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REVIEW

Individual Differences: Case Studies of Rodent and Primate Intelligence

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Early in the 20th century, individual differences were a central focus of psychologists. By the end of that century, studies of individual differences had become far less common, and attention to these differences played little role in the development of contemporary theory. To illustrate the important role of individual differences, here we consider variations in intelligence as a compelling example. *General intelligence* (*g*) has now been demonstrated in at least 2 distinct genera: primates (including humans, chimpanzees, bonobos, and tamarins) and rodents (mice and rats). The expression of general intelligence varies widely across individuals within a species; these variations have tremendous functional consequence, and are attributable to interactions of genes and environment. Here we provide evidence for these assertions, describe the processes that contribute to variations in general intelligence, as well as the methods that underlie the analysis of individual differences. We conclude by describing why consideration of individual differences is critical to our understanding of learning, cognition, and behavior, and illustrate how attention to individual differences can contribute to more effective administration of therapeutic strategies for psychological disorders.

Keywords: intelligence, working memory, reasoning, depression, attention

> There are as many different kinds of men in the world as there are mothers to bear them and experiences to shape them, and in the same wind, each gives out a different tune.
>
> —Jim Shepard, 2017

Few would dispute the obvious truth of the preceding quote by the brilliant fiction writer Jim Shepard. Mr. Shepard is not a trained psychologist, yet he naturally intuits what we have seemingly forgotten: individual differences are real, and they matter. Thus, it is reasonable to ask: Why are we so quick to disregard individual differences in favor of the "average standard value"? Beyond its obvious implication, the quote of Shepard's is even more prescient than it might initially seem, a point to which we will shortly return . . .

Correlational Methods and Individual Differences

In its infancy, Psychology was universally interested in, and often focused on, individual differences. This emphasis is illustrated by the prominence of the subject in our earliest textbooks. For instance, the classic introductory text of Seashore (1923) contains a chapter devoted to "Individual Psychology," while Boring, Langfeld, and Weld (1938) offered multiple chapters and subchapters on individual differences in learning and intelligence. The topic was considered so central to the broader discipline that doctoral students were commonly required to complete courses in Individual Psychology as late as the 1950s (George H. Collier, personal communication, 2003).

The formal study of individual differences and its preeminent place in the fabric of psychology (and related disciplines like neurophysiology; Donders, 1869; Helmholtz, 1863) waned by the middle of the 20th century. A cursory survey we did of at least a dozen widely used contemporary textbooks on introductory psychology found that none contained a dedicated chapter on individual differences. This decline in interest is, we believe, due to several key factors, not the least of which was the emerging dominance of *experimental manipulations* over correlational analyses (the latter of which are central to studies of individual differences). In a widely influential paper, Cronbach (1957) discussed these two distinct approaches to scientific psychology. According to Cronbach, the experimental approach attempts to understand reality by manipulating (under simplified conditions) variables between groups/treatments. In contrast, the correlational approach attempts to understand reality by estimating the influence of variables under complex conditions between individuals. Individual differences, critical for correlational analyses, are troublesome noise for the experimental psychologist, while the average outcome of group treatments, critical to the experimental approach, are of lesser interest to the correlational psychologist. Although both approaches are complementary and, as Cronbach argued, equally important to psychology, they are typically employed separately, reducing their true explanatory potential.

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Overall, and especially for the fields of learning and behavior, psychologists had been shaped through the decades to dismiss individual differences and to avoid correlational approaches in our design of studies. In a rare case of agreement, Edward Tolman (1924) and Clark Hull (1951) stated that correlational methods held little promise for the understanding of behavior. Tolman (1924) assumed that "individual difference variables [were] average standard values." According to Tolman, "we have tried to keep heredity normal by using large groups, age normal by using rats between 90 and 120 days old, previous training normal by using fresh rats in each new experiment, and endocrine and nutritional conditions normal by avoiding special dosages and also again by using large groups." (We could add to this list the complications of sex differences, which led to the practice of studying only male animals, an approach that is now explicitly eschewed by our funding agencies). Tolman was distrustful of the correlational approach, and stated that factor analyses (which epitomize the correlational method; see below) "do not seem to suggest any simple or agreed-upon results [and, for instance, in the case of intelligence research], the controversy rages from Spearman's one or two factors through Kelley's and Thurstone's three to nine factors." Even during the revolution in learning theory in the 1960s, all critical empirical data were derived exclusively from the experimental approach (for a review of this era of rapid change, see Rescorla, 1988).

Despite the general trend, correlational analyses have been quite productive in some fields like personality psychology, social psychology, psychometrics, clinical psychology, and developmental psychology. These fields all try to specify that which makes individuals vary, be it according to their personality, cultural background, cognitive abilities, extreme disorders, or age. (It is worth noting that "aging" is never induced; i.e., experimentally manipulated. Although a comparison of two ages under controlled laboratory conditions is often described as an *experiment*, the comparison of the performance of two groups of different ages is a highly constrained correlational analysis.) Acclaimed ideas like the self-determination theory (Ryan & Deci, 2000), general intelligence (Jensen, 1998), and Piaget's theory of cognitive development (Piaget & Inhelder, 1973) are all products of correlational research, and each has had broad impact and explanatory value.

largely abandoned for the six decades prior to this century. Thorndike's (1935), Tolman's (1924), and Tryon's (1940) classic studies of individual differences in general cognitive ability of rats were all concluded in the 1930s. However, for the last decade, interest in individual differences has seen a dramatic reemergence. In the present paper, we will review evidence from primates and rodents (with an emphasis on our work with mice) that supports the existence of a general cognitive ability, as well as individual differences in its expression. We will describe some implications of this work, as well as the power and broad utility of the procedures and statistical regimens employed in these analyses. Lastly, we will provide examples that highlight the critical and practical necessity to consider individual differences.

What Is "Intelligence"?

A committee of the American Psychological Association (Neisser et al., 1996) stated that "Individuals differ from one another in their ability to understand complex ideas, to adapt effectively to the environment, to learn from experience, to engage in various forms of reasoning, to overcome obstacles by taking thought. Concepts of 'intelligence' are attempts to clarify and organize this complex set of phenomena" (p. 77). While somewhat nebulous, our experience shows that this definition is remarkably in line with unpolished descriptions by college undergraduates in intro surveys. More importantly, the definition seems to capture that which is measured and predicted by common psychometric tests of intelligence. The rationale for many psychometric tests are roughly based on Spearman's early observation that performance on a wide range of cognitive tasks are positively correlated, and as such, can be reduced to a single index of aggregate performance. While controversy persists regarding exactly what is measured by psychometric tests of intelligence (e.g., the Stanford-Binet, Wechsler Adult Intelligence Scale, the Raven's Progressive Matrix), what is certain is that these tests are strongly predictive of important life outcomes, including educational and career success, longevity, health, happiness, the likelihood of criminal activity, drug dependence, and even marital success (Gottfredson, 1998; Jensen, 1998). To quote Gottfredson (1998), "No matter their form or content, tests of mental skills invariably point to the existence of a global factor that permeates all aspects of cognition [and which has] considerable influence on a person's practical quality of life" (p. 24).

To explore a trait analogous to intelligence in laboratory animals, we should devise tests that characterize the set of diverse skills encompassed by human IQ tests. To this end, the performance of nonhuman animals has been assessed on batteries of tests that represent diverse learning skills, reasoning abilities, inhibitory control, and the capacity for working memory and selective attention.

Individual Differences in General Intelligence in Nonhuman Animals

While it has been relatively common to compare the cognitive capacities of different species, there exist relatively few studies of variations (individual differences) in cognitive performance within species (for a recent review, see Burkart, Schubiger, & van Schaik, 2016). And so far, the most extensive efforts focused in mice and nonhuman primates (although recent evidence has also been obtained in wild birds; Shaw, Boogert, Clayton, & Burns, 2015).

