

ATTENTIONAL DISENGAGEMENT IS A STRONGLY PREDICTIVE FACTOR OF
GENERAL COGNITIVE ABILITY: INTELLIGENCE DEMANDS FLEXIBILITY

By

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ABSTRACT OF THE THESIS

Attentional Disengagement is a Strongly Predictive Factor of General Cognitive Ability
in Mice

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General cognitive ability (or general intelligence; g) has been widely recognized to influence a broad array of cognitive abilities of both humans and mice. Working memory has also become recognized as a strong predictor of g in both humans and mice. Recent evidence suggests that a component of working memory, selective attention, is responsible for the relationship between working memory and g . In three experiments, we test a hypothesis that emerges from human behavioral studies which suggests that attentional disengagement, a component of selective attention, critically mediates its relationship with g , and therefore should be most strongly predictive of general cognitive performance. Experiments 1 and 2 both assess the factor loadings of selective disengagement tasks on a general cognitive factor derived from larger batteries of cognitive tests and finds that selective disengagement loads more highly than any other measures that place less explicit demands on disengagement. In experiment 3 we demonstrate how groups with known differences in cognitive abilities (young vs. old

mice) differ significantly on measures of attentional disengagement. Our results provide support for the hypothesis that disengagement acts as the latent variable that determines intelligence.

INTRODUCTION

General cognitive ability (c.f. general intelligence; g) is a latent factor that has been demonstrated to play a mediating role in performance across a wide range of cognitive tasks, and is the variable captured by most common “intelligence tests” in both humans (for reviews on this literature, see Jensen 1998; Mackintosh, 1998) as well as in nonhuman animals (Galsworthy et al., 2002; Galsworthy et al., 2005; Matzel et al., 2003). While evidence suggests that g is expressed in these populations, empirical evidence indicates that performance on specific cognitive tasks is not only impacted by g , but also by domain-specific factors (e.g., spatial abilities; Kolata et al., 2008). These data support the hierarchical model of intelligence, which states that g is a high level control that mediates lower-level domain-specific abilities (e.g., reasoning, processing speed, spatial) that are in turn thought to most directly impact performance on tasks that measure those specific cognitive domains (Deary, 2014).

One domain-specific ability, working memory, has been well-documented as a covariate to g both in humans (Conway and Engle, 1995; Engle et al., 1999; Kyllonen and Christal, 1990; Matzel and Kolata, 2010; Süß et al. 2002) and in mice (Kolata et al., 2005; Kolata et al., 2007; Matzel and Kolata, 2010). Widely accepted definitions of working memory describe a cognitive system that uses both storage and processing components to mediate the maintenance of, as well as attention to, task-relevant information (i.e., distribute limited cognitive resources) appropriately in order to complete tasks (Baddeley and Hitch, 1974). This dual component (storage and processing) approach to working memory has led to subsequent findings that while

measures of the storage component of working memory (e.g., “simple span,” the ability to recall a list of words) do not correlate with g , measures thought to require the processing component of working memory (e.g., “complex span,” the ability to recall specific words from a series of sentences) did significantly correlate with g (Daneman and Carpenter, 1980). These results reported by Daneman and Carpenter have subsequently been supported by multiple behavioral studies (e.g., Ackerman, 1987; Colom et al. 2004; Conway and Engle 1995; Engle et al. 1999; Süß et al. 2002). Furthermore, suggestions that working memory efficacy may have a *causal* influence on g (Matzel and Kolata, 2010; Unsworth and Engle, 2007) have been supported by Light et al. (2010) who report that repeated training in tasks that require 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, a processing component of the working memory system. Previously reported empirical 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 the primary component of working memory that underlies the relationship between working memory and g (Kolata et al., 2007). Accordingly, the increases 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). Evidence from human brain imaging studies generally aligned with the reported studies in laboratory animals and has led to the assertion that selective attention is the component

of working memory that is most responsible for its relationship with *g* (for a review on the role of selective attention in working memory and *g*, see Matzel and Kolata, 2010).

