

Covariation of Learning and “Reasoning” Abilities in Mice: Evolutionary Conservation of the Operations of Intelligence

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Contemporary descriptions of human intelligence hold that this trait influences a broad range of cognitive abilities, including learning, attention, and reasoning. Like humans, individual genetically heterogeneous mice express a “general” cognitive trait that influences performance across a diverse array of learning and attentional tasks, and it has been suggested that this trait is qualitatively and structurally analogous to general intelligence in humans. However, the hallmark of human intelligence is the ability to use various forms of “reasoning” to support solutions to novel problems. Here, we find that genetically heterogeneous mice are capable of solving problems that are nominally indicative of inductive and deductive forms of reasoning, and that individuals’ capacity for reasoning covaries with more general learning abilities. Mice were characterized for their general learning ability as determined by their aggregate performance (derived from principal component analysis) across a battery of five diverse learning tasks. These animals were then assessed on prototypic tests indicative of deductive reasoning (inferring the meaning of a novel item by exclusion, i.e., “fast mapping”) and inductive reasoning (execution of an efficient search strategy in a binary decision tree). The animals exhibited systematic abilities on each of these nominal reasoning tasks that were predicted by their aggregate performance on the battery of learning tasks. These results suggest that the coregulation of reasoning and general learning performance in genetically heterogeneous mice form a core cognitive trait that is analogous to human intelligence.

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Studies of individual differences in mental abilities in nonhuman animals have increased dramatically during the past decade, and this work has served as an impetus to further delineate the behavioral processes and neural mechanisms that underlie general intelligence. Over a century ago, Spearman described “general intelligence” (i.e., “g”), noting that a single factor could account for a large portion of the underlying variance in performance across diverse cognitive tasks. Spearman (1904) concluded that regardless of the specific demands of a task, performance on that task is determined by both domain-specific abilities (e.g., spatial ability) as well as by g (i.e., general intelligence). It is the recognition of this latent influence on the execution of most cognitive tasks that underlies the rationale for contemporary tests of human intelligence.

Despite decades of often vigorous debate, a single, a widely accepted definition of “intelligence” has yet to be agreed upon. Nevertheless, consensus has emerged regarding the operations impacted by intelligence. In an article in the *Wall Street Journal*

(December 13, 1994) signed by 52 intelligence researchers, it was asserted that intelligence was “a very general mental capability that, among other things, involves the ability to reason, plan, solve problems, think abstractly, comprehend complex ideas, learn quickly and learn from experience.” A committee of the American Psychological Association (1995) stated that “Individuals differ from one another in their ability to understand complex ideas, to adapt effectively to the environment, to learn from experience, and to engage in various forms of reasoning to overcome obstacles. Concepts of “intelligence” are attempts to clarify and organize this complex set of phenomena.” While there is an apparent consensus regarding the functional consequences of intelligent behavior, these “definitions” are simultaneously nebulous in content and expansive in scope.

While a widely accepted definition of “intelligence” has not fully materialized, most descriptions (including those provided above) state that intelligent behavior involves the ability to “adapt to the environment” and to “learn quickly.” These characteristics, like colloquial impressions of intelligence, suggest that learning is a critical component of, if not critically influenced by, intelligence. For instance, rates of learning among humans are often predicted by psychometric tests of IQ (for reviews, see Gettinger, 1984; Jensen, 1989). In fact, Jensen has concluded that general *learning* factors (extracted from performance across *large* numbers of learning tasks) are so highly related to the general intelligence factor extracted from psychometric tests that “learning and psychometric abilities (general intelligence) are essentially one and the same” (Jensen, 1998). It is notable that occasional reports of a

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lack of correlation between performance on single learning tasks and measures of general intelligence may at times be attributable to the high *task-specific* variability inherent to measures of performance on a single task, such that the influence of a *general* factor on that task is relatively small (and thus, not detected by a probability test). Furthermore, on elemental tasks that all subjects can presumably master, any correlation between learning and general intelligence is dependent on the measurement of learning *rate* or speed of responding, a requirement that has at times been overlooked (see Jensen, 1998, p. 275 for discussion relevant to human learning, and Kolata, 2008, for a discussion relevant to the present utilization of measures of learning performance; for alternative data and interpretation, see Williams & Pearlberg, 2006).

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While the capacity for learning is indicative of intelligence, definitions of intelligence (such as those provided above) make reference to myriad processes beyond learning. Along with the ability to learn, most definitions of this trait make primary references to an individual's capacity to "think rationally," "reason," "engage in reasoning," or colloquially, "to figure out novel solutions" based on limited experience. Thus, the efficacy of reasoning is widely considered to be a critical component of intelligence (Manktelow, 1999), and most intelligence test batteries include components specifically intended to characterize an individual's capacity for reasoning. In fact, many modern tests of intelligence (e.g., the Raven's Progressive Matrix) are weighted almost exclusively toward this ability.

While it has been empirically determined that human intelligence (including its expression on tests of reasoning) and learning abilities covary (Gettinger, 1984; Jensen, 1989), there have been no attempts to assess the relationship between general learning abilities and reasoning in nonhuman animals. In this regard, it was until recently a common assertion that reasoning was beyond the capacity of nonhuman animals. In contrast to this assertion, demonstrations of behaviors that are nominally indicative of reasoning in nonhuman animals have begun to be reported. Briefly, species such as monkeys (McGonigle & Chalmers, 1977; Rapp, Kansky, & Eichenbaum, 1996), chimpanzees (Boysen, Berntson, Shreyer, & Quigley, 1993), rats (Dusek & Eichenbaum, 1997; Roberts & Phelps, 1994), and pigeons (Wynne, 1997; Lazareva, 2006 1853) have all demonstrated the capacity for transitive inference, an ability that, at least in some instances, has been asserted to depend on deductive forms of reasoning (for alternative explanations, see General Discussion & Shettleworth, 2010). Another task (that we will adapt here for the assessment of mice) that has been used to assess reasoning abilities in nonhuman animals is "fast mapping." Fast mapping is a mental process whereby a new concept can be learned based on a logical inference derived from a single exposure to limited information. Fast mapping (Care & Bartlett, 1978) is believed to play a critical role in the extraordinarily rapid and seemingly effortless 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 added to the otherwise familiar set ("inference by exclusion"), and this association requires no overt "pairing" of the novel word and its corresponding novel item. Over time, the word's approximate meaning becomes more refined as it is seen in other contexts.

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Logical inference, as exemplified here, is often described as a hallmark of reasoning.

Although fast mapping has been extensively studied in humans, there have been few attempts (except in two dogs and one chimpanzee) to assess whether nonhuman animals are capable of this cognitive process. Briefly, Kaminski, Call, and Fischer (2004), demonstrated that a Border Collie (also see Pilley & Reid, 2011) was able (on first command) to retrieve a novel object (identified by a novel term) from among set of over 200 previously learned objects. Kaminski et al. concluded that the Border Collie was able to correctly retrieve the novel object through the use of inferential exclusion principles, that is, the novel word used in the voice command was inferred to mean to retrieve the novel object. Hashiya and Kojima (2001) demonstrated that a chimpanzee was also able to use inferential exclusion in order to correctly match a novel voice to a novel portrait when two previously learned portraits (distracters) were present. Based on the limited observations of fast mapping in nonhuman animals, it is reasonable to ask whether mice are capable of utilizing similar basic reasoning, and whether the fast mapping abilities of mice covary with the general learning abilities of these animals.

Prior studies have demonstrated the existence of a general cognitive factor in genetically heterogeneous mice, and this latent influence on diverse learning abilities is in many ways analogous to general intelligence in humans. Specifically, we have shown that when genetically heterogeneous mice are assessed on batteries of as many as nine diverse learning tasks, as much as 28–50% of the variance in performance across these tasks can be accounted for by a single factor (Kolata et al., 2008; Kolata et al., 2010; Light, Kolata, Denman-Brice, Zagalsky, & Matzel, 2008; Matzel et al., 2003; Matzel et al., 2006; Matzel, Grossman, Light, Townsend, & Kolata, 2008; also, see Galsworthy, Paya-Cano, Monleón, & Plomin, 2002; Locurto, Fortin, & Sullivan, 2003). Moreover, it has been determined that the efficacy of processing components of working memory (i.e., capacity and selective attention) covary with an animal's general learning ability (Kolata et al., 2005, 2007), and furthermore, working memory training regimens promote an increase in animals' general learning abilities (Light et al., 2010; Matzel et al., 2011). These observations correspond with studies of humans which have indicated that working memory capacity covaries with an individual's general intelligence (Conway, Kane, & Engle, 2003; Engle, Laughlin, Tuholski, & Conway, 1999; Jaeggi et al., 2009). Thus, the processes that regulate the general learning abilities of mice are to some degree homologous with those implicated in establishing general intelligence in humans.

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As reasoning abilities are widely considered to epitomize the functional operations of "intelligence" (and comprise a core component of all definitions of intelligence), the work reported in the present article was aimed to determine whether laboratory mice are capable of behaviors that are analogous to behaviors described as "reasoning" among humans, and if so, whether the animals' capacity for this reasoning-like behavior covaries with their general learning abilities. To assess the hypothesis that general learning abilities and reasoning-like cognitive performance covary in laboratory mice, we first utilized a fast mapping-based task which is commonly asserted to reflect a subject's capacity for deductive reasoning (e.g., Carey & Bartlett, 1978).

