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Intelligence demands flexibility: Individual differences in attentional disengagement strongly predict the general cognitive ability of mice

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ABSTRACT

General cognitive ability (or general intelligence; *g*) is a latent variable that describes performance across a broad array of cognitive skills. This general influence on cognitive ability varies between individuals and shares a similar structure in both humans and mice. Evidence suggests that much of the variation in general intelligence is related to the efficacy of the working memory system. We have previously observed that one component of the working memory system, selective attention, disproportionately accounts for the relationship between working memory and general intelligence in genetically heterogeneous mice. In the three studies reported here, we test a hypothesis that emerges from human behavioral studies which suggests that attentional disengagement, a sub-component of selective attention, critically mediates its relationship with *g*. Studies 1 and 2 both assess the factor loadings (on a principal component analysis) of the performance of mice on an array of learning tasks as well as tasks designed to make explicit demands on attentional disengagement. We find that attentional disengagement tasks load more highly than measures of cognitive performance that place less explicit demands on disengagement and that performance in these disengagement tasks is strongly predictive of the general cognitive performance of individual animals. In Study 3 we observed that groups of mice (young and old) with known differences in general cognitive abilities differ more on a discrimination task that requires attentional disengagement than on a simple discrimination task with fewer demands on disengagement. In total, these results provide support for the hypothesis that attentional disengagement is strongly related to general intelligence, and that variations in this ability may contribute to both individual differences in intelligence as well as age-related cognitive declines.

1. Introduction

General cognitive ability (c.f. general intelligence; *g*) is a latent factor that describes performance across a wide range of cognitive tasks, and is the variable quantified by typical "intelligence tests" in both humans (for reviews on this literature, see Jensen, 1998; Mackintosh, 1998) as well as nonhuman animals (Galsworthy, Paya-Cano, Monleon, & Plomin, 2002, 2005; Matzel et al., 2003). Performance on any specific cognitive task, however, is not only impacted by *g*, but also by domain-specific factors (e.g., spatial

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abilities; Kolata, Light, & Matzel, 2008). This pattern is well summarized by the hierarchical model of intelligence, which states that *g* is a high-level construct that mediates lower-level domain-specific abilities (e.g., reasoning, processing speed, spatial naviagation) that are in turn thought to directly impact performance on tasks within that domain (Deary, 2014). Despite our recognition of the impact of *g* on cognitive performance, the nature of *g* itself is less clear, i.e., it could represent the influence of a fundamental cognitive process or processes, or could be a more elementary biological mechanism related to some ubiquitous cellular function (Geary, 2018). Understanding the relationship or influence of isolated cognitive processes on general cognitive performance could aid in resolving these different possibilities.

One domain-specific cognitive process, working memory, has been well-documented as a covariate to *g* in both humans (Conway & Engle, 1995; Engle, Tuholski, Laughlin, & Conway, 1999; Kyllonen & Cristal, 1990; Matzel & Kolata, 2010; Süß, Oberauer, Wittmann, Wilhelm, & Schulze, 2002) and in mice (Kolata et al., 2005; Kolata, Light, Grossman, Hale, & Matzel, 2007; Matzel & Kolata, 2010). Working memory has been described as a cognitive system that employs storage, processing, and attention to mediate the maintenance and manipulation (in memory) of task-relevant information (Baddeley, 2012; Baddeley & Hitch, 1974). It has been reported that the storage efficacy of working memory (e.g., measures of "simple span," or the ability to recall a list of words) is not consistently related to *g*, but the processing efficacy of working memory (e.g., "complex span," for example, the ability to recall specific words from a series of sentences that require comprehension) is significantly correlated with *g* (Daneman & Carpenter, 1980). These early results have been supported by multiple behavioral studies (e.g., Ackerman, 1987; Colom, Rbello, Palacios, Juan-Espinosa, & Kyllonen, 2004; Conway & Engle, 1995; Engle et al., 1999; Süß et al., 2002). Furthermore, suggestions that working memory efficacy may have a *causal* influence on *g* (Matzel & Kolata, 2010; Unsworth & Engle, 2007) have been supported by Light et al. (2010) who report that repeated training in tasks that tax the processing component of working memory resulted in increases in *g*.

Importantly, Light et al. (2010) reported that working memory training was associated with an increase in selective attention, and furthermore, working memory training that imposed fewer demands on attention had commensurately less impact on general cognitive performance. Previous studies have suggested that selective attention, defined as the ability to shift attention to relevant information needed to complete a task while ignoring irrelevant information, was a primary determinant of the relationship between working memory and *g* (e.g., Kolata et al., 2007). Evidence from human studies (Cohen et al., 1997; Friedman & Miyake, 2017; Friedman et al., 2006; Kane, Bleckley, Conway, & Engle, 2001) has generally aligned with the reported studies in laboratory animals and has led to the assertion that selective attention is critical to the relationship between working memory and *g* (for a review on the role of selective attention in working memory and *g*, see Matzel & Kolata, 2010). Accordingly, increases in selective attention abilities that resulted from working memory training provide a possible mechanism through which we can understand increases in *g* consequent to working memory training (Light et al., 2010).

Recent studies have focused on separating two underlying components of selective attention: maintenance and disengagement (Shipstead, Harrison, & Engle, 2016). Engle (2018) defined the two components of this system as follows: 1) *maintenance* is the "…ability to maintain information in the maelstrom of divergent thought," and 2) *disengagement* is the ability to "…unbind…and to functionally forget [information] when it proves to be unimportant or wrong." Human behavioral studies have sought to further the understanding of this component split by assessing relationships between *g*-related tasks to maintenance (e.g., operation span, symmetry span, and rotation span; Martin et al., 2020) and disengagement (e.g., Raven's Progressive matrix [RPM], letter set, and number series; Martin et al., 2020). Martin et al. (2020) found that when these two components can reliably be separated, the disengagement component is correlated with measures of *g* (such that individuals who can successfully disengage with irrelevant information achieve higher scores on the RPM) while the maintenance component has no significant correlation with *g* (also see Shipstead et al., 2016). These results are seemingly consistent with results from Sauce, Wass, Smith, Kwan, and Matzel (2014) who reported that in mice, performance on tasks that required control of internal sources of distraction (similar to control of disengagement) was significantly correlated with *g*, while performance in tasks that required control of external sources of distraction (comparable to maintenance) were not significantly correlated with *g*.

Much of the work described above led to an assertion by Engle (2018) that attentional disengagement, rather than maintenance, may be the critical aspect of the executive attention system that makes it such a useful predictor of *g*. However, this recent assertion has not been fully assessed. Evidence from an animal model would be useful in this regard, given the added benefits of being able to more carefully control the subjects' environments and task-relevant conditions. In the following three studies, we test in mice the hypothesis that the degree to which a cognitive task makes demands on attentional disengagement will directly determine its relationship to *g*, and relatedly, that individual differences in the capacity for attentional disengagement will be strongly related to variations in intelligence.

2. Study 1

Here we assessed the degree to which tasks that are varyingly dependent on attentional disengagement load on a factor (of a principal component analysis) that describes general cognitive performance. Eight measures of cognitive ability were obtained, six of which (learning tasks) did not make *explicit* demands on attentional disengagement, whereas the remaining two measures (disengagement tasks) were explicitly designed to require the disengagement from a previously instantiated learned response (i.e., these tasks required subjects to disengage from a previously learned response and reverse their responses in order to be completed). While it is presumed that all cognitive tasks are dependent to some extent on attentional disengagement, here we can test the hypothesis that the greater the explicit demands on that ability, the more heavily *g*-loaded that task will be. This allowed us to compare the *g* loadings of tasks with different nominal requirements for attentional disengagement.

2.1. Methods

Subjects. A total of 74 CD-1 outbred male mice from Harlan Laboratories (Indianapolis, IN) were used. Estimates of genetic variation in this line indicate that, despite over 50 years of laboratory breeding, they are very similar to wild mouse populations (Aldinger, Sokoloff, Rosenberg, Palmer, & Millen, 2009). Animals were housed individually in standard shoebox home cages in a temperature-controlled colony room using a standard 12 -h light-dark cycle. Animals arrived in the laboratory at 4–6 weeks of. Prior to testing, animals were handled (i.e., held and walked around the laboratory) by experimenters for 60 s each day for seven days to minimize effects that may occur due to animal stress from being handled. All procedures were conducted with approval with the Institutional Care and Use Committee (IACUC) at Rutgers University.

Food Deprivation. Seven of the eight cognitive tasks used for Study 1 (described below) were food-motivated, necessitating food deprivation. *ad libitum* food was removed from animals' home cages approximately 40 h prior to start of training for a task that required food deprivation. During deprivation, animals were provided food in their home cages for 120 min/day during the last two hours of the light cycle, resulting in animals being approximately 16 h food-deprived at the time of training or testing in any given task. This deprivation schedule was deemed "mild" as animals typically lost less than 5% of their free-feeding body weight during deprivation periods. Though mild, the deprivation was sufficient to maintain stable performance on the cognitive tasks.

