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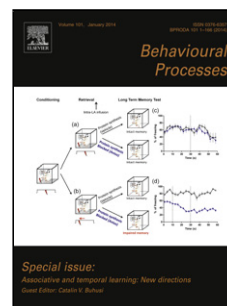
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Fast- and slow-exploring pigeons differ in how they use previously learned rules

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## Highlights

- Exploratory behaviour is related to performance on a line-orientation generalization
- Fast-explorers have steeper generalization gradients compared to slow-explorers
- There is a link between information use, post-acquisition, and personality.

## Abstract

Several studies report a correlation between exploratory behaviour and performance on tests of cognitive ability. Exploration may influence learning because less exploratory animals are less likely to come in contact with to-be-learned stimuli. Alternatively, the way information available in the environment is processed could influence the rate of exploration. Pigeons are one of the most-studied species used to examine the mechanisms underlying cognitive abilities, but have not been used to examine the relationship between these abilities and animal personality. Here, twelve pigeons were first tested in a novel environment to assess repeatability in exploratory behaviour. Pigeons were then trained to discriminate between two visual stimuli: lines oriented at 90° (vertical, the S+) and 135° (the S-). After training pigeons underwent generalization testing with ten additional visual line orientation stimuli. We found exploratory behaviour was related to generalization performance: fast-explorers had steeper generalization gradients compared to slow-explorers. This effect was only seen in the direction towards the S-. These results suggest that birds with different exploratory styles differ in how they use previously learned information. Further testing is needed to confirm which cue(s) (S+ or S-) control the behaviour of fast-explorers.

**Keywords:** Animal personality; Cognition; Exploratory behaviour; Generalization; Individual differences; Pigeon

## 1. Introduction

How an animal searches or explores the environment affects the amount of information that animal encounters. Then again, how an animal processes new or updates old information may affect that animal's movement through the environment. Exploratory behaviour is one of the most-studied animal personality traits (Reader, 2015; Reale et al., 2007; Stamps, 2015), has been shown to affect fitness (Dingemanse et al., 2004; Smith and Blumstein, 2007), and is heritable (Drent et al., 2003). Several recent empirical studies have examined the relationship between variation in exploration of a novel environment and variation in performance on cognitive tests (see Table 1). The results from this limited, but growing, body of work are inconclusive as to: (1) whether exploration and cognition co-vary and (2) what the nature of the relationship is (reviewed in Stamps, 2015; Griffin et al., 2015). Perhaps the strongest support for the former comes from studies conducted in laboratory mice showing that general learning ability is correlated with exploratory behaviour: mice that score higher in general learning ability (as measured across a suite of tasks) also explore more (Light et al., 2011; Matzel et al., 2006, 2003, see Table 1 for list of cognitive tasks used.)

In contrast to the idea of a general learning ability, studies examining performance on independent tasks have found evidence suggesting that the nature of the relationship between cognition and exploration is task dependent (Table 1, column headed: Outcome) and, in at least one case, sex-dependent (Titulaer et al., 2012). For example, Fast-explorers learn new appetitive tasks more quickly than slow-explorers (black-capped chickadees *Poecile atricapillus* Guillette et al., 2009; Panamanian bishop fish *Brachyrhaphis episcopi* DePasquale et al., 2014), whereas slow-explorers perform better than fast-explorers on reversal learning (black-capped chickadees Guillette et al., 2011; great tits Verbeek et al., 1994; but see Amy et al. 2012 where the opposite was found in great tits) or avoidance learning tasks (great tits

Exnerová et al., 2010). Most of the experiments on exploratory behavioural and cognition have focused on variation in learning speed (also called learning rate, e.g., trials to reach learning criteria, marked with ‘A’ for information acquisition in Table 1). Tests of other cognitive processes, notably how animals’ respond to novel stimuli, that share features with stimuli they have been previously trained with (i.e., generalization, marked ‘U’ for information use in Table 1) and other predictions laid out by Sih and Del Giudice (2012), are lacking. To better understand how cognition and personality may be related it is imperative to study cognition on more than just one level. That is, to examine more than just learning rate.

Thus, in the current study, our goal was to test if another aspect of cognition, generalization of previously learned rules, is related to how animals explore a novel environment. In this way we are testing if personality is related not to information acquisition, but to information use (i.e., processing once the information has already been acquired, Shettleworth, 2010). The current study was designed as a follow-up to a recent study (Guillette et al., 2015) we conducted with black-capped chickadees in which we examined performance accuracy in an acoustic discrimination task. In this experiment chickadees were trained to discriminate between two sets of acoustic stimuli, responses to exemplars from one category (S+) resulted in a food reward, and responses to exemplars from the other category (S-) did not. Once birds had reached a given performance criterion we measured performance accuracy to novel stimuli that shared acoustic features of the original S+ and S- categories. Accuracy was defined as the number of responses to the S+ stimuli divided by the total number of to all S+ and S- stimuli. We found no difference in performance accuracy when slow- and fast-exploring chickadees were tested with familiar exemplars (i.e., those used in training) after reaching criteria. There was a difference, however, in performance accuracy when chickadees were given novel-exemplars (i.e., those belonging to the same category, but not used in training): slow-exploring chickadees were more accurate than fast-explorers (Guillette et al.,

2015). We suggested that fast-exploring chickadees may learn more absolute features of stimuli, while slow-explorers may learn more general features of stimuli.

