Are cognition and personality related in budgerigars?

Jiani CHEN\textsuperscript{a,b,*}, Lu CHEN\textsuperscript{c}, Chuan YAN\textsuperscript{a}, Zibo YU\textsuperscript{d}, Yuqi ZOU\textsuperscript{b}, and Yue-Hua SUN\textsuperscript{b,*}

\textsuperscript{a}Institute of Innovation Ecology, Lanzhou University, Lanzhou 730000, China, \textsuperscript{b}Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China, \textsuperscript{c}College of Life Science, Hebei University, Baoding 071002, China, and \textsuperscript{d}School of Natural Conservation, Beijing Forestry University, Beijing 100083, China

*Address correspondence to Jiani Chen and Yue-Hua Sun. E-mail: chenjiani@lzu.edu.cn and sunyh@ioz.ac.cn.

Handling editor: Zhi-Yun Jia (贾志云)

Received on 9 June 2021; accepted on 17 August 2021

Abstract

In recent years, researchers have been attempting to relate differences in personality (e.g., boldness, aggressiveness, exploration tendency) to variation in cognition (performances in tasks that require learning, reasoning, attention, or memory, etc.) both theoretically and empirically. However, it is unclear on what basis personality and cognition might be associated with each other. Previous theory suggests a connection between fast–slow personality types and cognitive speed–accuracy tradeoffs. In this study, we tested this hypothesis in budgerigars and found that, in their 1st associative learning, birds with fast personality (less fearful of handling stress) were fast learners in the beginning, while slow personality individuals improved faster, but both types of birds did not differ in accuracy. However, these relationships were context-dependent. No significant relationship was found in subsequent learning tasks (reversal learning and a 2nd associative learning) in the familiar context (task setup and apparatus similar to the 1st associative learning). We then conducted a problem-solving experiment with novel setup and apparatus to test 1 possible explanation that the association between personality and cognition in the 1st associative learning might be caused by noncognitive constraint, such as fearfulness when facing novel task setup and apparatus. We found that fast individuals interacted more with the problem box and solved it, whereas the slow birds were not. We suggest that personalities can influence cognitive performances and trigger a cognitive speed-improvement tradeoff under the novel context. However, there are no consistent cognitive styles that co-varied with different personalities.

Key words: budgerigar, cognition, learning accuracy, learning speed, personality.
associated in numerous studies (Sih et al. 2004; Sih and Bell 2008). It has been suggested to extend this concept of behavioral syndromes to include cognition, with reference to a consistent cognitive style that is related to personality (Sih and Del Giudice 2012).

Compared with animal personality research, the study of animal cognition has a relatively long history, flourishing in the last half-century. With the rapid development of personality research, the integration between the 2 fields has attracted increasing attention in recent years. In contrast to personality research, much less work has been done to explore individual cognitive variation (Griffin et al. 2015), although striking individual cognitive variation is frequently observed (Thornton and Lukas 2012). Thus far, the underlying mechanisms of individual cognitive variation have not been well discussed from an ecological or evolutionary perspective. As a potential key determinant of individual variation, personality may be an important factor in cognitive performance (Carere and Locurto 2011). However, it is unclear on what basis personality and cognition might be associated with each other. Sih and Del Giudice (2012) proposed a hypothesis that received considerable attention: through a risk–reward tradeoff, individuals of fast personality type (referred to profiles that are more proactive, such as bold, active, aggressive, etc.), who are more willing to take risks, tend to express a cognitive style that emphasizes speed (the number of trials needed to reach a learning criterion; Griffin et al. 2015), over accuracy (the rate of correct/successful trials of a cognitive task) to quickly earn rewards, whereas individuals of slow personality type (shy, inactive, less aggressive, etc.) show the reverse in this personality–cognition chain.

