

Individual Differences and a Spatial Learning Factor in Two Strains of Mice (*Mus musculus*)

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Current theoretical approaches to animal intelligence either in the form of adaptive specializations or general processes make no explicit predictions nor do they provide substantial evidence concerning individual differences in problem solving. Two strains of mice (*Mus musculus*) were run through a battery of water escape tasks consisting of 4 spatial learning tasks, a visual discrimination task, and an activity control. The 2 strains were the second filial generation (F₂) from a cross between C57BL/6 and DBA/2Js inbred strains and a CD-1 outbred strain. Results indicated positive correlations across all learning tasks in both strains for latency and error measures. Factor analysis revealed a significant first factor for these measures in both strains. These results suggest that at least some spatial and visual tasks in mice under this motivational condition share common properties.

The past 2 decades have witnessed a growing interest in what has been termed comparative cognition or comparative intelligence, the study of complex processes in animals that in many respects parallels the study of similar processes in humans (e.g., Hulse, 1993; Hulse, Fowler, & Honig, 1978; Roitblat, Bever, & Terrace, 1984; Terrace, 1993; Weiskrantz, 1985). In one significant respect, however, the study of these processes in animals has proceeded along a quite separate path from the study of similar processes in humans. The case in point concerns the investigation of individual differences.

With respect to human intelligence, one of the most rigorously investigated issues since the inception of intelligence testing during the early part of this century has centered on the notion of a general intellectual ability (e.g., Cattell, 1963; Jensen, 1981). General intelligence refers to the fact that, within limits, individuals tend to retain their rank ordering across a series of different tasks such as those found on standardized intelligence tests. The result is a matrix of positive correlations across tasks, a "positive manifold" as it has been called (e.g., Jensen, 1992). Factor analysis of this matrix rather consistently yields a first factor or first principal component, the so-called general factor (*g*), that accounts for an appreciable proportion of the total variance in test scores, usually between 35 and 45% (e.g., Miller & Vernon, 1992).

To be sure, the identification of *g* has not proceeded without disagreements, and these disagreements have taken two forms. One form has asserted that the apparent presence

of *g* is a function of common elements in the administration and task demands of most standard human intelligence tasks and, therefore, indicates the presence of a test-specific or cultural-specific artifact, not a universal problem-solving mechanism (e.g., Gardner, 1983). A second form of disagreement concerns the best structural fit to the positive manifold. There has been debate, for example, concerning whether one need assume the presence of a general factor when a positive manifold may also be factored into a number of specific lower order factors such as spatial, memory, verbal, and other factors without also inferring the presence of a higher order general factor (Gould, 1981; Thurstone, 1947).

Despite these disagreements, there is at least rather robust agreement in the study of human intelligence that individuals rank ordered according to their performance on one task retain something of that same rank ordering on other tasks (Jensen, 1981; Locurto, 1997). The study of animal intelligence, on the other hand, evidences a different consensus. The prevailing view is that there is no coherent factor structure, with or without a general factor, in animals' performance across the types of tasks that would, if studied in humans, constitute components of general intelligence (Mackintosh, Wilson, & Boakes, 1985; Macphail, 1982; Scott & Fuller, 1965; Wahlsten, 1978). Warren (1977), for example, concluded that "one cannot speak of intelligence within a species of animals. No one has found evidence in support of a general level or capacity that result in an animal ... consistently performing above or below the level attained by other members of the species on several different tasks" (pp. 41–42). The term *animal intelligence*, although widely used, has become synonymous with the investigation of the characteristics of performance on specific problem-solving tasks such as serial position learning (e.g., Terrace, 1993), visual concept formation (e.g., Herrnstein, 1984), or any number of other complex cognitive tasks (e.g., Mackintosh, 1988), not with the study of individual differences.

This historical and contemporary difference in the approach to animal compared with human intelligence has far-reaching theoretical implications. If a factor structure,

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including perhaps a general factor, is present in human behavior but absent in animal behavior, this distinction may be as important as the long-standing controversy concerning whether animals and humans differ with respect to linguistic abilities (e.g., Rumbaugh, 1977). Macphail (1982, 1987), in fact, suggested that these two distinctions between animal and human intelligence may be linked, at least with respect to *g*: Linguistic abilities in humans may be the foundation for general intelligence in humans; the absence of comparable linguistic abilities in animals underlies the failure to observe general intelligence in animals.