Rodents

General cognitive ability. In our earliest work, we tested genetically diverse (outbred) CD-1 mice in a battery of five common learning tasks, each of which made unique sensory, motor, and information processing demands on the mice (Matzel et al., 2003). At least nominally, this test battery was analogous to the design of the first human intelligence tests, wherein various components of the battery are presumed to impinge on different information processing skills (i.e., cognitive "domains"). The tasks in this battery were rudimentary in nature (associative fear conditioning, passive avoidance, path integration, odor discrimination, and spatial navigation) such that all individual mice could eventually acquire the target responses with equal efficiency, but did so at different rates. Mice that performed well (i.e., exhibited relatively rapid acquisition) in one task tended to perform well in other tasks. Among the 56 mice tested, there was a positive correlation of individuals' rate of acquisition across all tasks (i.e., a "positive manifold"[1] existed), and principal component analysis[2] indicated that 38% of the variance was due to a single factor, which we originally described as "general learning ability." Published commentaries on this 2003 article suggested that the general ability we described was qualitatively and quantitatively analogous to the trait that is described in humans as *intelligence* (Blinkhorn, 2003), although it was only later that we acquired enough evidence to verify this claim. Since that first report, we obtained similar results in mice tested on as many as nine cognitive tasks, including tasks related to the utilization of working memory and attention (Matzel et al., 2003). Furthermore, a comprehensive test of 241 mice (Kolata, Light, & Matzel, 2008) revealed a hierarchical structure where the general learning factor influenced a domain-specific factor of spatial learning. This hierarchy is similar to that thought to underlie human intelligence (see Figure 1).

Using a similar strategy, Galsworthy, Paya-Cano, Monleón, and Plomin (2002) compared the performance of 40 genetically heterogeneous mice across a battery of cognitive tests distinct from those used by our group. All measures of cognitive performance loaded positively on a principal component that accounted for 31% of the variance across mice, again suggesting the presence of a common factor of general cognitive ability underlying performance on all tasks. Galsworthy et al. concluded that "a general cognitive ability appears to underlie the performance of mice on a battery tapping diverse cognitive demands" (p. 92). Thus, based on multiple test batteries administered by two different research teams, it is reasonable to conclude that genetically diverse mice express individual differences in a general cognitive ability.

It is worth noting that learning ability and intelligence are not homologous constructs. Many of the studies described above were limited to analyses of learning, and did not explicitly assess other cognitive functions (e.g., reasoning or attention). Despite this caveat, learning ability and general intelligence are so highly related that the distinction between them may be more semantic than real. Based on his extensive analysis, Jensen (1998)) concluded:

> A general factor common to all learning tasks [the RATE at which they are acquired] . . . is highly correlated with the *g* factor [general intelligence] extracted from psychometric tests. The general factor of both domains—learning and psychometric abilities—is essentially one and the same *g*. (p. 226)

Despite Jensen's conclusion, it would be premature to conclude that general learning ability and general intelligence are synonymous in mice. A more definitive conclusion would require a comparison of learning to other cognitive abilities, as well as some other critical noncognitive traits. Such analyses will be described in the next three sections.

Noncognitive influences on general learning ability. In previous work (Matzel et al., 2003), we also found a strong direct correlation between mice's level of exploration (relative time in unwalled areas of an open field) and their aggregate performance on a learning battery. It is notable that, in humans, the degree of preference for novelty by infants is positively correlated with later performance on IQ tests (Bornstein & Sigman, 1986; Vietze & Coates, 1986). These observations raise the possibility that differences in *exploratory tendencies*, which would increase an animal's engagement of its environment, could underlie some of the differences between mice in their abilities to learn. Or, at an extreme, that our "general learning factor" in mice could instead have been a simple "general exploratory" factor. In addition, given that exploration is influenced by stress reactivity (Kabbaj, Devine, Savage, & Akil, 2000; Kazlauckas et al., 2005), it was possible that differential *stress responses* could account for variations in nominal learning abilities, since stress can itself impair (or in some cases enhance) a rodent's performance on cognitive tests (Shors, 1998). Finally, it was also possible that variations in aggregate learning performance did not reflect differences in learning ability per se, but instead reflected variations in sensory or motor fitness. As could be inferred from this discussion of alternative possibilities, the principal factor identified in a factor analysis is not itself defined by the analysis. Rather, we as investigators must consider the pattern of factor loadings,[3] consider what the variables that load on a factor share in common, and attempt to characterize or

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[1] The "positive manifold" refers to the phenomena that performance among cognitive tasks with varied requirements all correlate positively, usually around 0.3–0.6. This positive manifold has been extensively studied in the field of psychometrics since its discovery and formal description by Spearman (1904). The positive manifold was the impetus for Spearman's idea of a *g* factor, and its meaning has been interpreted in multiple ways: some (including, famously, Arthur Jensen, 1993 believe the positive manifold is caused by a single physical trait such as the brain's processing speed (which, in other words, implies that *g* is a concrete entity that can be pointed to). Alternatively, others (such as Han van der Maas, 2006) believe that the positive manifold is created by multiple causes that emerge from a dynamic process during development (and, so, *g* is a property/process that involves these). For obvious reasons, the positive manifold and its interpretations will be extremely important in guiding future research in individual differences in animal intelligence.

[2] A principal component analysis (PCA) is one of the techniques related to factor analyses. A PCA is used to identify patterns that might exist in the individual differences among multiple variables. In other words, a PCA is an orderly simplification of interrelated measures. Functionally, the technique works by finding principal components that can best capture the variance in a dataset. The first principal component is the linear combination of all studied variables that result in the maximum variance (among all linear combinations), so it accounts for as much variability in the data as possible. The second component is the linear combination of all studied variables that accounts for as much of the remaining variation as possible, with the constraint that the correlation between the first and second component is zero. The third component on follows the same logic, and is orthogonal (zero correlation) with both the first and second components (the number of principal components possible will vary depending on the number of the studied variables). PCA is mostly used in psychology as a tool to explore and visualize complex data, as well as for (to an extent) making predictive models, such as the predictive component of general learning ability in mice described here.

[3] Factor analyses are remarkably useful for separating the different influences (or causes of variation) behind a trait. Factor loadings are the correlation between a factor (or latent variable) with each measured variable. If a set of variables show a consistently high to moderate loadings on a factor, it means that they all are influenced by/represent this latent trait. On the other hand, low loadings suggest that there is no relation with the measured variables. For example, a set of spatial learning tasks are expected to have a high factor loadings on a common factor, and this factor could reasonably be interpreted to represent spatial abilities. If you add a measure such as fear of water or exploration, this will show how much these also load in this "spatial learning" factor, and how much it loads into other, independent factors (such as a factor that represents stress reactivity). Therefore, it can be very useful in a study that aims to define a particular latent factor to include variables that are not expected to load on the principal factor.

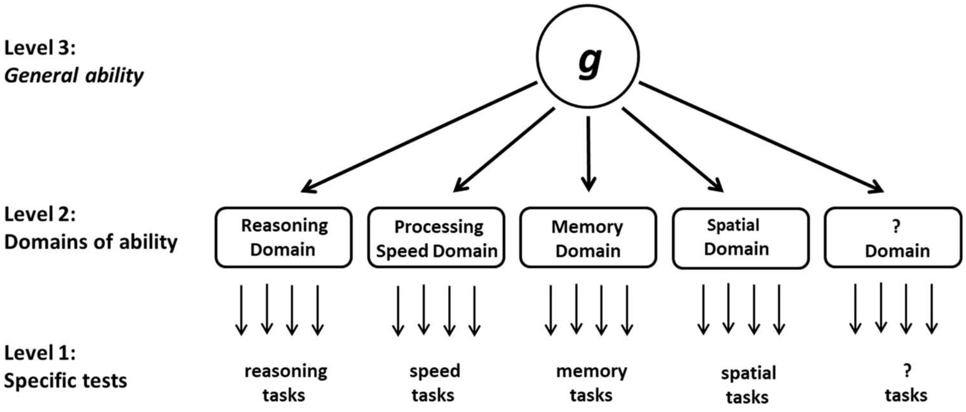

Figure 1. The hierarchical model of intelligence, where a general ability coexists with specialized abilities. At Level 1, people differ in their performance on specific tests that are representative of various cognitive domains (or "modules"). Within a domain, performance measures are highly correlated. Given this high correlation, a latent trait at the domain level (Level 2) would be identified through factor analysis. Level 3 represents a general influence that impacts performance regardless of domain, that is, people who do well in one domain also tend to do well in the other domains. It is this later observation that requires the existence of a general cognitive latent trait, or *g* (general intelligence). Nevertheless, correlations between tasks within a domain are typically higher than the correlations between tasks that reside in different domains, requiring the existence of domain-specific abilities. *Note.* The domains described in this figure are merely illustrative, as theoreticians differ as to the actual composition and number of domains that underlie human cognitive functions. The "? Domain" is intended to represent this uncertainty.

define the nature of that factor. Far from being exact, our definition of the latent influence captured by a factor is based on our best judgment and is always subject to interpretation. In this regard, we are reminded of Tolman's (1924) admonishment that factor analyses do not always "suggest any simple or agreed-upon results."

