

Article

Are cognition and personality related in budgerigars?

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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.

Various studies have documented animal personality across a broad range of taxa (Gosling 2001). Derived from psychological research, in which human personality has been shown to predict a range of health, social activity, and reproductive outcomes (Nettle 2005), animal personality is defined as consistent individual differences in behavior across time and/or contexts (Dall et al. 2004; Griffin et al. 2015; Wolf and Weissing 2012). It is directly comparable to human personality (Carere and Locurto 2011)

and likely has significant life-history consequences (Réale et al. 2010). In the last few decades, this thriving research area has shown that individual animals differ consistently in personality traits such as boldness, aggressiveness, exploration, and activity level (Gosling 2001; Groothuis and Carere 2005; Conrad et al. 2011). In addition, behavioral correlations have been found between different personality traits, resulting in behavioral syndromes; for instance, boldness and aggressiveness have been

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 (Bolhuis et al. 2004; Guillette et al. 2009; Reddon and Hurd 2009; Guillette et al. 2011; Carazo et al. 2014; Cussen and Mench 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 Klun 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 breast 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 ($15 \times 15 \times 20$ 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 ($28 \times 23 \times 25$ 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).

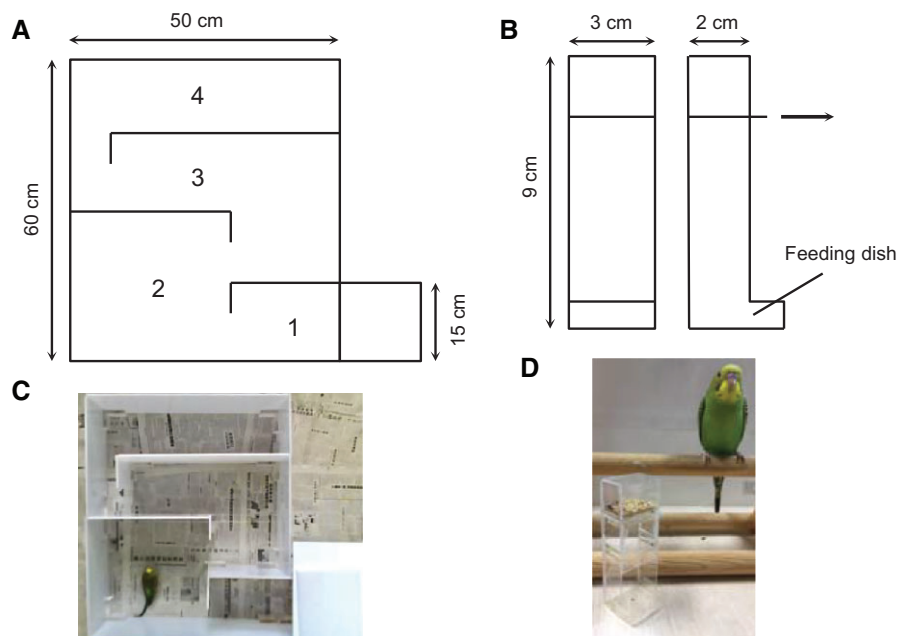


Figure 1. Apparatuses in the exploratory tendency test and problem-solving task. On the left, (A and B) the top view of the maze used in the exploration test. On the right, (C and D) the problem-solving box (the front and side views are shown in C).

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 variances, 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 (Carere 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 shallowly to gather more short-term gain, whereas slow animals take the time to collect more information to make more accurate inferences. We expected that fast animals would get more rewards (learn quicker) in the beginning, but make less accurate decisions by the end of the cognitive task, and slow animals vice versa. To determine whether personality actually links with learning in reference to speed, excluding other noncognitive aspects on which learning depends, we used the number of trials to a criterion to indicate learning speed (Griffin et al. 2015). To calculate the initial learning speed, we defined 5 correct choices in the 2 associative tasks and 8 correct choices in the reversal task as baseline learning criteria of the initial half of learning, because these 2 numbers were critical points indicating whether the subjects started to learn in the initial half of learning (chance level performances: 5 correct choices out of 10 trials in the 2 associative learning and 8 out of 15 trials in the reversal learning). Birds that did not learn would stay at a chance level, whereas fast learners needed less than 10/15 trials to accumulate 5/8 correct choices. For the convenience in interpretation, we divided the baseline learning criteria by the number of trials that the birds needed to reach these criteria (5/n in associative learning and 8/n in reversal learning) to represent the initial learning speed. A higher score indicated a higher initial learning speed. We calculated the percentage correct rate of the last 10 trials as the final accuracy and percentage correct rate of the total trials as the total accuracy. To further investigate how learning improved when the birds had different learning speeds and accuracies, we looked at the slope of the learning curve, which indicated how fast the learning improved and was defined as the improving rate. A logistic regression model was applied to the learning data of the individual birds using binary data (choice of S+/S-) as the dependent variable and trials as the independent variable to construct learning curves (Chen and ten Cate 2017). Generalized linear mixed models (GLMMs) with personality traits and sex (also interaction between personality scores and sex) included as fixed effects, the rewarding color types as random effects, were applied to investigate whether they explained differences in the initial learning speed, final accuracy, improving rate, and total accuracy of learning (e.g., initial learning speed \sim breathing rate + entering latency + sex + breathing rate \times sex + entering latency \times sex + breathing