The finding that in animals there is nothing similar to general intelligence as studied in humans may indeed reflect fundamental differences between animal and human intelligence. Alternately, it may be at least in part a function of the fact that there is no distinct tradition within animal intelligence of studying individual differences. As a result, there have been relatively few attempts to study the factor structure of problem-solving tasks in animals. Interest in this problem peaked during the 1930s and 1940s when Spearman's (1927) construction of human *g* became well known. Yet as early as 1942, Tryon indicated that there had been no substantially original studies on the problem of individual differences in animal intelligence since 1934: "Most psychological study of animals continues to consist of experiments showing the effects of laboratory-induced changes of conditions on the *average* animal. Systematic studies of the psychological nature and causation of individual differences are rare" (p. 358). A similar statement might be made about the subsequent literature. Royce, in reviewing the available animal literature in 1950 and again in 1966, noted that in the intervening 16 years between reviews there had been only four studies generally concerned with the factor structure of animal behavior, and none of these studies was concerned with intelligence. A review covering the entire history of studying general intelligence in animals drew the same conclusion (*viz.*, Locurto, 1997).

Naturally, the strength of the conclusion that there is no factor structure, with or without a general factor, in animal intelligence rests on the strength of the available literature. Unfortunately, not only have there been relatively few studies to investigate this issue, but there is also a question of whether any of them were sufficiently well designed to detect the presence of general intelligence or, for that matter, any factor structure. As P. E. Vernon (1971) noted with respect to battery development, "In general a minimum of three tests is needed to define a factor . . . if a battery consists only, or predominantly, of a specialized type of test (e.g., all tests of sensory-motor abilities), the *g* and major group factors may fail to reveal themselves" (p. 26). Vernon's comments apply to any factor structure investigation, but he was referring specifically to marking factors and identifying *g* within the framework of a hierarchical factor structure of the type that has become prevalent in the analysis of human intelligence. In this type of model, lower order factors (e.g., memory, spatial, verbal) are each measured or marked by a number of specific tests. No one test can be taken as unequivocal evidence of the presence of that factor. Similarly, the emergence of *g* itself depends on the measurement

of a number of lower order factors using a number of tests to reveal each lower order factor. Any two or more individual tests may correlate only modestly, depending on their particular *g* loading. It is even possible that, as Child (1990) observed, "in broad, heterogeneous factors [of which *g* would be a primary example], two variables [may] belong to the same factor, and yet have little or no correlation" (p. 33).

The implication of this need for task variety to mark a factor, and the need to mark lower order factors to reveal *g* if it emerges within a hierarchical framework, is that prior work in animal intelligence may not have been adequately designed to reveal the presence of any type of factor structure, especially a higher order factor structure that has *g* at its apex. It may well be a historical irony that the model of a hierarchical structure of human abilities and the methodological requirements to detect it became widely known only in the late 1940s, just as interest in a possible animal *g* had waned (see Burt, 1949, for a review of the development of hierarchical analyses). Both Eysenck (1987) and Humphreys (1987) argued that an appropriate psychometric assay of general intelligence in animals has yet to be accomplished (see, Locurto, 1997, for a similar conclusion). From this perspective, what is most striking is that nearly 70 years after Spearman first posited a general factor in human intelligence there has not been an adequately designed research program to assess the presence or absence of a factor structure in animal intelligence.