Results from initial behavioral studies in humans concerning selective attention and its relationship to *g* are consistent with those from animal studies, finding that measures of selective attention could successfully predict performance in *g* correlated measures (e.g., the prosaccade/antisaccade task; Kane et al., 2001). However, recent studies involving human intelligence have focused on further distinguishing between components of selective attention (i.e., separating the idea of “devoting attention to relevant information” from “disregarding irrelevant information”). Subsequent large-scale human behavioral studies focused on this relationship by assessing relationships between *g*-related tasks to 1) tasks of “direct attention” that aim to require devotion of attention with reduced emphasis on disengaging irrelevant attention (e.g., operation span, symmetry span, and rotation span; Martin et al., 2017) and 2) from tasks that specifically require attentional disengagement (e.g., Raven’s Progressive matrix [RPM], letter set, and number series; Martin et al., 2017). Martin et al. (2017) found that when these two variables can reliably be separated, the attentional disengagement component of selective attention is correlated with *g* measures (such that individuals who can successfully disengage with irrelevant information achieve higher scores on the RPM) while the “direct attention” component has no correlation with *g*. Similar conclusions were also reported by Shipstead et al. (2016).

Lastly, in mice, Sauce et al. (2014) reported that sources of distractions are relevant to the relationship between attention and general cognitive performance.

Namely, they report that attention which protects against environmental distraction (“external attention”) had only a weak correlation with general cognitive performance, while the ability to resist internal sources of distraction (“internal attention;” an attribute that closely resembles a process analogous to disengagement) was strongly correlated with general cognitive ability (Sauce et al., 2014). These results align with the aforementioned human behavioral studies, highlighting the importance of attentional disengagement and its relationship to g .

These studies, in part, led to an assertion by Engle (2018) that the attentional disengagement component of selective attention, rather than the direct attention component, may be the critical aspect of selective attention that makes it such a useful predictor of g . In the following three experiments, we test the hypothesis that, as the human data describes, measures of attentional disengagement in mice should be the mostly strongly predictive of g (i.e., be most heavily g loaded comparable to other measures).

EXPERIMENT 1

In the first experiment, we demonstrate how measures of attentional disengagement are g loaded within a novel battery of seven learning tasks. Five of the tasks were measures of acquisition of learned responses where no attentional disengagement was explicitly required. The remaining two tasks did require attentional disengagement, allowing us to compare the g loading of tasks that do not explicitly require attentional disengagement relative to those that do.

METHODS

Subjects. A total of 69 CD-1 outbred male mice from Harlan Laboratories (Indianapolis, IN) were used. Animals were housed individually in standard shoebox home cages in a temperature-controlled colony room using a standard 12 hour light-dark cycle. Animals arrived in the laboratory at approximately 4-6 weeks of age and were given ad libitum access to food and water except during testing that required food deprivation, where animals were given 120 min access to food starting on the day prior to testing, then each day following data collection. Prior to testing, animals were handled (i.e., held and walked around the laboratory) by experimenters for 60 secs 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.

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 sec 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 secs, 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 and the path taken by the animal to complete the trial were recorded during each trial. Each animal completed five trials.

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 at seven symmetric locations, "nodes," after an initial split dividing the maze in two symmetrical halves. At each of the 14 nodes within the maze, a small hole has been drilled to hold a recessed 14 mg Noyes pellet that serves as the food reward. Before the initial division in the maze sits an alley that originates from a starting box with a removable door where mice begin the experiment. This maze has previously been shown to load heavily (0.49) on a factor analysis describing a general intelligence factor (Waas et. al, 2012). This test involves mice navigating the branch-like structured maze to inspect each node for food. The object of this test is for mice learn the overall structure of the maze and formulate the optimally

efficient path through which it can search each potential food deposit while using the lowest amount of time and energy possible. Mice with high general intelligence will explore the maze in efficient paths (i.e., cross the same node only en route to an unexplored node) while mice with lower intelligences will often take meandering paths and make many errors in exploring the maze.