Although many studies have detected correlations between a range of traits in cognition and personality traits (Bohns et al. 2004; Guillette et al. 2009; Reddon and Hurd 2009; Guillette et al. 2011; Carazo et al. 2014; Cussen and Mensch 2014; Mamuneas et al. 2014; Trompf and Brown 2014; Guillette et al. 2015; Gibelli and Dubois 2017; White et al. 2017), the results that have attempted to explore these cognitive–personality connections seemed to illustrate inconsistent cognitive performances in relation to the same personality type (fast or slow) across different contexts. For example, in the experiment designed to encourage individuals to form routines, Guillette et al. (2009) found that fast explorers of black-capped chickadees learned faster than slow explorers. With the same species under a different experimental design, fast explorers were found to have lower accuracy in an acoustic discrimination test, but they did not outperform slow explorers in learning speed (Guillette et al. 2015). Similarly, in zebra finches, cognitive performance was not always associated with personality across contexts. Less neophobic finches learned faster in a less difficult color discrimination task, but learning speed was not associated with personality in a more difficult discrimination test or in a reversal task (Gibelli and Dubois 2017). In fish, bold female guppies confronted with a spatial associative learning task learned faster and more accurately than shy ones (Trompf and Brown 2014), but bolder trout were less successful in navigation and used cues to locate food (White et al. 2017). Interestingly, a nonlinear association between boldness and learning was found in lizards, and the individuals at the 2 extremes of the boldness index were found to be more successful learners (Carazo et al. 2014). Dougherty and Guillette (2018) conducted a meta-analysis using 25 studies and found an approximately equal number of studies showing a positive relationship between personality and cognition (fast animals learned quicker and had more correct responses) as showing a negative relationship (fast animals learned slower and had fewer correct responses).

In the current study, we conducted experiments to examine the relationship between cognition and personality in budgerigars. Many previous studies investigating cognition–personality connections assessed the performance of 1 cognitive task and attempted to link it with personality. This approach to link cognition and personality by looking at 1 cognitive test is conceptually and logically problematic, as consistency in cognitive performances (could be considered as cognitive style) has not been established first (Rowe and Healy 2014; Griffin et al. 2015). We conducted various tests in this study, investigating personality and cognition in multiple tasks to examine whether 1) there is a relationship between fast–slow personality and cognitive speed–accuracy tradeoffs and 2) personality predicts performance in multiple cognitive tasks.

**Materials and Methods**

**Subjects and housing**

Adult budgerigars from local breeders were housed in same-sex cages (93 × 40 × 60 cm, 6 birds/cage) under an 8.5:15.5 h dark–light photoperiod (light turned on from 6 am to 9:30 pm, temperature around 25°C) with ad libitum mixed seeds and water. A bath and food supplements, such as fresh vegetables, mineral grit mix, and cattle bones, were provided regularly.

**Personality tests**

**Response to handling stress**

Breathing rate under handling stress was measured. It is used to characterize reactivity in the parasympathetic nervous system (Koolhaas et al. 1999) and has been applied in personality tests to indicate animal responses to stressors (Carere and Oers 2004; Fucikova et al. 2009; Brommer and Klunen 2012; Krams et al. 2014; Mikus et al. 2016; Zhao et al. 2016) because breathing frequency responds to fear-inducing stimuli and reflects stress-induced tachycardia (Carere and Oers 2004). To the budgerigars, the breathing rate under handling stress reflects the fearfulness of the birds toward human hand. Individuals that are not afraid to perch on hand and can be pet by hand have significantly lower breathing rate under handling stress than those who cannot (mean ± Standard Error (SE) = 87.00 ± 3.36 time/min, N = 5 and 105.04 ± 3.38 time/min, N = 24, Wilcoxon test: P = 0.02; Chen, unpublished data).

Individual birds were caught and placed in a small cage (27 × 18 × 12 cm) for 3 min before the breathing rate test started. Immediately after catching and removing the bird from the small cage, the breathing rate was measured, as the number of breath movements in 1 min, whereas the bird was held firmly by hand (Carere and Oers 2004). This test was conducted by 2 researchers: one (always J.C.) managed the handling and counting, whereas the other timed the experiment. Twenty-one birds (8 females and 13 males) were tested in this way. The breathing rate of each bird was measured 3 times to check repeatability. The second measurement was performed 2 months after the 1st one and 2 weeks before the 3rd one. Body mass was also measured (sampled to 0.01 g) at the same time and used in the subsequent analyses to control for its effect on breathing rate.

**Novel environment test**

Novel environment test is used to measure boldness/fearfulness and exploratory tendency in animals (Carter et al. 2013). Twenty-one birds (8 females and 13 males) participated in this test. This test was conducted in an irregular maze (Figure 1A,B), which was divided into 4 compartments. The birds were placed in a small enclosed...
space (15 × 15 × 20 cm) with an entrance opening to the maze that was blocked by an opaque sliding door before the test. The birds stayed in this space for 20 min and were then given 2 h to explore the maze after the sliding door was gently opened. The latencies that birds took to enter the maze and the furthest compartment (from 0 to 4) they reached were measured. This test was conducted twice and was video recorded. The 2nd test was performed at least 2 weeks after the 1st one (3 males had a 3-week interval between the 1st and the 2nd test).