In the current experiment, homing pigeons (*Columba livia*) were used as a model species to examine if slow-exploring and fast-exploring birds differ in the way they generalize responses to novel visual stimuli, line orientations, after being trained on a binary line-discrimination task. Pigeons were first run in a novel environment task to assess exploratory behaviour. Each pigeon was then trained to discriminate between a reinforced (S+) and a non-reinforced (S-) visual stimulus (two different line orientations) in an operant chamber. Upon successfully learning the discrimination, the responses of each pigeon to novel line orientations with varying degrees of similarity to the trained S+ and S- stimulus were tested. The cognitive task in the current study is based on a classic psychological testing paradigm similar to that of Honig et al. (1963). We used a modified version of this task, where the stimuli vary in line orientation (different degrees of rotations, with 90° as vertical similar to Bloomfield 1967). The resulting generalization gradients allow comparison of discrimination performance: animals that produce steeper generalization gradients discriminate between test stimuli more precisely than animals that produce shallower gradients.

We predict that fast-explorers will learn more about the absolute features of a stimulus, as proposed by Guillette et al., (2015), and thus will respond less to novel modified stimuli resulting in steep generalization gradients. Slow-exploring birds, because they are more likely to learn about general features of stimuli, are more likely to generalize their learned response, thus responding more to novel stimuli and have shallower generalization gradients.

## **2. Material and methods**

### **2.1 Subjects**

Twelve homing pigeons (*Columba livia*; five male and seven female), were obtained from a local breeder (Vandermeer Farms, Sherwood Park, Alberta). Each pigeon was housed individually in a metal cage ( $42 \times 47 \times 42$  cm) in a colony room that was maintained on a 12:12-hour light:dark cycle with light onset at 08:00 h. Pigeons had visual and vocal, but not physical, contact with one another. Standard poultry grit and vitamin-supplemented water (Vetoquinol, Polytonine A Complex) were available *ad libitum* and each pigeon was maintained at 85% of its free-feeding weight on a diet of Kee Tee pigeon pellets. No pigeons had prior open field (i.e., novel environment) experience. All pigeons had been subjects in either touch screen or touch key operant experiments but were naïve to the current experimental stimuli.

All animal studies were conducted in accordance with the Canadian Council on Animal Care Guidelines and Policies and with approval from the Animal Care and Use Committee for Biosciences for the University of Alberta.

## **2.2 Apparatus**

### **2.2.1 Novel environment room**

The novel environment ( $185 \times 222$  cm; Figure 1) consisted of a room surrounded by 92 cm high uniformly white walls constructed from plastic. Above the walls, white curtains hung around the perimeter of the room, including the ceiling. The room was lit by four 40-watt fluorescent light bulbs located on the ceiling, which were hidden from view by the curtain. The floor was lined with approximately 4 cm of aspen chip bedding. A small transparent vertically-sliding door ( $38 \times 61$  cm) was located at the South end of the room, which connected to a start box ( $33.5 \times 23 \times 33.5$  cm), located on the outside of the room, that housed the bird at the start of each trial. Five uniformly gray free-standing partitions ( $30.5 \times 30.5 \times 11.5$  cm), were positioned at equally-spaced intervals throughout the room. The gray partitions served as visual

barriers, so that the pigeon was unable to view the entire novel environment room from the start location, or any other location within the novel environment room.

### **2.2.2. Operant chamber**

One operant chamber (74 × 31 × 40.5 cm) was used for both training and testing all pigeons. The custom-made chamber was composed of aluminum and stainless steel and had a 34 × 24.5 cm opening in the back wall for the flat-screen LCD color computer monitor (IBM ThinkVision) with attached infrared touch frames (CarrollTouch model no. D27566-001). The monitor screen was located 7 cm above the chamber floor and was covered with a thin sheet of Plexiglass that was located approximately 1.5 cm in front of the monitor. The touch frames had a resolution of 3 mm and detected individual peck responses. On the rear of the chamber, on either side of the monitor, was a food hopper, that when activated by a correct choice, provided the bird with a small amount of food. For the current experiment, both hoppers were activated each time reinforcement was provided, and the bird was able to choose which hopper to visit. A computer was located in the adjacent control room and controlled the stimulus presentation as well as recorded all data.

### **2.3 Stimulus preparation**

Using E-Prime (Psychology Software Tools, Pittsburgh, PA), twelve stimuli at fifteen degree rotation intervals were created (Figure 2). The stimuli were created to be similar to those used by Honig et al. (1963) and Bloomfield (1967). Each stimulus was a white circle (2.54 cm diameter) with a 1.60 mm wide black line through the center. Stimuli were always presented individually (dpi = 0.297) in the center of the monitor on a black background.