Behavioral Training and Testing. To quantify individual differences in general cognitive ability in mice, animals were assessed through a series of eight performance measures obtained through five tasks in the following order: spatial water maze, decision tree maze, straight alley (two measures: object permanence and simple discrimination) and the Lashley maze (two measures: navigation errors and object permanence puzzle), and Lashley maze reversal (two measures: reverse navigation errors and persistent searching). (Note that in order to assess individual differences, the order in which animals were trained on each task was deliberately *not* counterbalanced so that all animals will have been treated similarly.) In short, the spatial water maze requires animals to use spatial cues to escape a pool of water. The decision tree stresses inductive reasoning in efficiently navigating a unique, tree-shaped maze searching for randomly placed reinforcements. The straight alley requires animals to traverse a simple alley that terminates with a goal area in which they must 1) demonstrate object permanence by exploring a previously explored cup with a new obstacle added and 2) make a simple visual discrimination by ignoring non-target cups in favor of a visually marked food cup. The Lashley maze requires egocentric navigation to 1) efficiently reach the goal area for food retrieval and 2) demonstrate object permanence and puzzle-solving abilities by removing a novel, obstructing object from a previously reinforced food cup. The Lashley maze reversal requires animals to 1) efficiently navigate a previously learned maze in reverse direction and 2) ignore a previously heavily reinforced food cup in favor of a novel reinforcement location. A timeline of tasks can be seen in Fig. 1, and each task is described in detail below.

2.1.1. Learning tasks

Water Maze. A round black pool (122 cm in diameter, 41 cm deep) was filled to within 20 cm of the top of the pool with water. While the pool was being filled, water-soluble "super black" food coloring (Sunny Side Up Bakery company) was added to the water to give it an opaque, black coloring which hid the platform from the mice. This platform, 12 cm in diameter, was placed in the pool 1.5 cm beneath the surface of the water. This height was low enough to keep it hidden from the mice and high enough to let the mice rest mostly above the water when standing on it. Enclosing the pool were black curtains to which strings of lights were strung (forming several distinct patterns) to serve as spatial markers. A video camera was attached to the ceiling above the pool to record each animal's performance. On the day before testing, mice were placed in holding boxes in the testing room for 20 min prior to acclimation. Mice were then placed on the platform in the pool for 300 s to acclimate them. On the testing day, mice were again placed in holding boxes in the testing room for 20 min before testing began. Following the wait time, mice were placed into the pool at one of three starting locations, rotating each trial. Mice then swam until they reached the platform, stood on it using all four paws, and remained there for four secs. If a mouse failed to find the platform after 120 s, the animal was placed on the platform for four secs then removed, ending the trial. A 20 min inter-trial interval intervened prior to the subsequent trial. Two measures, the amount of time (secs) and the path taken (distance traveled in cm) by the animal to complete the trial were recorded during each trial. Each animal completed five trials. The average distance traveled (cm) across Trials 3–5 was used as the performance index in the principal component analysis.

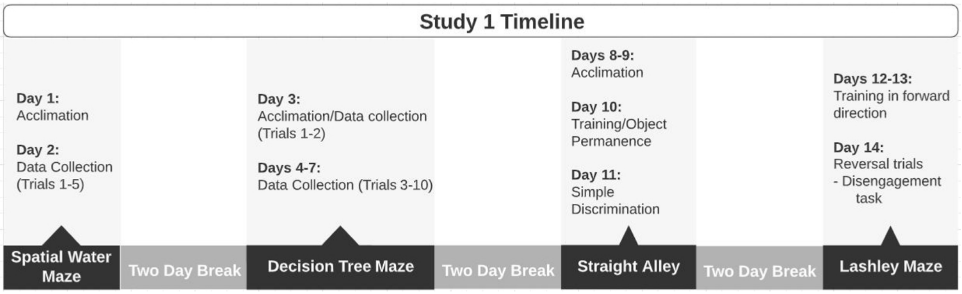

Fig. 1. A timeline of behavioral tasks in Study 1, including break days. A total of 20 calendar days was needed to complete all testing.

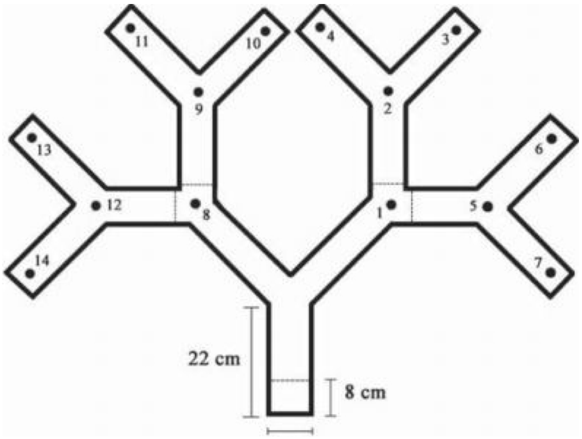

Fig. 2. Illustration of the decision tree maze. Animals were tasked with exploring each of the maze nodes (labeled 1–14 above) for a food reward during each trial. Four to eight random nodes were baited with food during each trial following an initial acclimation trial with all nodes baited, The efficiency of animals' maze navigation was determined by measuring the "streak" of necessary node crossings made before making an unnecessary crossing (figure source: Wass et al., 2012).

Decision Tree Maze. The Decision Tree maze is a "tree" shaped maze constructed from black Plexiglass with a start box and series of bifurcating arms. A holding box was located at the start of an initial straight alley. Mice were introduced to the maze from this start box that could be opened via a sliding Plexiglas door. After traversing an initial straight alley, the maze split into to symmetric halves. On each half, the maze then split three more times, for a total of six splits (after the initial split). At each split and at the terminal end of each branch a small hole (a "node") had been drilled that could hold a recessed 14 mg Noyes pellet that served as the food reward. In total, there were six nodes at the split points and eight nodes at the terminal ends (see Fig. 2).

Testing in this maze involved mice navigating the branch-like structure to inspect each node for food. The object of this test was for mice learn the overall structure of the maze and formulate the optimally efficient path through which it could search each potential food deposit (i.e., node) while crossing as few nodes as possible. Mice with high general intelligence would explore the maze in efficient paths (i.e., cross the same node only *en* route to an unexplored node) while mice with lower intelligences would take meandering paths and make many unnecessary node crossings (errors) in exploring the maze. The efficiency with which an animal searched the maze has been said to be emblematic of inductive reasoning, and performance in this maze (efficiency of search for food) has previously been shown to load heavily (0.49) on a factor analysis describing a general intelligence factor (Wass et al., 2012).

For the present test, the path animals took to explore each node in the maze was recorded. We used one measures from the maze, an animal's "streak", defined as the number of necessary node crossings an animal made before making an unnecessary crossing over a node it had previously explored. For additional details about the construction of this maze, see Wass et al. (2012).

Animals were food deprived for approximately 16 h before testing began. Testing in this maze lasted five days, with animals being tested in two trials per day for a total of 10 trials. On trial one, mice were placed in the start box for 10 s before the gate to the maze was opened. Mice were given access to the maze which had all 14 nodes baited with food. The path taken by the animal was recorded until all food pellets are retrieved. Mice were kept in the maze for 12 min. to allow further exploration. Mice were then removed and placed back in their home cages in the testing room for the 10 min ITI.

Trials 2–10 involved a similar procedure to trial one, with two major exceptions. The first exception was that during these trials, only four to eight of the nodes were baited with food. Standard arrangements of the food baiting were used to ensure consistency among animals. The number and location of nodes to be baited during each trial were selected randomly. The second exception from trial one was that these trials were not subjected to the 12 min time requirement. Rather, these trials ended when all available food had been eaten and all nodes had been explored. The average streak of correct choices across Trials 7–10 was used as the performance index in the principal component analysis.

The six remaining cognitive tests were conducted in a single piece of apparatus constructed as a convertible straight alley/Lashley maze hybrid-style maze. This battery of tests was comprised of the following component tests: straight alley, simple discrimination task, and Lashley maze (which included both acquisition and reversal measures).

Straight alley. Mice were placed in the start box of the maze for 5 s, the door was then opened and the mice were free to traverse the alley. When mice reached the goal area of the maze, access to the alley was blocked to enclose them in the goal area. The goal area contained a single platform with a food dish holding one piece of accessible food and one piece of inaccessible food. Time taken by the mouse to retrieve the food was recorded. This was repeated for a total of five trials with a 6 − 10 min ITI for each animal. Trial 6 proceeded as previous trials, with the exception of an added hexagonal lid placed on top of the food cup and recording of errors made by mice in removing the lid. An error was scored if an animal placed at least two paws on platform and withdrew from platform *or* made contact with a lid and failed to remove it. Errors were recorded if an animal approached a cup or made contact with the lid without retrieving the food. The trial was considered complete (and no error scored) if an animal removed the lid to retrieve the food reward. The total number of errors during Trial 6 served as the performance index for the principal component analysis.

For the simple discrimination measure, mice were again placed in the start box for 5 s and released to the straight alley. Four platforms, each with one food cup on them, were placed in the goal area. Each cup was baited with inaccessible food. During Trial 1, one cup (in position number three, counted from left to right) was covered with a hexagonal lid and baited with accessible food. The trial proceeded as previous trials in the straight alley, counting errors as previously described. Trials 2–12 ha d four cups in the goal area, all covered with hexagonal lids. One of the four cups was marked by a star as a discriminative cue and only this cup had accessible food. Lid errors were recorded as previously described, while animals could also make errors any time that they made contact with a non-target lid. Errors could occur multiple times at a single lid provided that the animal stepped off the platform after making initial error (i.e., attempts at same lid without leaving the platform count as a single error). The total number of errors committed between Trials 6–11 was used as the index of performance for the principal component analysis.

Lashley maze. For this portion of testing the maze was converted to its Lashley maze configuration. A single platform with an uncovered food cup baited with reinforcer was placed in the center back of the goal area. This phase of testing took place over three days in total, with two days of testing (Trials 2–12) in the forward direction of the maze and one day of reversal testing (Trials 13–18).