Experiment 1A

In order to assess whether an animal's general learning and deductive reasoning abilities were jointly regulated, we first characterized the general learning ability of individual animals in a five-task learning battery that has been previously described (e.g., Matzel et al., 2003, 2006). A principal component analysis was then applied to animals' performance on these five learning tasks in order to derive each animal's factor score (a measure of each animal's aggregate performance across all learning tasks; see below). Having ascertained the general learning ability of each animal, we then assessed the same animals on a fast-mapping task. Animals' general learning performance was then compared to their performance on the fast mapping task so as to determine the degree of covariance between individuals' capacity for deductive reasoning and general learning abilities.

Method

Subjects. A sample of 47 genetically heterogeneous male CD-1 mice were obtained from Harlan Laboratories (Indianapolis, IN) at 45 days of age. Owing to an experimenter error during fast mapping training, six animals could not be tested in this task. Upon arrival in our vivarium, animals were individually housed in standard shoe box cages and were allowed ad libitum access to food and water. All animals were allowed to acclimate to the vivarium, which was maintained on a 12 hour light/dark cycle, for a period of two weeks. During this period, the animals were handled by the experimenter for 90 sec/day in order to mitigate differential stress responses to the experimenter.

Learning battery. To quantify animals' general learning abilities, we evaluated animals' performance on a battery of five diverse tasks that impinged on different domains of learning, sensory/motor, and motivational systems. All of the animals were tested on these five tasks in the following order: Lashley III Maze, spatial water maze, passive avoidance, associative fear conditioning, and odor guided discrimination. Two days of rest intervened between each successive task in the learning battery. For tasks utilizing food reinforcers, animals were food deprived 48 hours prior to training by allowing only 90 min access to food within 2 hours of the end of the light cycle.

Lashley III maze. The Lashley III maze consisted of a start box, four interconnected alleys, and a goal box containing a food reward. (For an illustration of the Maze, see Matzel et al., 2003.) Efficient performance in the maze required that the animal make five spatial alternations to reach the goal box. Over trials, the errors (i.e., wrong turns or retracing) committed in the animal's approach to the goal box decreased. The maze (scaled for mice) was constructed of black Plexiglas. Each alley measured 58×6 cm, and had 16 cm high walls. A goal box was (20 cm long) was located 10 cm from the end of the last alley. A 2 cm diameter white cup was located in the rear portion of the goal box, and 45 mg BioServe (rodent grain) pellets served as reinforcers. Illumination was 80 Lux at the floor of the maze. The maze was isolated behind a shield of white Plexiglas to prevent the use of extramaze landmark cues.

Food-deprived animals were acclimated and trained on two successive days. On the day prior to acclimation, all animals were provided with three BioServe food pellets in their home cages to

familiarize them with the novel reinforcer. On the acclimation day, each mouse was placed in the four alleys of the maze, but the openings between the alleys were blocked (with black Plexiglas) so that the animals could not navigate between them. Each animal was confined to the start and subsequent two alleys for 4 min, and for 6 min in the last (goal) alley, where three food pellets were present in the food cup. This acclimation period promotes stable and high levels of activity on the subsequent training day. On the training day, each animal was placed in the start box and allowed to traverse the maze until it reached the goal box and consumed the single food pellet present in the cup. Upon consuming the food, the animal was returned to its home cage for a 20 min intertrial interval (intertrial interval, ITI), during which the apparatus was cleaned. After the ITI, the mouse was returned to the start box to begin the next trial, and the sequence was repeated for five trials. Both the latency and errors (i.e., a turn in an incorrect direction, including those which result in path retracing) to enter the goal box were recorded on each trial.

Spatial water maze. Animals were immersed in a round pool of opaque water from which they were able to escape onto a hidden (i.e., submerged) platform. The latency for animals to find the platform decreased across successive trials. In this task, performance of animals can improve across trials despite the animals beginning each trial from a new start location. Such a procedure mitigates egocentric navigation and promotes the animals' dependence on extramaze spatial landmarks. Typically, rodents' performance in the water maze does not rely on fixed motor patterns (i.e., performance improves despite the animal's irregular starting location) or the presence of discernable cues within the maze (e.g., visual, tactile, or olfactory signals). Instead, performance is dependent on the stability of extramaze cues, or "landmarks," and is said to reflect the animals' representation of its environment as a "cognitive map."

We employ a protocol in which mice exhibit significant reductions in their latency to locate the escape platform within 5–10 training trials. To support rapid acquisition, animals were confined in a clear Plexiglas cylinder on the safe platform for 6 min on the day prior to training. Second, a considerably longer ITI (10 min) was used than is typical (cf., 90 sec). Lastly, the maze, surround, and water were black and visual cues were constructed of patterns of lights.

A round black pool (140 cm diameter, 56 cm deep) was filled to within 24 cm of the top with water made opaque by the addition of nontoxic, water soluble, black paint. A hidden 11 cm diameter black platform was in a fixed location 1.5 cm below the surface of the water midway between the center and perimeter of the pool. The pool was enclosed in a ceiling-high black curtain on which five different shapes (landmark cues) were variously positioned at heights (relative to water surface) ranging from 24–150 cm. Four of these shapes were constructed of strings of white LEDs (spaced at 2.5 cm intervals) and included an "X" (66 cm arms crossing at angles 40° from the pool surface), a vertical "spiral" (80 cm long, 7 cm diameter, 11 cm revolutions), a vertical line (31 cm) and a horizontal line (31 cm). The fifth cue was constructed of two adjacent 7 W light bulbs (each 4 cm diameter). A video camera was mounted 180 cm above the center of the water surface. These cues provided the only illumination of the maze, totaling 172 Lux at the water surface.

On the day prior to training, each animal was confined to the escape platform for 360 sec.

Training was conducted on the two subsequent days. On Day 1 of training, animals were started from one of three unique locations on each of six trials. (The pool was conceptually divided into four quadrants, and one starting point was located in each of the three quadrants that did not contain the escape platform. The starting point on each trial alternated between the three available quadrants.) An animal was judged to have escaped from the water (i.e., located the platform) at the moment at which four paws were situated on the platform, provided that the animal remained on the platform for at least 5 sec. Each animal was left on the platform for a total of 20 sec, after which the trial was terminated. Trials were spaced at 10 min intervals, during which time the animals were held in their home cages. On each trial, a 90 sec limit on swimming was imposed, at which time any animal that had not located the escape platform was placed by the experimenter onto the platform, where it remained for 20 sec.

Animals were observed from a remote (outside of the pool's enclosure) video monitor, and animals' performance was recorded on video tape for subsequent analysis. Day 2 of training proceeded as did Day 1, albeit with only four trials. After the last training trial, a 90 min retention period began, after which animals were tested with a "probe" trial. On the probe test, the escape platform was removed from the pool, and all animals were started from the first position for that day. A 90 sec test was conducted in which the animals' time searching in the target quadrant (where the escape platform was previously located) and nontarget quadrants were recorded.

One-trial passive avoidance. Animals learn to suppress movement to avoid contact with aversive stimuli. This "passive avoidance" response is exemplified in step-down avoidance procedures, where an animal is placed on a platform, whereupon stepping off of the platform it encounters a footshock. Following just a single encounter with shock, animals are subsequently reluctant to step off of the safe platform. The animals' reluctance to leave the platform is believed to *not* reflect fear, because typical fear responses are not expressed in animals engaged in the avoidance response. Upon stepping off the platform, animals here were exposed to a compound of bright light and loud oscillating noise rather than shock, so as not to duplicate stimuli between tasks (see fear conditioning, below). Like more common procedures, our variant of this task supports learning after only a single trial (i.e., subsequent step-down latencies are markedly increased).

A chamber illuminated by dim (50 Lux) red light was used for training and testing. Animals were confined to circular ("safe") chamber (10 cm diameter, 8 cm high). The walls and floor of this chamber were white, and the ceiling was translucent orange. The floor was comprised of plastic rods (2 mm diameter) arranged to form a pattern of 1 cm square grids. A clear exit door (3 CM square) was flush with the floor of the safe compartment, and the door was able to slide horizontally to open or close the compartment. The bottom of the exit door was located 4 cm above the floor of a second circular chamber (20 cm diameter, 12 cm high). This "unsafe" chamber had a clear ceiling and a floor comprised of 4 mm wide aluminum planks that formed a pattern of 1.5 cm square grids oriented at a 45° angle relative to the grids in the safe compartment. When an animal stepped from the safe compartment through the exit door onto the floor of the unsafe compartment, a

compound aversive stimulus comprised of a bright (550 Lux) white light and "siren" (58 dBc above the 50 dB background, 2.4–3.7 kHz; Radio Shack sound oscillator, Model 273–057) was initiated.

Animals were placed on the platform behind the closed exit door. After 4 min of confinement, the door was retracted and the latency of the animal to leave the platform and make contact with the grid floor was recorded. Prior to training, step-down latencies typically range from 8–20 sec. Upon contact with the floor, the aversive stimulus (light, noise, and vibration) was presented for 3 sec. Upon initiation of the aversive stimulus, mice retract onto the safe chamber, at which time the platform door was closed and they were again confined for 4 min. At the end of this interval, the door was opened and the latency of the animal to exit the platform and step onto the grid floor (with no aversive stimulation) was again recorded. The ratio of posttraining to pretraining step-down latencies was calculated for each animal and served to index learning. It has previously been determined that asymptotic performance is apparent in group averages following 2–3 training trials; thus, performance after a single trial reflects, in most instances, subasymptotic learning.