**Associative learning and problem-solving tests**

**Color associative learning 1**

Twenty-one birds (8 females and 13 males), which had experienced the 2 personality tests, took part in this experiment and the following cognitive tasks. Birds were put individually in 1 cage (28 × 23 × 25 cm) during this and the following tasks. Two colored Petri dishes were provided to the subjects and they were required to choose and open the Petri dish with the reinforced color to get access to food. The birds were trained to open a transparent Petri dish before the color associative learning started. Afterward, colored papers were glued inside the Petri dish, making the food reward inside the dish invisible. One pair of colors—red and blue—was used in this associative learning. The subjects were food deprived from 18:00 the day before the associative learning task, which started the next day from 9:00. All birds were given 20 trials for learning the association between food and color during this task. In such a way, we can compare learning speed and learning accuracy among different individuals within a given number of trials. The color with which the reward was associated was randomly assigned to the subjects (9 birds were given blue as their reward-indicating color and 12 birds received red instead). Dishes with the reinforced color contained a small number of mixed seeds (S +), whereas dishes with the other color were empty (S −). The 2 dishes were placed in the cages as the subjects stood on the perch above. The subjects were only allowed to choose one of the dishes in each trial. If the bird chose the correct dish, they could eat the food after opening it. If wrong, they would find no food in the dish after opening it and probably turned to the other dish. We removed both dishes after the choice of a first dish and before the birds had turned to the other dish. The positions of the 2 dishes were switched randomly.

**Reversal learning**

In the reversal learning, the colors of S + and S − in the first color associative learning were reversed. All the procedures were identical to the associative learning task, except that all birds (8 females and 13 males) were given 30 trials in this task. Reversal learning was conducted after the completion of the 1st associative learning trials.

**Color associative learning 2**

Experiment 2 was conducted 16 days (18 days in 3 birds) after Experiment 1. This 2nd associative task was identical to the first one; only the previous pair of colors was replaced by yellow and green (10 birds were given green as their reward-indicating color and 11 birds received yellow instead). All birds (8 females and 13 males) were given 20 trials for learning the association between color and reward.

**Spontaneous problem-solving task**

The problem-solving device was a transparent acrylic puzzle box with a removable acrylic slice inserted into the upper part of the box, generating a space that could be filled with mixed seeds. The birds had to pull out the slice, releasing the seeds into the feeding dish (Figure 1C, modified from Cole et al. 2011). The puzzle boxes were placed in the birds’ cages for 2 h in the morning from 9:00 to 11:00 and 2 h in the afternoon from 15:00 to 17:00, allowing the birds to explore and spontaneously solve the task. No additional food was provided during these 2 h periods; the subjects had to obtain food from the problem-solving device. This procedure was repeated every day for 4 days and video recorded until the birds solved the problem or if they had not solved it by 4th day (16 h in total).

---

**Figure 1.** Apparatuses in the exploratory tendency test and problem-solving task. On the left, (A and B) the top view of the maze used in the exploration test. On the right, (C and D) the problem-solving box (the front and side views are shown in C).
Statistical analysis

The repeatability of the traits from the personality tests was calculated using a linear mixed model (repeatability = the between-individual variance/ the sum of the between-individual + within-individual variences, Nakagawa and Schielzeth 2010). The individual (bird ID) was included in the model as a random effect. Because of possible violation of model assumption, bootstrap and permutation tests were used to infer the confidence intervals and statistical significance (P < 0.05) of repeatability, respectively. The analysis was performed by R package ‘rptR’ in R software (Stoffel et al. 2017). Body mass was also included as a fixed factor in the model for breathing rate (Carrere and Oers 2004). If the behavior was repeatable, we would use the means of the measures in the personality tests as the score of personality traits. In this study, only breathing rate under handling stress and latency to enter the maze were repeatable, so we calculated the mean breathing rate of 3 times and the mean latency to enter the maze from the 2 replicate tests (referred to as breathing rate and entering latency for short hereafter) as the scores of personality for each individual and used them in the later analyses.