For Trials 1–5, animals were placed in the start box, released, and allowed to traverse the maze until it entered the arena and food was retrieved. Errors were recorded for the following actions: 1) back-tracking (complete reversal involving movement), 2) missed turn, i.e., passing a door without entering or 3) wrong direction of turn (i.e., exiting a door and turning in the wrong direction). Errors were not compounded, i.e., if an animal missed a door (error), then back-tracked to return to that door, the back-track was “necessary” and thus was not scored as an error. Likewise, if an animal made a wrong turn (error), it must back-track to return to the proper course and thus back-tracking was not an error. Errors could only occur if an animal was moving toward the goal, i.e., if the animal made an error that leads back through several doors before correcting and moving toward the goal, only the first error in the series was counted. Once the animal again progressed toward the goal, errors were again counted. Trials 7–14 followed this same procedure. Total errors committed between Trials 3–5 served as the performance index (Lashley Maze Errors) for the principal component analysis.

For trial 6, we repeated the procedure from Trials 1–5, with the exception that the food cup was covered by a blue ping-pong ball (puzzle). We recorded errors to enter the arena, then puzzle errors. An error was scored if an animal placed at least two paws on platform and withdrew from the platform or made contact with the ball and failed to remove it. Thus, approaches were recorded if an animal approached a cup or made contact with the ball without retrieving the food. The trial was completed (and no error scored) if an animal successfully removed the ball to retrieve the food reward. Total approaches during Trial 6 served as the performance index (Lashley Maze Puzzle Approaches) for the principal component analysis.

Following two refresher trials (Trials 13–14) at the start of day eight, we tested animals on four reversal trials (Trial 15–18) in the maze. A baited food cup was placed in what was previously the start box of the Lashley maze. Animals began the trial placed in the center of what had previously been the goal area facing a now empty food cup. Two types of errors were recorded: 1. Approach errors were recorded every time the animal approached the old (now empty) food cup. This was constituted any time that an animal placed at least two paws on the platform and withdrew or when its nose crossed the plane of the cup wall (in cases where the animal did not step on to the platform). The total number of approaches during Trials 16–18 served as the performance index (Lashley Maze Reversal Approaches) for the principal component analysis. 2. Maze errors were recorded as the animal traversed the maze toward what had previously been the start box (which now contained a baited food cup). These errors were scored as they were during forward Lashley maze training, although in this instance, the correct route was reversed. Animals were allowed to find and consume the food, and then removed to begin their inter-trial interval. The total number of maze errors committed during Trials 16–18 served as the performance index (Lashley Maze Reversal Errors) for the principal component analysis.

Statistical Analyses. All statistical analyses were completed using IBM SPSS Statistics Version 25. Two principal component analyses were conducted to assess the *g* loadings of individual tasks and generate factor scores that describe the average aggregate score for an individual across all of those tasks. One principal component analysis assessed *g* loadings and generated factor scores (Learning Task Factor Scores) for learning tasks only (as described above; i.e., all tasks other than disengagement tasks) while a second principal component analysis included both learning and disengagement tasks. Then a 2 × 2 factorial ANOVA was performed to assess differences between Smart (top quartile of performers as determined by Learning Task Factor Scores) and Dull (bottom quartile of performers) animals during acquisition and reversal test phases in the Lashley maze. Finally, simple linear regression was used to evaluate the predictive relationship of disengagement tasks and Learning Task Factor Scores.

2.2. Results

In this study, animals’ performance was recorded on eight tasks consisting of the Morris water maze, the decision tree maze, a straight alley object permanence task (requiring lid removal), a straight alley simple discrimination task, a Lashley maze navigation task, a Lashley maze object discrimination task, and two tasks that specifically require attentional disengagement: a Lashley maze reverse navigation task as well as a Lashley maze food cup disengagement task. We then performed two principal component factor analyses, one using the six learning tasks only (Table 1) and another using all the learning tasks as well as the two disengagement tasks (Table 3).

Learning Task Factor scores (indicative of an animal’s relative general cognitive performance) were obtained from the principal component analysis of learning tasks only. The factor score is essentially an average z-score for each animal for the six tasks, where each task was weighted according to its factor loading (as found in Table 1). Factor scores are reported such that lower scores indicate better aggregate performance, and we report factor scores for all 74 animals that ranged from -1.35 (best general cognitive

Table 1
Factor loadings from a principal component analysis (n = 74) of animals' performance on the six tasks of the learning battery computed without disengagement tasks.

	General Factor
Straight Alley Lid Fails	.77
Straight Alley Lid Discrimination	.67
Lashley Maze Errors	.70
Lashley Maze Puzzle Approaches	.60
Water Maze	.49
Decision Tree Maze	.34
Eigen value	**2.26**
% variance explained	**37.67**

performance) to +3.74 (worst general cognitive performance).

Results from the principal component analysis of the six-task cognitive battery (learning tasks only) reveals the degree to which each task loaded on the general factor is provided in Table 1 (Eigen value = 2.26; accounting for 37.67 % of the variance across all six tests). We found that task loadings ranged from 0.34 (decision tree maze) to 0.77 (straight alley lid fails). The degree to which the factor scores that resulted from this analysis were predicted by disengagement measures was assessed in subsequent analyses (see below).

Fig. 3 depicts acquisition and reversal performance (i.e., disengagement measures) in the Lashley maze. The figure illustrates the performance of all animals as well as the performance of animals who qualified as Smart (top quartile of performers) and Dull (bottom quartile of performers) as determined by each animal's Learning Task Factor score (i.e., that animal's average z-score on each task weighted by the factor loading of each task) derived from the principal component analysis of the six learning tasks (Table 1). In general, the learning curve illustrates that Smart animals committed fewer errors in the maze than average animals and Dull animals (i.e., factor scores are representative of animals' performance on this single task). Importantly, the reversal learning curve illustrates how animals representing the smart quartile were able to quickly learn a new route in the maze.

Fig. 4 summarizes the performance of all animals on the learning tasks (as determined by the principle component analysis reported in Table 1) as well as the top (Smart) and bottom (Dull) quartile performers, during acquisition and reversal in the Lashley maze. Animals were assigned mean scores representing their performance (average number of errors in the Lashley maze) across Trials 2–4 of acquisition and Trials 2–4 of reversal training. A two-way ANOVA was used to compare groups (All animals, Smart Quartile, and Dull Quartile) and phase of training (acquisition and reversal). A significant effect of group was observed ($F[1,68] = 18.48$, $p < 0.01$) such that the Dull group made more errors on average ($M = 22.25$, $SD = 13.68$) than the Smart group ($M = 10.92$, $SD = 9.13$). There was also a main effect of phase of training ($F[1,68] = 7.05$, $p = 0.01$) such that animals made more errors during the reversal phase ($M = 20.08$, $SD = 14.84$) compared to the acquisition phase ($M = 13.08$, $SD = 9.55$). There was no significant interaction effect ($F[1,68] = 0.61$, $p = 0.44$).

Prior to the principal component analysis of all eight dependent measures (performance on the six learning tests and the two reversal tests), a correlation matrix was constructed that included all of these variables. That matrix is provided in Table 2. All correlations in the matrix was positive, indicative of a common source of variance across all tasks. For the present purpose, the

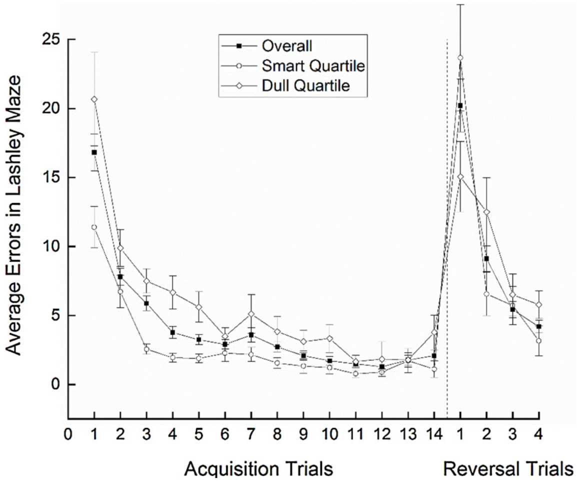

Fig. 3. Acquisition and reversal performance in the Lashley maze. Overall performance of all animals (n = 74) is plotted as is the upper and lower quartiles (ns = 18) of general learning abilities as determined by the factor scores obtained from the analysis of six tasks learning tasks. Error bars represent standard error.

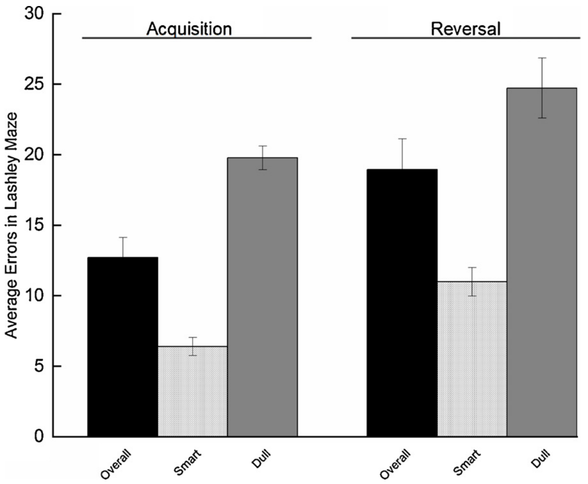

Fig. 4. Acquisition and reversal performance in the Lashley maze. Bars represent average performance of all animals (n = 74) alongside the top and bottom quartiles of performers (ns = 18; as determined by factor scores obtained from PCA described in Table 1 during both acquisition and reversal trials. In both phases, animals in the highest performance (smart) quartile group committed fewer errors than did those in the lowest performance (dull) quartile.