To assess these alternative explanations, we tested the relationship between 31 measures of sensory/motor abilities, fitness, fear/stress sensitivity, and the general learning abilities of individual mice (Matzel et al., 2006). First, in no instance was a relationship observed between the variation in simple fitness or sensory/motor function and the variation in general learning performance. A principal component analysis revealed that measures of balance, pain sensitivity, running speed, swimming speed, and overall activity all loaded weakly and inconsistently on factors on which learning tasks loaded highly. Again though, exploration of potentially stressful environments was positively correlated with performance on learning tasks. Exploration of the open quadrants of an open field or the open arms of an elevated plus maze is often interpreted as a tendency for novelty seeking, fear, and/or may reflect an animal's stress or anxiety in the unfamiliar open environments (Anderson, 1993; Kabbaj et al., 2000). Separating these influences, rather than leaving their interpretation to the whim of the experimenter, would be a *prototypic* application of factor analytic techniques. This is the strategy that we followed, observing that common measures of fear loaded weakly and inconsistently with measures of learning. (In particular, fecal boli counts during exploration of the open field, shock-induced freezing, and startle-induced escape responding were all unrelated to the mice's exploratory patterns or their general learning abilities.) Relatedly, we found no relationship between basal corticosterone levels (a stress hormone) and individual mice's propensity to explore the open quadrants of the open field or the open arms of an elevated plus maze. And corticosterone levels associated with a mild stressor (confinement on an elevated platform) were also unrelated to mice's level of activity in the open quadrants of an open field (Matzel et al., 2006; for similar results, see Dellu, Piazza, Mayo, Le Moal, & Simon, 1996; Overmier, Murison, & Johnsen, 1997; Piazza et al., 1991). This pattern of factor loading suggests that the relationship between exploration and learning was not attributable to variations in mice's expression of fear or their stress reactivity levels.

In total, this simultaneous consideration of learning, sensory/motor responses, stress, fear, anxiety and exploration provide further evidence for the existence of an influence on mice's learning abilities that transcend single domains of learning. Moreover, this general influence on learning does not appear to reflect variations in noncognitive variables related to fitness (also see Galsworthy et al., 2002; Locurto, Benoit, Crowley, & Miele, 2006; Locurto, Fortin, & Sullivan, 2003). Still though, we repeatedly observed a consistent relationship between mice's tendency to explore novel environments and their general learning abilities. Of course, it is possible that these two classes of behavior (learning and exploration/novelty seeking) are regulated in common but do not otherwise influence each other. A more intriguing possibility is that mice's propensity for exploration predisposes them to encounter those contingencies upon which learning depends, and thus is a direct determinant of general learning abilities. This possibility was assessed in two ways, both of which used an experimental approach in conjunction with correlational ones. First, Grossman et al. (2007) treated mice with a dose of an anxiolytic (chlordiazepoxide) that promoted an increase in exploratory behaviors but which had no measurable effect on sensory/motor behaviors or pain sensitivity. Despite the increase in exploration, no benefit of the anxiolytic could be observed on individual learning tasks or on aggregate performance in the battery of learning tests. In fact, nonsignificant tendencies were observed for the anxiolytic treatment to impair learning, an effect that has been observed elsewhere

(Kroon & Carobrez, 2009; Scaife et al., 2007). Light et al. (2008) provided a more direct test of the possibility that increases in exploration might promote a commensurate facilitation of general learning abilities. To this end, Light et al. exposed mice to a series of novel and varyingly complex environments over a sequence of 12 days. This "adaptation to novelty" promoted a profound and long-lasting (at least 30 days) increase in the propensity for exploration when the treated mice were tested in yet another novel environment (an elevated plus maze). Despite this increase in exploratory behavior, these mice exhibited no overall improvement in performance in our battery of learning tasks. Admittedly, this observation of Light et al. is rather tepid evidence, since it is possible that the adaptation to novelty had not reached some critical threshold beyond which it might have impacted rates of learning. Nevertheless, in combination, the results of Grossman et al. and Light et al. suggest that while general learning abilities and exploratory behaviors consistently covary, the degree of exploration need not have direct causal impact on mice's aggregate performance on batteries of diverse learning tasks. What then is the basis for this relationship between learning performance and exploration? Data from our laboratory suggests that far from being a "noncognitive" measure, an individual mouse's propensity for exploration is to some degree impacted by the rate at which it learns. According to this reasoning, exploration of the more stress-inducing areas of a novel environment (e.g., the open arms of an elevated plus maze) begins to emerge at the time at which mice adapt to the less stress-inducing aspects of that environment (e.g., the closed arms of an elevated plus maze). Consequently, faster learners adapt more quickly, and thus begin to explore new areas sooner. This conclusion is supported by the observation that early in their exposure to a novel field (i.e., the first 60–90 sec), both bright and dull animals explore at similarly slow rates. As the time in the novel field passes, brighter animals begin to enter the more stressful areas of the field sooner. Similarly, while bright and dull mice exhibit similar orientation to novel objects (e.g., a burst of noise or a flashing light), dull mice continue to orient after the response has dissipated (i.e., habituated) in bright mice (Light, Grossman, Kolata, Wass, & Matzel, 2011; for related results, see Poucet, Chapuis, Durup, & Thinus-Blanc, 1986). Again, these results suggest that brighter mice adapt or habituate at faster rates, which can in turn influence their patterns of exploration in novel environments.

General learning and reasoning abilities covary. Most formal definitions of intelligence make reference to the individual's capacity to "think rationally," and the efficacy of reasoning is considered a critical component of intelligence (Manktelow, 1999). While all intelligence test batteries include components that are specifically intended to assess an individual's capacity for reasoning, some (e.g., the Raven's Progressive Matrices; RPM) are based solely on tests of reasoning. Accordingly, performance on reasoning and other cognitive tasks covary, and we have assessed this relationship in mice. Before discussing this data, one caveat should be mentioned. Reasoning has been asserted by some to be the core ability that underlies general intelligence (Penrose & Raven, 1936; Raven, Raven, & Court, 1998), a theme that is at least as old as Aristotle. Since performance on an IQ test based solely on reasoning (like the RPM) correlates highly with tests of broader abilities (the concurrent validity coefficients between the RPM and the Stanford-Binet and Wechsler scales range between .54 and .88, with the majority of estimates in the .70s and .80s) and has similar predictive capacity, it would be easy to conclude that reasoning is indeed the core ability that underlies intelligence. However, it could also be true that reasoning abilities as well as other specialized abilities (such as spatial, speed of processing, mathematical, verbal) are all influenced by a more central core ability or even a common neurophysiological/molecular attribute. Separating these possibilities is enormously complicated, and alternatives to the "reasoning core" have been proposed (one of which will be discussed below). It is not our goal in this section to make claims regarding the causal direction of any relationship between reasoning ability and other cognitive abilities in mice. Rather, we will simply ask whether the reasoning abilities and more basic learning abilities of mice are related.