We looked at 4 parameters of cognitive performances in the associative and reversal learning tasks: the initial learning speed, final accuracy, improving rate, and total accuracy of learning. According to Sih and Del Giudice (2012), in a cognitive task, fast animals sample the improving rate. A logistic regression model was applied to the learning data of the individual birds using binary data (choice of S++) the improving rate. A logistic regression model was applied to the learning data of the individual birds using binary data (choice of S++). Percentage of correct choice.

| Trait               | No. of observations | Mean ± SE | Repeatability | P-value |
|---------------------|---------------------|-----------|---------------|---------|
| Breathing rate      | 21                  | 110.90 ± 3.34 (1st) | 0.49 | 0.002* |
| Entering latency    | 21                  | 28.10 ± 9.41 (1st)  | 0.44 | 0.022* |
| Furtthest position  | 21                  | 2.48 ± 0.31 (1st)   | 0.059 | 0.400  |

No. of observations is the number of repeated measures, 1st, 2nd, and 3rd indicate the time of each measurement. * Significant repeatability (P < 0.05). CI, confidence interval from 1,000 bootstrap iterations; Permutation P-value, P-value based on permutation test of 1,000 randomizations.

Table 1. Repeatability of behaviors

Table 2. Percentage of correct choice.

The table includes the performance of the birds in the cognitive tasks, with columns for the percentage of correct choices for the first and second associative tasks, as well as the reversal learning tasks. The data includes the average performance across blocks, with significant differences highlighted.

Rates of correct choices within given blocks (10 trials per block) in different learning tasks (1st associative learning, reversal learning, and 2nd associative learning).
Figure 2. Learning curves of individual birds in different learning tasks (A-C, 1st associative learning, reversal learning and 2nd associative learning respectively). Fitted curves were obtained by logistic regression models based on the responses to the learning trials and the distributions of these responses. Different color lines represent different individuals, describing the learning tendencies of individuals in the tasks and predicting the probabilities of successful choice at certain trials.

Figure 3. Relationships between breathing rate (time/minute, score indicating fearfulness of individual to handling stress) and cognitive performances across different learning tasks. (A–C) Relationships between fearfulness and initial learning speed. (D–F) Relationships between fearfulness and improving rate. (G–I) Relationships between fearfulness and final accuracy. (J–L) Relationships between fearfulness and total accuracy. Oblique lines (computed by simple linear regressions) indicate that fearfulness significantly predicts the cognitive traits ($P < 0.05$). All $N = 21$. 
Initial learning speed not correlated with each other (Figures 3a and 3b). Learning traits between different tasks are as follows: 1st associative and reversal tasks (all N = 21). Breathing rate significantly predicted the initial learning speed (t = -2.70, P = 0.014, N = 21) and the improving rate (t = 3.18, P = 0.005, N = 21). The birds with slower breathing rates were fast learners in the beginning (Figure 3a), but their learning was not able to improve as quickly as individuals with faster breathing rates (Figure 3d). However, in the reversal learning task, as well as in the 2nd color associative learning task, no relationships between breathing rate and these 2 learning traits were found (all P > 0.05; Figure 3). Breathing rate did not predict final and total accuracy across the 3 learning tasks (all P > 0.05).

In the spontaneous problem-solving task, 11 out of 21 birds spontaneously solved the problem. The birds that successfully operated the problem box have significantly slower breathing rates than the nonproblem solvers (W = 89.50, P = 0.017, N = 21, Figure 4). The solvers solved the problem in 6.42 ± 1.72 h (mean ± SE, N = 11), whereas the nonproblem solvers did not solve it during the total 16 h (N = 10). The frequencies of the birds trying to operate the box (bite the box) per hour were significantly different (W = 16.00, P = 0.007, N = 21, problem solvers: 5.25 ± 1.65 mean ± SE time/h, N = 11, nonproblem solvers: 1.29 ± 0.48 mean ± SE time/h, N = 10).

Entering latency did not predict learning traits across all learning tasks (all P > 0.05; in addition, no significant difference was found between entering latency of the problem solvers and nonproblem solvers in the problem-solving task: W = 46.00, P = 0.633, N = 21). Sex did not contribute to differences in most cognitive performances (all P > 0.05), except that the improving rate was significantly higher in females than in males in the reversal task (mean ± SE, 0.11 ± 0.02 for females and 0.02 ± 0.01 for males: t = -3.39, P = 0.003, N = 21).

Correlations across learning tasks
We found no significant correlation between learning traits in the 1st associative task and the reversal or 2nd associative tasks (Table 3). A positive correlation was found between the improvement rates in the reversal learning and 2nd associative learning tasks (Table 3). The final accuracies and total accuracies also tended to positively correlate between these 2 tasks (Table 3).