The efficiency with which an animal searches the maze has been said to be emblematic of inductive reasoning (Waas et al., 2012). The path an animal takes to explore each node in the maze were recorded. We used two measures from the maze: the number of times an animal crossed nodes in the maze (where a perfect score is 24 crossings) as well as the “streak,” or number of node crossings an animal made before making an unnecessary node crossing. For additional details about the construction of this maze, see Waas et al (2012).

Animals were food deprived for approximately 16 hours before testing will begin. 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 sec before opening the gate to the maze. Mice were given access to the maze which will have 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 mins to allow further exploration. Mice were then removed and placed back in its home cage 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 is 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 is 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 five 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 sec, the door was then be opened and the mice will be 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 be 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.

Simple discrimination. Mice were again placed in the start box for 5 sec 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 #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 had four cups in the goal area, all covered with hexagonal lids. One of the four cups were marked by a star as a discriminative cue and only this cup will have accessible food. Lid errors were recorded as previously described, while animals could also make errors any time that he 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).

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 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.

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 lid and failed to remove it. Thus, errors were recorded if an animal approached a cup or made contact with the lid without retrieving the food. The trial was completed (and no error scored) if an animal successfully removed the lid to retrieve the food reward. Trials 7-12 were identical to Trials 1-5.

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, not on a

platform, was placed in what was previously the start box. Animals began the trial placed in the center of the goal area facing an empty food cup platform. 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). 2. Maze errors were recorded as the animal traversed the maze toward the start box (which now contains 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.

Statistical Analyses. All statistical analyses were completed using IBM Statistics Version 25. To assess *g* loadings of each individual task and create factor scores, average aggregate score across each all tasks for an individual, we used a principal component analysis.

RESULTS

In this experiment, animals' acquisition were recorded on nine tasks consisting of the Morris water maze, the decision tree maze, a straight alley food retrieval latency measurement, a straight alley object permanence task with 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 a principal factor analysis to determine the *g* loading of each individual task. Results of this analysis are provided in Table 1. Factor scores were also obtained from the factor analysis. The factor score for each individual was a measure of the average aggregate performance of the individual across all nine tasks in the battery, weighed by the factor loading of each component part (found in Table 1). Factor scores are reported such that lower scores indicate better aggregate performance, and we report factor scores for all 69 animals that ranges from -1.19 to 4.21, where negative values indicate aggregate performance better than average, and positive values indicate aggregate performance that was worse than average.

Table 1

Factor loadings from a principal component analysis (n = 69) of animals performance on the nine component tasks of the learning battery. Measures of attentional disengagement are reported in boldface.

	General Factor
Straight Alley Latency	0.27
Straight Alley Lid Fails	0.73
Straight Alley Lid Discrimination	0.47
Lashley Maze Errors	0.68
Lashley Maze Puzzle Approaches	0.55
Lashley Maze Reversal Errors	0.79
Lashley Maze Reversal Approaches	0.82
Water Maze	0.35
Decision Tree Maze	0.26

Eigen value 3.07

% variance 34.11

Results from the principle component analysis of the nine component learning battery show how each component was *g* loaded, the presumed general factor described in Table 1 above (Eigen value = 3.07; describing 34.11% of variance). The analysis reports that the two measures of attentional disengagement, Lashley maze reversal and Lashley maze reversal approaches, had the two highest loadings on *g* (0.79 and 0.82, respectively) of all the nine component measures, which otherwise ranged from 0.26-0.73. This result is consistent with the hypothesis that measures of attentional disengagement are most highly representative of general cognitive performance.