## 2.4 Novel environment task

Each pigeon's exploratory behaviour was assessed in the novel environment prior to training and testing in the operant task. Individual birds were placed in the start box and the clear door that separated the start box from the novel environment allowed the birds to visually assess the room without being able to move into it. Birds were allowed ten minutes to habituate to the holding box and visually inspect the novel environment room before the door was lifted and the bird was given 30 minutes to explore. Each bird's activity within the room was recorded by a video camera suspended from the ceiling. Once 30 minutes had elapsed, the room lights were extinguished, the bird was immediately removed from the novel environment room and returned to its colony room cage. Thirty-five days after each bird's first session in the novel environment room, it participated in a second session, with all procedures carried out exactly as during the first session. All novel environment trials were conducted between the hours of 10.00 and 14.00 between 16 October and 27 November 2011.

## 2.5 Operant Task

*Autoshaping.* The purpose of autoshaping was so that the pigeon forms an association between the presentation of a visual stimulus presented on the screen and access to food. The pigeon is not required to peck the stimulus for access to food. Each pigeon was given an initial *Autoshaping* phase to re-establish reliable pecking. *Autoshaping* paired the presentation of a white stimulus (2.54 cm diameter, see Figure 2, stimulus on the left), with access to the food hoppers. Each trial started with a 10 s inter-trial-interval (ITI) with no stimulus presentation, followed by 45 s stimulus presentation with both hoppers activated. The trial ended 5 s after the infrared beam in one of the hoppers was broken or timed-out after 45 s if the beam in a hopper was not broken. Each daily session lasted until the bird received 30 food presentations (i.e., broke the hopper beam while the stimulus was presented), or until 45 minutes elapsed,

whichever occurred first. The criterion to complete *Autoshaping* was entering a hopper on each of 30 opportunities per daily session for one day. After completing *Autoshaping*, pigeons moved onto *Peck Training I*.

2.5.1 *Peck Training I*. The purpose of *Peck Training I* was to train the pigeon to peck the stimulus on the screen to receive access to food. In *Peck Training I* the first peck on the stimulus (white circle, 1 cm diameter) was rewarded with a 2 s access to the food hoppers. Each trial began with a 10 s ITI with no stimulus presentation followed by a 60 s stimulus presentation. The first peck on the stimulus resulted in activation of both food hoppers. The opportunity for reinforcement remained available for 5 s. After the infrared beam in a hopper was broken and a 2 s access to food was given, followed by a new trial. Failure to peck on the stimulus after 60 s elapsed ended the trial, and following a 10 s ITI, a new trial began. Each daily session continued until the pigeon received 60 reinforcement opportunities, or until 45 minutes had elapsed, whichever occurred first. The criterion to complete *Peck Training I* was one daily session where the pigeon responded to each stimulus presentation.

If a pigeon failed to peck during the stimulus presentation on two consecutive daily sessions it was moved to *Remedial Autoshaping* training. In *Remedial Autoshaping* training, all rules from *Autoshaping*, outlined above, remained in place, with the exception of the following: both food hoppers were activated 5 s after the stimulus was presented on each trial. The criterion to complete *Remedial Autoshaping* was entering a hopper on each of 30 opportunities per daily session for one day. Birds then moved back to *Peck Training I*. After completing *Peck Training I* pigeons moved onto *Peck Training II*.

2.5.2 *Peck Training II*. The purpose of *Peck Training II* was to train the pigeon to respond to the reinforced stimulus (S+). To introduce the S+, the same white stimulus as was used in the

preceding phases was displayed, but with the addition of a 90° (vertical) black line through the center (see Figure 2, stimulus presented in the middle). The stimulus was fixed on the screen for the entire daily session (i.e., no ITI) and the bird was reinforced for each peck on the S+. Once the S+ was pecked, both hoppers were activated and the opportunity for reinforcement remained available for 5 s. As in the previous phase, once the infrared beam in a hopper was broken, the pigeon had 2 s access to food. Each daily session ended when the bird received 40 reinforcements or after 45 minutes elapsed, whichever occurred first. The criterion to complete *Peck Training II* was one daily session in which the bird responded 40 times. After completing *Peck Training II* pigeons moved onto *Variable Interval S+ Training*.

**2.5.3 Variable Interval S+ Training.** The purpose of *Variable Interval S+ Training* was so that the pigeon learned that the reward for a correct response occurs after a random interval, rather than a fixed interval. Variable interval training promotes a high rate of responding, such that decrements in response rate can be measured in future phases. In this phase there were 55 trials per daily session. Each trial started with a 10 s ITI with no stimulus presentation followed by the S+ displayed on the centre of the screen. Each pigeon was reinforced on a variable interval (VI) 30 s schedule with 2 s access to food for its first peck on the S+ after a random amount of the time had elapsed from the start of the trial (range = 3-57 s). Each trial ended once the bird received reinforcement, or after 60 s elapsed with no response, whichever occurred first. The criterion to complete *Variable Interval S+ Training* was a difference in average response rate no greater than 10% across the last three days, after a minimum of 10 days of training. After completing *Variable Interval S+ Training* pigeons moved onto *Discrimination Training*.