Associative fear conditioning. In this task the animals received a tone (conditional stimulus, CS) paired with a mild footshock (US). Two distinct experimental chambers were used (a training context and a novel context). Each box was contained within a sound and light-attenuating chamber. The training box (16.5 × 26.5 × 20 cm) was brightly lit (50 Lux) with a clear Plexiglas front/back, and one stainless steel and one clear Plexiglas side wall. The floor was composed of a steel grid (5 mm spacing) from which a 0.6 mA constant current footshock could be delivered from a shock scrambler (Lafayette Instruments, Lafayette, IN). The novel chamber (23 × 21.5 × 19 cm) was dimly lit (4 Lux) and all of the walls and the floor were composed of clear Plexiglas. In both boxes the tone (60 dB, 2.9 kHz) was delivered by a piezoelectric buzzer (Med Associates, EV-203a).

The animals were acclimated to the training and novel contexts by placing each animal in both boxes for 20 min on the day before training. Training on the subsequent day occurred in a single 18 min session during which the animals received three tone-shock pairings after 4 min, 10 min, and 16 min. The CS presentation consisted of a pulsed (0.7 sec on, 0.3 sec off) 20 sec tone. Coincident with the offset of the tone, shock (US) was presented for 500 msec. The following day the animals were placed in the novel chamber where they received the same presentation of tones but without the shock. (As it was critical to measure performance during acquisition, tests of the tone in the novel chamber are not reported here. This test was conducted simply to maintain comparability to previous work in our laboratory.)

To quantify conditioned fear responses, the animal's behavior was videotaped and both the time spent freezing 20 sec prior to the initiation of the tone as well as freezing during the tone was determined. Freezing was defined as period of 1 sec or greater when all of the animal's paws remained anchored in-place to the grid floor and the animal's ears were retracted. Freezing responses were scored by an observer who was unaware of the animal's performance on other behavioral tests. Conditioned responses to the CS were defined as freezing during the tone presentation minus freezing prior to the tone. For purpose of ranking the animals, CS freezing during the second training trial was used.

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Odor guided discrimination. Rodents rapidly learn to use odors to guide appetitively reinforced behaviors. Here, mice learned to navigate a square field in which unique odor-marked (e.g., almond, lemon, mint) food cups were located in three corners. Although food was present in each cup, it was only accessible to the animals in the cup marked by mint odor. An animal was placed in the empty corner of the field, after which it explored the field and eventually retrieved the single piece of available food. On subsequent trials, the location of the food cups was changed, but the accessible food was consistently marked by the same odor, mint. On successive trials, animals required less time to retrieve the food and made fewer search errors (see below) directed at food cups in which food was not available. With this procedure, near errorless performance is typically observed within 3–4 training trials.

A black Plexiglas 60 cm square field with 30 cm high walls was located in a dimly lit (10 fc) testing room with a high ventilation rate (3 min volume exchange). Three $4 \times 4 \times 2.0$ cm (l, w, h) aluminum food cups were placed in three corners of the field. A food reinforcer (30 mg portions of chocolate flavored puffed rice) was placed in a 1.6 cm deep, 1 cm diameter depression in the center of each cup. The food in two of the cups was covered (1.0 cm below the surface of the cup) with a wire mesh so that it was not accessible to the animal, while in the third cup (the “target” cup), the food could be retrieved and consumed. A cotton-tipped laboratory swab, located between the center and rear corner of each cup, extended vertically 3 cm from the cups’ surface.

Immediately prior to each trial, fresh swabs were loaded with 25 μ l of either lemon, almond, or mint odorants (McCormick flavor extracts). The mint odor was always associated with the target food cup. It should be noted that, in pilot studies, the odor associated with food was counterbalanced across animals, and no discernible differences in performance were detected in response to the different odors. On the test day, animals received four training trials in the field with three food cups present. On each trial, an animal was placed in the empty corner of the field. On Trial 1, the reinforcing food was available to the animal in the cup marked by mint odor. The trial continued until the animal retrieved and consumed the food from the target cup, after which the animal was left in the chamber for an additional 20 sec and then returned to its home cage to begin a 6 min ITI. On Trials 2–4, the location of the food cups was rearranged, but the baited cup was consistently marked by the mint odor. Both the corner location of the mint odor and its position relative to the remaining odors were changed on each trial. On each trial, the errors committed by the mouse were recorded. An error was recorded any time an animal made contact with an incorrect cup, or its nose crossed a plane parallel to the perimeter of an incorrect cup.

Fast mapping procedure. Two weeks after the completion of the previous test, animals’ capacity for deductive reasoning was determined based on their performance in a fast mapping task (illustrated in Figure 1). On the first day of training, animals were placed in a square open field constructed of white Plexiglas ($46 \times 46 \times 13$ cm) for 15 min. Located within the field were eight uniformly distributed objects (small plastic figurines, Mattel Corp., 01-09TL) that would later be used to form paired associates. This initial exposure was intended to familiarize animals to these objects, as two of the eight objects would otherwise only be encoun-

tered on the final (critical) test trial. (This procedure would be repeated on the day prior to the critical test.)

On Day 2 of training, animals were acclimated to the training apparatus which was constructed of black Plexiglas. The training apparatus consisted of a start box measuring $20 \times 14 \times 20$ cm and a field portion. The walls (46 cm in length and 20 cm high) of the field portion radiated from the start box at an approximate 145 degree angle and were connected to the back wall of the field which was measured 60 cm in length and 20 cm high. Located within the start box was a square block of black Plexiglas measuring $7.5 \times 7.5 \times 1.5$ cm which was fastened to the base of the apparatus by Velcro. In the center of the block was a food port measuring 1.5 cm in diameter and 1 cm in depth. This served as the reinforcer (45 mg BioServ dustless precision pellets) location. Three identical blocks were also placed in the field portion of the apparatus. An inaccessible food port (to which a food reinforcer was loaded in all cups) measuring 1 cm in diameter was drilled into the side of each food cup. A 2 mm hole was drilled directly into the center of the inaccessible food port until it protruded into the accessible food port. Food placed in the port served as an odor stimulus to ensure that the smell of food in the target cup could not differentially guide the animal’s behavior during training or testing. During this acclimation phase all of the possible food locations (a total of four locations) were baited. Initially the animals were confined to the start box for a period of five minutes. After this time period had elapsed the clear Plexiglas door (separating the start box from the field) was removed allowing the animal to venture into the field portion of the apparatus where it was confined for another period of 5 min.

On Day 3, the training process was begun. The animals were trained in two distinct phases. During the first phase, animals were placed in the start location with a sample object (chosen from the eight figures that the animals were exposed to on Day 1) that had a reinforcer located in a recessed cup beneath it. Once the animal retrieved the reinforcer, the door was opened and the animal was allowed to venture into the field portion where only the sample object’s paired associate (target object) was located. Under this target object was a second reinforcer. Training using this same procedure was continued (with a 6 min intertrial interval) for the two additional paired associates. This procedure was repeated for 4 days (a total of eight exposures to each of the three stimulus pairs), with the order of exposure to each pair randomly determined on each day. After paired associate training (Phase 1) was complete, Phase 2 of training began on the subsequent day, at which time animals were exposed to an object from one pair (the sample) and were allowed to collect food from under its paired associate (the target). However, on these trials the target object was placed in a field containing two distracter objects (objects that had previously been paired with a different sample object). Six such training trials were conducted per day such that each pair of objects was encountered two times each day. This phase of training spanned 8 days (a total of 16 additional exposures to each stimulus pair), at the end of which all animals performed near errorlessly, choosing the correct target on at least five of the last six trials.