rate \times entering latency + [1|color]). The binomial distribution family was used for GLMMs of final accuracy and total accuracy, and the Gaussian distribution family was used for GLMMs of initial learning speed and improving rate. We performed backward model selections of the full models and kept only significant terms to obtain the best-fitting models for statistical inference.

Spearman correlation was applied to check the relationships between different learning traits across cognitive tasks. Wilcoxon test was conducted to compare the differences between the personalities of the problem solver and nonproblem solver birds in the spontaneous problem-solving task. Fisher's exact test was conducted to detect whether the problem solver and nonproblem solver birds differed in sex. Statistical tests were implemented using the *base* (version 1.3-24), *logistf* (version 1.24), *lme4* (version 1.1-26), and *lmerTest* (version 3.1-3) packages (Bates et al. 2014;

Table 1. Repeatability of behaviors

Trait	N	No. _{obs}	Mean \pm SE	Repeatability (CI 5–95%)	P-value
Breathing rate (time/minute)	21	3	110.90 \pm 3.34 (1st) 110.33 \pm 3.33 (2nd) 120.45 \pm 3.98 (3rd)	0.49 (0.17–0.72)	0.002*
Entering latency (minutes)	21	2	28.10 \pm 6.94 (1st) 40.13 \pm 9.38 (2nd)	0.44 (0.03–0.71)	0.022*
Furthest position (Compartment)	21	2	2.48 \pm 0.31 (1st) 2.57 \pm 0.28 (2nd)	0.059 (0–0.491)	0.400

No._{obs} 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 2. Percentage of correct choice.

Individual	Block	1 st associative (%)		Reversal (%)			2 nd associative (%)	
		1	2	1	2	3	1	2
1		60	90	30	50	60	40	60
2		50	80	50	40	90	70	100
3		70	100	40	90	90	70	100
4		90	90	30	80	40	40	50
5		70	60	30	40	70	30	70
6		60	100	50	90	100	60	90
7		50	50	10	40	60	50	90
8		60	90	20	60	70	70	100
9		50	70	50	70	70	60	60
10		60	80	20	60	20	70	60
11		80	60	40	30	80	80	80
12		40	70	40	60	60	50	60
13		80	90	20	40	30	60	80
14		60	60	30	80	60	90	90
15		50	80	50	90	70	70	100
16		60	90	50	10	20	70	40
17		60	70	50	80	60	80	60
18		70	70	20	30	40	30	70
19		100	80	50	40	40	30	70
20		80	90	40	60	40	70	100
21		80	90	20	70	80	60	60

Rates of correct choices within given blocks (10 trials per block) in different learning tasks (1st associative learning, reversal learning, and 2nd associative learning).

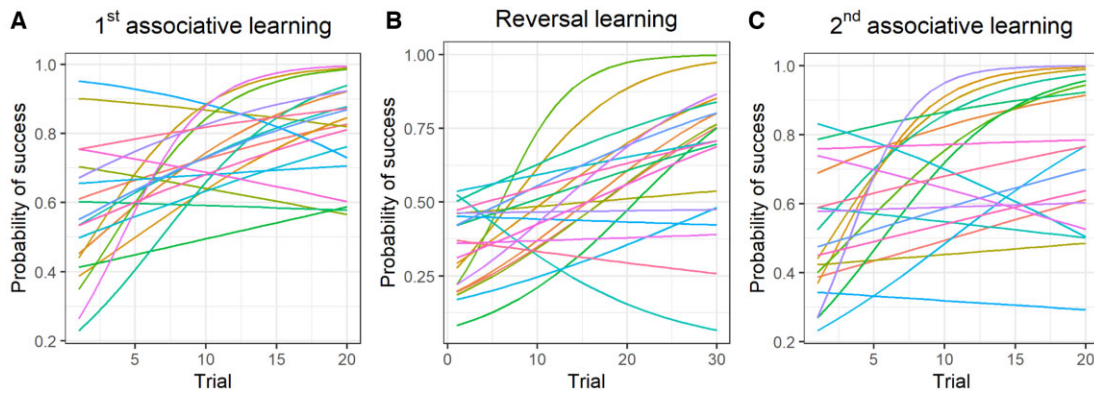


Figure 2. Learning curves of individual birds in different learning tasks (A-C, 1st associative learning, reversal learning and 2nd associative learning respectively). Fitted curves were obtained by logistic regression models based on the responses to the learning trials and the distributions of these 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.