**2.5.4 Discrimination Training.** The purpose of *Discrimination Training* was to train the birds to respond more to the reinforced (S+) than to the non-reinforced (S-; 135° line, see Fig. 5-2,

stimulus on the right) stimuli. Each pigeon received 54 trials in each daily session (27 S+ and 27 S- presentations). Responses to the S+ were reinforced on a VI 30 schedule, with trials ending after the fixed 2 s access to the food hoppers. No reinforcement was provided for pecking on the S-. Trials were separated by a 10 s ITI. The presentation order of the S+ and S- were pseudo randomized so there were never more than two consecutive presentations of any stimulus type. The lengths of the S- trials were yoked to the lengths of the S+ trials in a random order, so the duration of daily experience with both the S+ and S- stimulus was equivalent. S+ trials timed out after 60 s with no response. The criterion to complete *Discrimination Training* was a discrimination ratio (DR) of 0.75 for three consecutive sessions where at least 19 of the 27 S+ presentations were rewarded. The DR was calculated by dividing the number of pecks on the S+ by the total pecks per session (i.e., the sum of the number of pecks on the S+ and the number of pecks on the S-). Discrimination is at chance (DR = 0.50) when the animal is responding equally to both stimulus types and perfect (DR = 1.00) when the animals is only responding to presentation of the S+. After completing *Discrimination Training* pigeons were moved onto *Generalization Testing*.

Some pigeons performed *Discrimination Training* with high DRs but did not receive the minimum number of reinforcements (19 per daily session), meaning they were pecking on the S+ more than the S-, but were not pecking enough to obtain at least 19 reinforcements. These pigeons were returned to *Variable Interval S+ Training*, and in some cases, to *Peck II Training*, and then were returned to *Discrimination Training*. If a bird still did not meet the minimum required number of reinforcements, it was moved onto *Generalization Testing* (described below) after 35 cumulative daily sessions of *Discrimination Training*.

**2.5.6 Generalization Testing.** The purpose of *Generalization Testing* was to examine how new stimuli controlled the behaviour of the pigeons. For example, high rates of responding to novel

stimuli indicate that the pigeon perceives this stimulus as similar to the trained S+. Twelve stimuli of 15-degree increment line orientations, including the S+ and S- (see Figure 2, Panel b), were presented once per block, in six blocks, randomized for order in each daily session. Each trial began with a 5 s ITI with no stimulus presentation, followed by a stimulus presentation where the stimulus remained fixed on the screen for 30 s. All stimuli, including the S+, were presented under extinction, that is, they never yielded a food reward. Testing continued for two daily sessions. All pigeons completed the stimulus generalization operant task between 10 January 2012 and 27 May 2012. Six pigeons were run in a squad; each pigeon was run seven days a week, at the same time each day, between 09 00 and 14 00 hr. After each daily session of training or testing, pigeons were returned to the colony room and fed each day at approximately 15 00 hr.

## **2.6 Data collection**

### **2.6.2 Novel environment**

The novel environment room was divided into thirty  $37 \times 37$  cm squares, which were not visible to the pigeons, but were used by experimenters to quantify the amount of novel area explored (see Figure 1). The exploration score was the sum of the novel squares entered (out of 30 total) by each pigeon for the duration of each 30 minute trial. If a pigeon failed to leave the start box, it received an exploration score of zero. For statistical analyses examining the relationship between behaviour in the novel environment task and performance in the operant task, the sum of the exploration scores from the two sessions was used. This sum provided more complete information about how each pigeon behaved across the 60 minutes it was allotted to explore the novel environment room.

### 2.6.3 Operant task

During *Generalization Testing* the number of pecks to each of the 12 stimuli were summed over the six presentations per daily session and a generalization gradient (stimuli on  $x$ -axis, number of pecks on  $y$ -axis) was constructed. We measured the slope of the line between the responses to two stimuli. The slope measures the amplitude of the difference in response levels between two stimuli. For stimuli that fell to the left of the stimulus of peak responding, the value were calculated to be positive (e.g., the slope of the line between peak responding and the stimulus  $30^\circ$  to the left = (# pecks to stimulus with peak responding - # pecks to the stimulus  $30^\circ$  to the left)/ 30) while for stimuli that fell to the right of the stimulus of peak responding the stimuli were calculated to be negative (e.g., the slope of the line between peak responding and the stimulus  $30^\circ$  to the left = (# pecks to the stimulus  $30^\circ$  to the left - # pecks to stimulus with peak responding)/ 30). Slope is considered to be the most sensitive measure of stimulus control (Honig and Urcuioli, 1981). If the absolute value of the slope is large, then the animal is discriminating more expertly between two stimuli than when the slope is smaller, or close to zero. We calculated the slope between the stimulus where peak responding occurred for each individual and the stimuli at  $15^\circ$ ,  $30^\circ$  and  $45^\circ$  angle rotations to each side. Stimuli rotated to the left are in the direction away from the trained S-, and stimuli rotated to the right are in the direction towards the trained S-. This resulted in six slope measurements. Lastly, we chose to use the stimulus that evoked the maximal responding for each individual, rather than the trained S+ (unless the maximal responding was to the S+) because of a phenomenon called the peak shift effect. The peak shift effect is a product of the intradimensional discrimination procedure that we implemented for training and testing and is when maximal responding occurs not to the trained S+, but to another stimulus along the dimension in the direction away from the S- (Hanson, 1959). Given our training procedure, it would be expected that individuals,

during generalization testing, would respond more to the stimulus with the line orientation that is shifted 15° or possibly even 30 ° to the left of the trained S+.