To assess reasoning in mice, we used two tasks. The first was a Binary Tree Maze, which, like a flow diagram, is a decision tree that bifurcates (at decision points) into branches. Each decision point is a potential goal location (where food might be found), and the end of each branch terminates in two leaves, each of which also contains potential goal locations. In the maze that we used, there were a total of 14 potential goals (only a random selection of which contain food on any trial), and the mice's task was to navigate the maze so as to inspect every potential goal for a piece of food. While there are many possible search strategies (or paths) to visit every node in a decision tree, the vast majority of these paths would be inefficient, that is, they would involve unnecessary retracing of a path or crosses of a location that had already been explored. The degree to which a mouse could comprehend the structure of the maze and implement that information from its current location is a reflection of what Aristotle called inductive reasoning. Using the most efficient strategy, a mouse would pass a maximum of 24 goal locations. What distinguishes the Binary Tree Maze from a maze learning task such as the Lashley Maze is that no single path is best, that is, many routes are equally efficient, and a mouse can perform at maximum efficiency across trials, yet not follow the same route on successive trials. In our tests, the efficacy with which mice navigate the maze stabilized very quickly (within 3–5 trials), suggesting that the mice quickly comprehended the structure of the maze and developed a strategy for its navigation. When we compared the number of choice points crossed by each mouse to their factor scores from a learning battery (indicative of general learning ability), there was a strong correlation of .60. To insure that mice did not simply follow a rote path to navigate the maze, on several trials one of the options at one of the second level decision junctions was blocked (thereby disrupting any potential fixed path). Despite forcing the mice to deviate from their initial path, the correlation between their maze performance and factor scores from the learning battery remained strong, $r = .51$ (Wass et al., 2012).

After testing in the Binary Tree Maze, we tested the same mice on a second reasoning task based on the concept of *fast mapping*, a process whereby a new concept can be acquired based on logical elimination, corresponding with Aristotle's description of deductive reasoning. Fast mapping (Carey & Bartlett, 1978) is believed to play a critical role in the extraordinarily rapid acquisition of information during early human development, and explains (in part) the prodigious rate at which children gain vocabulary. For example, when faced with a group of familiar items described by familiar words, an individual will quickly associate an unfamiliar word with a novel item that is added to the set, and this association requires no overt "pairing" of the novel word and its corresponding novel item. To test fast mapping in mice, we first taught each mouse to associate pairs of objects (small plastic toys) by exposing them to one (sample) object and then letting the mouse retrieve a piece of food that was hidden under the sample object's paired associate. After learning a series of such object pairs (much like words and objects can be associated through pairing), the mice were required to find the relevant paired associate within a field that contained several objects, all of which had been previously associated with a different sample. After a moderate amount of training, mice perform this task almost without error. After this training, the mice were finally tested for their capacity for fast mapping (i.e., the ability to form an association with no explicit training). On these trials, the mice were exposed to a sample object that had not previously been encountered, and then were allowed to explore the test field which contained one novel object among a set of familiar objects (ones that had an established "meaning" based on prior training). Under these circumstances (according to the principle of fast mapping), the mouse should rationally infer that since the sample object was novel, the food reward will be located under the unfamiliar object in a field of otherwise familiar objects. Following a series of four such trials (interspersed among trials with known paired associates), the number of fast mapping errors (incorrect choices) committed were compared to factor scores indicative of each mice's general learning ability. Better learners tended to make fewer fast mapping errors, with a correlation of .44 between factor scores and fast mapping performance (Wass et al., 2012). It is also worth noting that the average performance of all mice exceeded what would be expected were the animals choosing randomly, suggesting that along with humans and dogs (Kaminski, Call, & Fischer, 2004; Pilley & Reid, 2011; Tomasello & Kaminski, 2009), fast mapping is within the cognitive capacity of rodents.

In total, mice's performance in the Binary Tree Maze and the fast mapping task suggests that mice are capable of constructing rational plans and making rational choices. Furthermore, the degree of "rationality" exhibited by individual mice was strongly and consistently correlated with their general learning abilities. Thus much like what is observed in humans (Jensen, 1998, p. 226), learning abilities and reasoning abilities are highly related processes in mice.

The relationship of working memory to general cognitive abilities. The working memory system encompasses the short-term storage of information (encompassing both the number of stored items as well as the stability/duration of storage) as well as the processing of information under conditions of interference, the latter of which is strongly dependent on selective attention (Baddeley, 2003; Jarrod & Towse, 2008). Thus the working memory system is comprised of storage components (span, or number, as well as duration) and selective attention. It is not surprising then that to varying degrees, performance on any cognitive test is dependent on the application of working memory, and working memory has come to be viewed by some as a potential latent factor that underlies or regulates general cognitive abilities (Colom, Rebollo, Palacios, Jaun-Espinosa, & Kyllonen, 2004; Engle, Tuholski, Laughlin, & Conway, 1999; Matzel, Sauce, & Wass, 2013). In a series of allied correlational and experimental studies, we have asked if the variation in working memory in mice (as well as its direct manipulation) contributes to individual differences in intelligence.

To asses working memory in mice, we used a variant of a task originally described by Roberts and Dale (1981). Essentially, mice were trained to asymptotic levels of performance in two radial arm mazes that were located in the same room (thus sharing a set of extra maze visual landmark cues). The mice were then required to concurrently work in both mazes, that is, several choices in one maze alternated with several choices in the other maze. Since the spatial cues used to guide the mice's choices were shared across the two mazes, this manipulation was thought to tax a process analogous to *working memory capacity* (defined as the ability to retain, segregate, and act upon information under conditions of interference). As anticipated, the interference that accumulates when working simultaneously in two mazes (imagine trying to remember two new phone numbers simultaneously) promoted an increase in errors (returns to locations at which food had already been retrieved). Importantly, the number of errors committed by individual mice was inversely related to their aggregate performance on a battery of learning tests (Kolata et al., 2005).

Recall that the working memory system is comprised of storage components (span or number, as well as duration of storage) and selective attention. To begin to separate the contribution of these potential sources of variation to general cognitive performance in mice, Kolata, Light, Grossman, Hale, and Matzel (2007) assessed the simple short-term storage abilities of mice by requiring them to maintain the memory of up to six visual symbols associated with food rewards. There was a moderate correlation ($r = .38$) between this measure of simple storage and individuals' general learning performance. A second task was then employed with which we could measure individual differences in the duration of a simple isolated memory (i.e., choice location in a **"T"** maze), and the duration of the memory trace correlated weakly with the mice's general learning performance. Finally, mice were tested on a task modeled after the human Stroop test (Stroop, 1935) to assess selective attention. In a typical Stroop test of humans, a subject is required to identify the color of a word that is briefly presented. In the simple form of this test, subjects' accuracy is normally quite good. However, if the color of the font conflicts with the meaning of the word, (e.g., if a red font spells the word *BLUE*) performance degrades such that the latency to respond increases and/or response errors occur. This degradation in performance is thought to reflect a highly specific failure of selective attention. In the Stroop-like task that we developed for mice, the mice learned a three-choice visual discrimination in a distinctive context (Context VIS) and a three-choice olfactory discrimination in a different (Context OLF). After stable (typically errorless) performance had been attained in both tasks, mice were occasionally tested under conditions of high interference, that is, both odor and visual cues were simultaneously presented in Context VIS (the context which signaled the relevance of visual cues) or in Context OLF (the context which signaled the relevance of olfactory cues). During these trials of high interference, errors increased, and the error rate of individuals was strongly correlated ($r = -.50$) with their aggregate performance in the battery of learning tests. This suggests that absent any explicit demands on memory, attentional abilities are related to general cognitive performance. With these three sets of observations (of short-term memory [STM] span, STM duration, and selective attention) in hand, we then applied a principal component analysis to mice's performance on the tests of simple memory span, memory duration, and selective attention, as well as on six tests of learning. One factor accounted for 44% of the total variance in performance across all of these tasks. On this factor, STM duration loaded at a negligible level (.14), simple span abilities loaded at a moderate level (.50), and our measure of selective attention loaded heavily (.78). These results suggest that, at least in mice, span, duration, and attention differ dramatically in their weight/importance in regulating the relationship between working memory and general cognitive abilities.