It should be said that despite the accepted conclusion concerning general intelligence in animals, a number of studies conducted during the 1930s and early 1940s reported positive correlations across various types of maze tasks (e.g., Campbell, 1935; Commins, McNemar, & Stone, 1932; see Munn, 1950, for a review of this early work). Additionally, although contemporary work has not been concerned with identifying an animal *g*, there has also been a number of studies that point in the direction of positive correlations across spatial-maze tasks (e.g., Anderson, 1993; Crinella & Yu, 1995; Davenport, Hagquist, & Rankin, 1970; Livsey, 1970; Thompson, Crinella, & Yu, 1987). The reliable finding of a positive manifold across maze tasks would itself be important in suggesting the presence of a spatial factor, apart from considerations of whether that factor correlated with other types of tasks, thereby indicating the presence of higher order factors. Spatial behavior consistently emerges as a highly *g*-loaded factor in hierarchical analyses of human intelligence, and it also emerges as a separable factor in models that do not posit a general factor, as it did as one of Thurstone's Primary Mental Abilities (1947; Cardon, Fulker, DeFries, & Plomin, 1992; McClearn et al., 1997; Plomin, 1988; P. E. Vernon, 1971). Further, brain regions that appear to mediate the expression of spatial performance in rodents are analogous to regions associated with similar memory and cognition functions in humans (Aggleton, Hunt, & Rawlins, 1986). It should also be noted that spatial learning appears to be genetically mediated in both animals and humans (Plomin, 1988; Upchurch & Wehner, 1989).

Given the lack of historical and contemporary interest in this issue, no single study can at this juncture serve as an omnibus test of a factor structure in animal intelligence,

much less serve to mark the presence of a general factor. We have little if any systematic evidence of the presence of a positive manifold across any set of tasks, even those that presumably tap common functions such as spatial learning. In this light, the present study may be seen as a first stage in the longer term development of a test battery to determine whether a factor structure of any sort exists in animal intelligence.

The strategy at this first stage was to develop a set of spatial tasks to explore the presence of a spatial factor within one motivational system. We chose water escape motivation for all tasks after pilot testing indicated that it was easily implemented and highly reliable across repeated test sessions. Tasks were chosen that had a long history of use in assaying spatial learning: The Hebb-Williams maze has received extensive attention since its development (*viz.*, Hebb & Williams, 1946), and, unlike most animal conditioning tasks, considerable standardization data have been published (e.g., Rabinovitch & Rosvold, 1951), although relatively few data have been published using mice in a water escape format. Reversal learning tasks are typically included among tasks that assay animal intelligence (e.g., Macphail, 1982) and, in particular, between-species differences in intelligence (Bitterman, 1965, 1975; Mackintosh, 1969). We included both spatial and visual forms of this task to assess the generality between spatial tasks and a visual learning task. The Morris maze has been used extensively as a measure of what may be termed *place learning* (see Brandeis, Brandys, & Yehuda, 1989, for an extensive review). We included a "transfer" phase of this task, which has been described as an example of spatial learning sets (Whishaw, 1985). We also used a second-place learning task that has been used as a marker of this form of spatial behavior (Lassalle & Wahlsten, 1992).

Method

The study was run using two different mouse (*Mus musculus*) strains: the second filial generation (F_2) cross between C57BL/6 and DBA/2Js inbred strains and a CD-1 outbred albino strain. The F_2 mice were run first, and small samples of the F_2 mice were used to pilot the development and standardization of each task before that task was run on a larger sample of subjects. This procedure did not allow for full counterbalancing and also led to temporal delays between tasks as the larger sample of F_2 mice proceeded through the entire battery of tasks. The CD-1 mice were then run as a replication study that included full counterbalancing and no temporal delays between tasks. Results for the two strains are herein presented together for ease of comparison.

Animals

F_2 mice. The F_2 sample consisted of 34 males obtained from the Pennsylvania State University's Center for Developmental and Health Genetics. Testing began when the F_2 mice averaged between 75 and 110 days of age. All animals were maintained on a 12:12-hr diurnal cycle, with testing occurring during the dark cycle. Food and water were constantly available in the home cages. This particular F_2 cross was chosen because one of the long-term goals of this project is to pursue genetic analysis of any observed factor structure. A considerable amount of genetic work has been

accomplished on recombinant inbred strains developed from these F_2 mice, particularly with respect to identifying candidate genes that may be syntenic with human genes (see McClearn, Plomin, Gora-Maslak, & Crabbe, 1991; Plomin, DeFries, & McClearn, 1990, Figure 3.7, p. 56).

CD-1 mice. The CD-1 outbred albino strain consisted of 41 offspring that were randomly selected from five timed-pregnant females obtained from Charles River Laboratories (Wilmington, MA). There were 21 females and 20 males. Animals were weaned at 24 days and housed in same-sex sibling groups of 2 to 4 per cage. Testing began at an average of 84 days of age. Thirty CD-1 mice were used in the visual discrimination task, and all 41 were run through the remaining tasks.