EXPERIMENT 2

As in the prior experiment, 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 experiment, five of the six tasks that were used were different than those used in Experiment 1, and the reversal task required that the animals adapt to a new escape location in a spatial water maze (as opposed to the reversal of a previously learned egocentric path as was the case in Experiment 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, Sokoloff, Rosenberg, Palmer, & Millen, 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-hour light/dark cycle. In order to minimize any differential stress responses due to experimenter handling, we handled the mice for 90 secs a day for a period of seven days prior to the start of the experiment. 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 hours prior to the start of training (and thus encompassing the "rest" day between successive tasks). During the deprivation period, animals were provided food in their home cages for 90 min/day during the last 2 hrs of the light cycle, and thus were approximately 16 hrs 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 (Matzel et al., 2006, 2008; Kolata et al., 2007, 2008). All animals were tested in a series of six independent learning tasks in the following order: Lashley III maze, passive avoidance, spatial water maze, odor discrimination, and reinforced alternation) that 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. The spatial water maze encourages the animals to integrate spatial information to efficiently escape from a pool of water. 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 food. Testing order was designed so that tasks that impinge on similar information processing, motor, or motivational demands were separated to the greatest possible extent. Each test is described in detail below.

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 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 x 12 cm (l x w) and that is illuminated by a dim red light was used for both acclimation and testing. An enclosed platform (70 x 45 x 45 cm, l x w x 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 leaves the platform and makes contact with the grid floor it initiates the aversive stimuli.

Animals are 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 sec. 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.

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 secs. 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 sec. After locating the platform or swimming for 90 secs, the animals were left or placed on the platform for 10 secs. Upon a trial's completion, the animals were removed for 20 mins 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.

To assess the animals' capacity to disengage from a well-learned response, a third day of training was added 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 sec 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 to find the platform was recorded for each trial. Each animal's performance on Trials 5 and 6 was averaged and served as that animal's index of learning for purposes of principal component analysis.

Odor Discrimination (OD). Rodents are adept at using odor to guide their reinforced behavior. This task is modified from one developed by Sara, Rouillet, & Przybyslawski (1999) but scaled for use with mice. In this task, mice navigate through a field using unique odors to guide them. The animals learn to choose the food cup that contains 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 food cup was placed in three corners of the 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 a food cup. On each trial, food could be retrieved from the cup marked by the mint odor. At the end of each trial the food 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 an incorrect food 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 sec, 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 sec ITI. On the second trial, this procedure was repeated, but the right door was closed and the left door open. After a 20 sec 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 sec 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 centimeters from a 15 cm diameter central hub. The maze was elevated 25 centimeters 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.

RESULTS

In this experiment, 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 in a factor analysis of general cognitive performance, and the degree to which the reversal performance was indicative of an individual animal's cognitive ability. 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 from this analysis were used to characterize each animal's general cognitive ability. The results of this analysis are provided in Table 2. 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).

Table 2

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

	General Factor
Passive Avoidance	.22
Lashley Maze	.48
Reinforced Alternation	.63
Odor Discrimination	.38
Radial Arm Maze	.76
Water Maze	.47

Eigen value 1.63

% variance 27.10

Figure 1 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; $n_s = 14$) of general learning abilities as determined by the factor scores obtained from the analysis summarized in Table 2. 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 during the first 30 sec of Trial 1 during reversal (Smart mean = 44.1%, s.e. = 5.2%; Dull mean = 37.8%, s.e. = 4.9%; $t[1,26] = .87$, ns).