Table 2
Correlations between animals' performance on all six learning tasks as well as the two reversal tasks are presented. (For the intent of this analysis, Lashley Maze reversal errors and reversal approaches are not represented on the column of variables, thus isolating columns of tasks from those two variables.). WM = Water Maze; TM streak = streak length in decision Tree Maze; SA lid fails = lid puzzle failures in the Straight Alley; SA discrimination = discrimination errors in the Straight Alley; LM acq errors = errors during Lashley Maze acquisition; LM puzzle errors = puzzle errors in the Lashley Maze.

	WM	TM streak	SA lid fails	SA discrimination	LM acq errors	LM puzzle errors	LM reveersal errors	LM reversal approaches
WM	——	.026	.220	.176	.249*	.175	**.214**	**.290***
TM streak	.026	——	.128	.202	.221	.011	**.153**	**.213**
SA lid fails	.220	.128	——	.351**	.420**	.349**	**.418****	**.423****
SA discrimination	.176	.202	.351**	——	.380**	.446**	**.320****	**.359****
LM acq. errors	.249*	.221	.424**	.382*	——	.384**	**.463****	**.501****
LM puzzle errors	.175	.011	.349**	.446**	.360**	—	**.396****	**.341****
mean	.169	.117	.294	.311	.326	.273	**.327**	**.354**

Table 3
Factor loadings from a principal component analysis (n = 74) of animals' performance on the eight component tasks of the learning battery computed with disengagement tasks (denoted in bold).

	General Factor
Straight Alley Lid Fails	.72
Straight Alley Lid Discrimination	.55
Lashley Maze Errors	.69
Lashley Maze Puzzle Approaches	.55
Water Maze	.46
Decision Tree Maze	.32
Lashley Maze Reversal Errors	**.79**
Lashley Maze Reversal Approaches	**.81**
Eigen Value	3.18
% variance explained	39.72

correlations of the learning tasks with two measures obtained during reversal (disengagement) training in the Lashley Maze (reversal errors and approaches to the empty food cup) are most informative. These correlations are relatively high, and in fact the mean correlations obtained for Lashley Maze reversal errors and approaches to the empty food cup are (nominally) the highest in the set.

The most critical analysis of the present experiment is the principal component analysis of all eight task cognitive battery measures (learning and disengagement tasks). Results are provided in Table 3 and reveal the degree to which each task loaded on the general cognitive factor (Eigen value = 3.18; accounting for 39.72 % of the variance across all eight tests). Of the six learning tasks, factor loadings ranged from 0.32 (decision tree maze) to 0.72 (straight alley lid failures). Importantly, the two explicit measures of

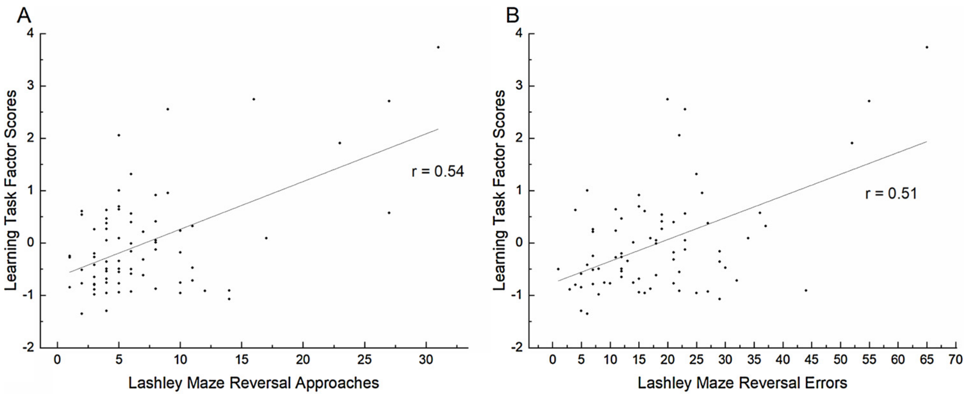

Fig. 5. Linear regressions of the two disengagement tasks and Learning tasks factor scores. **A)** Linear regression of Lashley maze reversal approaches and learning task factor scores. **B)** Linear regression of Lashley maze reversal errors and learning task factor scores. Both graphs illustrate that animals that performed poorly in Lashley maze reversal tasks (indicated by larger numbers of approaches/errors) tended to have higher learning task factor scores (indicating lower general cognitive ability).

disengagement (Lashley maze reversal errors and reversal approaches) loaded more heavily (0.79 and 0.81, respectively) than any of the remaining tasks (which had lower nominal requirements for disengagement).

The relationship between learning-task factor scores and the two attentional disengagement tasks were assessed using simple linear regressions. A significant regression was found ($r[1,72] = 0.54$, $p < 0.001$) between learning task factor scores and Lashley maze reversal approaches (Fig. 5A). Likewise, a significant regression was found ($r[1,72] = 0.51$, $p < 0.001$) between learning task factor scores and Lashley maze reversal errors (Fig. 5B). In both cases, animals that made a larger number of approaches/errors during reversal had a higher learning task factor score (indicating lower general cognitive ability).

3. Study 2

As in the prior study, here we assessed the degree to which attentional disengagement was "*g* loaded." For this purpose, animals were assessed on a series of learning tasks, one of which included a phase where after super-asymptotic levels of performance were reached, the animals were required to reverse a previously learned behavioral tendency, i.e., had to disengage from the previous pattern of behavior and adopt a new response. In the present study, five of the six tasks that were used were different than those used in Study 1, and the reversal task required that the animals adapt to a new escape location following extensive training in a spatial water maze.

3.1. Methods

Subjects. A total of 58 CD-1 outbred male mice from Harlan Laboratories (Indianapolis, IN) were used. Estimates of genetic variation in this line indicate that, despite over 50 years of laboratory breeding, they are very similar to wild mouse populations (Aldinger et al., 2009). The mice arrived in our laboratory between 8–10 weeks of age, and were singly housed in clear shoe box cages inside a temperature-controlled colony room under a 12-h light/dark cycle. In order to minimize any differential stress responses due to experimenter handling, we handled the mice for 90 s a day for a period of seven days prior to the start of testing. Handling consisted of removing each mouse from his home cage and holding it while walking throughout the laboratory space. At start of testing, animals were approximately 12 weeks of age.

Food Deprivation. For the cognitive tasks that required food deprivation, *ad lib* food was removed from the animals' home cages at the end of the light cycle approximately 40 h prior to the start of training (and thus encompassing the "rest" days between successive tasks). During the deprivation period, animals were provided food in their home cages for 90 min/day during the last 2 h of the light cycle, and thus were approximately 16 h food-deprived at the time of training or testing. This deprivation schedule was deemed "mild" (animals typically lost less than 5% of their free-feeding body weight during this period), but was sufficient to maintain stable performance on these tasks. In the one task that required water deprivation, the same schedule was followed except that free access to water was limited to 60 min per day.

Behavioral Training and Testing. To quantify individual differences in general cognitive performance among mice, animals were tested on six distinct tasks that have previously been found to be influenced by a single source of underlying variance (Kolata et al., 2007; Matzel, Grossman, Light, Townsend, & Kolata, 2008; Matzel et al., 2006, 2008). All animals were tested in a series of six independent learning tasks in the following order: Lashley III maze, passive avoidance, odor discrimination, and reinforced alternation, and spatial water maze. These tasks place unique sensory, motor, motivational, and information processing demands on the animals. Briefly, passive avoidance is an operant conditioning paradigm in which the animals must learn to be passive in order to avoid aversive light and noise stimulation. Odor discrimination is a task in which animals must discriminate and use a target odor to guide their search for food. In the reinforced alternation task, animals must alternate between left and right arms in a t-maze to obtain

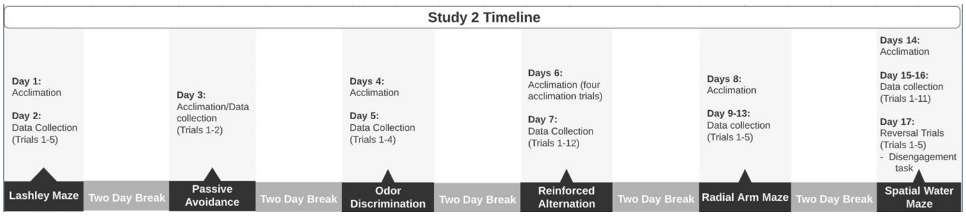

Fig. 6. Timeline of behavioral tasks in Study 2, including break days. A total of 27 calendar days was needed to complete testing.

food. The spatial water maze encourages the animals to integrate spatial information to efficiently escape from a pool of water. Testing order was designed so that tasks that impinge on similar information processing, motor, or motivational demands were separated to the greatest possible extent. A timeline for behavioral tasks in Study 2 is shown in Fig. 6, and each test is described in detail below.

3.1.1. Learning tasks

Lashley III Maze (LM). This maze consists of a start box, three interconnected alleys and a goal box. Previous studies have shown that over successive trials, the latency and number of errors to find the goal decreases. When extra-maze cues are minimized, the animals tend to use egocentric methods (e.g., fixed motor patterns) to locate the goal box.

A Lashley III maze scaled for use with mice (see Matzel et al., 2003) was constructed from black Plexiglas and located in a dimly lit room (10 Lux at the floor of the maze). A 3 cm diameter white circle was located in the center of the goal box, and 45 mg Bio-serv food pellets (dustless rodent grain) was placed in the cup to motivate the animal's behavior.