One day after the completion of Phase 2 paired-associate training, the animals were again placed in the open field (as described above) with the six paired-associate objects and two novel objects (previously encountered only in the open field) uniformly distributed throughout the field. Again, this was intended to moderate

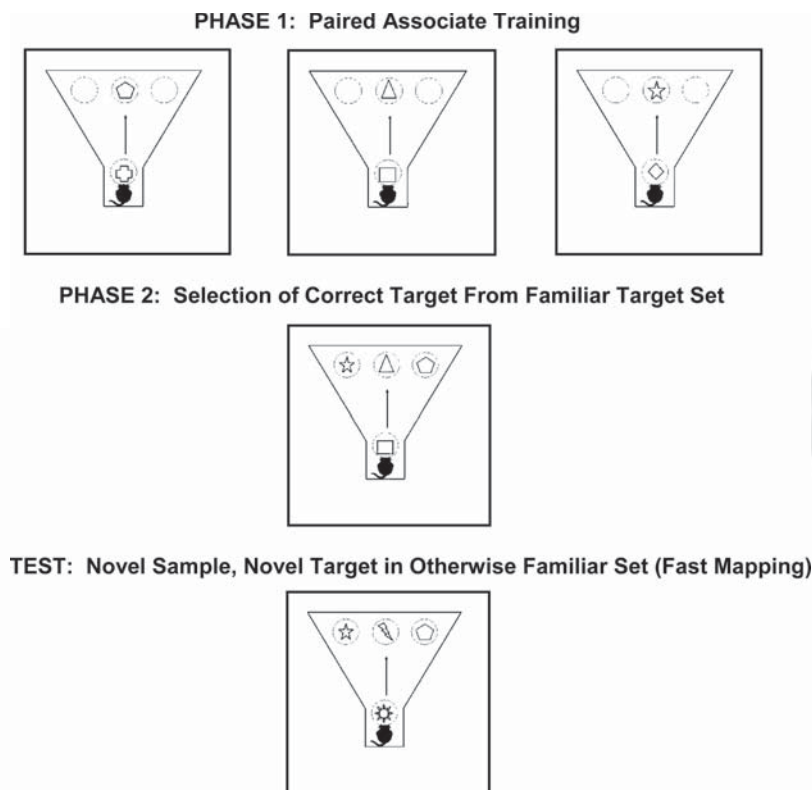


Figure 1. An illustration of the procedure for the “fast mapping” task. During Phase 1, animals were taught to associate pairs of objects (“paired associates”). In Phase 2, animals were allowed to find the relevant paired associate within a field that contained several objects, all of which had previously undergone paired associate training. In Phase 3, a “fast mapping” test was administered. On this test trial, animals were exposed to a novel sample object, and then allowed to explore the test field which contained a set of familiar objects (ones that had an established meaning based on prior paired-associate training) and one novel object. (Note: For simplicity, the directional arrows illustrated above all point to a correct target object located in the center position of the test field. During actual trials, the location of the correct target was randomly determined).

any differential responding to the two novel objects that animals would encounter on the critical fast mapping test trial. On the subsequent day, animals received a single test trial to assess their capacity for fast mapping. A fast mapping test trial consisted of exposure to a novel (previously unencountered) sample object and a novel target object placed within a field of three objects, two of which were previous paired associates (i.e., which had acquired specific meaning). After exposure to the novel sample and retrieval of the reinforcer located beneath it, the animals were allowed to explore the field of three objects (two previously trained on one novel to the test context). Target choices were then recorded until the piece of food located under the novel object was collected.

Results and Discussion

Here, we assessed 41 genetically heterogeneous CD-1 mice on a battery of five learning tasks (i.e., Lashley III maze, passive avoidance, odor guided discrimination, Morris water maze, and associative fear conditioning) designed to tax different sensory/motor, and information processing systems. These tasks placed unique sensory, motor, motivational, and information processing demands on the animals, thereby maximizing the likelihood that

the underlying influence across all tasks was domain-independent (i.e., “general”).

The performance of individual animals across all learning tasks was first analyzed with a principal component analysis. This is a variable reduction procedure that uses an orthogonal transformation to convert a set of independent observations (potentially correlated variables) into a set of uncorrelated variables (i.e., principal components). The goal of this analysis is to provide a reasonable characterization of the complete data set by reducing a correlation matrix to the fewest number of factors that can describe the pattern of correlations. The principal factor is that factor which can explain the largest amount of variance. Previous work has indicated that as much as 28–48% of the variance in performance across the five learning tasks reported here can be accounted for by a single factor (see Kolata et al., 2008, for a complete description). In the present study, a principle component factor analysis of animals’ performance on the five learning tasks (see Table 1) indicated that performance on all tasks were influenced by a single source of variance. That factor (eigenvalue of 1.72) accounted for 29% of the variance in the performance across all of the learning tasks. From that analysis, a general learning factor score was

Table 1
Factor Loadings From The Principal Components Analysis (n = 41) For Animals' Performance On The Five Learning Tasks In Experiment 1A

	General learning factor
Lashley III Maze	-.60
Fear Conditioning	-.52
Passive Avoidance	-.72
Odor Discrimination	-.61
Morris Water Maze	-.40
eigenvalue	1.72
% variance	.29

calculated for each of the animals. A factor score is analogous to an average *z* score of an animal's performance on the five learning tasks, with each score weighted according to the individual tasks loading on the primary (general learning) factor. Thus, an animal's factor score is a quantification of that animal's position in the distribution of general learning abilities.

In subsequent analyses, animals would be compared based on their aggregate performance across all learning tasks. This was accomplished by separating animals into groups comprised of high, intermediate, and low factor scores (based on the principal components analysis presented above). That is, the factor scores (of each individual) were ranked, and the top, middle, and bottom thirds of these ranked scores were used to construct groups of animals representing high, intermediate, and low general learning abilities. Figure 2 presents the learning performance on each learning task of animals characterized as having high or low general learning abilities. As is evident from this figure, animals so classified are clearly distinguishable, not only according to their aggregate performance, but also on individual learning tasks.

After completion of the learning battery, animals began training on a task intended to assess fast mapping. Animals were first required to learn associations between three pairs of objects (small plastic figurines) in order to obtain a food reward, and their capacity for fast mapping was then evaluated. A fast mapping test trial consisted of exposure to a novel (previously untrained) sample object and a novel (previously untrained) target object that was located in a field of three objects (where the remaining two objects were previously paired associates). Target choices were then recorded until the reinforcer located beneath the novel object was collected. If animals were employing inferential exclusion, they should make the inference that since the sample object located in the start box was novel, they should direct their choice toward the novel object in the test field. The number of errors (incorrect target choices) that the animals made was recorded and compared to their factor scores (their aggregate performance in the learning battery, where *lower* scores = higher aggregate learning performance) which revealed a significant correlation, $r(39) = .44, p < .01$, indicating that animals with higher aggregate learning abilities also made fewer fast mapping errors. This correlation was reflected in marked differences in performance across animals of high, intermediate, and low general learning abilities (see Figure 3). A comparison of the fast mapping errors of these three groups using a one way ANOVA revealed a main effect of group (i.e., learning ability), $F(2, 38) = 5.53, p = .008$. An LSD post hoc analysis

revealed a significant difference between the best and the worst learners, $p < .002$. No other comparison was significant, although a trend toward a difference was observed when the intermediate learners were compared to the animals of low learning abilities, $p < .09$.

It is important to note that across the entire sample of 41 animals, 22 animals made *no* fast mapping errors, and on average, animals made only .4 errors. This number of errors is far below that which would occur by chance (where one [or potentially more if errors were repeated] errors would be expected in a random search), $\chi^2(41, 2) = 22.87, p < .0001$, indicating that rodents are indeed capable of nominal deductive reasoning as represented by performance on a fast-mapping task.

One might interpret the results of this experiment as the consequence of the animals simply approaching the novel object in the field rather than deducing that the novel target object was the correct choice in response to the novel sample object. However, it should be reiterated that prior to and again at the completion of paired-associate training, animals were exposed equally to *all* sample and test objects to mitigate this potential influence. Nevertheless, the "novel" test object was designated as novel based on its having undergone no prior paired associate training, and as such, was *less* familiar to the animals than were the two distractor objects (that *had* undergone previous paired associate training). A more complete test of the possibility that the relative novelty of the test object, as opposed to fast mapping, could account for the results presented here is provided in Experiment 1B.

Experiment 1B

With a task that was procedurally and conceptually analogous to fast mapping, in Experiment 1A, we ostensibly demonstrated that mice were capable of making choices based on inferential exclusion. Furthermore, performance on the fast-mapping task was significantly correlated with animals' aggregate performance in battery of learning tests, suggesting that nominal reasoning and general learning abilities were jointly regulated. However, on the critical fast mapping test trial, a correct choice was indicated by an animal approaching a test stimulus (in response to a novel sample) that was less familiar than the comparison objects (that had undergone paired-associate training). A correct choice was presumed to reflect the animal's decision that in a field of familiar objects, the novel sample must be associated with the more novel test object. In that task, animals had been preexposed (in a nontest environment) to all stimuli so as to reduce the nominal novelty of the sample and test stimuli at the time of test. Nevertheless, at the time of the critical test, the novel test stimulus was *less* familiar to the animals than were the previously trained stimuli, raising the possibility that animals were simply attracted to the more novel stimulus, rather than selecting that object through the process of inferential exclusion. Given that the animals were food deprived and the familiar objects in the test field were previously paired with food, this seemed an unlikely explanation for the animals' performance. Nevertheless, based on the procedure in Experiment 1A, this possibility cannot be excluded.