Tasks and Apparatus

Hebb-Williams. The original Hebb-Williams maze (1946) consisted of a series of 12 problems, each of which partitions an enclosed space so that a different route to the goal area is required; the start and goal areas remained the same for each problem. Our water maze version of this task was run in a 50.8×50.8 cm enclosed space constructed of Plexiglas with 10.2 cm between adjacent alleys. Water temperature for this task and all others was maintained at $26^\circ\text{C} \pm 1^\circ\text{C}$. A solid Plexiglas platform 12.7 cm high and 10.2 cm^2 was submerged just below water level to serve as the goal.

After piloting, a final version of the maze was developed by selecting the five problems from Rabinovitch and Rosvold's (1951) standardization of Hebb-Williams that loaded highest on a first factor constructed from water escape latencies obtained in pilot testing ($n = 20$ for this pilot study). These problems were Numbers 1, 3, 4, 5, and 8 from Rabinovitch and Rosvold's series. Practice Problems A and D from that series were used during adaptation sessions. Errors were redefined from Rabinovitch and Rosvold's work such that each problem had 4 possible errors, thereby resulting in 120 possible errors over six trials per problem and five problems. Errors were defined as 7.6-cm entries into an incorrect turn or blind portion of the maze. Each problem was run for six trials, and only one problem was administered to a subject on a given test day. An adaptation session was used before the first practice problem. This session consisted of open-field exploration with a platform set in one corner of the field. Maximum time per trial was set at 75 s, with 20 s between trials. Subjects not finding the platform within the time limit were placed on the platform for 20 s.

Morris maze. The version of the Morris maze developed for this work consisted of a circular pool 154 cm in diameter. Animals were run for 30 trials, with 6 trials per session and a maximum of 75 s per trial. The start and goal locations remained the same on each trial. After this acquisition phase, subjects were exposed to a transfer of training procedure for three sessions in which the escape platform was located in a different quadrant each day and subjects were started from six different compass positions each session. Only latencies were recorded for this problem. Separate analyses are reported for acquisition and transfer on this task.

Spatial reversal. The water maze version of this task was conducted in a T maze constructed of black Plexiglas. Each arm measured 45.7 cm in length, 30.5 cm deep, and 15.2 cm wide. The escape platform was a 15.2-cm cube placed at the end of a designated arm. Subjects received a maximum of 40 s to locate the submerged platform. Subjects were run for 50 trials over three sessions with one designated side correct, at which point the opposite arm was designated correct and 50 additional trials were conducted over three sessions. A subject's score reflected the combined average of initial acquisition and reversal learning

scores. An error was defined as entry of 15.2 cm into an arm after the subject left the start arm and included returns to the start arm. If a subject did not locate the platform within 40 s, it was placed on the platform for 10 s.

Place learning. Our water escape version of this task was conducted in a plus (four-arm) maze; each arm had the same dimensions as for spatial discrimination. Subjects were given 9 trials per session, run in blocks of 3 trials, with a total of 45 trials. Within each block of 3 trials, subjects were started from each of three arms and had to locate the platform, which remained fixed in the fourth arm, within 40 s. This task, therefore, required a subject to execute a left turn, right turn, and straight-alley path within each block of 3 trials.

Visual reversal. This water escape task was also run in a T maze with the same dimensions as that used in spatial discrimination. Removable Plexiglas arm liners, either black or white, served as discriminative stimuli. The initial discrimination and reversal learning were run for 50 trials each over three sessions. Initial acquisition and reversal scores were averaged to produce a single score for each subject. Temporal parameters were the same as those used for spatial discrimination learning. A random number sequence was used to determine placement of the arm liners, with the restriction that in any session no more than three trials in a row had the same side arm designated correct.

Activity Controls

F₂ mice. Activity assessment was conducted in the enclosure used for the Hebb-Williams maze, with a platform in one corner. Subjects were run before any Hebb-Williams training on two consecutive sessions of 6 trials each.

CD-1 mice. Activity assessment was conducted in a straight alley measuring 108.7 cm in length, 30.5 cm deep, and 15.2 cm wide. The alley was demarcated into five sections of 21.6 cm each. The number of sections entered during two sessions of 3 min each served as a measure of activity.