Food-deprived animals first received a day of acclimation to the maze, followed by a single training day. Prior to the day of acclimation, all animals received three pellets of the reinforcer in their home cage. On the acclimation day, each mouse was confined in each of the first two alleys of the maze for 4 min, and in the final alley (containing the goal box) for 6 min. On this acclimation day, three pellets were placed in goal box. At the end of each period, the animal was physically moved to the next alley. This acclimation exposure was intended to adapt the animals to the apparatus prior to actual training. On the subsequent training day, each animal was placed in the start box and allowed to freely navigate the maze, during which time their latency to locate their food and the number of errors were recorded. (An error was constituted by either a wrong turn or a re-tracing of the animal's path.) Upon locating and consuming the food pellet, the animal was returned to its home cage for a 25 min inter-trial interval (ITI) during which time the maze was cleaned. (In this and other multi-trial tasks, long inter-trial intervals were used, as our previous work has determined that the longer ITI supports more stable/rapid acquisition of the learned response.) The animals completed five trials during the single training day. For the purpose of characterizing individual mice for the principal component analysis, the number of errors committed by each animal on trials three and four were averaged and served as each animal's index of performance.

Passive Avoidance (PA). In this test, animals learn to suppress their exploratory tendency in order to avoid aversive stimuli. The animals are placed on a platform, and when they step down, are exposed to an aversive stimulus compound comprised of a bright light and loud oscillating tone (i.e., "siren").

A chamber with a white grid floor 16 × 12 cm (l × w) and that is illuminated by a dim red light was used for both acclimation and testing. An enclosed platform (70 × 45 × 45 cm, l × w × h) constructed of black Plexiglas and elevated 5 cm above the grid floor was located at the back of the chamber. It has only one opening facing the grid floor which allows the animal to step down onto the floor. The exit from the platform can be blocked remotely by a clear Plexiglas guillotine-style door. When an animal left the platform and made contact with the grid floor it initiated the aversive stimuli.

Animals were placed on the platform with the door closed, confining them in the enclosure. After 5 min, the door is opened and the latency of the animal to leave the platform and make contact with the floor was recorded. After they make contact, the aversive stimuli are initiated and the platform is lowered, exposing them to the stimuli for 4 s. after which they are allowed access to the enclosure again. They were then again confined on the platform for 5 min, after which the door opened and their latency to walk onto the grid floor was recorded for a second time. For purpose of principal component analysis, the ratio of the post-training step latency to pre-training step latency served as the index of performance.

Odor Discrimination (OD). Rodents are adept at using odor to guide their reinforced behavior. This task is modified from one developed by Sara, Roullet, and Przybyslawski (1999) but scaled for use with mice. In this task, mice navigated through a field using unique odors to guide them. The animals learned to choose the food cup that contained the target smell when given three choices. The food cup locations are rearranged on each trial but the accessible food is always marked by the same target odor (in this case mint).

The odor discrimination chamber consisted of a black Plexiglas 60 cm square field with 30 cm high walls which was located in a dimly lit room with a high rate of air turnover. Three aluminum food cups were placed in three corners. Only one cup (the target cup) contained accessible food, while the other two cups had food located in a covered hole drilled into the side with a ventilation hole allowing the mice to smell the food but not access it. One 30 mg portion of chocolate flavored puffed rice acted as a reinforcer and was placed in a depression on top of the target cup. A cotton-tipped laboratory swab (2 cm long) was loaded before each trial with 25 ul of lemon, mint or almond flavored extract and extended vertically from the back corner of each cup. Mint was always the target odor.

Each animal had one day of acclimation and one day of testing. The night prior to the acclimation day, food was removed from each animal's home cage. The next day, to adapt the animals to the test chamber, each mouse was placed in the box for 20 min without the food cups present. At the end of the day each animal received three pieces of the reinforcer in their home cage. On the training day, a baited food cup and two non-target cups were placed in three separate corners of test chamber, and each animal received four trials (with a 20 min ITI) in which they were placed in the corner of the training chamber which did not contain the food cup or a non-target cup. On each trial, food could be retrieved from the food cup marked by the mint odor. At the end of each trial the food cup and non-target cups were rearranged to occupy different corners, but mint always remained as the target odor. For each trial, the number of errors were recorded (where an error was constituted by making contact with or sniffing within 2 cm of non-target cup). For purpose of the principal component analysis, the average number of errors across Trials 2 and 3 served to index each animal's learning performance.

Reinforced Alternation (RA). In this task, animals are started at the bottom of a "T" maze, and learn to alternate between entering one of two arms that intersected at the top of the T. On each trial a food reinforcer was present in the end of one arm. The location of the reinforcer shifted to the alternate arm after each successful retrieval of food. In order to perform efficiently in such a task the animals had to alternate choices on successive trials (win-shift) in order to minimize the amount of effort it required to locate the food.

The apparatus was constructed of black Plexiglas and consisted of a start arm (7.5 cm wide x 17 cm long) that intersected at the middle of an alley (92 cm long x 6 cm wide) that forms the top of a T. The entire maze was enclosed in a 5 cm high wall. The initial 10 cm segment of the start arm was segregated by a guillotine door that was remotely operated by the experimenter. This segment of the arm constituted the start box. At the entry of each choice arm there was another experimenter-operated guillotine door (see below). On the walls of the right arm there were alternating 20 cm wide vertical white and black stripes. On the walls of the left arm there were alternating horizontal black and white stripes. These stripes were intended to aid the animals' discrimination of the arms.

Training was conducted over two consecutive days. On Day 1, animals were acclimated to the maze and allowed to make four *forced* choices across successive trials. On the first trial, the animal was held in the start box for 30 s, after which it was allowed to traverse the maze; the door into the left arm was closed, and the right door was open. A 14 mg Bio-Serv pellet (dustless rodent grain) was located in the food cup at the end of the right arm. After consuming the food, the animal was returned to the start box for a 20 s ITI. On the second trial, this procedure was repeated, but the right door was closed and the left door open. After a 20 s ITI, this sequence was repeated for two additional trials. Through this sequence of four forced choices, the animals were acclimated to the maze.

On the subsequent day, animals were trained. On all training trials, each choice door was fully open. On Trial 1, a reinforcer was available in both food cups and the animal could make a free choice. On the second trial, reinforcement was available in the arm not entered on the first trial. If an animal chose the correct arm, the location of the reinforcer alternated on the following trial. If an incorrect choice was made, the animal was allowed to correct its mistake and locate the food in the other arm. In either case, after the reinforcer was consumed, the animal was placed back in the start box to begin a 20 s ITI. Animals' choices were recorded on each trial for 12 trials. For purposes of the principal component analysis, each animal's percent of correct choices across Trials 6–12 was used as that animal's index of performance.

Spatial Memory in a Radial Arm Maze. To assess spatial memory in a maze distinct from the water maze, animals were tested in a radial arm maze. The maze was constructed of black Plexiglas where eight arms extended 40 cm from a 15 cm diameter central hub. The maze was elevated 25 cm above the ground. A small depression was located at the end of each arm in which a reinforcer (a single 14 mg Noyse pellet) was placed. To mitigate any reliance on odor cues emanating from the food rewards, a cup containing 10 food pellets was placed under the end of each arm of each maze. The maze was located in a dimly-lit room on which patterns of LED lights (that could serve as spatial location cues) were located on the walls.

Training occurred on six successive days. On Day 1, each food-deprived animal was placed in the central hub of the maze and was allowed to explore the maze (with no food rewards present) for 6 min. On Days 2–6, each animal received a single training trial in the maze. On each of these trials, an animal was placed in the central hub and allowed to explore the maze and to retrieve the food reinforcer that was located in the cup at the end of each maze. After retrieving all of the food, the animal was returned to its home cage. On each trial, we recorded the number of errors committed by each animal, where an error was constituted by an animal's re-entry (where its hind legs crossed 1 cm into the arm) into an arm in which it had already obtained food. For purposes of the principal component analysis, each animal received a score that reflect its average performance across Trials 4–5.

Water Maze (WM). This task requires the animals to locate a submerged platform in a pool of opaque water (from which they are motivated to escape). Absent distinct inter-maze cues, animal's performance in this maze is highly dependent on their integration of spatial cues (Morris, 1981). The latency and the path length to locate the platform decrease over successive trials, despite entering the pool from different locations on each trial.

A round pool (140 cm diameter, 56 cm deep) was filled to within 20 cm of the top with water that is clouded with a nontoxic, water soluble black paint. A hidden 14 cm diameter black platform was located in a fixed position 1 cm below the surface of the water. The pool was enclosed by a ceiling high black curtain on which five different light patterns (which served as spatial cues) were fixed at various positions. These light cues provided the only illumination of the maze, which was 16 fc at the water's surface.

On the day prior to training, each animal was confined to the platform by a clear Plexiglas cylinder that fits around the platform for 360 s. On the next two training days, the animals were started from one of three positions for each trial such that no two subsequent trials start from the same position. The animal was said to have successfully located the platform when it remains on the platform for 5 s. After locating the platform or swimming for 90 s, the animals were left or placed on the platform for 10 s. Upon a trial's completion, the animals were removed for 20 min. and placed in a holding box before the start of the next trial. Each animal completed 11 total trials (6 on the first training day, 5 on the second). We have previously observed that with these training parameters, most animals reach asymptotic levels of performance between Trials 6 – 10.

3.1.2. Disengagement task

To assess the animals' capacity to disengage from a well-learned response, a third day of training was added to the water maze protocol in which the location of the platform was moved to a quadrant of the pool opposite the prior location. The animal's performance on five such reversal trials was assessed in the manner described for initial acquisition. During the first 30 s of the first of these trials, we recorded the percentage of time that each animal spent swimming in the *prior* target quadrant. This served as a measure of the strength of the prior learning, and is usually interpreted as an index of the degree to which an animal has established a spatial strategy to locate the platform. Of particular interest across these five reversal trials was the rate at which each animal abandoned its previously established pattern of navigation, and adopted the pattern that was appropriate for the new target location.