In order to ascertain whether the subjects' performance on the fast mapping test in Experiment 1A was influenced by a propensity for novelty seeking, in Experiment 1B we implemented a relevant control procedure into the fast mapping task. Using a group of

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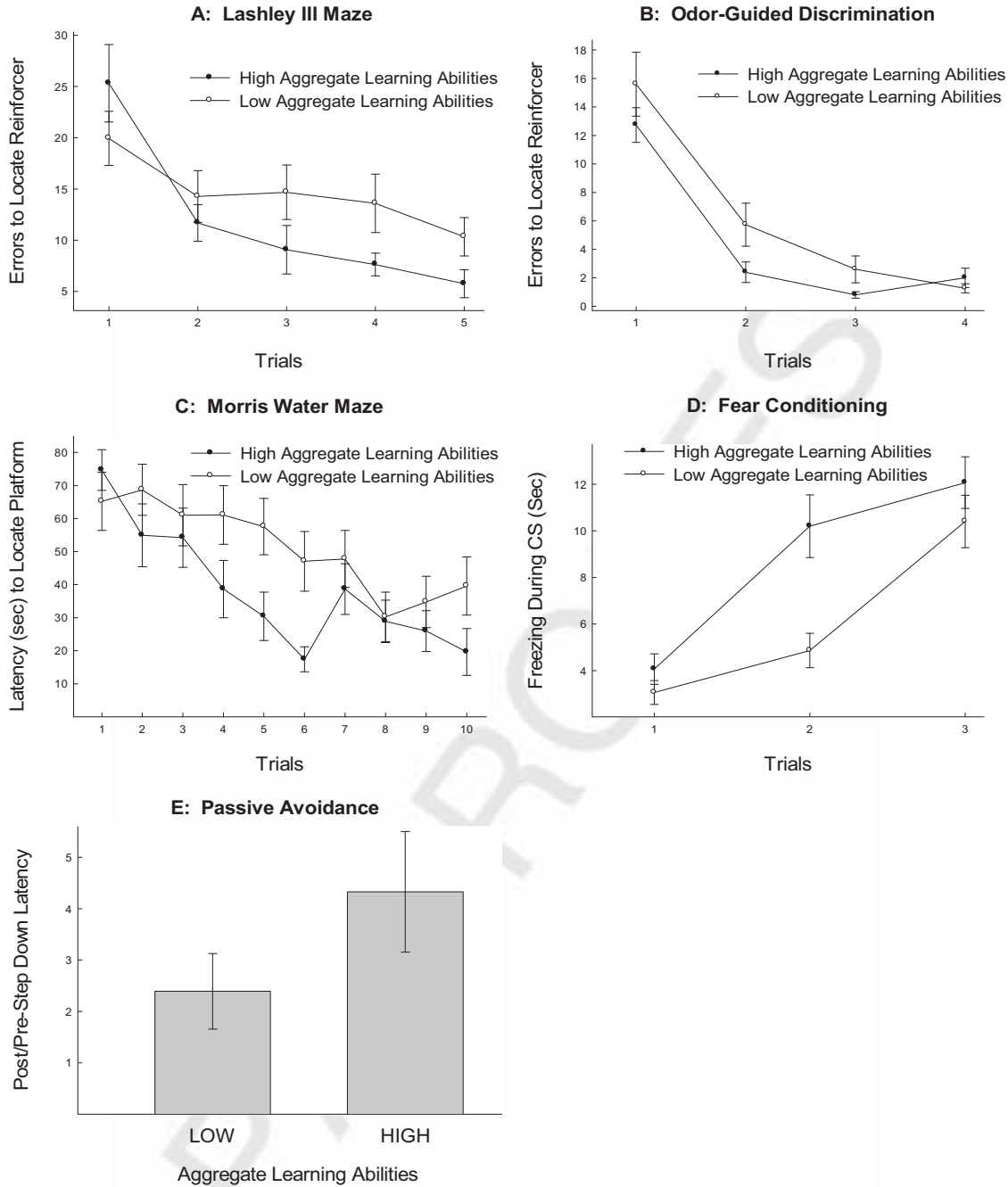


Figure 2. Performance on individual tasks of animals of highest and lowest general cognitive abilities. General learning abilities were determined by factor scores (of individual animals) derived from a principal component analysis of the acquisition data from all five learning tasks. Illustrated is the mean performance of animals of high and low general learning abilities (for clarity, animals of intermediate abilities are not illustrated.) Animals with high general learning abilities outperformed animals of low general learning abilities in each of the five individual tasks (Lashley Maze [A], odor-guided discrimination [B], Morris Water Maze [C], fear conditioning [D], and passive avoidance [E]). Brackets indicate standard error of the mean.

experimentally naïve animals, this experiment followed the general procedure of Experiment 1. However, at the time of testing, our sample of mice was divided into two groups (with statistically equal general learning abilities). One group received a standard

fast-mapping test trial, where a novel sample stimulus was followed by the subjects' choice among a field of two familiar objects (previously paired associates) and one novel object. On this test trial, a second group was exposed to a *familiar* sample, two

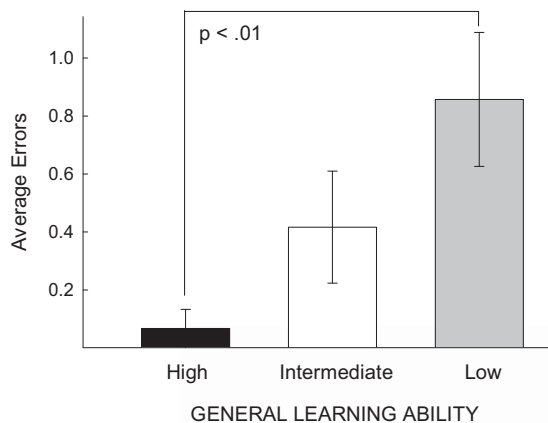


Figure 3. Fast mapping test performance, Experiment 1A. Three groups of animals were formed based on the upper, middle, and bottom third of factor scores (reflective of general learning performance) obtained from the principal component analysis of learning test performance in Experiment 1A. Plotted is average number of errors (\pm standard error) on the fast mapping test trial of the animals that performed best (High), intermediate, and worst (Low) on the battery of learning tasks. For this task, one error (on average) would be expected in a random search (assuming that repeated errors were not committed, in which case, the number of errors could increase).

familiar choice objects (one of which was the correct paired associate), and one novel object. If the choice of the novel object was directed by the animals' propensity to choose novelty, both of the groups in this experiment should choose the novel object on this test trial. However, if animals' performance was guided by inferential exclusion, only animals administered the standard fast-mapping test should choose the novel object. In addition to an assessment of novelty-seeking as an explanation of animals' fast mapping performance, Experiment 1B also served to assess the reliability of the results described in Experiment 1A.

Method

Subjects. A new sample of 25, experimentally naïve genetically heterogeneous male CD-1 outbred mice were obtained from Harlan Laboratories (Indianapolis, IN) at 45 days of age. Housing and maintenance conditions were identical to Experiment 1A.

Learning battery. Animals were first assessed in the learning battery as described in Experiment 1A. Testing in the learning battery provided a second opportunity to assess the relationship between fast mapping performance and general learning abilities. Furthermore, having characterized each animal's aggregate learning performance, we were able to assign an equal distribution of learning abilities to both of the groups represented in this experiment.

Fast mapping. Two weeks after the completion of the learning battery, the initial group of 25 animals was separated into two groups which will be referred to as "Group FM" (Fast Mapping) and "Group NS" (Novelty Seeking). Group FM ($n = 13$) animals would undergo the fast mapping training and testing as described in Experiment 1A. Group NS ($n = 12$) would undergo a near identical training and testing procedure with one critical difference intended to ascertain whether Group FM's performance was due to

their propensity for novelty seeking or if these animals' performance was indicative of fast mapping. Specifically, on the critical test trial Group NS would be exposed to a familiar sample, followed by a choice from among three test objects that included the correct paired associate, an incorrect paired associate, and a novel object.

On the first day of training, all 25 animals were placed in a square open field constructed of white Plexiglas ($46 \times 46 \times 13$ cm) for 15 min. For Group FM, there were eight uniformly distributed objects (small plastic figurines, Mattel Corp., 01-09TL) located within the field, of which six would later be used to form paired associates. The remaining two objects would later be used as the critical (novel) sample and test objects. In contrast, the test objects were absent for Group NS so that the remaining objects in the field would be the six objects that would later form paired associates. This initial exposure was intended to familiarize both the experimental and control groups to the objects that would later constitute paired associates. By not exposing Group NS to the two test objects, it insured that those objects would be entirely novel at the time of testing (so as to maximize any influence of novelty seeking).

On Day 2 of training, all 25 animals were acclimated to the training apparatus (which was identical to the one used in Experiment 1A). Animals then underwent paired-associate training as in Experiment 1A, and on the day following completion of this training, the animals were again placed in the open field (as described above). Group NS was only exposed to the six paired-associate objects and Group FM was exposed to those six objects as well as the two that would comprise the sample and test stimuli on the critical test trial.

On the subsequent day, Group FM received a single test trial to assess their capacity for fast mapping. The fast mapping test trial consisted of exposure to a novel (previously unencountered in paired-associate training) sample object and a novel target object placed within a field of three objects, two of which were previous paired associates. After exposure to the novel sample and retrieval of the reinforcer located beneath it, the animals were allowed to explore the field of three objects (two previously trained and one novel to the test context). Target choices were then recorded until the piece of food located under the novel object was collected. For Group NS, a previously reinforced sample object was placed in the start box and its paired associate was located within the field with two distracter objects (a total of three objects). One of the distracter objects was an incorrect paired associate whereas the second object was a novel object to which the animal had not previously been exposed. Target choices were recorded until the animal chose the correct paired associate.