Given the central role seemingly played by selective attention in the regulation of intelligence, we wanted to further understand the structure of this cognitive ability. To do so, Sauce, Wass, Smith, Kwan, & Matzel (2014) devised a battery of attention tasks (analogous to our learning battery) where some tasks were designed to tax internal attention (attention against internal impulses, such as when a student needs to ignore thinking about the party last night when taking an exam) and other tasks to tax external attention (attention against external distractions, such as when a student needs to ignore the fan noise when taking an exam). These different types of attention were assessed in mice using four tasks. Two of these tasks were intended to isolate external sources of distraction, and included the mouse "Stroop" test described above (where the mouse must ignore its learned impulse to follow an olfactory cue in a box where performance was guided by a visual cue) and the dual-radial arm maze also described above (where the mouse must ignore cues that guide performance in the maze adjacent to the actual test maze). Two other tasks were intended to isolate internal sources of distraction. The first was a variant of latent inhibition, where essentially the animal must ignore previous learning that a cue was "safe" when the cue began to signal danger (i.e., a footshock). The second test of internal attention required the animal to reverse a previously learned response in a **"T"** maze (e.g., if the previous correct response was to turn left, the animal must now learn to turn right). Put more simply, the first two tests (the Stroop test and the Dual-radial arm maze) in this attentional battery required that the animals ignore external sources of interference, whereas the second two tests (latent inhibition and **"T"** maze reversal) required the animal to ignore an internal source of interference that was based on previously learned response tendencies (and is thus analogous to response inhibition). After the completion of testing on these four tasks, a confirmatory factor analysis[4] was conducted where we assessed a model (a hypothetical explanation of the results) where all tests load to one latent construct (general attention) versus an alternative model with two alternative constructs: internal attention and external attention. We found that the second model had a better fit to the data, which suggests that attentional abilities in mice were not only related (performance on all attentional tasks were positively correlated), but also segregate depending on the source of interference (internal vs. external). In addition, we also performed a factor analysis (similar to a principal component analysis [PCA] described above) with the factor scores from a learning battery and the attention tasks. Our results indicate that external attention is more highly related to learning scores (i.e., is more highly correlated) than internal attention. This is a good example of finding and pulling the "hidden strings" of Nature, which is how Cronbach (1957) poetically described the value of the correlational approach in psychology. It is difficult to imagine how experimental studies alone could answer similar types of questions.

To summarize the relationship of working memory (which includes attention) to broader cognitive abilities, as in humans, the efficacy of mice's working memory system covaries with their general cognitive ability. To assess the directionality (cause vs. correlation) of this relationship, Light et al. (2010) provided mice with complex working memory "exercise" by training them repeatedly (over a period of weeks) in the dual-radial arm maze task described above (Kolata et al., 2005). This training promoted superior performance when the mice were later tested in our mouse analog of the Stroop task, a measure of selective attention. Furthermore, complex working memory exercise promoted an increase in the mice's performance in a six-task learning battery. These results suggest that the efficacy of the working memory system is causally related to the expression of general intelligence, a result that is supported by work with humans (Jaeggi, Buschkuehl, Jonides, & Perrig, 2008; but see Moody, 2009; Redick et al., 2012; Shipstead, Redick, & Engle, 2012).

Summary of the analysis of individual differences in the intelligence of mice. The general cognitive performance of mice varies dramatically across individuals. Some are characteristically "smart" while others appear more "dull". As with the distribution of human intelligence, many mice are just average in a normally distributed range of abilities. At a structural level, intelligence in mice is similar to human intelligence: a general influence on cognitive ability contributes to performance on domain-specific abilities (e.g., spatial abilities) as well as diverse individual cognitive tests (Kolata et al., 2008). And lastly, like human intelligence, the general ability of mice appears to place constraints on learning, reasoning, working memory, and attention.

Nonhuman Primates

Studies of primate intelligence have traditionally followed a very different approach to those that have been employed with mice. Most studies of nonhuman primate intelligence would be more familiar to the comparative psychologist in that they often focus on cognitive differences between species. In this tradition, it has been possible to determine the relative intelligences of various species (i.e., capital letter *G*), and these efforts have been instrumental in the development of theories on the evolution of general intelligence (Burkart et al., 2016). In one meta-analysis, Deaner, van Schaik, and Johnson (2006) compared 24 primate taxa on nine cognitive tests. Not only was a consistent G observed for these species, but G strongly predicted the species intelligence rank. A similar analysis in 2014 compared the performance of 62 primate species on five cognitive domains (tool use, foraging, tactical deception, social learning, and innovation) and found that a single factor accounted for over 60% of the variance across all tasks. Thus, like humans (and mice!), primates appear to consistently express (at least across species) a trait analogous to "general intelligence."

In contrast to cross-species comparisons of G, far fewer studies have attempted to describe individual differences in *g* (general intelligence) within a species. And owing perhaps to the complexities and costs associated with primate research, these studies have been somewhat less extensive than those reported for mice. Moreover, studies of cognitive abilities of primates have often focused

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[4] While exploratory factor analyses (a version of which is the PCA described above) are used to explore without preconceptions the possible underlying constructs behind a set of observed variables, a confirmatory factor analysis (CFA) allows us to test the hypothesis that a relationship between observed variables and their underlying latent constructs exists. In other words, a CFA tests if a model postulated a priori (the structure and relationships between variables and constructs) actually fits the observed data. In addition, a CFA also allows us to compare models statistically by estimating which has a better relative fit.

on those abilities that are sometimes regarded as unique to these species; for example, tool implementation (which may reflect reasoning), social awareness, social transmission of a learned skill, or number use. Thus, it is sometimes difficult to infer that performance on these tasks is indicative of a general cognitive ability.

Perhaps most systematically, Herrmann, Hernández-Lloreda, Call, Hare, and Tomasello (2010) tested 106 chimpanzees on a battery of 15 cognitive tasks. These tasks included skills representative of spatial memory, object rotation, spatial transposition, addition, and causality estimation. No tasks were included that could be described as "elemental" in nature (i.e., sufficiently simple that all chimpanzees could eventually perform them at 100% accuracy), and none were representative of basic learning skills. In these latter regards, these test batteries differ from the tests that have been designed for mice. The tasks administered by Herrmann, Hernández-Lloreda et al. did impinge on several different motivational systems (and thus were unlikely to capture a general motivational state). Nine of the tasks could be categorized as belonging to a "physical domain" (representing space, quantity, or causality) and six were categorized as belonging to a "social domain" (social learning, communication, and theory of mind). A general factor was differentially expressed across individuals, as was a domain factor representative of spatial ability (for similar results with mice, refer to the previous description of Kolata et al., 2008). However, no independent factors emerged that captured physical and social cognition. Interestingly (and representative of the "comparative" approach), Herrmann, Hernández-Lloreda et al. also tested 105 two-year old human infants on a similar battery of tests. While the human infants expressed a general factor and a specific spatial ability, they also expressed domain-specific physical and social abilities. (It is worth noting that the adult chimps and infant humans performed remarkably similarly in test of physical cognition, while the chimps were consistently worse, and in two instances, quite poor, on tests of social cognition. It is of course possible that a domain-specific social ability might be revealed were the tests designed to support a higher level of performance among the chimps.) These findings support the conclusion that humans and nonhuman apes share certain cognitive skills and a similar hierarchy of abilities, but also suggest that humans (and other primates) may have evolved specialized skills in the domain of social cognition, a theme that is pervasive in theories of the evolution of intelligence (Dunbar & Shultz, 2017; Holekamp & Benson-Amram, 2017)

While most studies of nonhuman primates have been designed to compare species and to maximize the influence of distinct cognitive domains, one study was designed explicitly to assess individual differences in the expression of a general cognitive influence within a single species. Banerjee et al. (2009) administered to 22 tamarin monkeys a large and diverse battery of cognitive tests. The cognitive tasks covered a wide range of cognitive skills and domains, including occluded reach, targeted reach (reward retrieval from a moving pendulum), adaptation to an observed change in reward location (a measure of executive control), reversal learning, novel object exploration (which is impacted by rate of learning; Light et al., 2011), numerical discrimination, acoustic habituation, object tracking (an index of attention), social tracking (gaze at a conspecific), hidden reward retrieval after various delays, and a food retrieval puzzle (which was asserted to tax reasoning). With minor exceptions (targeted reach and social tracking), the cognitive processing required by these tasks is an obvious (and principal) contributor to variations in performance, and in this regard, the study by Banerjee et al. (2009) is unique among studies of general cognitive ability in primates.

