Variability in ambient temperature promotes juvenile participation and shorter latency in a learning test in zebra finches

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Recent increase in climate instability and unpredictability can pose challenges to the behaviour and survival of animals. Effective cognitive mechanisms could provide adequate responses for individuals to adapt to changing habitats and should be selected for. Studying the direct impact of the unpredictably changing environment on learning performance is particularly important in juvenile animals, because their learning abilities are in development and any impairment can affect their fitness. In this study, we bred zebra finches, Taeniopygia guttata, in stable or variable ambient temperature conditions. At hatching, half of the birds in each family were cross-fostered to a different condition while the other half remained in their original one. Just prior to their independence, we assessed their associative learning performance of 209 juveniles. Using a novel colour associative test apparatus, we compared the participation rate, latency to choice and learning performance between the experimental groups. We found that the juveniles that originated from the stable condition and that experienced environmental instability after hatching had the highest participation rate and the shortest latency to choice. Our results also showed that individuals that made quicker choices performed significantly better in the learning test than the slower birds. This finding was opposite to the often-postulated speed–accuracy trade-off, usually manifested by more accurate learning of slower individuals. There was no direct effect of temperature variability on the learning performance. However, we suggest that the differences in activity and latency (measures often used as proxies of personality traits) could be attributed to personality bias which may indirectly affect the outcome and interpretation of cognitive research. We discuss our results in relation to the long-term effects of environmental variability on animal activeness and cognitive abilities as well as the mechanisms responsible for the variation in learning performance.

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Cognitive performance is a significant component of the phenotype, which in each generation may be shaped by genes, parental effects and the environment (Cauchox et al., 2018; Healy, 2019; Tang et al., 2014). Relationships between cognition and fitness have long been a subject of research. Currently, given global warming and the increase in climate unpredictability and short-term variability, it is particularly important to understand the consequences of environmental variation for cognitive performance.

Associative learning is a domain of cognitive function defined as the modification of a behaviour followed by reinforcement based on the association between stimuli, responses and events (Griffin et al., 2015; Shettleworth, 2010). It is one of the most critical aspects of cognitive performance through its relevance for survival and foraging by adapting behaviours to an environment (Veit et al., 2015). In passerines, associative learning is responsible for relating novel predator sounds to conspecific mobbing calls which increases the survival rate through predator avoidance (Dutour et al., 2019). Associative learning ability can also facilitate better foraging by utilizing different stimuli in a variable/unpredictable environment (Franks & Thorogood, 2018).

While learning performance has great impact on the fitness of individuals, it inevitably carries costs, including high metabolic costs of developing and maintaining a big brain (Foley et al., 1991; Longman et al., 2017; Maille & Schradin, 2017). Larger brains are suggested to have evolved to enhance behavioural flexibility and allow the animals to deal with changes in the environment (Sol, 2009). Large-brained avian species have higher survival rates than small-brained species when introduced in a novel environment (Sol et al., 2005). Despite these advantages, it is assumed that effectively using the brain, for example during the learning process,
brings about additional metabolic costs (Jaumann et al., 2013; Mery & Kawecki, 2004). Consequently, any circumstances that reduce the resources available to the developing organism should affect the allocation of resources to cognitive abilities.

Environmental severity can originate from various factors, such as the intensity and duration of rainfall/droughts, parasite loads, competitors and availability of nutrients. Indeed, early life nutritional stress has been shown to have a negative effect on cognitive performance (Brust et al., 2014). Yet, one of the most basic environmental variables is temperature. Fluctuation in ambient temperature alone could induce physiological (e.g. metabolic and cardiovascular) costs (do Carmo et al., 2017; Yahav et al., 1997), especially in small endotherms (Naya et al., 2018). Short- and long-term heat stress could negatively affect cognitive abilities (Soravia et al., 2021). For instance, learning and motor performance in foraging tasks decrease at high air temperatures for zebra finches, *Taeniopygia guttata* (Danner et al., 2021). This could be because oxygen consumption and heat dissipation are important for brain functioning (Bliss et al., 2021; Bryan & Jones, 1980) and could thus mediate the effect of ambient temperature on cognitive behaviour.