Design and Procedure

F₂ mice. All F₂s received the activity control first. Hebb-Williams and Morris mazes were then administered in counterbalanced order to two subgroups. All subjects received the remaining tasks in the same order: spatial reversal, visual reversal, place learning. The first three tasks were run consecutively without delays between tasks. The last three tasks were developed individually thereafter; pilot testing intervened between the running of each

task on the larger group of F₂ mice. As a result, temporal delays averaging 3 to 4 weeks intervened between the running of the third task and each of the remaining three tasks. Subjects used in pilot testing were not part of the larger sample of F₂ mice.

CD-1 mice. Subjects were divided into seven subgroups of 5 to 6 mice each, and these subgroups were run through the test battery in counterbalanced fashion such that each of the five learning tasks occurred in each ordinal position at least once. No more than 3 to 7 days intervened between tasks.

For both strains, each task was preceded by adaptation to the apparatus. Adaptation consisted of allowing each subject to explore all arms or areas of the enclosure. Platforms were placed in each arm or corner of the enclosure during this period. For each subject's first learning task 2 days of adaptation were used; thereafter, 1 day of adaptation was used. If a subject did not find the platform within 40 s during adaptation, the subject was placed on the platform for 10 s. Each subject was given six trials in this manner. Running a subgroup through the test battery required 40 sessions, including adaptation sessions, distributed as follows: Hebb-Williams maze, 8 sessions; Morris maze, 9 sessions; spatial discrimination, 7 sessions; place learning, 6 sessions; visual discrimination, 7 sessions; activity testing, 2 sessions; and one additional adaptation session for the first task.

Latency and error measurements were recorded by research assistants. Error ratings were practiced until rater reliability exceeded .85 for all tasks. Factor analysis was accomplished using Systat 5.0's Iterated Principal Axis (IPA) option with significant eigenvalues set at a minimum of 1.0.

Results

Descriptive data for the F₂ and CD-1 samples are presented in Table 1. There was no consistent pattern of differences between the two samples on these measures, although some differences were significant: F₂ mice produced lower latencies than CD-1 mice on the Morris acquisition task and a lower proportion of errors on the place learning task, whereas CD-1 mice produced shorter latencies on the Hebb-Williams maze and the visual discrimination task. For the CD-1 mice, sex differences were also analyzed for each task; no significant differences were found and are not presented here.

The correlation matrices for the F₂ and CD-1 samples are presented in Tables 2 and 3, respectively. Latency measures were recorded for each task. Errors were recorded for all

Table 1
Descriptive Data and *t* Values for F₂/CD-1 Comparisons

Group	Latencies						Errors*			
	H-W	M:acq	M:trans	Spatial	Place	Visual	H-W	Spatial	Place	Visual
F ₂										
<i>M</i>	37.49	30.71	39.33	13.29	14.72	14.53	0.76	0.31	0.36	0.43
<i>SD</i>	20.56	22.99	33.25	5.07	10.91	6.66	0.14	0.16	0.18	0.10
CD-1										
<i>M</i>	25.63	48.16	54.11	10.63	12.60	8.59	0.79	0.39	0.57	0.45
<i>SD</i>	12.85	18.52	24.43	6.44	6.77	5.34	0.10	0.20	0.12	0.08
<i>t</i>	3.05*	-3.59*	-1.85	1.93	1.03	3.90*	-1.30	-2.00	-6.11*	-0.68

Note. H-W = Hebb-Williams maze; M:acq. = Morris maze acquisition phase; M:Trans = Morris maze transfer phase.

*Errors are expressed as the proportion of trials with an error.

**p* < .01.

Table 2
Correlation Matrix for F_2 Sample

Variable	H-W	M:acq	M:trans	Spatial	Place	Visual	Activity
Latency							
H-W	—						
M:acq	.66*	—					
M:trans	.61*	.89*	—				
Spatial	.48*	.47*	.44*	—			
Place	.22	.28**	.40*	.38**	—		
Visual	.39*	.50*	.46*	.69*	.39**	—	
Activity	.35**	.34*	.64*	.14	-.06	.19	—
Errors							
H-W	—						
Spatial	.23			—			
Place	.42*			.10	—		
Visual	.23			.41*	.14	—	
Activity	.27			-.20	.08	.16	—

Note. H-W = Hebb-Williams maze; M:acq = Morris maze acquisition phase; M:trans = Morris maze transfer phase.