Results and Discussion

A principal component analysis of the 25 animals' performance on the five learning tasks indicated that performance on all of the tasks was influenced by a single source of variance (see Table 2). That factor accounted for 32% (eigenvalue 1.9) of the variance in the animals' performance across all learning tasks. From that factor analysis we were able to derive factor scores (as described above) for each individual animal. Those factor scores (which ranged from:

Table 2
Factor Loadings From The Principal Components Analysis (n = 25) For Animals' Performance On The Five Learning Tasks In Experiment 1B

	General learning factor
Lashley III Maze	-.62
Fear Conditioning	-.76
Passive Avoidance	-.51
Odor Discrimination	-.32
Morris Water Maze	-.55
eigenvalue	1.9
% variance	.32

-2.39 to 1.83, where lower values indicate *better* aggregate learning performance) were then used to divide the subjects into two groups (Groups FM and NS) of roughly equal general learning abilities (with an equal representation of animals of high, intermediate, and low general learning abilities). Following their assignment to groups, the mean factor score of these two groups was .034 and .048 (Groups FM and SM, respectively) and the groups did not differ statistically, $t(23) = .03$.

If animals' propensity for novelty seeking determined their performance on the putative fast mapping test trial, then Group NS would be expected to choose the novel object in the test field despite the presence of a familiar sample and test stimulus (the correct paired associate) on the critical test trial. However, 10 out of the 12 animals in Group NS made no errors, choosing the correct paired associate test object on their first choice. Of the two subjects that did make an error, they incorrectly chose the distracter paired associate object, not the novel test object, and then proceeded to the correct paired associate. Of the 12 animals, 0/12 chose the novel test stimulus on either their first or second choice. This number of choices of the novel stimulus is below that which would occur through even a random search, $\chi^2(2) = 14, p < .001$, indicating that the animals are utilizing a process that was independent of novelty seeking to guide their behavior.

Unlike Group NS, Group FM was presented with both a novel sample object and a novel test object among a field containing two familiar objects (with a history of paired associate training). Inference by exclusion would dictate that under these circumstances, animals would be disposed to choose the novel test stimulus. In this instance, six of 13 animals chose the novel test stimulus on their first choice, but given the relatively small sample size, this pattern was not significantly different than chance. However, an inspection of the subgroup of these animals with the highest general learning scores ($n = 8$) revealed that these animals performed well above chance levels, choosing the correct (novel) test object on six out of eight first choices (from the set of three possible choices), $\chi^2(2) = 6.24, p < .05$. This pattern, like that described in Experiment 1, indicates a capacity of these animals for inference by exclusion. In addition, this result indicates the importance of considering the performance of individual animals when assessing animals' capacity to perform on a task that is at the upper limits of their cognitive abilities.

Having demonstrated that animals' fast mapping performance was not related to their propensity for novelty seeking, a subsequent analysis of Group FM's performance (errors) in the fast

mapping task was compared to their aggregate performance across all learning tasks (i.e., their factor scores). That comparison revealed a significant correlation, $r(11) = .67, p < .02$, which indicates that animals with higher general learning abilities made fewer fast mapping errors. A further analysis examining the top third of the distribution (animals with high GLA scores), the middle third (intermediate GLA scores) and bottom third (animals with low GLA scores) of the distribution using a one way ANOVA revealed a main effect of group $F(2, 9) = 5.39, p < .03$. An LSD post hoc analysis revealed a significant difference between animals of high general learning abilities and low general learning abilities, $p < .01$. No other comparisons were significant, but a trend toward a significance was observed when animals of intermediate learning abilities and low learning abilities were compared, $p < .056$. These results are illustrated in Figure 4.

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Experiment 2

It was established in Experiment 1A and 1B that the general learning ability of mice was correlated with their performance on a nominal deductive reasoning (fast mapping) task. The aim of Experiment 2 was to assess whether animals' general learning and inductive reasoning abilities were also coregulated. For this purpose, animals that had been characterized for general learning performance in Experiment 1A were used here (so as to compare these abilities within a single group of animals). After the completion of Experiment 1A, the animals that participated in that experiment were assessed on a task which could be most efficiently performed through the application of inductive reasoning. To assess inductive reasoning abilities, we developed a task in

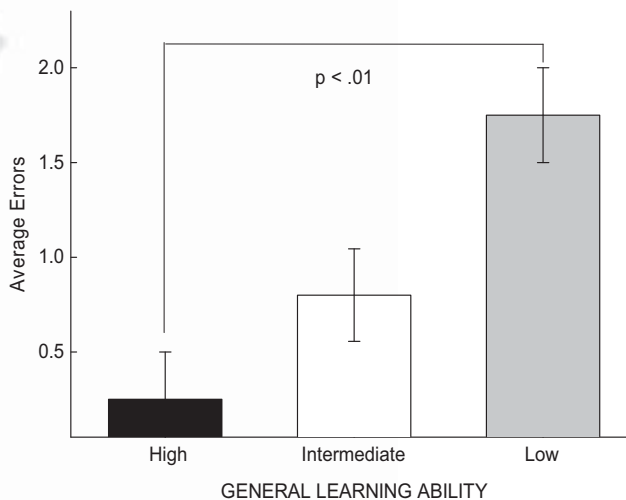


Figure 4. *Fast mapping test performance, Experiment 1B.* Three groups of animals were formed based on the upper, middle, and bottom third of factor scores (reflective of general learning performance) obtained from the principal component analysis of learning test performance in Experiment 1B. Plotted is average number of errors (\pm standard error) on the fast mapping test trial of the animals that performed best (High), intermediate, and worst (Low) on the battery of learning tasks. For this task, one error (on average) would be expected in a random search (assuming that repeated errors were not committed, in which case, the number of errors could increase).

F5 which animals could discern an efficient search strategy based on their experience with the overall structure of a “decision-tree” (or binary) maze (graphically represented in Figure 5). Binary trees are used in operations research to identify strategies that are most efficient in reaching a goal. (A colloquial version of the decision tree is exemplified by the process utilized to identify an object in the game of “20 Questions.”) Of note, this task is not simply a maze-learning task, such as the Lashley III Maze used in the learning battery. In a typical egocentric maze (like the Lashley Maze), the food is consistently located in a goal box and the animals learn that one path is most efficient in reaching that goal. Once learned, execution of a route does not involve active searching. By comparison, in this binary tree maze, both the location and amount of food is randomly distributed throughout the maze at various choice points, and there are many possible routes (of varying degrees of efficiency) with which to explore the maze to find the available food. Thus, by design, the requirements of this maze promotes the implementation of a search strategy. It is the efficacy of that strategy that will serve as our index of inductive reasoning.

AQ: 10

Method

Subjects. The 47 animals that served in Experiment 1A were used here. Housing and maintenance conditions were as described above.

Decision tree maze. Two weeks following the completion of Experiment 1A, animals began training in the decision tree. As depicted in Figure 5, the maze walls, floor, and doors were

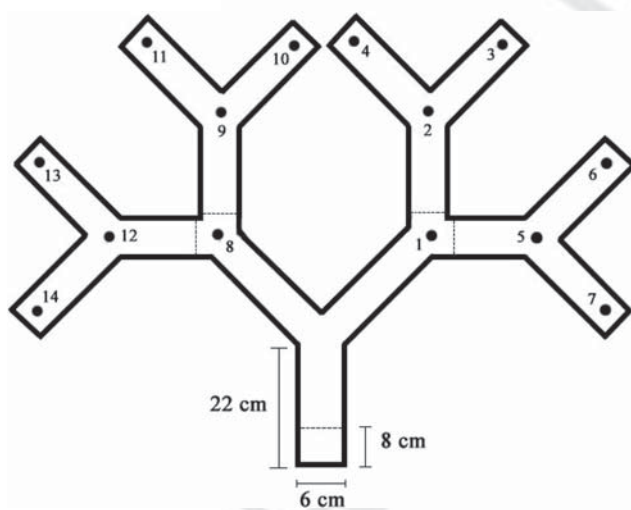


Figure 5. Illustration of the binary decision maze. Here, the animals’ task was to navigate the maze so as to inspect every potential node (labeled 1–14) for a payoff (a piece of food recessed in the floor). At the beginning of each trial, food was randomly placed in 4–8 locations. Since the animal could not know the location of food or the number of goal locations that were actually baited, an efficient search would inspect all nodes with minimal duplication of effort. Using an optimal search strategy, the animal would pass a maximum of 24 nodes (as would be required were the animal to search, without unnecessary duplication, every node in one half of the maze, exit that side of the maze, then search every node in the other half of the maze).

constructed of black Plexiglas, and a transparent sheet of Plexiglas covered the top of the maze. The maze consisted of a start box and a series of bifurcating arms. The maze bifurcated along each branch at seven symmetrically arranged locations and terminated in dead ends (“leaves”). Other than at the first bifurcation (which divided the maze into two symmetric halves), each bifurcation and each leaf constituted a “node” at which a reinforcer (20 mg BioServe chocolate flavored pellet) could be hidden in a recessed cup in the floor.

The apparatus consisted of a start box ($8 \times 6 \times 7$ cm) located at the base of the decision tree which was separated from the maze by a removable door (represented by a dashed line in Figure 5). Extending from the start box was the first alley of the decision tree which, like all other alleys, measured $22 \times 6 \times 7$ cm. At the end of the first alley was the first bifurcation point in which there was no food port located. The locations of the food cups are depicted in Figure 5 as dots located at each bifurcation point (except the initial bifurcation point) as well as at the end of each leaf. The food cups were recessed holes in the base of the maze. If baited with a reinforcer, the reinforcer would be below the level of the floor ensuring that the animal was unable to see the reinforcer as it approached the port. Each food port measure 1 cm in diameter and 1.5 cm in depth. A 2 mm hole was drilled directly into the center of each cup which protruded through the base of the maze. This hole served as an odor port for inaccessible food reinforcers (80 mg) that were placed beneath each food cup (to provide a uniform distribution of olfactory cues).