Environmental severity could also shape certain aspects of cognition in a positive way (Roth and Pravosudov, 2010) and environmental complexity could induce evolutionary emergence of a learning ability (Dridi & Lehmann, 2016). At the individual level, blue jays, *Cyanocitta cristata*, subjected to a variable environment track their surroundings closely and are able to respond to the changes more efficiently after experiencing this variability (Dunlap & Stephens, 2012). At the comparative scale, passerine species that encounter variable precipitation (Medina & Francis, 2012) and mockingbird species subject to more variable and unpredictable precipitation and temperature have more elaborate song displays (Botero et al., 2009), a cognitive ability important for courtship and reproduction. At the between-population scale, black-capped chickadees, *Poecile atricapillus*, from a harsh environment outperform their conspecifics from a mild environment in food caching and recovery and associative learning (Pravosudov & Clayton, 2002) and problem-solving tasks (Roth et al., 2010). The effect is probably attributable to genetic differences between the populations, but the experimental set-up used in this study does not allow maternal effects or the influence of early life developmental conditions to be ruled out.

Maternal effects are nongenetic modifications of the offspring traits generated by the environment provided by the mother during development (Mousseau, 1998). Temperature-related maternal effects in zebra finches have been found: eggs incubated at a high temperature had significantly greater long-term survival than those incubated at a lower temperature (Berntsen & Bech, 2016). Avian mothers may vary yolk hormone levels in response to ambient temperature (Ruuskanen et al., 2016), yet it is not known whether this is an adaptation to prepare offspring for conditions they may experience later in life. A remarkable study showed that zebra finch mothers may acoustically signal to their embryos when ambient temperature exceeds 26 °C. In turn, this signalling affects the choice of nest site and reproductive success in adulthood of the resulting offspring (Mariette & Buchanan, 2016). The effects of ambient temperature at the embryonic stage has been documented in birds (Berntsen & Bech, 2016; Mariette & Buchanan, 2016); however, it remains unknown whether prehatching maternal effects could constitute an adaptive trait preparing the offspring for unpredictable temperature fluctuations.

Our main aim in this study was to determine the impact of unpredictable versus stable temperature conditions experienced by juvenile songbirds during development on their learning performance. Determining the direct impact of fluctuating ambient temperature on learning in juveniles is particularly important because their learning abilities are in development and any impairment can decrease their fitness and survival. The majority of cognitive studies on zebra finches that are related to foraging and survivability have been conducted on adults (e.g. Brust et al., 2013; Guillette & Healy, 2014; Howell et al., 2019; Katz & Lachlan, 2003; but see Rojas-Ferrer & Morand-Ferron, 2020). Associative learning in juvenile zebra finches has not been investigated previously. To investigate the potential modulation of the environmental conditions by maternal effects, we cross-fostered half of the offspring at hatching and thus created four treatment groups, determined by the match and mismatch of their pre- and posthatching ambient temperature conditions (Fig. 1). We assessed the juveniles’ learning performance using a custom-built colour associative test apparatus (Fig. 2). We chose to conduct two learning tests per individual to address any side preference, but, at the same time, to achieve a high throughput cognitive test to capture the learning performance of a large number of juveniles. We tested hypotheses that the original and rearing conditions and their interaction would affect juveniles’ (1) participation rate, (2) latency to choice and (3) learning performance. If variable temperature conditions entail costs to learning, we expected the juveniles reared in such conditions to show cognitive impairment. Alternatively, if effective food acquisition ability helps to improve the physiological state of the individual in unpredictable

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**Figure 1.** Illustration of the experimental design. The timeline of the study with the timing of cross-fostering at hatching are shown. Both climatic chambers had a night-time temperature of 17 °C.
conditions, we would expect cognitive resilience in learning (Maille & Schradin, 2017). When the offspring environment matches that of the mother, prenatal programming during egg laying could potentially alleviate the effect of developing in a variable environment. In this case, anticipatory maternal effects are expected and the consequences of developing in variable ambient temperatures would have a smaller impact on learning (Burgess & Marshall, 2014). On the other hand, prenatal programming in unpredictable environments may not be ideal (Krause & Naguib, 2014). The developmental plasticity of the offspring themselves may be responsible for the variation in their learning performance.