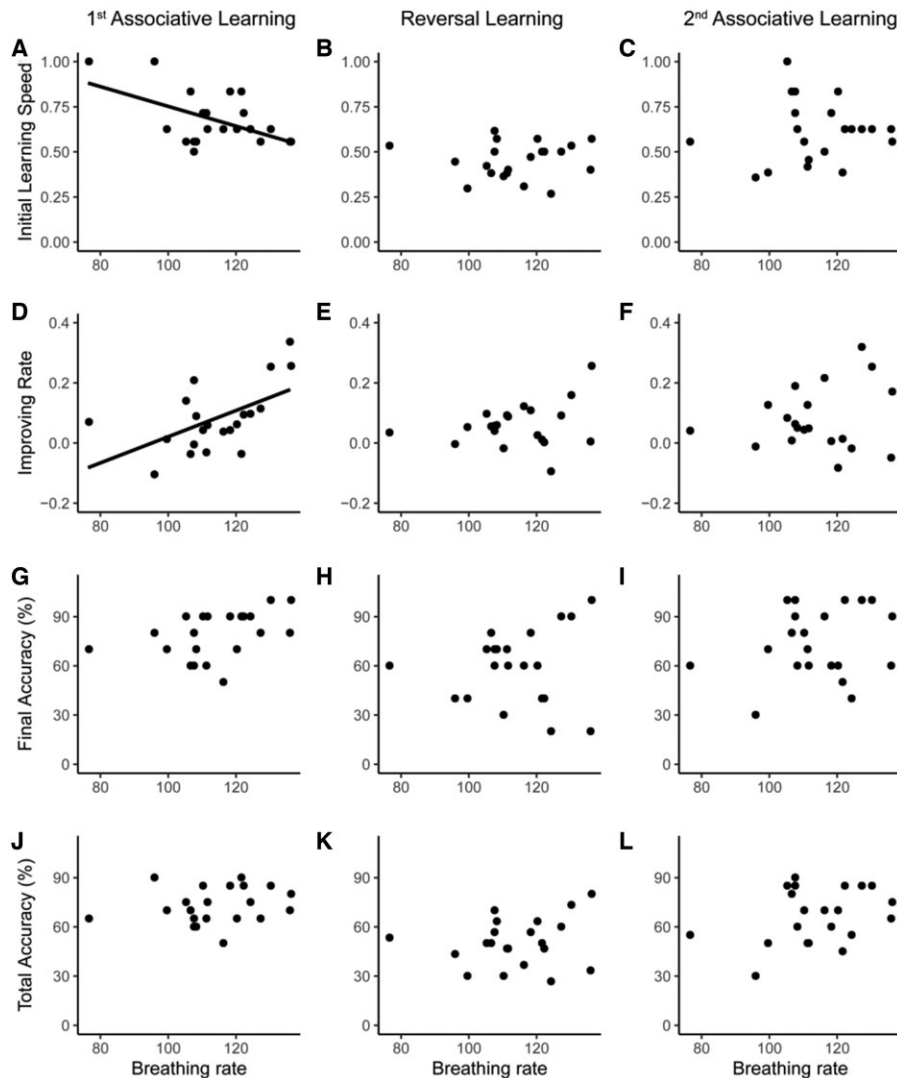


Figure 3. Relationships between breathing rate (time/minute, score indicating fearfulness of individual to handling stress) and cognitive performances across different learning tasks. (A–C) Relationships between fearfulness and initial learning speed. (D–F) Relationships between fearfulness and improving 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 $N = 21$.

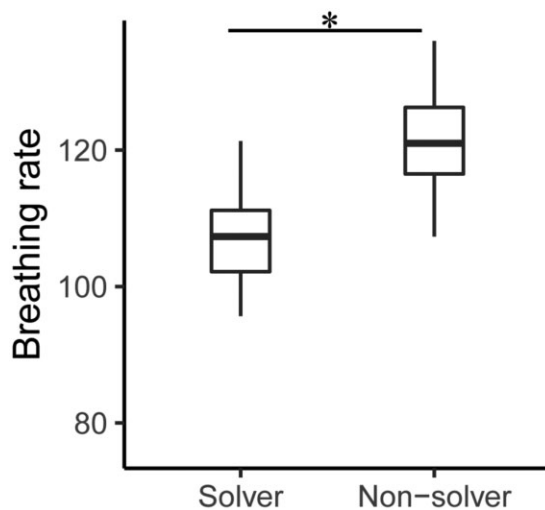


Figure 4. Breathing rate (fearfulness scores) of solver and nonsolver individuals in the spontaneous problem-solving task. *Significant difference ($P < 0.05$), $N = 21$.