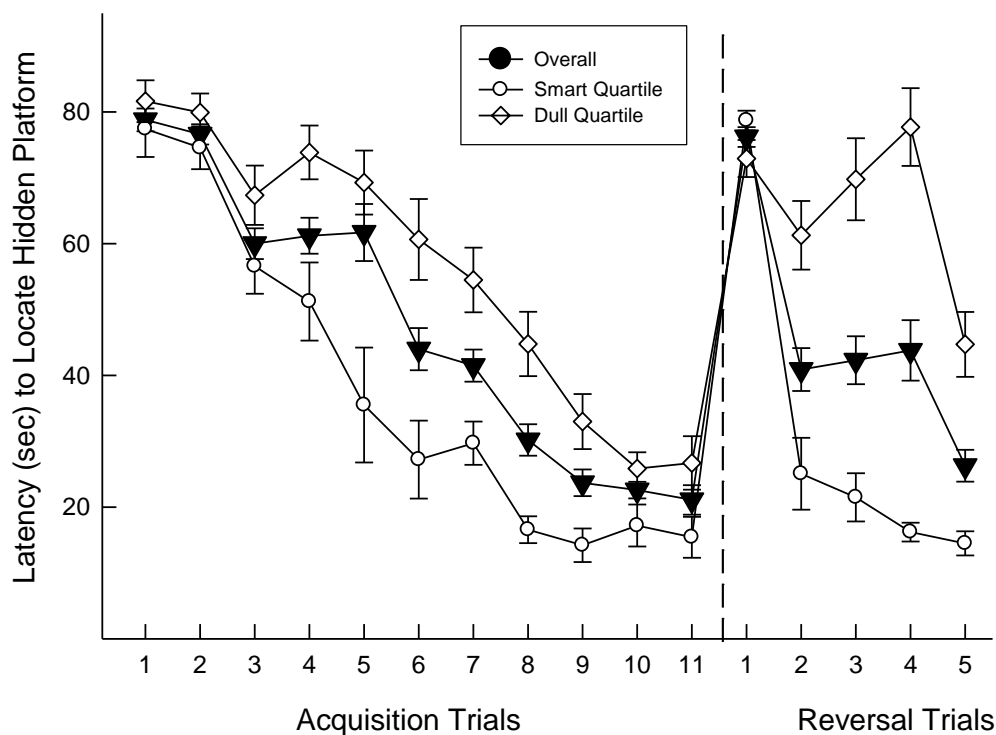


Figure 1. Acquisition and reversal performance in the spatial water maze. Illustrated is the average performance of all animals ($n = 58$), as well as the performance of the animals representing the upper and lower quartiles ($n_s = 14$) of general learning abilities as determined by the factor scores obtained from the analysis summarized in Table 3. 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.

Figure 2 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 and dull animals was significantly greater during reversal than during acquisition.