Banerjee et al. observed positive correlations in animals' performance across all tasks, suggesting that a general factor contributed to performance on all of the tests. Employing a technique closely resembling a factor analysis, they found that all tasks loaded positively on a common factor, with weights described as *weak* to *moderate* (0.24–0.54). Interestingly, the tasks with the least obvious cognitive demands (targeted reach and social tracking) loaded most weakly. In total, these results provide evidence for individual differences in the expression of a general cognitive ability among tamarins; and moreover, that the general factor's influence is directly related to the level of the cognitive demand.

A trait analogous to intelligence is heritable among nonhuman primates. Hopkins, Russell, and Schaeffer (2014) tested 99 chimpanzees using 13 of the cognitive tasks originally developed by Herrmann, Hare, Call, and Tomasello (2010). A principal component analysis revealed a general cognitive factor influenced the performance of animals across most tasks. Moreover, using an approach that considered sibling, half-sibling, and parent–offspring comparisons, they found substantial heritabilities for these tasks (with estimates as high as .74 on a 0–1 scale). In a follow-up analysis of the same data, Woodley of Menie, Fernandes, and Hopkins, (2015) reported that the higher a task's "g-loading" (i.e., the degree to which a task is impacted by a general ability), the higher the task's heritability. Thus like humans and mice, chimpanzees express variations in general cognitive abilities, and these variations are at least in part heritable (for more on heritability, see the next section, The Origins of Individual Differences in Cognition). Moreover, this analysis of chimpanzees is consistent with the assertion that intelligence is among the most heritable of psychological traits (Jensen, 1980, 1998; Plomin, 1999).

The Origins of Individual Differences in Cognition: An Interaction of Genes and Environment

The heritability[5] of intelligence in humans can exceed 0.8 (on a scale of 0–1) at 50 years of age. Other psychological traits described as highly heritable rarely approach the degree of heritability of IQ (see Bouchard, 2004, for extensive examples). The most

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[5] Heritability is a statistic that captures how much of the variation on a trait is due to genetic differences. Heritability can be estimated for any trait (a method will be described below), and it ranges from 0.0 (meaning that variation in the trait has no genetic component) to 1.0 (meaning that the trait is completely heritable). Importantly, heritability is not the same as genetic inheritance. Technically, a trait that is completely controlled by genes could have a zero or very low heritability, such as number of fingers. Our five fingers on each hand are determined by genetics during early development, but most of the variation in number of fingers in human populations is due to accidents, not genetic mutations. The same holds true for the inverse: highly heritable traits could in principle have low genetic inheritance. Despite its limitations, heritability has been used productively for decades in fields as diverse as molecular biology, quantitative genetics, population genetics, evolutionary biology, conservation ecology, and medicine. The uses of heritability range from predicting the response to selection for nitrogen absorption in plant breeding (which probably saved millions of lives from starvation during the Green Revolution; for a brief overview, see Moose & Mumm, 2008), to studying the malleability of intelligence (which could potentially change our welfare policies as well as the educational system; Plomin & Spinath, 2002).

comparable is schizophrenia (heritability of 0.64; Lichtenstein et al., 2009), while alcoholism (heritability of 0.50), neuroticism (heritability of 0.48; Riemann, Angleitner, & Strelau, 1997), and major depression (heritability of 0.40; Sullivan, Neale, & Kendler, 2000) are markedly lower. Given the relative paucity of work with nonhuman animals, we know far less about the heritability of intelligence among the species reviewed above. However, we do know that laboratory animals can be selectively bred to promote specific learning abilities, as demonstrated in classic studies of the heritability of maze learning in rats. For instance, Tolman (1924) tested 82 male and female rats in a maze learning task. The nine "brightest" males and females and the nine "dullest" males and females were selected for mating. The offspring of these rats exhibited levels of learning more closely resembling their parents. However, owing to presumed technical complications, this pattern of heritability began to dissipate in the subsequent generation. Across the next decade, a similar but more extensive analysis was conducted by Tolman's former graduate student Robert Tryon, who mated bright and dull rats for 20 generations. (It is notable that in Tolman's laboratory, Tryon developed procedures to increase the reliability of behavioral measures and standardized the animals' living conditions, and used rats that expressed more genetic diversity than those used in Tolman's prior study; see Innis, 1992, for discussion). Once again, divergence in maze performance was observed, plateauing at seven generations with bright rats making about 40% of the errors made by dull rats (with some dull rats making up to 20 times the errors of a bright one!). Both of these early studies (progenitors in the field of behavior genetics) are evidence for the heritability (and genetic contribution) of individual differences in maze learning ability (also see Heron, 1935). However, it must be noted that the results of these analyses do not inform us about the heritability of a general cognitive ability. Tolman's (1924) and Tryon's (1940) results (as well as Heron's) did not appear to generalize beyond the specific maze in which their rats were tested. Moreover, it is impossible to conclude that the rats in these studies were selected for learning abilities per se, but rather, may have been selected for some hidden variable (e.g., sensitivity to deprivation or visual acuity) that indirectly influences learning. This highlights the limitations of conclusions based on a single measure of cognitive performance. Nevertheless, the outcome of these early experiments was by no means obvious in the 1920s and 1930s, as the vocal majority of this era insisted that variations in behavior were solely the product of the animal's history with its environment.

Based on Tolman and Tryon's analyses, we can conclude that something is inherited that can impact maze learning. We also know from our own work that smart and dull animals are genetically different (Kolata et al., 2010). But what can be said about the actual degree to which general cognitive ability is heritable? Galsworthy et al. (2005) directly calculated (using a classic sibling analysis[6]) the heritability of a general cognitive ability in mice. They tested outbred mice on a battery of seven cognitive tasks that were dependent on at least four different motivational states, and which required the engagement of a range of sensory and motor systems. The authors then found that a single factor accounted for 36% of the variability in the aggregate performance of individuals across all tasks (i.e., mice varied in their general learning ability). In a second experiment, approximately 90 sibling pairs were tested, allowing Galsworthy et al. to estimate the correlation of the general abilities between siblings. From this analysis, the heritability of general cognitive ability was estimated at approximately 0.4, suggesting a moderate genetic contribution to the expression of this trait.

The results of Galsworthy et al. provide evidence that general cognitive abilities in mice are moderately heritable. However, this estimate of heritability is markedly lower than that which is typically reported for adult humans (which is commonly estimated to range from 0.7–0.8 in adulthood; (Bouchard, 2004, 1997; Haworth et al., 2010). This may be a real difference, or may simply reflect the additional error that would be expected in a newly developed battery of cognitive tests applied to mice (recall Tryon's difficulty in developing reliable methods for testing the cognitive abilities of rodents). However, a much more intriguing possibility exists. Unlike typical humans, laboratory mice are maintained in a behaviorally sterile environment that is homogeneous across mice. Thus, these mice cannot select the environments or challenges that might maximize cognitive differences, that is, they cannot select an environment that is matched to their cognitive ability. The importance of this constrained environment on the heritability of intelligence will be become evident below.

Among humans, the heritability of eye color approaches 1.0 and this value is observed regardless of the age at which eye color is assessed. In contrast, while the heritability of body weight is quite high at 5 years of age (heritability = 0.95), it typically decreases across the life span, plateauing at approximately 0.60 by 50 years of age. This decline in heritability reflects the fact that while genes set some initial parameters for body weight, lifestyle choices become a more dominant determinant of body weight as we age. The decreasing heritability of body weight shows that this trait is not fixed at birth, but, rather, is quite malleable despite the initially strong genetic influence. This example highlights a common misperception about the nature of heritability: Heritability needn't determine the expression of a trait, but rather, reflects the outcome of a gene–environment interaction.