## 2.7 Statistical Analyses

To test for repeatability of exploration in the novel environment across time (the two sessions of the novel environment task), an Intraclass Correlation Coefficients was calculated (Lessells and Boag, 1987). To examine if exploratory behaviour in the novel environment can be predicted by performance during generalization testing following intradimensional discrimination training, a step-wise linear regression was conducted where all variables were considered for entry (probability of  $F$ -to-enter  $\leq 0.05$ ) or removal (probability of  $F$ -to-remove  $\geq 0.1$ ) at each step. The linear regression had the six slope measurements available to predict exploration in the novel environment. All statistics were conducted with IBM SPSS Statistics v23.

## 3. Results

Exploratory behaviour was not significantly repeatable; although the number of squares entered was positively correlated across the two sessions in the novel environment, the correlation failed to reach statistical significance, ICC  $r(12) = 0.612$ ,  $p = 0.06$ , see Figure 3. The step-wise linear regression revealed that exploration in the novel environment was significantly related to performance in the cognitive task: The slope of the line between the peak response and the stimulus rotated 15° to the right (towards the S-) significantly predicted the total number of squares entered in the novel environment,  $F(1,10) = 6.688$ ,  $R^2 = 0.401$ ,  $p = 0.027$ ,  $\beta = -0.633$ . Pigeons with steeper slopes entered a greater number of squares in the novel environment, see Figure 4.

#### 4. Discussion

The results revealed that exploratory behaviour in a novel environment was not significantly consistent across time, but marginally so (i.e.,  $p = 0.06$ ). This suggests that exploration is either; (1) not completely consistent in pigeons over a short (i.e., 35 days) time period or (2) that the novel environment was not novel after the first session, and pigeons with different behaviour profiles attenuated (or habituated) to the novel environment at different rates. The latter explanation is likely true, considering the variation in exploration scores as evidenced after the first session of the novel environment. That is to say, if one individual entered the novel environment and explored extensively during the first session, while a second individual did not, then the novelty during the second session of the novel environment room varied by individual. It should also be noted that there were only 12 pigeons in this study and future work should seek to replicate and expand these results with more subjects.

How pigeons behave in a novel environment is related to their performance in a cognitive task. Fast exploring pigeons discriminated among test stimuli to a greater degree than slow-exploring pigeons. This result is in line with predictions derived from Guillette et al. (2015) that fast-exploring birds would be more expert discriminators compared to slow-exploring birds. Verbeek previously found that fast-exploring birds did not alter their behaviour in reaction to environmental stimuli; rather they form a routine and stick to it (e.g., Verbeek et al. 1994). If a fast-exploring pigeon learned the rule “peck to the S+ and only the S+” they could perform with a high discrimination ratio in the training phase. If these pigeons perseverated with the same response strategy during the test phase, “only respond to the S+” then they would have steep generalization gradients indicating behaviourally, that they are expert discriminators, even if they were not attending to all environmental stimuli (i.e., the lack of reinforcement or the presence of novel stimuli or the trained S-). Said another way, a fast-



exploring pigeon need not have been sensitive or aware of anything in the environment with the exception of the S+ to achieve perfect discrimination.

While this interpretation seems plausible, it does not, however, account for the complete pattern of results we obtained. For instance, if the fast-exploring, active pigeons were only responding according to the rule “only respond to the S+” then we would expect that the slope of lines between the S+ and the stimuli rotated in both directions (towards and away from the S-) to be predictive of behaviour. However, in regression equations that significantly predicted exploration, only the slope of line between the stimulus with peak responding and stimuli rotated towards the S- were predictive. Steeper slopes indicated more control (behavioural inhibition) by the S-, and fast-exploring pigeons had steep slopes on the side towards the S-. This indicates that fast-exploring pigeons were not likely relying on the strategy of “only respond to the S+”. This idea, that the fast-exploring pigeons were more sensitive to the S- could be tested by training the pigeons with the same S+ (vertical line, 90°), and then training with two S-s, one at 135° as in the current experiment, and the other at 45°, the mirror image of 135°. With these methodological changes the prediction would be that the slope of the lines to both sides of the S+ would be steeper for fast-exploring pigeons.

Recent work looking at neural responses in live, awake zebra finches performing a go/no-go acoustic operant discrimination task, show that fast- and slow-learners treat trained ‘go’ and ‘no-go’ responses differently (Bell et al., 2015). Fast-learners showed stronger memory for trained no-go stimuli and were more likely to classify novel, ambiguous stimuli as belonging to the ‘no-go’ category. To the contrary, slow-learners had stronger memory for trained ‘go’ trained stimuli and were more likely to classify novel, ambiguous stimuli as belonging to the ‘go’ category. It would be informative to see how these zebra finches would behave in a novel environment.