The latency and path (distance traveled in cm) to find the platform was recorded for each trial. Each animal's performance on Trials 4 and 5 was averaged and served as that animal's index of learning for purposes of principal component analysis.

Statistical Analysis. All statistical analyses were completed using IBM SPSS Statistics Version 25. Two principal component analyses were conducted to assess the g loadings of individual tasks and generate factor scores (the average aggregate score for an individual across all of those tasks). One principal component analysis assessed g loadings and generated Learning Task Factor while a second principal component analysis included both learning and disengagement tasks. A two-way ANOVA was then performed to assess differences between Smart and Dull animals during acquisition and reversal test phases in the spatial water maze. Finally, simple linear regression was used to evaluate the predictive relationship of disengagement tasks and Learning Task Factor Scores.

3.2. Results

In this study, animals' acquisition was assessed on six cognitive tasks (passive avoidance, Lashley Maze, reinforced alternation, odor discrimination, radial arm maze, and water maze), as was their ability to reverse (disengage from) a previously learned response (in the water maze). Of particular interest was the degree to which reversal performance (cognitive disengagement) loaded on a factor indicative of general cognitive performance, and the degree to which the reversal performance was indicative of an individual animal's cognitive status. Consequently, two principal component factor analyses were performed. The first of these analyses only included the six measures of acquisition obtained from every animal, and factor scores (Learning Task factor scores) from this analysis were used to characterize each animal's general cognitive ability. The results of this analysis are provided in Table 4. Based on this principal component analysis, factor scores were computed for each animal and those scores ranged from -1.98 to 3.34 (where lower values indicate better aggregate performance, i.e., a faster rate of acquisition across the six tasks).

Fig. 7 illustrates acquisition and reversal performance in the spatial water maze. Illustrated is the average performance of all animals, as well as the performance of the animals representing the upper and lower quartiles ("smart" and "dull"; ns = 14) of general cognitive abilities as determined by the factor scores obtained from the analysis summarized in Table 4. As is evident in the figure, generally fast and generally slow learners differed during both the acquisition and reversal phases of water maze learning. (It is important to note that factor scores used to classify animals included measures of acquisition in the water maze but did not include measures of reversal. Thus performance during reversal is consistent with the independent measures obtained during acquisition.) This differentiation was observed despite their being no difference in the performance of smart and dull animals during the first trial of reversal, indicating that both subgroups were similarly disrupted by the change in conditions. Furthermore, both groups spent a similar percentage of time searching for the escape platform (in the quadrant of the maze that previously contained the escape platform) during the first 30 s of Trial 1 during reversal (Smart mean = 44.1 %, s.e. = 5.2 %; Dull mean = 37.8 %, s.e. = 4.9 %; t [126] = .87, ns).

Fig. 8 summarizes the performance of all animals and the subgroups of smart and dull animals during acquisition and reversal in the water maze. Animals were assigned a mean score representing their performance across Trials 2–5 of acquisition and Trials 2–5 of reversal training. A two-way ANOVA was computed for this data, comparing groups (Smart and Dull) and phase of training (Acquisition and Reversal). Significant effects of phase of testing (F[1, 56] = 37.1, p < .001), subgroup (F[1, 56] = 70.9, p < .001), and an interaction of phase and subgroup (F[1, 56] = 9.23, p < .01) were observed. This indicates that the differentiation between smart

Table 4
Factor loadings from a principal component analysis (n = 58) of animals performance on six learning tasks only.

	General Factor
Passive Avoidance	.22
Lashley Maze	.48
Reinforced Alternation	.63
Odor Discrimination	.38
Radial Arm Maze	.76
Water Maze	.47
Eigen value	2.22
% variance explained	31.74

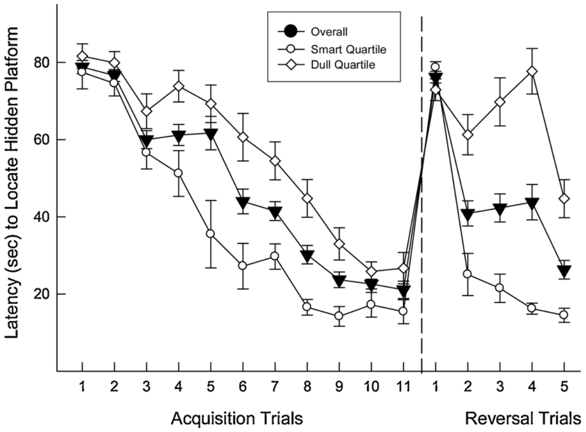

Fig. 7. Acquisition and reversal performance in the spatial water maze. Illustrated is the average performance of all animals (n = 58), as well as the performance of the animals representing the upper and lower quartiles (ns = 14) of general learning abilities as determined by the Learning Task factor scores obtained from the analysis summarized in Table 4. Smart and dull animals did not differ during the first trial of reversal (and both subgroups exhibited similar spatial performance during this trial), but rapidly diverged during the subsequent reversal trial, with dull animals exhibiting significant deficits in their ability to disengage from the previously instantiated behavioral tendency.

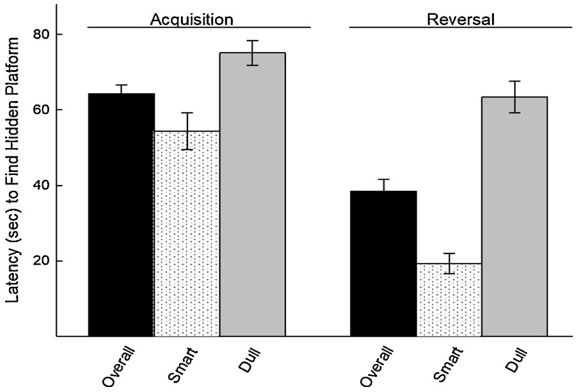

Fig. 8. Acquisition and reversal performance in the spatial water maze. Bars represent average performance of all animals (n = 58), as well as by upper and lower quartiles (ns = 14) of general learning abilities as determined by factor scores obtained from analysis summarized in Table 4. Results for both acquisition and reversal trials are reported. During acquisition trials, smart animals learn, on average, faster than both dull animals and the overall average. Dull animals learn slower than both the overall and smart animals. These results are also seen during reversal trials.

and dull animals was significantly greater during reversal than during acquisition.

Given the sensitivity of reversal to individual differences in general cognitive ability, we asked about the degree to which the measure of reversal in the water maze would load on a primary factor indicative of general cognitive performance.

Prior to the principal component analysis of all seven dependent measures (performance on the six learning tests and the one reversal test), a correlation matrix was constructed that included all of these variables. That matrix is provided in Table 5. All but one unique correlation in the matrix was positive, indicative of a common source of variance across all tasks. For the present purpose, the

Table 5

Correlations describing animals' performance between all seven dependent measures (six learning tasks and one reversal task) are presented. PA = Passive Avoidance; LM = Lashley Maze; RA = Reinforced Alternation; OD = Odor Discrimination; RAM = Radial Arm Maze; WMacq = Water Maze acquisition; WMrev = Water Maze reversal.

	PA	LM	RA	OD	RAM	WMacq	WMrev
PA	—	.038	.121	.305*	.219	−.017	**.036**
LM	.038	—	.169	.093	.171	.037	**.227**
RA	.121	.169	—	.119	.252	.115	**.385****
OD	.305*	.093	.119	—	.199	.071	**.239**
RAM	.219	.171	.252	.199	—	.241	**.456****
WMacq	−.017	.037	.115	.071	.241	—	**.547****
mean	.133	.101	.155	.157	.216	.089	**.315**

Table 6
Factor loadings from a principal component analysis (n = 58) of animals' performance on six learning tasks and during reversal of a previously learned response in the water maze.

	General Factor
Passive Avoidance	.12
Lashley Maze	.39
Reinforced Alternation	.57
Odor Discrimination	.37
Radial Arm Maze	.70
Water Maze ACQUISITION	.61
Water Maze REVERSAL	**.86**
Eigen value	2.22
% variance explained	31.74

correlations of the six learning tasks with performance during water maze reversal is most informative. These correlations are relatively high, and the mean correlation between water maze reversal and other tasks was substantially higher than the mean correlation between any other individual task and the other learning tasks.

The results of the principal component analysis are provided in Table 6. The loading of the measure of reversal was high relative to other measures (all of which reflected acquisition of a learned response), again suggesting that attentional disengagement was highly sensitive to animals' general cognitive ability.

A simple linear regression was calculated to predict learning task factor scores based on reversal trial performance in the water maze (Fig. 9). A significant regression was found ($r[1, 56] = 0.65$, $p < 0.001$) such that animals who made more errors during reversal trials also had higher factor scores (indicative of poorer performance) obtained from the battery of learning tasks.

4. Study 3

In the two studies described above, an individual differences approach was used to assess the degree to which attentional disengagement was representative of animals' general cognitive ability. In both of those studies, measures of reversal (the ability to disengage from a learned behavioral tendency) loaded highly on a principal factor that represented general cognitive performance, and moreover, strongly differentiated between animals that were designated as "smart" or "dull." In Study 3, a different approach was used to address this same question. In this study, two groups of animals (young and old) were used that we (and others) have previously established to express distinct differences in general cognitive abilities (Matzel et al., 2008; Matzel, Wass, Kolata, Light, & Colas, 2009; Matzel et al., 2011). The performance of young and old animals was assessed on a mouse analog of a "Stroop Test" (Stroop, 1935), in which the mice must ignore a previously reinforced olfactory discriminative cue in order to efficiently use a visual cue to guide their search for food. As suggested by the two studies reported above, we anticipated that performance during the Stroop testing would be highly sensitive (relative to simple discrimination learning) to cognitive differences between young and old animals such that young mice would be able to disengage from previously relevant information more efficiently than old mice.