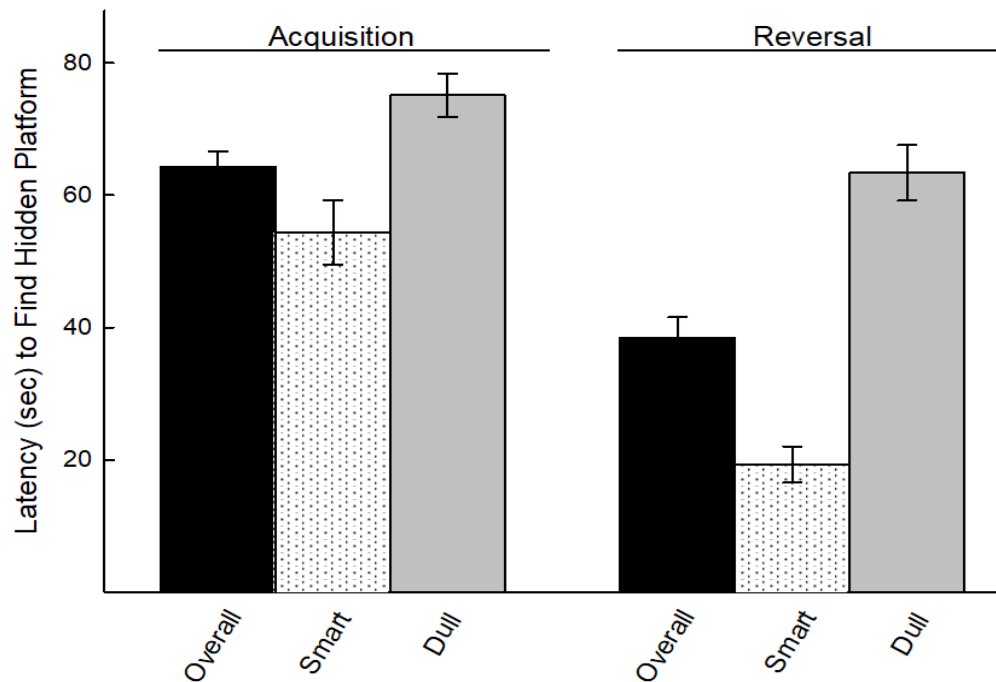


Figure 2. Acquisition and reversal performance in the spatial water maze. Bars represent average performance of all animals ($n = 58$), as well as by upper and lower quartiles ($ns = 14$) of general learning abilities as determined by factor scores obtained from analysis summarized in Table 3. Results 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.

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. The results of the principal component analysis are provided in Table 3. 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 cognitive disengagement was highly sensitive to animals' general cognitive ability.

Table 3

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 31.74

EXPERIMENT 3

In the two experiments 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 experiments, 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 Experiment 3, a different approach was used to address this same question. In this experiment, 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, Grossman, Light, Townsend, & Kolata, 2008; Matzel et al., 2011; Matzel, Wass, Kolata, Light, & Colas, 2009). 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 experiments reported above, we anticipated that performance during the Stroop testing would be highly sensitive to cognitive differences between young and old animals.

METHODS

Subjects. Two groups of male CD-1 mice were used in this experiment. 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 equivalent to 20 and 70 year-old humans; Crawley, 2000). At the start of behavioral testing, young mice ranged from 26.4-36.4 g, and aged mice from 31.1-42.9 g.

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

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 navigate through a square field using a distinct odor to guide their search for food. This odor discrimination task was similar to that described in Experiment 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 x 7.5 x 1.5 cm. In the center of the block was a food port measuring 1.5 cm in diameter and 1 centimeter 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 x 17 x 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 sec, 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 sec. 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.

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 day of training) 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 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 animals' general cognitive performance (Kolata, Light, Grossman, Hale, & Matzel, 2007).

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. Figure 3 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.