METHODS

Subjects and Breeding

We used domesticated zebra finches resulting from the interbreeding of populations maintained in Kraków, Poland and Max Planck’s Department of Behavioural Neurobiology in Seewiesen, Germany. Birds in the colony are usually maintained in semi-sheltered outdoor aviaries where they experience a range of ambient temperatures between ca. −10 °C and 38 °C. Breeding took place in climactic chambers after 2 months of acclimatization. The chambers were equipped with controlled lighting (13:11 h day:night), humidity (60%) and temperature. One chamber maintained a stable daytime temperature of 21 °C and 17 °C at night. The other chamber was set for a nighttime temperature of 17 °C and a variable daytime temperature: each day the temperature was drawn randomly from a normal distribution with a mean of 21 °C and SD of 5 °C, and the range was truncated to 11−30 °C. This procedure ensures that the mean daytime temperature calculated over different timescales (a week or a month) was ca. 21 °C in both groups (see the Supplementary material for the temperature and humidity record during the experiment). Importantly, temporal dynamics of the changes in the variable conditions were similar to those observed in the native habitats of zebra finches in Australia, where the maximum daytime temperature from day to day might differ by over 20 °C (e.g. Mariette & Buchanan, 2016).

Two months before pairing the birds, they were transferred to individual cages housing either two males or two females per cage, for acclimatization to the new temperature in the chambers. During breeding, each pair was placed in the individual cage (75 × 70 cm and 40 cm high) with two perches, a transparent feeder standing on the floor with ad libitum mixture of yellow millet, canary seed, red millet and black seed (Megan, Krakow, Poland) and a drinker hanging on the wall of the cage. A mix of minced eggs and carrot was provided on alternating days. Cardboard nestboxes were attached to the inside of the breeding cage in a top corner and shredded paper towels and wood wool were provided as nesting materials. Breeding pairs were monitored daily for nest building, egg laying, incubation and hatching. At hatching, each chick was marked by nail clipping and half of the hatchlings in each clutch were cross-fostered to another nest in the other chamber which had a matching number of offspring (+1 chick). All cross-fostering was carried out as soon as all the offspring in a nest had hatched. Juveniles were ringed at the age of 2 weeks. The learning phase was initiated at 40 days of age of the oldest chick in the clutch. Learning performance was measured at 55–65 days of age 2 weeks after the onset of the learning phase. Birds remained in their new or original nests until developmental independence (ca. 65 days). Further details of breeding and cross-fostering are given in Appendix 1.

Cognitive Assay

The learning phase took place in the home cages and was therefore influenced by the experimental temperature condition of a given individual. All procedures related to the cognitive tests, which were carried out outside the home cages (habituation, motivation and testing), were performed at 21 °C for all birds. The testing room contained a small aviary and a flock of zebra finches, which could be heard but not seen by the focal birds.

Learning phase

Two different opaque colour feeders were placed in each of the home cages for a minimum of 2 weeks. The colour feeders were hung on the front mesh of the home cage slightly above the height of the perches. Each cage was randomly assigned a colour combination; one colour feeder was filled with seed mix (reward feeder) and the other remained empty (empty feeder). The regular feeders were removed from the home cages during this phase. The feeders were coloured red, blue, green, graphite, pear, purple and yellow. The combination of the colour feeders was assigned based on prior analyses which confirmed the distinction between the colours measured by a spectrophotometer (see Appendix 2).

Habituation

All juveniles from a given cage were habituated to handling on the same days. Each individual was captured and transferred alone to the fasting cage (70 × 30 cm and 40 cm high with two perches and no food or water) for a 30 min habituation session every other day over the week. Three habituation sessions per bird were carried out 1 week before testing.

Motivation

The tests were performed after food deprivation to increase motivation to perform the tasks. On the day before testing, focal birds were transferred to the fasting cages 30 min before lights-off (2000 hours) for overnight fasting and at least 2 h of food and water deprivation in the following morning until 0900 hours. Individuals from the same home cage were put together in the same fasting cage overnight and remained together until the tests.

Apparatus

The testing cage was divided into an observation chamber and a choice chamber by a mesh divider (Fig. 2). The observation chamber was covered on three sides, except the meshed wall between the two chambers to provide a view of the feeders. The colour
The scores had inactive/no choice made (0) in each test session. The scores for the performance outcome was scored as correct (0.5), incorrect (0), one correct and one inactive (0.5), both sessions incorrect and one inactive (0), both incorrect and one inactive (0), both incorrect and one inactive (0.5), both sessions correct (1)

The birds that were tested first were chosen randomly from one of the two rearing conditions to be tested on the day and the following individuals were taken from alternating conditions each of the two rearing conditions to be tested on the day and the respective home cages immediately after testing; all were healthy and showed no signs of abnormal behaviour. All tested birds were monitored daily; none died or was injured.