This study is another in a growing body of work (see Table 1) showing that how an animal explores a novel environment is related to some aspect of cognitive performance. Initial investigations of the personality/cognition relationship focused on learning speed suggested perhaps that acquisition rate (i.e., learning) is faster when an animal explores more because exploration, *ipso facto*, put animals in contact with more to-be-associated stimuli compared to animals that explore less (Dugatkin and Alfieri, 2003; Guillette et al., 2009; Sneddon, 2003). Although the parsimony of this explanation is appealing the influence of exploration tendency in a learning task can be removed methodically by, for example (1) habituating the subject to, and (2) training them how to use the experimental apparatus before acquisition training (to measure learning speed) begins (e.g., Guillette et al., 2015, 2011b). Alternatively, a learning task that does rely on exploratory behaviour, for example, classical conditioning, can be used (Griffin and Guez, 2016). Evidence from several studies in mice that increased exploration rate in novel environments, either by exposing animals repeatedly to different novel environments (Light et al., 2008) or by administering anxiolytic drugs (Grossman et al., 2007) found no corresponding increase in general learning ability (GLA). A corresponding increase in GLA would be expected if exploration had either a causal effect on learning speed or if stress mediated both exploration and learning.

Alternately, the rate at which animals process information they receive from the environment may mediate how quickly they can move through their environment. That is, animals that are slower to process new information may take longer in one area before moving onto another area, with potentially novel information. In this view, novel environment exploration can be considered a cognitive task *sensu* (Light et al., 2011). It is not clear how best to test these hypotheses linking learning speed to exploration.

Leaving aside learning speed, there are other ways to test if cognitive abilities are related to exploration. One way to do this is to test an animal's performance *after* they have

reach asymptotic performance on a cognitive task. This can begin to assess *how* the animal may have been able to solve the task, that is, what features of the stimuli used in training may be controlling the behaviour of the animal. The relationship we currently find is not due to processing speed, rather, how information is acted on once acquired. The current results thus suggest that links between cognition and personality are not limited to information acquisition, but extend into how animals use information.

In conclusion, we designed a novel environment test that can be used to examine exploratory behavior in a pigeon model. We also found that fast-exploring pigeons were better discriminators and slow-exploring pigeons were more likely to generalize, sampling novel stimuli that were similar to trained stimuli. Further tests with either aversive stimuli, or the use of multiple unreinforced stimuli during training are needed to confirm current results. Extant long-term datasets on cognitive abilities in animals may be sufficient to allow for cursory analyses of individual differences in cognitive abilities, when the same subjects have been used in multiple cognitive tests (Griffin et al., 2015; Thornton and Lukas, 2012; Vonk and Povinelli, 2011).

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### Figure Captions

Figure 1. Panel a - Top-down schematic of novel environment room and start box (S). The gray partitions are represented by the gray boxes. The lines partitioned the novel environment into 30 distinct areas that were visible to the researchers and used to quantify exploration and activity scores. These lines were not visible to the pigeons. Panel b – picture of pigeon in the novel environment room.

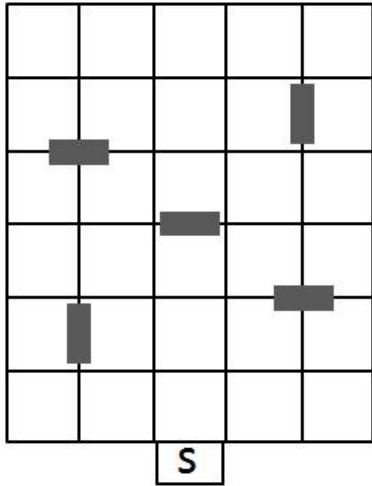
Figure 2. Panel a - Operant task training stimuli. Circle with no line was the stimulus used in Autosshaping, Remedial Autosshaping, and Peck training; 90° line orientation S+ used in Peck training, Discrimination, and Generalization testing; 135° line orientation S- used in Discrimination and Generalization testing. Panel b - Twelve line orientation stimuli ranging from 0° to 165° in 15° increments used in Generalization testing

Figure 3. Plots of exploration score, the number of novel squares entered during the first session (*X*-axis) and in the second session of the novel environment (*Y*-axis).

Figure 4. The exploration score (the number of novel squares entered, out of 60 total, *X*-axis) in the novel environment and the slope of the line between the stimulus at peak responding and the stimulus rotated 15° to the right (towards the S-, *Y*-axis). As the absolute value of the numbers on the *y*-axis increase, the slope of the line becomes steeper.

Figure 1.

a)



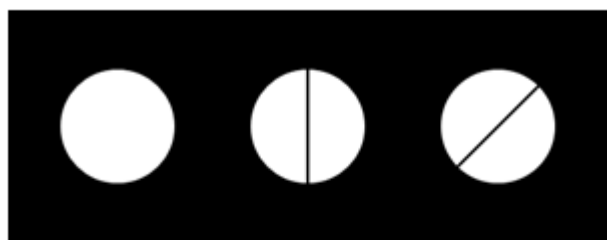
b)





Figure 2.

a)



b)