Forty-eight hours prior to the acclimation day the animals were food deprived and allowed 90 min of free access to food toward the end of their light cycle. Also, on the day prior to acclimation, the animals were given three reinforcers to familiarize them with the novel reinforcers to be used in the binary maze. On the acclimation day the animals were confined to the start box for a period of 30 sec. After 30 sec, the removable door separating the start box from the first alley was removed, allowing the animal to enter the maze. During this first exposure to the maze, all 14 nodes were baited. The animal was allowed 20 min to freely navigate the maze and find all possible reinforcers before being brought back to the vivarium.

On 10 subsequent testing days (i.e., trials), as few as four and as many as eight nodes were randomly baited, with a minimum of two baited nodes on each half of the maze (all animals received the same baited nodes). Since the actual location and number of baited nodes varied randomly across trials, it was advantageous to the animals to adopt a strategy for inspecting all nodes with equal likelihood. On these critical test days, the animal was once again confined to the start box for 30 seconds, released, and allowed to explore the maze until all the reinforcers were retrieved and all nodes were crossed at least once.

To determine if the animals had implemented a flexible search strategy or were simply following a rote path, after the 10th day of testing, a new procedure was instituted. Three trials were administered (on successive days) where when an animal reached its first terminal leaf, the second level junction adjacent to the one occupied by the animal was blocked. There were four possible locations that could have potentially been blocked and these are represented as dashed lines in Figure 5. As above, animals were allowed to continue through the maze until all food had been retrieved.

To assess animal's search efficiency, "streak" lengths were recorded (i.e., the number of nodes crossed prior to an animal unnecessarily crossing a node that had already been visited) for both stages of testing (Trials 1–10 and 11–13). For the first stage of testing (Trials 1–10), a maximally efficient search would require 24 node crossings. During the second stage (Trials 11–13), an efficient search would result in 18 nodes being crossed (since one branch was rendered inaccessible to the animals).

Results and Discussion

In their initial 1–4 exposures to the decision tree maze, no systematic pattern of exploration could be detected across the group of animals or within individuals (i.e., the animals' pattern of behavior suggested a disorganized random search). However, within 4–6 trials, the patterns of individual animals stabilized and remained stable for the remaining 4 days of testing (see Figure 6). Although several animals performed at optimal efficiency during the last four trials, other animals' performance remained unsystematic. Streak lengths ranged from 4–24 (maximal efficiency) on each of the last four trials (indicative of wide variability in animals' performance).

The average streak length on the last four trials was compared to factor scores (indicative of general learning abilities) obtained from the principal component analysis of learning performance (described in Experiment 1A). These two independent measures were significantly correlated, $r(45) = -.46, p < .01$ (Figure 7A), indicating that the more efficient search (as indicated by longer streaks) was associated with better aggregate learning abilities (as indicated by lower factor scores). As evident in Figure 7B, the streak lengths differed between animals of high, intermediate, and low general learning abilities (the bottom, middle, and top third of factor scores), $F(2, 44) = 7.65, p < .001$. A LSD post hoc analysis revealed a significant difference between the streak lengths of

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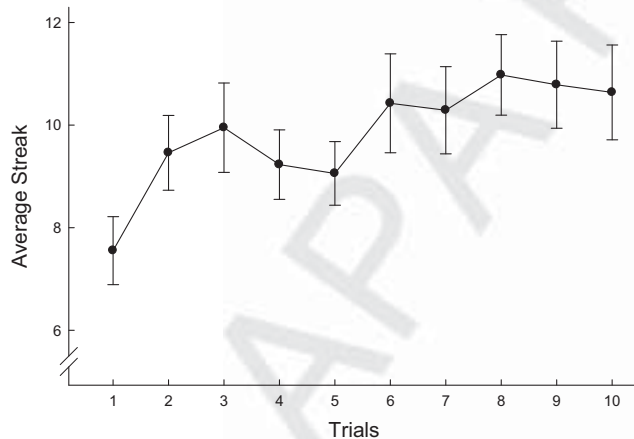


Figure 6. Performance in the binary decision tree. Plotted is the average streak length of all 47 animals tested in this maze, where a streak of 24 would reflect optimal efficiency. Animals' performance was initially erratic, but stabilized within six trials and remained stable thereafter. Although several animals performed at optimal efficiency during the last four trials, other animals exhibited unsystematic performance. Streak lengths (across animals) ranged from 4–24 on each of the last four trials. Brackets indicate standard error of the mean.

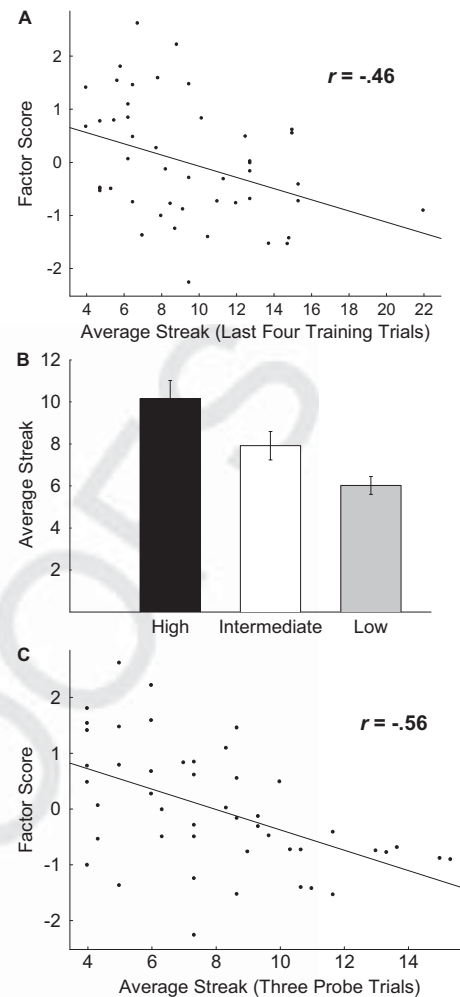


Figure 7. Individual animals' performance in the binary decision maze is predicted by their aggregate (general) learning ability. Panel A: Factor scores for each animal were derived from a principal component analysis of all animals' performance on five learning tasks. These scores reflect animals' aggregate performance across all five tasks. (Note that lower factor scores = better aggregate learning performance.) A significant correlation was observed between animals' factor scores and the number of node crossings prior to unnecessarily crossing a node ("streak" performance) on the last four (of 10) test trials. Thus, the efficacy of an animal's search (a form of inductive reasoning) was predicted by their general learning ability. Panel B: Three groups of animals were formed based on the upper, middle, and bottom third of factor scores (reflective of general learning performance). The average streak length (indicative of search efficacy) differed across these three groups. Plotted is the animals that performed best (High), intermediate, and worst (Low) on the battery of learning tasks. Brackets indicate standard errors. Panel C: After an animal reached its first low-level terminal node, the adjacent entry point was blocked with a sliding door. This was intended to disrupt any rote path (i.e., algorithmic strategy) that an animal may have developed in lieu of comprehension of the overall structure of the maze. Plotted is the average streak during three such probe trials against factor scores obtained from the principal component analysis of learning performance. (Note that lower factor scores = better aggregate learning performance.) Again, a significant correlation between general learning abilities and search efficacy was observed.

animals of low general learning abilities and animals of either intermediate or high abilities, $p < .01$. No difference in streak length was observed between animals of high and intermediate learning abilities.

Following the initial 10 trials, we determined if animals were relying on rote paths through the maze or whether they were engaging in an active search of the maze (a requisite for inductive reasoning). To make this determination, each animal was allowed to begin its exploration of the maze, and upon making its first entry into a second level branch, the adjacent branch was blocked by lowering a black guillotine door. Had an animal been following a rote (but nominally efficient) path through the maze, this manipulation would have disrupted the utilization of that rote path. Animals' streak lengths under these conditions were assessed on three trials. Despite the imposed disruption of the path, the correlation between the animals' average streak and factor scores (aggregate learning performance) was still strong, $r(45) = -.56$, $p < .01$ (Figure 7C). The average streak lengths for these three trials differed between animals of high, intermediate, and low general learning abilities, $F(2, 44) = 9.44$, $p < .001$ (means \pm sem = 10.2 ± 0.86 , 7.9 ± 0.68 , and $6.0 \pm .42$, respectively, where a perfect streak = 18). LSD post hoc analysis revealed a significant difference between animals of high and intermediate abilities, $p < .02$, as well as between animals of high and low abilities, $p < .001$. Lastly, a significant difference between animals of intermediate and low abilities was observed, $p < .05$.