Table 3. Correlations (r) of learning traits between associative and reversal tasks

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

^{*}Significant correlation (after Bonferroni correction, $P < 0.017$). All $N = 21$.

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: $79.05 \pm 3.08\%$ SE, $N = 21$; reversal learning: $59.52 \pm 4.95\%$ SE, $N = 21$; 2nd

associative learning: $73.80 \pm 4.65\%$ SE, $N = 21$). In the 1st color associative learning task, 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 quicker 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 \pm 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 \pm SE time/h, $N = 11$, nonproblem solvers: 1.29 ± 0.48 mean \pm 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 \pm 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; Klun 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

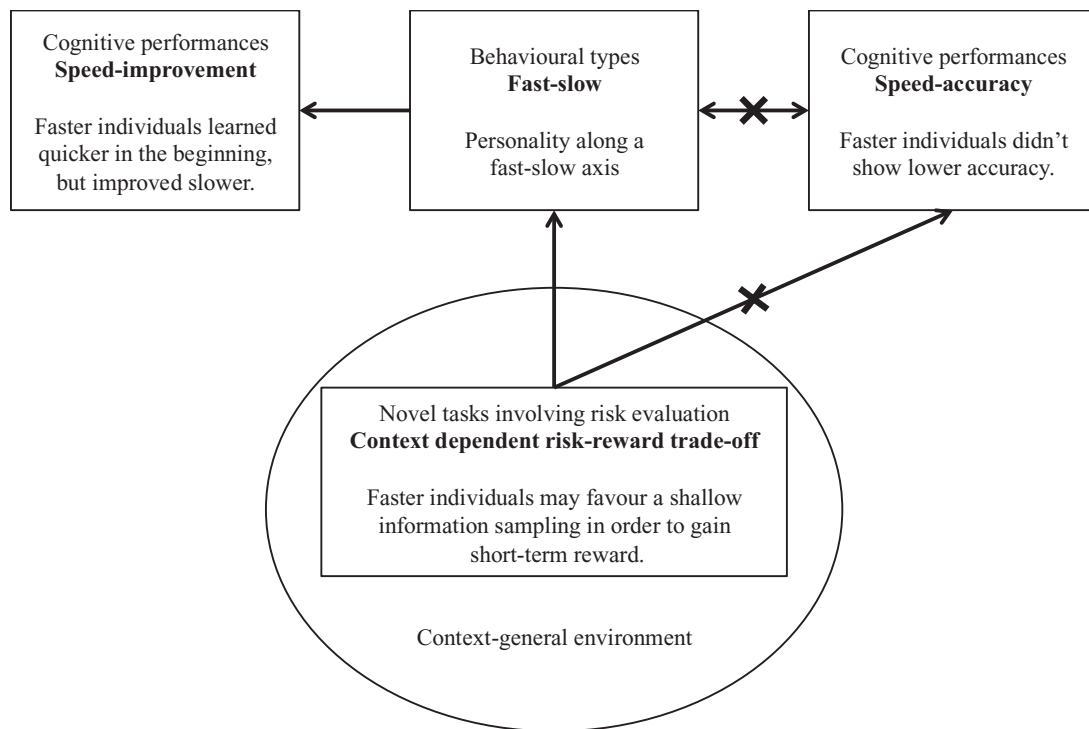


Figure 5. Hypothesized relationships between cognition and personality. It shows the relationships that are supported and not supported (crossed paths) by the results of this study. We suggest that personalities can influence cognitive performances only under the context involving risk evaluation and there are no consistent cognitive performances linked to different personalities.

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 shy 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. Owing 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 for the cognitive process ([Chittka et al. 2009](#); [Sih and Del Giudice 2012](#)) and thereafter improve their accuracy more quickly than the faster ones using this information. For instance, slow initial learners could collect more information from both correct and wrong choices. 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.

Ethics

This research was approved by the Animal Care and Use Committee of the Institute of Zoology, Chinese Academy of Sciences, and complied with local, institutional, and national rules of animal care and use, conforming to all applicable governmental regulations concerning the ethical use of animals and biodiversity rights.

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Conflict of Interest

The authors declare that they have no competing interests.

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