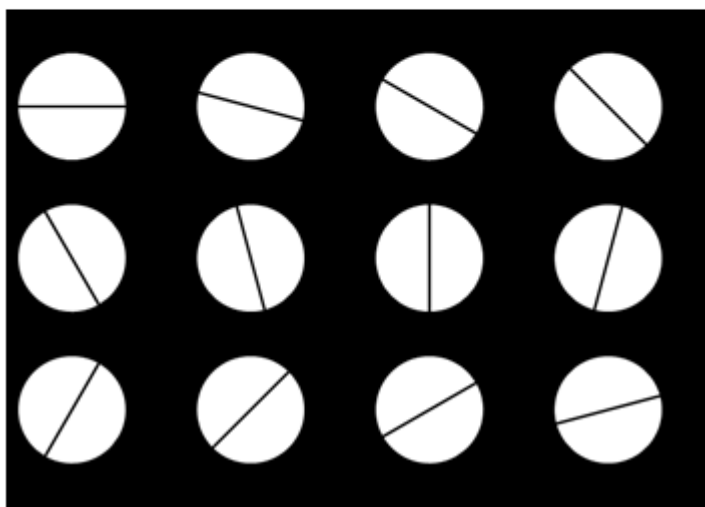


Figure 3.

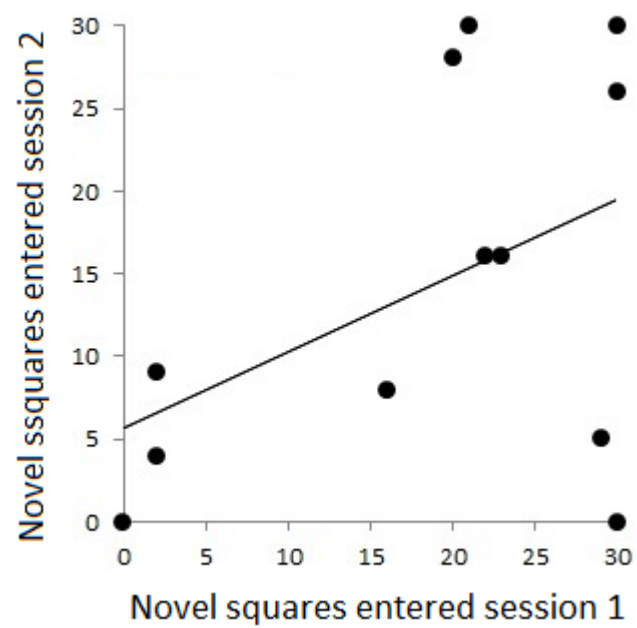


Figure 4.

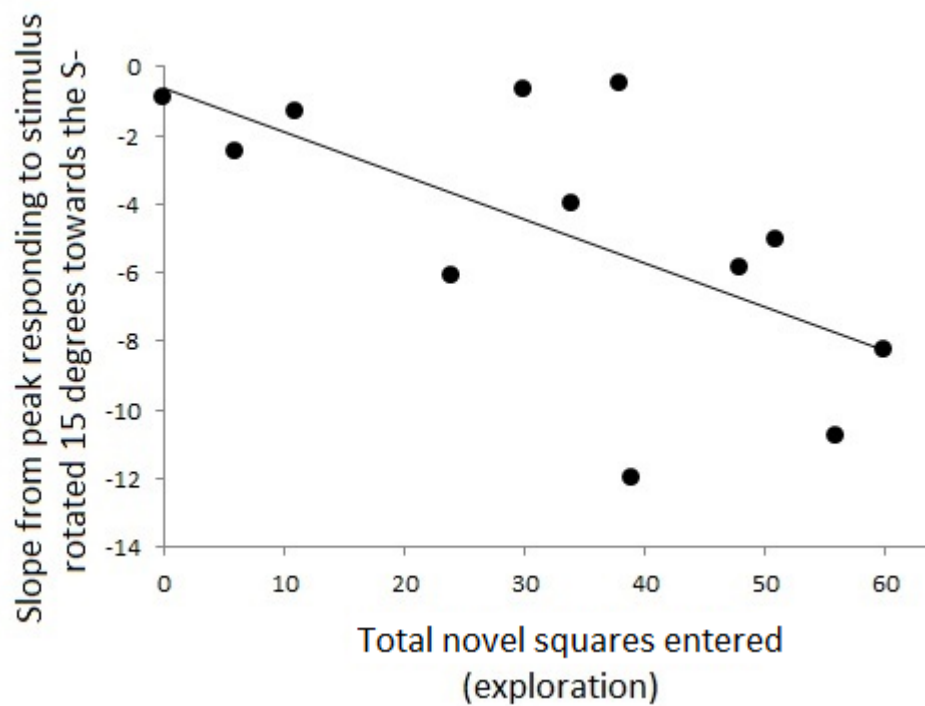


Table 1. Relationship between exploration score in a novel environment behavioural test and cognitive test(s). F indicates faster explorers and S indicates slower explorers, SL indicates selection lines for F and S exploration, and  $\approx$  indicates no statistically significant relationship. Sex of subject was either both or not reported, unless otherwise stated. \*It is not clear which cognitive ability underpins problem solving (Griffin and Guez, 2014; Morand-Ferron et al., 2015; Rowe and Healy, 2014) if any (van Horik and Madden, 2016). For the cognitive task it is indicated whether the ‘A’ acquisition or ‘U’ use of previously acquired information was measured. A ‘?’ indicates that it is not clear whether information acquisition or use were measured (e.g., number of errors for a set number of trials).

