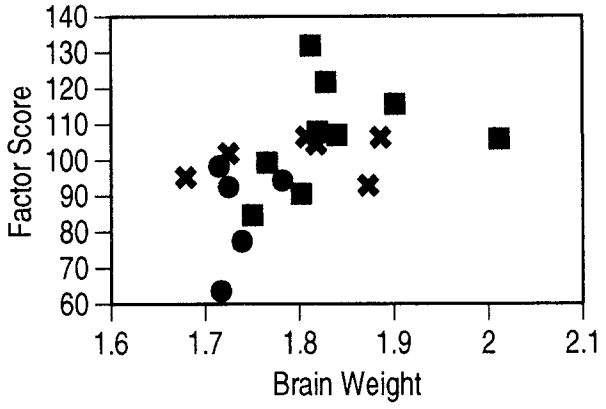

Fig. 1. The relationship of brain weight and factor score are shown. The factor score is a unitless number standardized to a mean of 100 and a standard deviation of 15. The factor score was calculated from applying the factor scoring coefficients from the principal factor analysis to the behavioral measures of 20 male rats. The brain weight is reported in grams and was obtained fresh at the time of sacrifice. The treatment group membership of the individual rats is designated by different symbols. Sal/H2O (squares) refers to control animals; MAM/H2O (circles) refers to animals exposed to methylazoxymethanol on gestational day 15 and water on postnatal days 1–21; and MAM/NTX (x) refers to animals that received naltrexone on postnatal days 1–21 in addition to the methylazoxymethanol. Other analyses showed that eliminating the difference in factor score due to differences in brain size eliminated any treatment effect.

The conclusions of this study are that four cognitive measures in the rat show a positive correlation manifold, factor analysis of the intercorrelated ability measures yields a general factor, and this general factor correlates to brain size. If our aim is to discover the biological basis of intelligence, then this derived measure, representing the latent structure of a battery of cognitive tests, may prove to be a valuable correlate for hypothesized biological markers.

The rat tests applied here were selected to measure characteristics like reasoning and problem solving, which are frequently considered as intelligent in humans [17]. The response flexibility apparatus is by its nature a novel problem requiring a solution. The reasoning accuracy measure also assesses novel problem solving. In this paradigm a rat is required to deduce a unique solution that will lead him to reward. Since the animal never runs a previously reinforced route for reward, a reasoned, rather than a learned, solution is required. The speed of solving the reasoning problem also appears relevant as it is not only accuracy but speed of problem solving that influences our colloquial perception of an individual's intelligence. The preference for novelty measure differs from the other 3 tasks in not being a hunger-motivated task. It also is unique in not being a problem solving measure. Its selection was motivated by the recognition

that a similar measure in human infants correlates to later measures of I.Q. [5, 8, 20].

There is no gold standard of intelligence, against which this factor, derived from measures of rat performance, can be correlated to assess construct validity. It is reported here that the intercorrelations of the four behavioral variables are positive and are statistically consistent with a general factor. This does not allow one to conclude that a one-factor model is necessary but the results do suggest that a zero-factor model is not valid and that a two-factor model does not significantly enhance the descriptive power of the solution.

The general factor is a reflection of consistent individual differences across tasks for the Long–Evans rat. How can the general factor be best conceived? The factor is not simply an apparatus effect since 3 different apparatuses were used. The factor cannot be hunger or a typical form of motivation since the preference for novelty task was not a rewarded task and loaded comparably to the other variables on this general factor. Since the tasks are all complex behavioral measures of cognitive ability, the general factor may best be conceived of as relating to individual differences in cognitive ability. Further evidence supporting a cognitive designation for the general factor is that the factor score of the rat correlates to brain size. Human intelligence also correlates to brain size [21]. The failure of prior studies to demonstrate a positive correlation manifold for normal rats administered cognitive tasks may be explained by differences in task selection. Prior attempts have emphasized learning measures.

Does it make sense to speak of rat intelligence? This is something we best 'Let the Jesuits debate... (Anonymous reviewer, personal communication)'. A hypothetical construct such as intelligence can neither be proven nor disproved. Rats serve as useful models of autoimmune, pulmonary, and assorted organ system diseases. Rats have brains that are distinctly similar in their anatomy and physiology to human brains [12]. If rats also show a general factor derived from the intercorrelations of ability measures and this 'g' factor relates to brain size, then that should be sufficient to encourage pursuing the biological correlates of general cognitive ability in rats. Why suppose a qualitative break in the phylogenetic continuum with respect to the neurocognitive system?

A break is often posited because humans employ language in communicating, but it has not been demonstrated that language is necessary for intelligent behavior [10]. Conceptually and practically the measurement of intelligence can occur in humans without linguistic material and even before verbal capacity [5, 8, 20]. The differences in the spheres of rat and human problem solving may reflect different manipulated items and differences in the complexity of processing abilities rather than differences in the basic processes of manipulation. If so, then studying the biological correlates of individual differences in the abilities of rats to manipulate cognitive items may show where to look for similar correlates in humans.

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