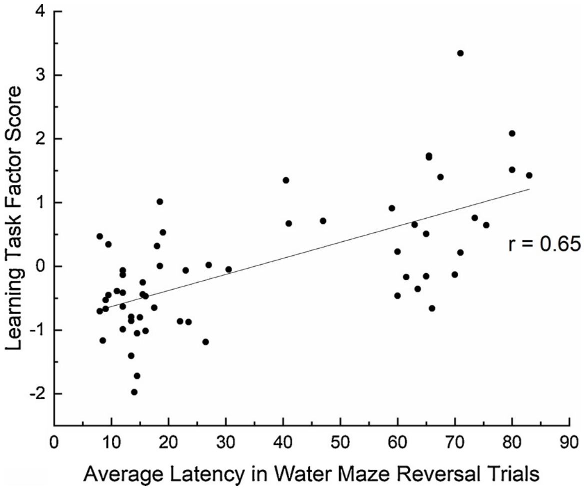

Fig. 9. Linear regression of learning task factor score as predicted by water maze reversal performance. Animals that performed poorly in water maze reversal (indicated by high average latency during reversal trials) tended to have higher learning task factor scores (indicating lower general cognitive ability).

4.1. Methods

Subjects. Two groups of male CD-1 mice were used in this study. One group of animals arrived in our laboratory at approximately 45 days of age (“YOUNG”; n = 10) and a second group arrived at approximately 15 months of age (“OLD”, n = 11). At the time of critical behavioral testing, the two groups were approximately 4 and 18 months of age (roughly estimated as the equivalent of 20 and 70 year-old humans; Crawley, 2000). A the start of behavioral testing, young mice ranged from 26.4 to 36.4 g, and aged mice from 31.1 to 42.9 g.

Animal housing, maintenance, and food deprivation followed the same protocols as described for the prior two studies.

4.1.1. Learning tasks

Odor and Visual Discrimination Training. To assess differences in selective attention it was first necessary to train the animals to perform an odor discrimination and visual discrimination in two distinct contexts (Context ODOR and Context VISUAL, respectively).

Odor Discrimination: In this task, mice were required to obtain a food reward by approaching a corner of the test chamber marked by a single target odor. This odor discrimination task was similar to that described in Study 2 above, although in this case, each animal was required to choose a target odor among four odors, and all animals were trained beyond asymptotic levels of performance.

The odor discrimination chamber consisted of a 60 cm square black Plexiglas field with 30 cm high walls which was located in a dimly lit room (approximately 10 Lux) with a high rate of air turnover. Each corner of the chamber was fitted with a 10 cm wide wall (aligned 45° to each side wall, creating a 10 cm wide flat surface in each corner), which was also constructed of black Plexiglas. Affixed to the base of these interchangeable walls were food cups which were affixed flush with the base of the wall. The flat surfaces of these corner panels could be backlit by a white LED, and each panel had a distinct pattern of holes forming one of four shapes: a circle, an X, a triangle, and two parallel horizontal lines. For odor discrimination training, these patterns were never illuminated.

The food cup affixed to the base of these interchangeable inserts was a square block of black Plexiglas measuring 7.5 × 7.5 × 1.5 cm. 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 (30 mg portion of chocolate flavored puffed rice) location. This food port was covered during training and testing with a sliding piece of opaque Plexiglas measuring 42 × 17 × 1.5 mm. This cover could pivot (in either direction) to expose the food port. All cups also contained inaccessible food in a chamber covered with screen cloth directly beneath the food port. This was intended to distribute the odor of the food reinforcer across all of the food cups, thus insuring that the scent of the reinforcer would not guide the animals’ behavior toward the target cup. A cotton tipped laboratory swab was loaded before each training trial with 25 ul of lemon, mint, cinnamon, or almond flavored extract (McCormick *PURE* Flavor Extracts) extended vertically (2 cm) from the back corner of each cup. Mint was always the target odor and was associated with the only cup that contained the accessible food reinforcer.

Each animal received one day of acclimation and four days of training. On the acclimation day, the animals received four trials in order to train them to push the pivoting door to allow access to the food ports. During these acclimation trials the cotton tip laboratory swabs were placed in their relevant locations, but were not loaded with odor extract and only one (of the four) food ports was baited with a reinforcer. On the first acclimation trial the animal was placed into a perforated transparent Plexiglas cylinder (11 cm in diameter and 12.7 cm in height) located in the center of the training chamber for 20 s, after which the cylinder was removed to allow the animal to venture into the field. On this trial, the pivoting doors on the food cups covered only half of the food port. On the three subsequent trials (6 min ITI), the pivoting door was progressively closed so that by the fourth trial the food port was completely covered. The location of the baited food cup occupied a different corner of the field on each of these four trials.

On the subsequent four training days, each animal received five training trials on each day. During this phase, the cotton tipped swabs were loaded with 25 ul of either mint, lemon, almond, or cinnamon extract. On these trials, an accessible food reinforcer was located under the pivoting door associated with the mint odor. (On only the first trial, an additional reinforcer was placed on the edge of the target cup.) At the beginning of each training trial the animals were once again placed in the clear Plexiglas cylinder located in the center of the apparatus for 20 s. The animal was then released, and remained in the field until the food associated with the target odor was retrieved. At the end of each trial, the animal was returned to a holding chamber for a 6 min ITI, during which time the food cups were rearranged (i.e., located to different corners), but mint always remained as the target odor. For each trial, the number of errors to retrieve food was recorded. An error was constituted by the animal pushing a nontarget pivoting door enough to expose the food port, and/or returning to a previously opened nontarget cup.

Visual Discrimination: In this task, the animals performed in a unique chamber and learned to choose the target visual symbol among four possible choices to locate food. The visual discrimination box was made distinct from the odor discrimination box by the addition of vertical white stripes on the walls measuring 1.9 cm in width and spaced 1.9 cm apart. The procedure was the same as described for odor discrimination with the exception that the cotton laboratory swabs were not loaded with extract and that the visual cues (back lights) were illuminated. The LED backlights were formed by a pattern of backlit holes that formed one of four shapes, each approximately 6 cm high: a circle, an X, a triangle, and two parallel horizontal lines. Here the mice were trained to associate the two horizontal lines with the location of the reinforcer. Again, the animals received five training trials/day for four days.

4.1.2. Disengagement task

Attentional Disengagement Testing. Following training on odor and visual discrimination, the animals were given additional overtraining trials upon which they received four odor discrimination trials and four visual discrimination trials separated by four hours on each of three training days. After seven total days of training on both the odor and visual discrimination (with 32 training trials on each task), all animals had reached asymptotic levels of performance (defined as a total of two or fewer errors over the final

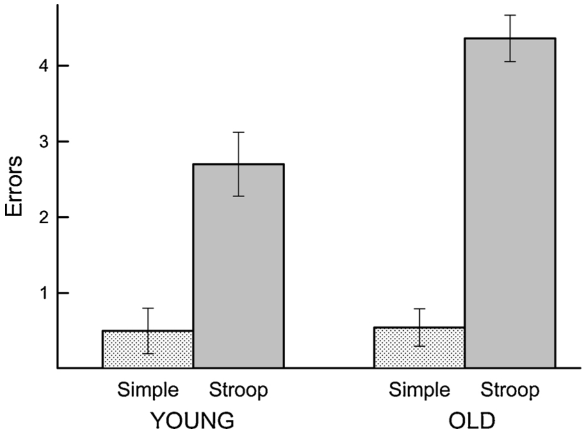

Fig. 10. Average performance on simple discrimination and Stroop test separated on the basis of age (OLD v. YOUNG). During the simple discrimination task, OLD and YOUNG animals make a similar number of errors, on average. Performance in the Stroop test (which requires that animals ignore, or disengage from a relevant distractor) shows that OLD animals make significantly more errors than YOUNG animals.

four training trials in either the visual or odor discrimination task). Following these overtraining trials the animals performed a complex discrimination task to assess attentional disengagement. On these trials, the odor cues from odor discrimination training were introduced into the VISUAL discrimination box, and thus acted as salient task-relevant distracters. (The mint odor, which served as the target cue during odor discrimination training, was always located on a food cup that conflicted with the target visual cue.) Failure to ignore the odor cues would impair visual discrimination performance. Animals received four such trials, and the total number of errors was once again recorded. Previously, using a similar task, the ability to effectively attend to target cues and to ignore task-relevant distracters has been reported to be a measure of selective attention and was found to be related to be related to animals' general cognitive performance (Kolata et al., 2007).

4.2. Results

Of principal interest was the performance of YOUNG and OLD animals on the simple visual discrimination, and subsequently, on the visual discrimination in the presence of the conflicting odor cues. Fig. 10 illustrates the performance of YOUNG and OLD animals on the last four trials of the simple visual discrimination, and on the four trials of visual discrimination when the odor distractor was present in the test chamber.

All animals received extensive over-training on the simple visual discrimination, thus it is not surprising that OLD animals attained a level of competence similar to YOUNG animals (Matzel et al., 2009). When the odor distractor was added to the visual test box, all animals exhibited an impairment in choice performance (i.e., an increase in errors), although the OLD animals appeared more severely impaired than the YOUNG. This was confirmed by a two-way ANOVA (simple vs. complex discrimination; OLD vs. Young), where a main effect of age was observed ($F[1, 38] = 5.23$, $p < .03$), an effect of type of discrimination was observed ($F[1, 38] = 64.51$, $p < .001$), and an interaction of age and type of discrimination was observed, ($F[1, 38] = 4.66$, $p < .04$). A planned comparison revealed a significant difference between YOUNG and OLD animals during the Stroop phase of testing ($F[20] = 5.92$, $p < .02$]).