Like body weight, the heritability of intelligence also changes across the life span. However, the pattern for intelligence is quite

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[6] Sibling analyses are techniques used in quantitative genetics to estimate genetic effects (and, therefore, heritability) by using family relatedness as a proxy to DNA/gene variation. Simply put, if there are genetic effects behind the variation of a trait, we expect a correlation to exist between the trait values among family members. And the magnitude of that correlation will, of course, depend on how related the people are. In the case of sibling analyses, it will be 100% in the case of monozygotic, identical twins, 50% (on average) in the case of dizygotic fraternal twins and also in the case of standard full siblings, and 25% in the case of half siblings. For a full sibling study, for example, heritability is twice the observable phenotypic correlation between the siblings. This estimation, however also includes confounding factors from the environment that are shared by the siblings such as maternal effects. Because of that, the heritability estimate from a full sibling study is considered to be an upper bound estimate; it gives the maximum genetic influence for that trait. There are ways to eliminate these confounding factors, as, for example, in twin studies when comparing identical twins to fraternal twins. The assumption of twin studies is that the shared family environment experienced by identical twins (among them) and fraternal twins (among them) will be relatively similar, while only the shared genetic material will differ. Therefore, the discrepancy between how similar identical and fraternal twins are can be used to get a more precise estimate of heritability than by simply using only standard full siblings. (For more on the twin method and other models for estimating heritability, see Tenesa & Haley, 2013).

different than that observed for body weight (and for many other traits). In humans, intelligence can be reliably quantified by about 4 years of age, at which time, the heritability of IQ is estimated at approximately 0.22. By 16 years of age, the heritability of IQ increases to 0.60, and by age 50 (at which time the heritability of body weight has declined precipitously), the heritability of IQ is estimated to be as high as 0.80 (Bouchard, 1997; Haworth et al., 2010). This increase in the heritability of IQ is not simply a measurement artifact. The increase in heritability of IQ with age probably reflects an underlying role of gene–environment interactions (and correlations, i.e., self-selection of an environment based on IQ) in creating IQ differences between individuals.

An individual's IQ is an important determinant of their attraction to a particular cognitive environment and cognitive challenges. While the genome is largely established at birth (except for age-dependent genes), the environment that one selects (or is forced into) is subject to constant change. This suggests that the increase in heritability observed across the life span is, in large part, an interplay of the genome with the environment. But why does the heritability of IQ increase (rather than decrease like traits such as body weight)? Small genetic differences in IQ during early childhood can be amplified by the accumulation of cognitive challenges offered by different environments (Lykken, Bouchard, McGue, & Tellegen, 1993; McGue, Bacon, & Lykken, 1993). Children with slightly higher IQs interact with the environment (and choose an environment) that is appropriate for their cognitive abilities, which can in turn promote further gains in intelligence. Conversely, children with slightly lower IQs may gravitate toward less challenging environments, and may come to have relatively lower IQs as adults. As this occurs, those that are genotypically similar become phenotypically more similar, and estimates of heritability increase. The same pattern of changes in heritability that occurs across the life span occurs consequent to changes in socioeconomic status and adoption (Turkheimer, Haley, Waldron, D'Onofrio, & Gottesman, 2003) and even across generations in response to rapid industrialization (Dickens & Flynn, 2001; Flynn, 1984). All of these observations indicate the important role that a variable environment (and its interaction with genes) has in the determination of IQ and ultimately, in the heritability of IQ (for an extensive review, see Sauce & Matzel, in press).

So, a wealth of data suggests that despite its high heritability, human intelligence is also highly malleable; and moreover, that estimates of heritability are highly sensitive to variations in the environment in which heritability is estimated (see Sauce & Matzel, in press, for a detailed analysis). This is reminiscent of the quote by Jim Shepard (2017): "There are as many different kinds of men in the world as there are mothers to bear them and experiences to shape them, and in the same wind, each gives out a different tune." Mothers (and of course fathers) provide the genotype which establish the parameters for an individual's intelligence. But environments, and the individual's choices in those environments, determine how those genes will ultimately be expressed. Each contributes and interacts to establish the individual's tune (or in this case, intelligence).

One final point on this topic should be addressed. Estimates of IQ's heritability in humans are usually described as high, but studies across SES reveal quite low heritabilities in poor populations. That discrepancy, we believe, is (at least in part) due to the environments in which these samples are drawn. Most studies of intelligence are in fact obtained from high SES samples, that is, the participants are drawn from middle class and above, who reside in wealthy countries. In these populations, an abundance of opportunities and good conditions can amplify small genetic differences in intelligence via gene–environment interactions. The same is not true of estimates obtained from low-SES samples, where environments are necessarily more restricted. In the case of high-SES samples, the favorable environment can inflate estimates of the heritability of IQ (leaving the impression that genes underlie the high estimates). This pattern is interestingly relevant for studies of intelligence in animals. Let's return to the observation of Galsworthy et al. (2005) that the heritability of general cognitive ability in mice (0.4) is low relative to that observed in humans. But "typical" estimates of heritability in (wealthy) humans are made in favorable environments in which individuals can "self-select" the conditions appropriate for their cognitive abilities, and are freer to meet a vast array of experiences—which leads to more opportunities for gene-environment interactions (more opportunities, e.g., for a genetically gifted student to go to grad school, an experience that will increase her IQ more than it will her less gifted classmate). Recall that Galsworthy et al.'s mice were raised and maintained in a standard (sterile) laboratory environment. The cognitive opportunities for these mice were necessarily restricted and homogeneous, analogous to the low-SES environment of humans from which estimates of the heritability of IQ are correspondingly low. This presents the intriguing possibility that like humans, in a more favorable environment, mice might encounter cognitive challenges appropriate for their genotype, and estimates of heritability might increase. This represents one of the great virtues of animal research. While this possibility, although consistent with interpretations based on correlational data, can never be directly tested in humans (owing to ethical considerations), environmental manipulations can be administered to laboratory mice, and such an experiment could help resolve the role of Gene × Environment interactions in the determination of the heritability of intelligence. We are currently conducting exactly this experiment in our laboratory.

Modularity, General Abilities, and Evolutionary Constraints

A recurring controversy surrounds the degree to which cognitive abilities are modular and isolated from one another versus the degree to which cognitive abilities are regulated in common. In fact, many theoreticians have specifically denied the existence of a general cognitive ability by asserting that the mind (at least in primates) is comprised of independently evolved specialized modules (which in this case, refers only to independent domains of cognitive abilities; Fodor, 1983; Gallistel, 1990; Pinker, 1997). While not always acknowledged, a similar idea underlies much of the work aimed at localizing the areas responsible for specific cognitive abilities (a tradition emerging from the early studies of Lashley [reviewed in Lashley, 1958] and later observations of the amnesic H.M.). So ingrained is this idea, a member of an NIH grant review panel once commented to one of us (Louis D. Matzel) that the "premise of a general cognitive ability flies in the face of 50 years of neuroscience research."

In mammals, different specific cognitive abilities (i.e., domains) do appear to have evolved independently in different species

(Barton & Harvey, 2000). It is generally assumed that such modularity increases the likelihood of an animals' survival in the conditions that are specific to its environmental niche, that is, modules independently evolve to solve species- or environment-specific problems (Gallistel, 1990; Shettleworth, 2010; Tomasello & Call, 1997).

Evidence for modularity takes many forms, two of which are particularly relevant here. First, if it is demonstrated that one species outperforms another on one task, but underperforms that species on a different task, domain-specific cognitive modules can be inferred. This type of evidence is quite common in studies of primates. For instance, Herrmann, Hare et al. (2010) compared bonobos to chimpanzees (human's two closest relatives). While genetically similar, these animals inhabit very different environments and express distinct behavioral tendencies. For instance, chimpanzees are "extractive" foragers, using tools to obtain otherwise difficult-to-retrieve food (a feat suggested to reflect causal reasoning; Boesch & Boesch, 1990). In contrast, bonobos use tools much less frequently in their natural environments, but are renowned for their cooperative social interactions (and rampant sexual promiscuity). These two species were tested on cognitive tasks that taxed their aptitude on physical and social challenges. Bonobos performed better on tasks related to theory of mind and social causality, while chimpanzees were more skilled at tasks requiring the use of tools or causal reasoning. These species differences support the contention that ecological pressures shape cognitive specialization (and do so over relatively short periods of evolution). Second, it is also possible to examine the factors that emerge (on for instance, a principal component analysis) when animals are tested on a wide range of cognitive tasks. This approach has been taken by Amici, Barney, Johnson, Call, and Aureli (2012), who analyzed data from seven primate species tested on 17 tasks that were representative of four cognitive domains (inhibition, memory, transposition, and social support). Different domain-specific factors were associated with different species, again supporting the hypothesis that the mind of primates is at least partially modular, and that domain-specific abilities arise in response to different evolutionary pressures.