* $p < .01$. ** $p < .05$.

tasks except the Morris maze. For all tasks, errors were represented as the proportion of trials with at least one error across all sessions. The tables reveal similar findings. Most important, all correlations across the learning tasks were positive for latencies and errors in both samples, a total of 42 correlations. For the F_2 mice, the average latency correlation across the learning tasks was .46 and average error correlation was .26. For the CD-1 mice, the average latency correlation was .44 and average error correlation was .30.

Additionally, the activity measures evidenced similar patterns, although, given the different activity tasks used for the two samples, care must be taken in interpreting the sign of the correlations. For the F_2 mice, the activity control was run in an open enclosure with a platform present. As a result, higher scores indicated slower location of the platform. This measure correlated positively with all learning latency measures except place learning, with an average correlation

of .27. This measure bore a much smaller and nonsignificant relationship with errors, however, with an average correlation of .08. For the CD-1 mice, the activity measure consisted of the number of sections traversed in a straight alley. As a result, higher scores indicated higher activity levels. This measure consistently correlated negatively with latencies, with an average of $-.31$, indicating, as may be expected, that higher latencies covaried with less activity. The relationship between this activity measure and errors was again inconsistent and small, with an average correlation of $-.15$.

The consistency of findings across these two samples can also be seen in the factor analysis of latency and error measures given in Table 4. For latencies, the analysis for F_2 mice revealed a significant first factor that accounted for 61% of variance, and all tasks, including the activity measures, loaded positively on that factor. For the CD-1

Table 3
Correlation Matrix for CD-1 Sample

Variable	H-W	M:acq	M:trans	Spatial	Place	Visual	Activity
Latency							
H-W	—						
M:acq	.46*	—					
M:trans	.32**	.69*	—				
Spatial	.58*	.28**	.27**	—			
Place	.68*	.21	.16	.57*	—		
Visual	.58*	.40**	.21	.67*	.65*	—	
Activity	-.34**	-.30**	-.38*	-.34**	-.18	-.35**	—
Errors							
H-W	—						
Spatial	.18			—			
Place	.25**			.37*	—		
Visual	.44*			.29**	.32**	—	
Activity	-.19			-.09	.09	.13	—

Note. H-W = Hebb-Williams maze; M:acq = Morris maze acquisition phase; M:trans = Morris maze transfer phase.

* $p < .01$. ** $p < .05$.

Table 4
First Factor Loadings, Eigenvalues,
and Variance Accounted for

Learning task	F ₂		CD-1	
	Latency	Errors	Latency	Errors
H-W	0.67	0.70	0.84	0.65
M:acq	0.90	—	0.81	—
M:trans	0.79	—	0.60	—
Spatial	0.73	0.56	0.83	0.84
Place	0.58	0.46	0.79	0.49
Visual	0.89	0.57	0.76	0.67
Activity control	0.84	0.24	-0.51	-0.20
Eigenvalue	4.2	1.4	3.9	1.9
Percentage of variance	61.0	28.0	55.0	37.0

Note. H-W = Hebb-Williams maze; M:acq = Morris acquisition phase; M:trans = Morris transfer phase.

mice, that same analysis of latencies revealed a first factor that accounted for 55% of variance, and all tasks again loaded positively on that factor. The negative loading for the activity measure reflects its negative correlation with latencies, indicating again that higher values on this measure covaried with shorter latencies.

It was also the case that for both the F₂ and CD-1 samples, factor analysis of latencies revealed second factors with eigenvalues of 1.1. These second factors accounted for 16% of variance for both samples. The characteristics of this second factor differed in the two samples. For the F₂ sample the two Morris maze measures, place learning, and the activity measure loaded positively on this second factor, whereas for the CD-1 mice all but the two Morris measures loaded positively on this factor.

For error measures, a similar pattern occurred, although the first factor accounted for less variance than was true for latencies: 28% in the case of the F₂ mice and 37% for the CD-1 mice. It was also the case that activity measures showed far lower loadings on the first factor for errors than was true for latencies. There was no second factor in either sample for errors with an eigenvalue greater than 1.0.