Discussion
In this study, we found budgerigars had a consistent breathing rate under handling stress. Breathing rate under handling stress is considered to indicate the fear response to stressors. It was found to be lower in individuals with fast personality types (more aggressive, bold, and active) than with slow individuals in birds (Carere et al. 2001; Carere and Oers 2004; Kluen et al. 2014).

Our results show that fearfulness toward handling stress predicts learning performance in a novel context where task setup and apparatus were introduced to the individuals for the first time, but not in the familiar context where the setup and apparatuses were similar to what the individuals had encountered previously. Individuals with high fearfulness to stressors needed more trials to reach the learning criterion during the 1st associative task. When facing the problem-solving task, fearful birds were more reluctant to operate the box per unit time and did not solve the puzzle box to get access to food. However, individuals did not adopt the fast/slow strategy or express this fast/slow style of learning during the reversal and the 2nd associative learning, where experimental setup and apparatuses were similar to those in the 1st associative learning. Similar results were

| Learning traits between different tasks | r | P-value |
|----------------------------------------|---|---------|
| Initial learning speed                 |   |         |
| 1st and 2nd associative and reversal   | -0.28 | 0.215 |
| 1st and 2nd associative                | -0.41 | 0.068 |
| Reversal and 2nd associative           | 0.30  | 0.184  |
| Improving rate                         |   |         |
| 1st and 2nd associative and reversal   | 0.23  | 0.316  |
| 1st and 2nd associative                | 0.27  | 0.243  |
| Reversal and 2nd associative           | 0.53  | 0.014  |
| Final accuracy                         |   |         |
| 1st and 2nd associative and reversal   | 0.05  | 0.835  |
| 1st and 2nd associative                | 0.07  | 0.753  |
| Reversal and 2nd associative           | 0.50  | 0.020  |
| Total accuracy                         |   |         |
| 1st and 2nd associative and reversal   | -0.17 | 0.460  |
| 1st and 2nd associative                | -0.24 | 0.287  |
| Reversal and 2nd associative           | 0.47  | 0.030  |

*Kuznetsova et al. 2017; Heinze et al. 2020* in the R environment (version 3.6.3, R-Core-Team, 2020).

**Results**

**Personality**

The breathing rate under handling stress and the latency to enter the maze were significantly repeatable, but the furthest position they got in the maze was not (Table 1). These 2 personality parameters were not correlated with each other (r = 0.28, P = 0.268, N = 23).

**Relationship between personality and cognitive performance**

Most of the birds had learned the tasks (performed above chance level; Table 2 and Figure 2). Percentage of correct choices of the final 10 trials in the 1st associative learning: 79.05 ± 3.08% SE, N = 21; reversal learning: 59.52 ± 4.95% SE, N = 21; 2nd associative learning: 73.80 ± 4.65% SE, N = 21). In the 1st color associative learning task, breathing rate significantly predicted the initial learning speed (t = -3.18, P = 0.005, N = 21). The birds with slower breathing rates were fast learners in the beginning (Figure 3a), but their learning was not able to improve as quickly as individuals with faster breathing rates (Figure 3d). However, in the reversal learning task, as well as in the 2nd color associative learning task, no relationships between breathing rate and these 2 learning traits were found (all P > 0.05; Figure 3). Breathing rate did not predict final and total accuracy across the 3 learning tasks (all P > 0.05).

In the spontaneous problem-solving task, 11 out of 21 birds spontaneously solved the problem. The birds that successfully operated the problem box have significantly slower breathing rates than the nonproblem solvers (W = 89.50, P = 0.017, N = 21, Figure 4). The solvers solved the problem in 6.42 ± 1.72 h (mean ± SE, N = 11), whereas the nonproblem solvers did not solve it during the total 16 h (N = 10). The frequencies of the birds trying to operate the box (bite the box) per hour were significantly different (W = 16.00, P = 0.007, N = 21, problem solvers: 5.25 ± 1.65 mean ± SE time/h, N = 11, nonproblem solvers: 1.29 ± 0.48 mean ± SE time/h, N = 10).

Entering latency did not predict learning traits across all learning tasks (all P > 0.05; in addition, no significant difference was found between entering latency of the problem solvers and nonproblem solvers in the problem-solving task: W = 46.00, P = 0.633, N = 21). Sex did not contribute to differences in most cognitive performances (all P > 0.05), except that the improving rate was significantly higher in females than in males in the reversal task (mean ± SE, 0.11 ± 0.02 for females and 0.02 ± 0.01 for males: t = -3.39, P = 0.003, N = 21).