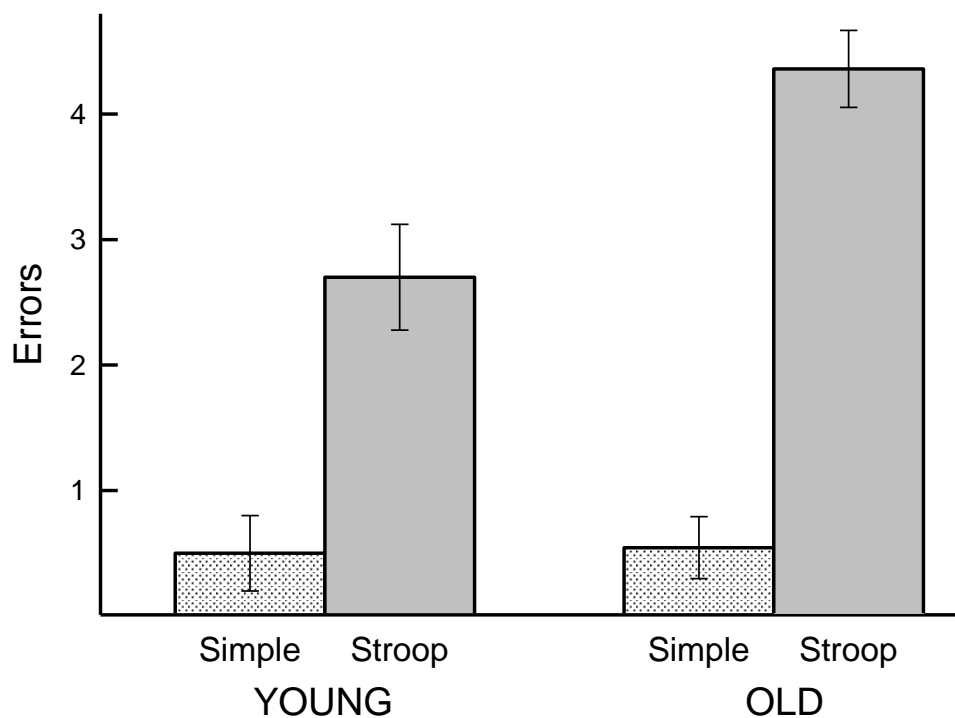


Figure 3. Average performance on simple discrimination and Stroop test separated on the basis of age (OLD v. YOUNG). During the simple discrimination task, OLD and YOUNG animals make a similar number of errors, on average. Performance in the Stroop test shows that OLD animals make significantly more errors than YOUNG animals.

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. 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.

DISCUSSION

In each of the first two experiments described above, we find that measures of attentional disengagement are significantly *g* loaded relative to other measures of cognitive ability that are less explicitly dependent on such disengagement. From Experiment 1, we find that the two tasks that are most heavily *g* loaded amongst the nine tasks examined in our battery (see Table 1) are the two tasks that specifically require attentional disengagement to complete the Lashley maze reverse navigation task (0.79) and the Lashley maze reversal approaches measure (0.82). 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 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 over-trained during the initial Lashley maze procedure. Mice in this phase have all learned that following a specific, rigid path (e.g., turn right, then turn left, then turn right...) will successfully lead to reinforcement. The reversal task measurement captures how quickly and efficiently an individual can ignore 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 measures 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 measures of g .

In Experiment 2, a task that specifically requires attentional disengagement, the water maze reversal task, was more heavily g loaded (0.86; Table 3) 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 1). 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 Experiment 1, we found that mice with high g scores were able to more quickly succeed in this reversal paradigm, resulting in a high loading of the reversal trial measurement on the g factor (0.86; Table 3).

Experiment 3 further addressed our hypothesis that measures of attentional disengagement should be strongly representative of general intelligence by examining performance on the Stroop test (a task that requires 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; Matzel et al., 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. In this simple discrimination, 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 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 Figure 3). This supports the hypothesis that attentional disengagement (in this case, performance on the Stroop test) can serve as a proxy for general cognitive ability.

There are, however, examples of studies in the literature that report contradictory findings to ours. For example, a human behavioral study performed by Redick et al. (2016) found that for some multitasking measures, the attentional component of selective attention (i.e., “direct attention,” actively attending to relevant information rather than disengaging from irrelevant information) 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 arguably reflect a more broadly encompassing measure of *g* in mice (Matzel et al., 2003; 2006, 2008; Kolata et al., 2007, 2008).

Additionally, a recent animal study makes a contradictory conclusion about the role of reversal behaviors (i.e., attentional disengagement). Madden et al. (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 et al., 2012) compared to those who were quick to reverse (i.e., those which exhibited decreased attentional disengagement also expressed increased behavior indicative of high g , contradicting our results). However, this study was confounded by the fact that animals were never trained to the same level of competency in the discrimination tasks. 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 strongly instantiated behavioral tendency. This is a confound that our study does not have, as we trained every animal to asymptotic levels of initial competence before implementing a reversal procedure.

In total, we found that results from these three experiments 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., 2017; Shipstead et al., 2016), we report that tasks which intentionally require disengagement from old, now irrelevant information provide the most predictive information about general cognitive ability. Based on these similarities to the human literature, future studies aimed at developing tasks analogous to tests of the “direct attention” component of selective attention, rather than attentional disengagement, to confirm it is uncorrelated to g as suggested by the human literature (Engle, 2018; Martin et al., 2017; Shipstead et al., 2016) may be warranted. 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 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.

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