The reliabilities and intercorrelations for latencies and errors in each sample are given in Table 5. All reliabilities were calculated as a form of split-half reliability, either first- versus second-half of training or, in the case of the discrimination problems, initial discrimination versus reversal. In both samples, latency reliabilities were considerably higher than errors. Latency reliabilities averaged .83 for the F₂ mice and .79 for the CD-1 mice. Error reliabilities averaged .48 for the F₂ mice and .52 for the CD-1 mice. Latency-error intercorrelations averaged .43 for the F₂ mice and .48 for CD-1 mice.

Discussion

The study of comparative intelligence has made significant progress in detailing similarities and differences between species, including comparisons between humans and other animals (e.g., Hulse, 1993; Wasserman, 1993). Al-

though our knowledge of these parallels and their limitations is undoubtedly far from complete, it may well be that we know less about the structure of individual differences in animal intelligence, how that structure may differ between species, and whether it parallels or diverges from the structure of individual differences in human intelligence than about any other aspect of comparative intelligence (Locurto, 1997).

Within that framework, the present results, in conjunction with earlier findings, offer the beginnings of a foundation from which to explore the structure of individual differences in animal intelligence. These findings indicate reliable individual differences across visuospatial tasks in two strains of mice, although it is not yet apparent what sort of factor this observed commonality represents. Its nature may be restricted in several ways: to the tasks chosen, to the species or strains studied, to the motivational condition used, or perhaps to a combination of these and other factors.

An additional interpretative issue concerns differences in the measures reported: latencies and errors. Both measures revealed a significant first factor, although the analysis of latencies suggested a much stronger first factor. The moderate correlations between latencies and errors suggest that these measures reflect somewhat different though certainly not independent aspects of performance, perhaps accuracy-precision versus speed of task solution. It is also the case that, as might be expected, latency measures, but not error measures, included or reflected to some extent general activity. It is not possible from these data to determine with certainty to what extent latencies reflect activity per se apart from the more directional notion of speed of task solution, but it should be noted that in standardized tests of human intelligence both accuracy and speed of solution are typically measured (Anastasi, 1989). Additionally, advances in the study of the processes underlying human intelligence suggest that both speed of information processing, as reflected in reaction time measures on elementary cognitive tasks, and the accuracy of simple perceptual judgments both correlate substantially with standardized psychometric measures of intelligence (Deary & Stough, 1996; Locurto, 1997; P. A. Vernon, 1987).

The differences between latencies and errors may also reflect differences in the reliabilities of the two measures. It is clear that latency measures were more reliable than error measures (see Anderson, 1993, and Tolman & Nyswander,

Table 5
Latency and Error Reliabilities and Latency-Error
Intercorrelations for F₂ and CD-1 Samples

Task	F ₂			CD-1		
	Latency	Errors	L-E	Latency	Errors	L-E
H-W	.95*	.71*	.32**	.79*	.69*	.33**
Spatial	.84*	.43*	.49*	.86*	.34**	.69*
Place	.86*	.44*	.62*	.72*	.63*	.36*
Visual	.66*	.33**	.28**	.78*	.42*	.55*

Note. H-W = Hebb-Williams maze; L-E = latency-error.
p* < .01. *p* < .05.

1927, for other reports of error reliabilities). The lower reliabilities for errors cannot be due to rater reliability because, as noted earlier, rater reliabilities were uniformly high in this study. It appears that error measures, at least in the preparations studied here, are less reliable than latencies for reasons yet to be understood. Naturally, these lower reliabilities affected error correlations between tasks and, in turn, the factor analysis of error measures, including factor loadings and eigenvalue estimates.

These interpretative difficulties aside, it can be said that the observed spatial factor, whatever its limitations, possesses some generality as well. It appears to be uniform across at least two strains of mice and across variations in testing procedures that were evident between the two samples. It also appears to include problems that require the use of explicit visual cues. A similar finding has been reported for rats in land-based tasks: Rajalakshmi and Jeeves (1968) observed correlations that ranged between .37 and .63 between Hebb-Williams maze performance and acquisition and reversal of complex visual discriminations (horizontal vs. vertical). It may not be surprising that spatial and visual tasks invoke common mechanisms given that spatial learning involves the use of proximal and distal visual cues (e.g., Morris, 1981), but this commonality does at the least suggest some flexibility in the invocation of the mechanisms underlying the observed spatial factor.