Correlations across learning tasks
We found no significant correlation between learning traits in the 1st associative task and the reversal or 2nd associative tasks (Table 3). A positive correlation was found between the improvement rates in the reversal learning and 2nd associative learning tasks (Table 3). The final accuracies and total accuracies also tended to positively correlate between these 2 tasks (Table 3).

**Discussion**

In this study, we found budgerigars had a consistent breathing rate under handling stress. Breathing rate under handling stress is considered to indicate the fear response to stressors. It was found to be lower in individuals with fast personality types (more aggressive, bold, and active) than with slow individuals in birds (Carere et al. 2001; Carere and Oers 2004; Kluen et al. 2014).

Our results show that fearfulness toward handling stress predicts learning performance in a novel context where task setup and apparatus were introduced to the individuals for the first time, but not in the familiar context where the setup and apparatuses were similar to what the individuals had encountered previously. Individuals with high fearfulness to stressors needed more trials to reach the learning criterion during the 1st associative task. When facing the problem-solving task, fearful birds were more reluctant to operate the box per unit time and did not solve the puzzle box to get access to food. However, individuals did not adopt the fast/slow strategy or express this fast/slow ‘style’ of learning during the reversal and the 2nd associative learning, where experimental setup and apparatuses were similar to those in the 1st associative learning. Similar results were
found in other studies, such as Gibelli and Dubois (2017) and Ducatez et al. (2015). The former study shows that more neophobic zebra finches were slower to reach the learning criterion in their first learning task, whereas the latter study found that shyer wild-caught carib grackles needed more trials to achieve problem-solving success in the first learning task. However, neither study found a relationship between personality and cognitive performance in subsequent learning tasks.

Previous studies and our data show that the effect of personality on learning seems to occur only in novel contexts. Novel context may introduce more stressors to birds of slower personality type. In our study, the nature of the 2 associative learning tasks was closer, so one would expect similar learning scores of these 2 tasks. However, learning scores seemed more similar between the reversal and the 2nd associative learning tasks. The improving rates in reversal learning and 2nd associative learning tasks were significantly correlated. The final and the total accuracies in these 2 tasks also tended to correlate. The inconsistency of the learning scores between the 2 associative learning tasks and the similarity of the learning scores between the reversal learning and the 2nd associative learning may indicate a style of risk-taking. In novel context, individuals of slow personality type may tend not to take risk to make a certain choice based on sampling with relatively few trials. In familiar context, as the risk had already been evaluated previously, individuals of slow personality type may have not been hampered by the fearfulness of taking the risk. Therefore, the performances in the learning tasks in the familiar context may reflect the actual learning capacities of individuals, whereas performances in novel context may not, resulting in inconsistency of the learning scores in novel and familiar contexts.

Although the influence of slow personality only occurred in a novel context, it was still associated with lower benefits, such as learning slower in the 1st associative task or being reluctant to solve the problem box induced less or no food rewards. If this slow personality only hampered the animals without additional benefit, the evolution of the personality would not be possible. Sih and Del Giudice (2012) proposed that the disadvantage of having a slow personality could be balanced out through a speed–accuracy tradeoff, where individuals that are slower on cognitive tasks are more accurate, and those that are fast are inaccurate. Owning to this tradeoff, individuals who favor speed or accuracy on cognitive tasks yield similar overall benefits. In this study, we found no tradeoff between speed and accuracy, but a speed-improvement tradeoff instead. In the 1st associative task, birds with higher fearfulness to stressors had slower initial learning speeds but higher improving rates on learning and get similar final and overall accuracy with their faster conspecifics. These results show that connections between fast–slow personality and associative learning exist in certain (novel) contexts, via a speed-improvement route instead of a cognitive speed–accuracy tradeoff. Individuals with slow personality types may benefit from being slow, during which period they can collect more information and get similar final and overall accuracy with their faster conspecifics. Therefore, they were able to catch up with the faster individuals and receive similar overall benefits.