These results indicated that with sufficient training (on a sufficiently simple task), young and old animals can attain similar levels of competence (also see Matzel et al., 2009). However, despite this similar performance, old animals were more severely impacted by the introduction of task-relevant distractors, i.e., they were less able to disengage from previously learned behavioral tendencies.

5. Discussion

In the first two studies described above, we observed that measures of attentional disengagement were heavily "*g* loaded" relative to other measures of cognitive ability that are less explicitly dependent on such disengagement. In Study 1, we found that the two tasks that were most heavily *g* loaded amongst the eight tasks examined in our battery (see Table 3) are the two tasks that specifically require attentional disengagement to complete: Lashley maze reverse navigation errors (0.79) and Lashley maze reversal approaches to a now empty food cup (0.81). These two tasks are proposed to be measures of attentional disengagement because they both specifically require an animal to disregard previously (but no longer) relevant information and/or response tendencies and to adopt a new (competing) set of rules/responses to receive reinforcement. In the case of the Lashley maze reversal measurement, successful mice are required to abandon (i.e., disengage from) a set of learned egocentric navigational information that has recently been overtrained (during initial acquisition). Mice in this phase learned a specific path (e.g., turn right, then turn left, then turn right…) that was the most efficient route to reinforcement. The reversal task measurement captures how quickly and efficiently an individual can abandon that previously learned tendency and learn a new path through the maze to find reinforcement. Individuals who can efficiently disregard previously learned navigation rules and learn a new path through the maze were found to have higher overall estimates of *g*. This was also true of our second measure of attentional disengagement, the Lashley maze reversal approaches. In this measurement, we capture how quickly an individual can disengage from the recently over-trained tendency to approach a food cup (in what was previously the “goal area” of the maze) containing reinforcement. Individuals that are able to quickly abandon this in favor of approaching a new area for reinforcement (i.e., those who can disengage quickly) were found to have higher overall estimates of *g* as evidenced by the significant linear regressions using the reversal measures to predict *g* (see Fig. 5).

In Study 2, a task that specifically requires attentional disengagement (the water maze reversal task) was more heavily *g* loaded (0.86; Table 6) than six leaning tasks that were not explicitly dependent on disengagement. In fact, while water maze acquisition was moderately “*g* loaded” (0.61), water maze *reversal* loading was substantially higher (0.86). This result was obtained despite all animals obtaining similar levels of spatial navigation performance during initial acquisition (see Fig. 7). Like the reversal trials of the Lashley maze, this reversal procedure required the animals to abandon old, now irrelevant information (in this case, the previously learned location of the escape platform) and devote its cognitive resources to locating the platform in its new location and developing a new spatial map to continue to locate this new location in future trials. Similar to the results discussed from Study 1, we found that mice with high *g* scores were able to more quickly succeed in this reversal phase of training, resulting in a high loading of the reversal trial measurement on the general cognitive factor (0.86; Table 6). Furthermore, we found that the water maze reversal measure (similar to the Lashley maze reversal tasks in Study 1) was a significant predictor of general cognitive ability (see Fig. 9).

Study 3 further addressed our hypothesis that measures of attentional disengagement should be strongly representative of general intelligence by examining performance on the Stroop test (which is dependent on attentional disengagement) across individuals with demonstrably different general cognitive abilities. Previously published literature has established that general cognitive abilities decline significantly across the lifespan of mice (Matzel et al., 2008, 2009; Matzel et al., 2011). Mice in both the “old” and “young” conditions were initially over-trained in a simple discrimination task that required the mice to learn context-specific cues (visual or odor cues) to find a reinforcement. Specifically, in the “visual box” mice were trained that reinforcement would always be marked by a specific visual cue, while in another context (the “odor box”), reinforcement would always be marked by a specific odor cue. This simple discrimination tasks makes specific demands on attentional maintenance *only* (i.e., no demands on attentional disengagement; animals need only to attend to a single rule with no interference from previously learned rules). Accordingly, all animals (young and old) were able to achieve similar levels of performance (also see Matzel et al., 2009). Following the simple visual and odor discrimination tasks, odor distractor cues were introduced to the “visual box” to create a paradigm that mimics that of the human Stroop test. To be successful in the Stroop test, an individual must be able to attend to information specific to the current test conditions (e.g., a context) and disengage from information that is irrelevant to that test condition (e.g., in the visual box, an individual must attend only to visual information and disengage from any conflicting odor stimuli it may encounter). As expected, older mice (who exhibit significant declines in general cognitive performance) made significantly more errors during this test relative to younger mice (see Fig. 10). In sum, all animals were able to perform similarly in the simple discrimination task (requiring only attentional maintenance), while young mice excelled in the Stroop test (which requires attentional disengagement) relative to the older mice. These results support the hypothesis that attentional disengagement can serve as a significant predictor of general cognitive ability.

Overall, the results described here suggest that *g* is strongly related (and possibly dependent) on an animal’s capacity to disengage from irrelevant distractors, supporting a recent assertion by Engle (2018). However, seemingly contradictory results have appeared in the literature. For example, a human behavioral study performed by Redick et al. (2016) found that for some multitasking measures, the maintenance component of selective attention was the most highly correlated with measures of general intelligence. These differences seem contradictory to our results reported here, though it is important to note that their measure of *g* was performance on a reading comprehension test, while the test batteries used in our report might reflect a more broadly encompassing measure of *g* in mice (Kolata et al., 2007, 2008; Matzel et al., 2003, 2006, 2008).

Additionally, a recent animal study makes a conclusion that is nominally inconsistent with the present results. Madden, Langley, Whiteside, Beardsworth, and van Horik (2018) reported that pheasants which are slow to reverse learned behavior (in this case, spatial and color discrimination tasks) exhibited *increased* survival rates (a measure that correlates with *g* in humans, see Ford, Bergmann, Boeing, Li, & Capewell, 2012) compared to those who were quick to reverse (i.e., those which exhibited less attentional disengagement expressed increased behavior indicative of high *g*). However, this interpretation is complicated by the fact that animals were not initially trained to the same level of competency in the discrimination tasks (an objective that is difficult to attain when working with animals in the wild). In other words, it is not possible to say whether an animal was truly “slow to reverse” relative to another since we cannot determine if they were initially trained to the same asymptotic level, i.e., “smarter” animals appeared to obtain initially higher levels of competency and thus would be less inclined to adopt a reversal of this more strongly instantiated behavioral tendency. In the present studies, all animals were trained to a similar stable asymptotic level of initial competence before implementing the reversal procedure(s). Additional work will be necessary to determine if this can account for the seemingly contradictory results, and more generally, whether the capacity for attention disengagement is a principal determinant of variations in intelligence.

It should be noted that the interpretation of the general cognitive factor that we have reported is itself complicated. While we interpret the principal factor derived from a battery of cognitive tests to be reflective of animals’ general cognitive capacity, other general influences could also be reflected in this factor. In a series of prior papers, general influences such as stress reactivity, exploratory tendencies, and anxiety have been dissociated from the principal factor, leading us to favor the interpretation that this factor is reflective of a general influence on cognitive abilities (e.g., Grossman, Hale, Light, Kolata, & Matzel, 2007; Light et al., 2008; Matzel et al., 2006). However, a further complication is the uncertain nature of *g* itself. For many years it has been a common assumption that *g* is a latent cognitive variable that determines performance on cognitive tests and ultimately explains the ubiquitous positive manifold (i.e., positive correlations between cognitive abilities). In recent years there have been a number of alternative theories proposed to explain *g* that are important to consider in conjunction with our findings. One of these alternative explanations, the mutualism theory, explains the positive manifold by way of initially uncorrelated cognitive abilities becoming correlated through mutually beneficial interactions (van der Maas et al., 2006). Through this lens, attentional disengagement might load most heavily on *g* due to its necessity in shifting between cognitive abilities (i.e., each time control is shifted from one cognitive ability to another, attentional disengagement must be exercised to cease a previous behavior before engaging in a new one). A second alternative theory of *g*, the process-overlap theory, explains the positive manifold through overlapping demands placed on domain-general executive processes by cognitive tests (Kovacs & Conway, 2016). Again, attentional disengagement loading heavily on *g* aligns with this theory, as cognitive tasks in nature will rarely depend on the consistent taxing of a single domain of ability. Attentional disengagement is required to mediate the transition of control between these various domain-general executive processes and thus would load heavily across a battery of intelligence tests encompassing multiple domains of cognitive abilities as it has shown to in the present studies.

In total, results from these three studies provide support for the hypothesis that measures of attentional disengagement are strongly predictive of general cognitive ability. Similar to data reported in human behavioral literature (Engle, 2018; Martin et al., 2020; Shipstead et al., 2016), we report that tasks which intentionally require disengagement from old, now irrelevant information are strongly predictive of general cognitive ability. Based on these similarities to the human literature, future studies aimed at developing tasks analogous to pure tests of the maintenance component of selective attention (rather than disengagement) would allow us to more precisely determine its relationship to *g*, a strategy that has been employed in the human literature (Engle, 2018; Martin et al., 2020; Shipstead et al., 2016). Furthermore, future studies should evaluate how attentional disengagement compares and contrasts with internal attention. Given that the two share qualitative characteristics (e.g., both involve a momentary hierarchy of information relevance and a "decision" as to what to engage/disengage with) as well as similar predictive relationships with *g* (Sauce et al., 2014), it would be of great interest to fully understand this relationship.

Author statement

All authors contributed to the collection of data and data analysis reported here. Crawford, Matzel, and Sauce wrote the manuscript.

All authors have approved this submission.

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