Reference	Species	Cognitive ability	Cognitive task/type A = acquisition, U = use	Outcome
	<b>Great tits <i>Parus major</i></b>			
Verbeek <i>et al.</i> 1994	Male	Spatial learning	Reversal (A)	F < S
Exnerová <i>et al.</i> 2010	Male, SL	Discrimination learning	Avoidance learning (A)	F < S
		Memory	24-hour retention interval (U)	$\approx$
Cole <i>et al.</i> 2011	Wild	?*	Puzzle box (?)	$\approx$
Amy <i>et al.</i> 2012	Male, SL	Discrimination learning	Colour discrimination - foraging board (A)	$\approx$
		Discrimination learning	Reversal (A)	F > S
Titulaer <i>et al.</i> 2012	Wild-caught	Discrimination learning	Colour/location discrimination - foraging board (A)	$\approx$
		Discrimination learning	Reversal learning (A)	F < S (females) F > S (males)
Morand-Ferron <i>et al.</i> 2015	Wild	Discrimination learning	Colour discrimination - operant paradigm (A)	$\approx$
	<b>Three-spined stickleback <i>Gasterosteus aculeatus</i></b>			
Brydges <i>et al.</i> 2008	Wild caught	Spatial learning	Foraging (A)	$\approx$
		Spatial learning	Reversal (A)	$\approx$
	<b>Black-capped chickadees <i>Poecile atricapillus</i></b>			
Guillette <i>et al.</i> 2009	Wild caught	Discrimination learning	Acoustic discrimination (A)	F > S

Guillette <i>et al.</i> 2011	-	Discrimination learning	Acoustic discrimination (A)	≈
		Discrimination learning	Reversal (A)	F < S
Guillette <i>et al.</i> 2015	-	Discrimination learning	Acoustic discrimination (A)	≈
		Generalization	Novel acoustic exemplars (U)	F < S
		Discrimination learning	Reversal (A)	≈
		Discrimination learning	Colour discrimination - Foraging board (A)	≈
		Discrimination learning	Reversal (A)	≈
		Behavioural inhibition	Detour reaching (A)	≈
		<b>Eastern water skink <i>Eulamprus quoyii</i></b>		
Carazo <i>et al.</i> 2014	Wild caught	Spatial learning	Refuge location (A)	≈
		<b>Panamanian bishop fish <i>Brachyrhaphis episcopi</i></b>		
DePasquale <i>et al.</i> 2014	Wild caught	Associative learning	Cue predicts food availability (A)	F > S
		<b>Florida scrub-jay <i>Aphelocoma coerulescens</i></b>		
Bebus <i>et al.</i> 2016	Wild	Discrimination learning	Colour discrimination - Foraging board (A)	≈
		Discrimination learning	Serial reversal (A)	≈
		<b>Mallard <i>Anas platyrhynchos</i></b>		
Bousquet <i>et al.</i> 2015	Captive wild-type female	Spatial learning	Maze - move to correct goal location (?)	≈
		<b>Common carp <i>Cyprinus carpio</i></b>		
Mesquita <i>et al.</i> 2015		Discrimination learning	Colour discrimination – foraging (A)	F < S
		<b>CF1 mice</b>		
Kazlauckas <i>et al.</i> 2005	Male	Behavioural inhibition	Inhibitory avoidance -Platform test (?)	F > (higher inhibition) S
		Spatial leaning	Lashley maze (?)	F > S
		<b>CD-1 outbred mice (Harlan Sprague Dawley)</b>		
Galsworthy <i>et al.</i> 2002	Male	General learning (PCA score)	Route learning, Hebb-Williams maze; Spatial learning, Morris water maze; Problem solving: (Burrowing task, Contextual memory, Plug puzzle) (?)	≈
Matzel <i>et al.</i> 2003	-	General learning (PCA score)	Associative fear conditioning; passive avoidance; odour discrimination; Route learning, Lashley maze; spatial learning, Morris water maze (?)	F > S

Matzel <i>et al.</i> 2006	-	General learning (PCA score)	Associative fear conditioning; passive avoidance; odour discrimination; Route learning, Lashley maze; spatial learning, Morris water maze (?)	F > S
Light <i>et al.</i> 2011	-	General learning (PCA score)	Associative fear conditioning; passive avoidance; odour discrimination; Route learning, Lashley maze; spatial learning, Morris water maze (?)	F > S

Table 2. The number of pecks to the stimulus of peak responding (peak) and to the stimuli rotated 15°, 30° and 45° to the left (L) and the right (R) for each subject during generalization testing.

Subject	# of pecks to stimuli						
	45 L	30 L	15 L	Peak	15 R	30 R	45 R
1	2	4	6	26	12	10	19
2	66	15	317	354	317	330	208
3	15	58	97	124	104	84	28
4	31	56	81	101	9	44	19
5	33	35	50	74	64	17	16
6	8	19	75	223	163	213	167
7	15	0	17	44	36	0	0
8	199	341	408	415	235	43	48
9	146	99	160	200	112	118	61
10	18	14	40	130	54	51	54
11	314	237	280	417	255	62	39
12	180	266	253	277	153	124	55