We also found that budgerigars were consistent in the latency of entering the maze. However, relationships between entering latency and learning performance were not found across all learning tasks in this study. Similar to the response to handling stress, latency to enter a novel environment was also used as an indicator of boldness/fearfulness (Carter et al. 2013). In a recent meta-analysis to explore the relationship between personality and cognition, the authors found that only boldness in response
to predators, but not in response to novel objects or food, showed a significant relationship with cognition (Dougherty and Guillette 2018). Our results seem to find similar relationships between personality and learning with Dougherty and Guillette (2018). As being bred in captivity, budgerigars are unlikely to encounter real predators. However, catching and handling by humans is a stressor similar to that caused by predators, giving rise to panicked behavior in budgerigars. Handling stress is more similar to predation and latency to enter the maze may be considered as a response to novel objects. What mechanism is responsible for the formation of these relationships is unknown and research on it is needed.

Although partly in agreement with Sih and Del Giudice (2012), who proposed a bidirectional interaction between personality and cognition that is connected by a risk–reward tradeoff, our results suggest that risk-taking/risk–reward tradeoff style (taking risk or not in a novel context) that linked to personality (fast–slow) might influence learning performances and trigger a cognitive tradeoff (speed–improvement tradeoff in our case) in a novel context (Figure 5). The relationship between them was context-dependent as it was only found in tasks with setup and apparatuses that were presented to the individuals for the first time. A meta-analysis using 19 species of animals showed that there is a small but significant relationship between personality and cognition in absolute value; however, the direction of this relationship is highly variable when considering the positive and negative effect sizes (Dougherty and Guillette 2018). We suggest that there may be no consistent cognitive style predicted by personality, and the relationship between personality and cognition may depend on contexts.

Acknowledgments
We are very grateful to the 3 anonymous reviewers for their helpful comments and suggestions on our paper.

Funding
This study was supported by the National Natural Science Foundation of China (Project No. 31501868 and No. 32070443) and Fundamental Research Funds for the Central Universities (Project No. lzujbky-2020-czy02).

Conflict of Interest
The authors declare that they have no competing interests.