The degree to which an animal can devise an efficient strategy to search a maze in which the location and number of reinforcers continuously changes is at least nominally indicative of inductive reasoning. While numerous search strategies may be utilized to navigate this maze, one search strategy in particular, the depth-first search, would be the most efficient. Other search strategies such as the breadth-first search or random searching would be relatively inefficient strategies owing to their necessitating unnecessary node crossings. It should be noted that performance in this task should not be considered to be exclusively an expression of a learned route, as of the various number of routes that could be learned, no single route is most efficacious, and furthermore, would be severely disrupted by blocking the animals' path. Also, throughout this task the number of reinforcers available as well as the locations of the reinforcers varied each day, ensuring that the animal wasn't learning fixed reinforcer locations. These manipulations, therefore, tested an animal's ability to implement an efficient search strategy in an environment that was explicitly unstable.

We have suggested that a more intelligent animal would be able to form a more complete representation of the structure and requirements of the maze, and would thereby implement a more efficient search strategy. It should also be noted that other factors such as the efficacy of an animal's working memory may have influenced their performance in this task. Working memory specifically has been shown to correlate with general learning abilities in mice as well as in humans (Buehner, Krumm, & Pick, 2005; Engle et al., 1995; Kolata et al., 2005, 2008; Light et al., 2010; Sub, Oberauer, Wittman, Wilhelm, & Schulze, 2002). However, the implementation of an efficient search strategy in this task would minimize any reliance on working memory. It is also recognized that performance in this maze would be described in other contexts as a form of "foraging" (for review, see Rashotte, O'Connell, & Djuric, 1985). Thus, an animal's reasoning abilities

may directly relate to the animal's performance in a foraging task and have obvious and direct implications for survival in more ethologically relevant environments.

Upon completion of Experiment 2, an additional principal component analysis was conducted that included the learning data reported in Experiment 1A, fast mapping performance from Experiment 1A, and decision tree performance from Experiment 2. (Data from Experiment 1B was not included in this analysis as it was obtained from a separate sample of animals that were not assessed in the decision tree maze.) Only animals ($n = 41$) that contributed to both the fast mapping task (Experiment 1A) and the decision tree task (Experiment 2) were included in this analysis. A single factor accounted for 27% (eigen value = 1.92) of the variance across all performance measures, and performance on both the decision tree and fast mapping tasks loaded moderately and in the same direction as performance on all of the learning tasks (see Table 3). This analysis suggests that a single underlying source of variance influences performance on all of these diverse cognitive tasks.

General Discussion

Over a century ago, Spearman reported the existence of a general intelligence factor in humans (Spearman, 1904). The concept of general intelligence has facilitated studies of individual differences in the expression of this ubiquitous cognitive trait (Jensen, 1998). Recent work with nonhuman animals has implicated the existence of a general learning ability in genetically heterogeneous mice, as well as individual variations in this trait (Galsworthy et al., 2002; Kolata, Light, Grossman, Hale, & Matzel, 2007; Kolata et al., 2005; Locurto et al., 2003; Matzel et al., 2006). Although it has been asserted that this general learning ability mice is psychometrically and structurally analogous to "intelligence" in humans (Kolata et al., 2008; see Blinkhorn, 2003, for commentary), it was not previously known whether general learning abilities in mice were coregulated with the animals' capacity for reasoning. Since reasoning is considered a central function of intelligent behavior, here we aimed to address this issue, using tasks based on ones that are often asserted to reflect the capacity of humans for reasoning.

Human reasoning abilities have been found to be highly predictive of a person's general intelligence. It is in this regard the

Table 3
Factor Loadings From The Principal Components Analysis (n = 41) For Performance On The Five Learning Tasks As Well As Fast Mapping Performance (Experiment 1A) and The Average Streak Length In The Decision Tree Maze (Experiment 2)

	General cognitive factor
Lashley III Maze	-.23
Fear Conditioning	-.55
Passive Avoidance	-.28
Odor Discrimination	-.8
Morris Water Maze	-.68
Decision Tree	-.49
Fast Mapping	-.31
eigenvalue	1.92
% variance	.27

Raven's Progressive Matrix (RPM) test has been asserted to be one of the purest measures of general intelligence (Babcock, 1994; Fry & Hale, 1996; Dawson, Soulieres, Gernsbacher, & Mottron, 2007; Jensen, 1998), and has largely supplanted many historically prevalent adult intelligence tests. The RPM measures one's ability to infer rules, think rationally, reason by analogy, and to organize spatial information into related wholes. Therefore, if the purest measure of human general intelligence was based on one's ability to reason, and nonhuman animals' general learning abilities were in fact indicative of intelligence, it would follow that the reasoning and general learning abilities of mice should be positively correlated.

Following Aristotle, it is often asserted that reasoning can take one of two general forms. In the first, one attempts to understand the "whole" by considering only the component parts. In the second, one attempts to characterize a class of objects by considering the common features of each object in that set. To assess reasoning in laboratory mice, we devised two novel tasks which reflect each of these forms of rational behavior. First, animals' performance was assessed on a fast mapping task. Fast mapping is a mental process whereby a new concept can be learned based on a logical inference derived from a single exposure to incomplete information. This corresponds with what is described as "deductive" reasoning, that is, an attempt to characterize a class of objects by considering the common features of each object in that set. Fast mapping is believed to play a critical role in the extraordinarily rapid and seemingly effortless acquisition of information during early human development, and explains (in part) the prodigious rate at which children gain vocabulary (Carey & Bartlett, 1978). In addition to fast mapping, animals' performance was assessed in a "decision" or binary-tree maze. Decision trees are commonly used in operations research, specifically in decision analysis, to identify strategies that are most efficient in reaching a goal. While many search strategies (or paths) could be utilized to visit every node in the decision tree, the vast majority of these paths would lead to an inefficient search, that is, one which unnecessarily retraces paths or crosses goals that had already been explored. Thus, the degree to which an animal can comprehend the whole structure of the maze and implement that information from its current location would be a reflection of a type of "inductive" reasoning.

Given the focus of the present work on what is described as the capacity for "reasoning" by mice, it should be acknowledged that more elemental psychological processes (e.g., associative learning) have been proposed to underlie other apparent instances of reasoning in nonhuman animals (Dwyer, Starns, & Honey, 2009; Haselgrove, 2010; see Shettleworth, 2010 for relevant discussion; but see Lazareva & Wasserman, 2006 for response). Similar explanations (devoid of reference to reasoning) could be applied to many instances of presumed reasoning by humans. We concede that what might nominally be described as "reasoning" may, at least in some instances, actually be the product of more elemental processes. Were this the case, the relationship between human learning abilities and intelligence (as indexed by reasoning-based psychometric tests) may reflect the correlation of two traits that are dependent on the same (or related) underlying processes (e.g., associative learning). The same may be true in the present case, where we have concluded that animals' performance (on the fast mapping and decision tree tasks) is dependent, at least in part, on forms of reasoning. In this regard, it was not our intention to argue

that performance on any particular task is exclusively indicative of the implementation of reasoning. Rather, the rationale for the present experiments was that if performance by humans on a task (e.g., fast mapping) is said to rely on reasoning, then the same description can be applied to the analogous performance of a nonhuman animal. Our goal was not to unequivocally demonstrate the capacity for reasoning in laboratory mice, but rather, to determine if performance on tasks that are attributed to reasoning (as they would be when performed by humans) are predicted by the general learning abilities of these animals.

The findings of the current study indicate that nonhuman animals are indeed capable of behaviors that are at least nominally indicative of various forms of reasoning (also see Blaisdell, Sawa, Leising, & Waldmann, 2006; Dusek & Eichenbaum, 1997; Povinelli, 2000; Pilley & Reid, 2011). More relevant to our present purpose, the efficacy with which mice performed on the two reasoning tasks reported here was directly predicted by their aggregate performance across a battery of five diverse learning tasks. These observations support the hypothesis that reasoning and general learning abilities of mice are the mutual expression of a core cognitive ability that among humans would be described as "intelligence."

The observation here that reasoning and general learning abilities are correlated should be considered in light of previous observations that the general learning abilities of mice are predicted by variations in selective attention and working memory capacity (Kolata et al., 2005, 2008; for review, see Matzel & Kolata, 2010; for analogous results from tests of humans, see Halford, Cowan, & Andrews, 2007; Unsworth & Engle, 2007). To return to one of the definitions of intelligence provided above, concepts of "intelligence" are attempts to classify "the 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." While this and similar definitions were conceived to describe a human cognitive trait, this same definition appears relevant in summarizing the performance of mice on this diverse set of cognitive tasks. Thus, like humans, mice appear to express individual variations in intelligence, and these variations have profound functional consequences for the animals' negotiation of their environments. Overall, our observation of the coregulation of diverse cognitive abilities in mice suggests that the operations of intelligence may have been evolutionarily conserved across distant mammalian species (see also Banerjee et al., 2010).

It is worth noting that subregions of the prefrontal cortex may mediate "intelligence" through their regulation of attentional control and/or working memory capacity (Durstewitz, Seaman, & Sejnowski, 2000; Kolata et al., 2010; Sawaguchi & Goldman-Rakic, 1991; Thurley, Senn, & Luscher, 2008; for review, see Matzel & Kolata, 2010). In fact, Kolata et al. (2010) have reported that a cluster of dopamine D1-related genes in the prefrontal cortex are overexpressed in animals of high versus low general learning abilities. Since general learning abilities, attentional control, and reasoning abilities appear to be coregulated, it is tempting to speculate that dopaminergic signaling in the prefrontal cortex might serve as one of the (among potentially other) determinants of variations in intelligence.

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