Although these results do not favor any broader conclusions about the structure of intelligence in mice under these circumstances, they do call into question "anarchic" approaches to intelligence, to use Spearman's (1927) original term for this approach (i.e., approaches that assume that any problem-solving task invokes mechanisms specific only to that task). That said, what must be emphasized at this juncture is how little we know about individual differences and the structure of animal intelligence. We do not know whether, for a given species, spatial tasks cohere into a single factor or whether spatial behavior is best characterized as partitioned into separable factors that are tangentially related or even functionally independent. In addition, if we do not know the structure of spatial behavior itself, surely no claims can be made about the relationship of a spatial factor to other factors or about the presence of an animal *g*.

It might be asked whether the work required to demarcate further a spatial factor, apart from the far more prodigious effort that would be needed to mark an animal *g*, would be worth the effort. After all, historically the study of individual differences in animal intelligence has not attracted sustained attention, and current theoretical approaches to animal intelligence make few allowances for individual differences. The adaptive specialization approach, as an example, posits that aspects of animal problem solving may have evolved to meet the requirements of the specific ecological niche occupied by a species (Rozin & Kalat, 1971). Although this approach has been expanded by Sherry and Schacter (1987) to include the evolution of processes that serve more general functions, it nonetheless provides no elaborated basis for understanding the origins and functional significance of a coherent structure of individual differences in animal intelligence.

A different approach has been advanced by Macphail (1982, 1985, 1987), who proposed that, in cases in which species differences have been reported, results might instead be due to subtle contextual variables that were processed differently by different species, thereby evoking differences in perception, motivation, or performance, but not learning differences. As a corollary to this approach, once these contextual variables have been taken into account, it may be that identical problem-solving mechanisms are quite common, perhaps universal, across different species. The presumed lack of between-species differences in these mechanisms need not indicate anything about individual differences, but Macphail suggested that "one implication, though not a necessary consequence, of this hypothesis, is that there are no within-species differences (that is, individual differences) in intellect in nonhuman vertebrates" (Macphail, 1985, p. 234).

Although current theory offers little guidance concerning the nature of individual differences, their inclusion in the study of animal intelligence would have both theoretical and practical import. The impact on theory may be more apparent given the current focus on species-level specializations or their absence, but there are as well important practical implications. At present, we have little idea of "what goes with what," so to speak (i.e., which tasks cohere into which factors). As a practical matter, then, one cannot select a task or set of tasks for a specific purpose, such as assaying spatial learning, without making quite arbitrary choices: If one wants to measure spatial learning, does it matter whether one uses the Morris maze or spatial reversal learning? The answer may indeed be yes, particularly given that the Morris maze, as typically implemented, provides only latency scores and these have now been shown to be related to general activity, whereas the same influence of activity is not found in error measurements that are available in spatial reversal learning as well as other spatial tasks.

The idea that the study of individual differences may impact both theory and practice was advanced with respect to human behavior much earlier by Chronbach (1957) in his classic essay on psychology's two disciplines: the experimental and the correlational-psychometric. Chronbach reasoned that the two approaches were inherently complementary and noted

Nature has been experimenting since the beginning of time, with a boldness and complexity far beyond the resource of science. The correlator's mission is to observe and organize the data from Nature's experiments. As a minimum outcome, such correlations improve immediate decisions and guide experimentation. At the best, a Newton, a Lyell, or a Darwin can align the correlations into a substantial theory. (p. 672)

Perhaps of greater interest to students of comparative intelligence, Chronbach also noted that historically the study of individual differences had been considered part and parcel of a truly comparative psychology. Broadly conceived, comparative psychology in the early 20th century included comparisons between individuals, species, cultures, and even different developmental periods. Chronbach lamented the fact that, although other psychologists (e.g., personality, developmental, and differential psychologists) interested in

individual differences remained at least "loosely federated" (p. 672), it was the animal behaviorists who turned their discipline from this truly comparative approach into the experimental study of one or a few species.

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