References
Bates D, Mächler M, Bolker B, Walker S, 2014. Fitting linear mixed-effects models using lme4. arXiv Preprint arXiv 1406. 5823. doi:10.18637/jss. v067.i01
Bolhuis JE, Schouten WG, de Leeuw JA, Schrama JW, Wiegent VM, 2004. Individual coping characteristics, rearing conditions and behavioural flexibility in pigs. Behav Brain Res 152:351–360.
Brommer JE, Kluen E, 2012. Exploring the genetics of nestling personality traits in a wild passerine bird: testing the phenotypic gambit. Ecol Evol 2:3032–3044.
Carazo P, Noble DW, Chandrasoma D, Whiting MJ, 2014. Sex and boldness explain individual differences in spatial learning in a lizard. Proc R Soc B 281:20133275.
Carere C, Locurto C, 2011. Interaction between animal personality and animal cognition. Curr Zool 57:491–498.
Carere C, Oers KV, 2004. Shy and bold great tits Parus major: body temperature and breath rate in response to handling stress. Physiol Behav 82:905–912.
Carere C, Welink D, Drent PJ, Koelhaas JM, Groothuis TG, 2001. Effect of social defeat in a territorial bird Parus major selected for different coping styles. Physiol Behav 73:427–433.
Carrer AJ, Feeney WE, Marshall HH, Cowlishaw G, Heinsohn R, 2013. Animal personality: what are behaviour ecologists measuring? Biol Rev 88:465–475.
Chen J, ten Cate C, 2017. Bridging the gap: learning of acoustic nonadjacent dependencies by a songbird. J Exp Psychol Animal Learn Cogn 43:295–302.
Chittka L, Skorupski P, Raine NE, 2009. Speed-accuracy tradeoffs in animal decision making. Trends Ecol Evol 24:400–407.
Cole EF, Cram DL, Quinn JL, 2011. Individual variation in spontaneous problem-solving performance among wild great tits. Anim Behav 81:491–498.
Conrad JL, Weimersmith KL, Brodin T, Saltz J, Sih A, 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. J Fish Biol 78:393–435.
Cussen VA, Mench JA, 2014. Personality predicts cognitive bias in captive pittacines Amazona amazonica. Anim Behav 89:123–130.
Dall SR, Houston AI, McNamara JM, 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecol Lett 7:734–739.
Dougherty LR, Guillette LM, 2018. Linking personality and cognition: a meta-analysis. Philos Trans R Soc B 337:20170282.
Ducatez S, Audet JN, Lefebvre L, 2015. Problem-solving and learning in Carib grackles: individuals show a consistent speed-accuracy trade-off. Anim Cogn 18:485–496.
Fucikova E, Drent PJ, Smits N, Van Oers K, 2009. Handling stress as a measurement of personality in great tit nestlings Parus major. Ethology 115:366–374.
Gibelli J, Dubois F, 2017. Does personality affect the ability of individuals to track and respond to changing conditions? Behav Ecol 28:101–107.
Gosling SD, 2001. From mice to men: what can we learn about personality from animal research? Psychol Bull 127:45.
Griffin AS, Guillette LM, Healy SD, 2015. Cognition and personality: an analysis of an emerging field. Trends Ecol Evol 30:207–214.
Groothuis TG, Carere C, 2005. Avian personalities: characterization and epigenesis. Neurosci Biobehav Rev 29:137–150.
Guillette L, Hahn AH, Hoeseche M, Przyluski A-M, Sturdy CB, 2015. Individual differences in learning speed, performance accuracy and exploratory behaviour in black-capped chickadees. Anim Cogn 18:165–178.
Guillette L, Reddon AR, Hoeseche M, Sturdy CB, 2011. Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. Proc R Soc B 278:767–773.
Guillette L, Reddon AR, Hurd PL, Sturdy CB, 2009. Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, Poecile atricapillus. Behav Proc 82:265–270.
Heinze G, Ploner M, Dunkler D, Southworth H, 2020. logistf: Firth’s Bias-Reduced Logistic Regression. http:// cran.r-project.org/web/packages/logistf/
Klunen E, Sittari H, Brommer JE, 2014. Testing for between individual correlations of personality and physiological traits in a wild bird. Behav Ecol Sociobiol 68:203–213.
Koelhaas JM, Korte SM, De Boer SF, Bij VDV, Van Reenen CG et al., 1999. Coping styles in animals: current status in behavior and stress-physiology. Neurosci Biobehav Rev 23:925–935.
Krams IA, Vrublevska J, Sepp T, Abolms-Abols M, Rantala MJ et al., 2014. Sex-specific associations between nest defence, exploration and breathing rate in breeding pied flycatchers. Ethology 120:492–501.
Kuznetsova A, Brockhoff PB, Christensen RH, 2017. lmerTest package: tests in linear mixed effects models. *J Stat Softw* 82:1–26.
Mamuneas D, Spence AJ, Manica A, King AJ, 2014. Bolder stickleback fish make faster decisions, but they are not less accurate. *Behav Ecol* 26:91–96.
Mikus AA, Hope SF, Ketterson ED, 2016. Effect of acute stressor on reproductive behavior differs between urban and rural birds. *Ecol Evol* 6:6546.
Nakagawa S, Schielzeth H, 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol Rev* 85:935–956.
Nettle D, 2005. An evolutionary approach to the extraversion continuum. *Ecol Hum Behav* 26:363–373.
R-Core-Team, 2020. *R: A Language and Environment for Statistical Computing*. https://www.R-project.org/.
RÅale D, Garant D, Humphries MM, Bergeron P, Careau V et al., 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos Trans R Soc B* 365:4051–4063.
Reddon AR, Hurd PL, 2009. Individual differences in cerebral lateralization are associated with shy-bold variation in the convict cichlid. *Anim Behav* 77:189–193.
Rowe C, Healy SD, 2014. Measuring variation in cognition. *Behav Ecol* 25:1287–1292.
Sih A, Bell A, Johnson C, Ziembas R, 2004. Behavioral syndromes: an integrative overview. *Q Rev Biol* 79:241–277.
Sih A, Bell AM, 2008. Insights for behavioral ecology from behavioral syndromes. *Adv Stud Behav* 38:227–281.
Sih A, Del Giudice M, 2012. Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philos Trans R Soc B* 367:2762–2772.
Stoffel MA, Nakagawa S, Schielzeth H, 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol Evol* 8:1639–1644.
Thornton A, Lukas D, 2012. Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philos Trans R Soc B* 367:2773–2783.
Trompf L, Brown C, 2014. Personality affects learning and trade-offs between private and social information in guppies, Poecilia reticulata. *Anim Behav* 88:99–106.
White S, Wagner T, Gowan C, Braithwaite V, 2017. Can personality predict individual differences in brook trout spatial learning ability? *Behav Process* 141:220–228.
Wolf M, Weissing FJ, 2012. Animal personalities: consequences for ecology and evolution. *Trends Ecol Evol* 27:452–461.
Zhao QS, Hu YB, Liu PF, Chen LJ, Sun YH, 2016. Nest site choice: a potential pathway linking personality and reproductive success. *Anim Behav* 118:97–103.