So, the mind of primates (and seemingly other animals) is comprised (at least in part) of modules that support distinct cognitive skills or domains. However, as described above, it is also indisputable that these animals express general cognitive abilities (for a more extensive recent review, see Burkart et al., 2016). In this regard, we find the debate regarding modularity versus generality as superfluous. Others (e.g., Amici et al., 2012; Burkart et al., 2016; Matzel & Gandhi, 2000) have pointed out that properties of the brain (e.g., size, proportion of gray matter, speed of transmission) could have a general effect on all brain areas (or modules), and could underlie correlations between performance dependent on otherwise independent modules. But such a general neurophysiological influence could also be accompanied by (or underlie) a general psychological process that is implemented during the execution of any cognitive tasks. Working memory (or its reliance on selective attention) could play such a role, as it is hard to imagine a cognitive task that is not to some extent dependent on the implementation of working memory (Colom, Jung, & Haier, 2007; Conway, Kane, & Engle, 2003; Cowan et al., 2005; Engle et al., 1999; Matzel & Kolata, 2010; Matzel et al., 2013). We need only assume that regardless of its "modularity", some process can impact all modules. For instance, processes such as attention or working memory may evolve independently of other domains. This is exactly one of the rationales that led to the hypothesis that working memory might contribute to general intelligence (for review and extensive development, see Mackintosh, 1998).

As described in the earlier section on General Cognitive Ability (and Figure 1), the existence of modules that are impacted by a more general process is exactly the rationale for contemporary hierarchical models of intelligence, where a higher order factor (*g*) influences second-order factors, or modules, like verbal ability, quantitative ability, special ability, reasoning, and so forth. In other words, a general factor coexists with more modular abilities.

Why Would Individual Differences in G Exist?

Given the evidence for individual differences in general cognitive abilities, the premise that these variations are heritable, and the obvious and documented functional consequences of variations in intelligence (Deary, 2001; Gottfredson, 1998), one might ask why so much variation in this ability exists across individuals of a species. It would be reasonable to expect that higher intelligence would be broadly selected for. Two explanations have been proposed to resolve this paradox. First, animals of lesser physical prowess may have evolved compensatory cognitive abilities to facilitate their survival within the group. This conclusion is consistent with a general theme that has been advanced in recent years among evolutionary biologists and psychologist (Holekamp, 2007; Kamil, 2004; McNally, Brown, & Jackson, 2012). Direct experimental support for this hypothesis has been limited, although such a trade-off between cognitive abilities and fitness (larval competition) has been previously observed in *Drosophila* (Mery & Kawecki, 2003) and wild birds (Cole & Quinn, 2012). Most relevant to the present discussion, we have recently reported that in the absence of adult experience with social hierarchies or social defeat, the predisposition for social subordination was associated with superior general cognitive ability in genetically diverse mice, suggesting that submissive tendencies may be associated with superior cognitive potential, and this can reflect a native predisposition that precedes exposure to social pressures. (Note that if exposed to social defeat, mice commonly develop cognitive deficits*;* Colas-Zelin et al., 2012; Fitchett, Collins, Barnard, & Cassaday, 2005).

Mery and Kawecki (2003) suggested a very different interpretation of the relationship between cognitive abilities and fitness: better cognitive abilities have costs that render the beneficiaries of improved cognition less physically fit. Indeed, the development and maintenance of the neural architecture that supports learning and memory storage is associated with high energetic costs (Johnston, 1982; Laughlin, 2001). Of course, it is entirely possible that cognitive abilities are compensatory and simultaneously mitigate fitness. Regardless, the above observations support the possibility that socially subordinate animals evolved compensatory strategies to facilitate their survival, but also indicate that cognitive "superiority" is but one route to immediate or evolutionary success.

Conclusions and Implications

The evidence is clear that at least several species of animals express individual differences in a general cognitive ability. In humans, this trait is colloquially described as *intelligence*, and can be accurately quantified with several modern IQ tests. Given the capacity of an IQ score to predict functional life outcomes (e.g., academic and career success, health, longevity, happiness, propensity for crime and addiction), it is immediately clear why individual differences matter, and why they should matter for related psychological traits such as learning, attention, and reasoning. Nevertheless, as a topic for research, studies of individual differences, and the correlational methods that they require, have been somewhat neglected, particularly within the field of learning.

To further illustrate the need to attend to individual differences, a broader example may be informative. The removal of an expected reward is known as *extinction*, which leads to a decrease in goal-directed behavior. The prototypic extinction curve (which typically illustrates the average response of a group of individuals) suggests that the decrease in behavior is gradual and relatively homogeneous across individuals. In fact, however, this decrease in responding can emerge at dramatically different rates across individuals (Andrews & Debus, 1978; Quinn, Brandon, & Copeland, 1996), and the typical extinction curve is of little use in describing the behavior of any individual. These variations in response to extinction have been studied extensively in human infants by Michael Lewis and colleagues. In a series of such studies, it has been observed that upon extinction, some young infants exhibit persistent responding accompanied by facial displays of anger (Alessandri, Sullivan, & Lewis, 1990; Crossman, Sullivan, Hitchcock, & Lewis, 2009; Sullivan, Lewis, & Alessandri, 1992), while others quickly stop responding during extinction, and show facial expressions of sadness (Lewis & Ramsay, 2005). These distinct individual differences in response to extinction suggest the possibility that these two populations reflect differences in a broader phenotype, a possibility that has been largely ignored within the field of learning. In collaboration with Lewis, we have begun to study this phenomenon in genetically heterogeneous CD1 mice (Sauce, Wass, Lewis, & Matzel, in press). We have observed that upon extinction of a running response for food, some mice quickly abandon the running response, while some actually exhibit an initial increase in running speed, followed by a much slower dissipation of running. (Notably, when reduced to an "average value," a smooth, gradual extinction curve is revealed.) These two classes of animals exhibit other distinct characteristics. Those that are more persistent during extinction also engage in prolonged patterns of search-like behavior in the extinction apparatus. Furthermore, they also take longer to abandon swimming in a pool of inescapable water, a kind of persistence known to predict resilience against depression in animal models (for a review on the topic, see Porsolt, Brossard, Hautbois, & Roux, 2001). We have concluded that these two classes of animals are emblematic of distinct phenotypes representing persistence and resignation, the latter of which may be more susceptible to depression.

Pronounced individual differences in response to extinction have broader implications, and might be informative about the predisposition of individuals to psychiatric disorders such as major depressive disorder. Although major depression is highly heritable, it has become increasing apparent that despite identical genetic markers, some individuals will develop depression while others will not. For example, Caspi et al. (2003) studied the risk of depression in individuals with a variant in the promoter region of the serotonin transporter (5-HTT) gene that leads to lower levels of the transporter in the brain (a target for modern antidepressants such as Prozac). While they could find no main (independent) genetic effect of this gene, carriers of the 5-HTT gene variant had a higher risk of developing depression following stressful life events and childhood maltreatment (Caspi et al., 2003). This study has become remarkably influential in the clinical field, and is a fascinating case of a Gene × Environment interaction underlying the emergence of a psychological trait. Relatedly (though perhaps not surprisingly), it is widely recognized that despite their ubiquitous administration, antidepressant drugs such as Prozac are effective on only a small minority of recipients. In fact, extensive meta-analyses indicate that modern antidepressant drugs may be effective on less than 20% of the individuals that actually receive them (Kirsch, 2008). In a commentary on the NIH website, former NIMH director Thomas Insel (2011) remarked that "mild depression tends to improve on placebo so that the difference between antidepressant use and placebo effect is very small, or at times, absent." So, our disregard for individual differences in response to treatment has dramatic functional consequences (both in terms of patient health, time, and monetary investment). The development of simple screening assays (e.g., an individual's response to extinction?) might be exactly the type of diagnostic device that could result in the effective assignment of treatment options. Of course such an approach requires that we recognize individual differences, and attend to their significance. To return to the point made by Jim Shepard, individual differences are real and they matter.

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