**Statistical Analyses**

Analyses were carried out in R (version 3.6.2, R Core Team, 2019) with packages lme4 (Bates et al., 2015), ordinal (Christensen, 2019) and emmeans (Lenth, 2020). Variation in learning performance due to the experimental treatment of a 2 × 2 full factorial set-up (original condition during egg laying × rearing condition during juvenile period, henceforth Origin and Rearing, respectively) was assessed by mixed-effect models. All models had fixed effects of Origin, Rearing and the interaction between them. Models also contained covariates and random effects, as detailed below. Any effect that appeared nonsignificant (P > 0.05) was removed from the model via stepwise selection and comparison of the Akaiake information criterion score of the models to increase the power of the tests. This procedure was used to analyse variation in the following response variables: (1) probability of making a choice, (2) latency to choice and (3) outcome of learning performance. All individuals tested were included in the model to assess task participation (N = 209). Only individuals that made a choice were included in the other models (N = 133).

Using a chi-square test we confirmed the lack of side preference in the first session, with 53 birds choosing the right and 53 the left side (chi-square test: $\chi^2 = 0.1$, P = 1). There was also no side preference in the second session, with 61 birds choosing the left and 68 the right side (chi-square test: $\chi^2 = 0.38$, P = 0.54). During the second session, a given individual was more likely to choose the feeder that was on the opposite side of the first session (chi-square test: $\chi^2 = 45.53$, P < 0.01). This indicates that the birds were choosing the feeders based on the colour they selected in the first test session.

**Task participation**

We used generalized linear mixed models (GLMM) with a binomial response variable of participation (0 and 1) and fixed effects of Origin, Rearing, Sex, Age at testing (days), Start time (minutes since 0700 hours) and the interaction between Origin and Rearing. Start time and Age at testing were transformed by centring when the models suggested rescaling of the variables due to a large eigenvalue ratio. BoxPair (the combination of the origin and rearing cage ID) was included as a random effect. The random effect of ColourPair (the combination of the colour feeders placed in the home cage) was removed from this model, as it explained no variance. Post hoc analysis on the interaction effects was performed using estimated marginal means (EMMs) after a significant effect of the interaction was found.

**Latency to choice**

The linear mixed-effect models (LMEM) included fixed effects of Origin, Rearing, Sex, Age at testing. Start time and the interaction between Origin and Rearing. BoxPair and ColourPair were included as random effects. Latency as the response variable was transformed by square rooting to meet the assumptions of the model. Post hoc analysis on the interaction effects was performed with EMMs.

**Learning performance**

Cumulative link mixed models (CLMM) were used to analyse the ordinal response variable of the performance outcome. CLMM models correctly treat the ordered categorical data which provide a flexible regression framework for analyses (Christensen, 2019). The model included fixed effects of Origin, Rearing, Latency, Sex, Age at testing, Start time and the interaction between Origin and Rearing.

**Ethical Note**

The study was carried out with the permission from the 2nd Local Institutional Animal Care and Use Committee (IACUC) in Kraków, Poland; permit no. 155/2019. Breeding and housing of the birds complied with the European Union Law for experimentation with animals and the colony was monitored weekly by a veterinarian. Birds in both temperature conditions had ad libitum access to food and water. We checked the birds and replenished the food and water daily. All focal birds were transferred back to their respective home cages immediately after testing; all were healthy feeders were hung at the end of the choice chamber on the opposite side of the cage with a single perch placed next to the feeders. Only the rewarded feeder was filled with a layer of seeds while the other remained empty. There was an opaque divider between the two feeders so the bird could not see the other feeder once a choice was made.

**Test phase**

Test sessions ranged from 0900 until 1600 hours. The same rewarded and empty feeders in the home cages during the learning phase were transferred and hung inside the test cage. The experimenter captured the focal bird from the fasting cage and transferred it into the observation chamber. After 5 min, the mesh divider was gently lifted at the start of the test, allowing the bird to move to the choice chamber and choose one of the two sides. The starting side of the rewarded feeder was selected randomly and alternated after every bird. The experimenter quietly observed the focal bird from behind the observation chamber. Each test session ended once the bird had chosen a feeder by looking at least one head movement towards the inside of the feeder, or after a maximum of 10 min if no choice was made. The chosen colour and side were recorded, and if the rewarded feeder was chosen, the bird was allowed to feed on the seeds for 30 s. The experimenter then gently encouraged the bird to return to the observation chamber and replaced the mesh divider. The positions of the two feeders were swapped while the mesh side of the observation chamber was covered by opaque plates to prevent the bird from seeing the swap. The second test session started after 2 min of resting in the observation chamber. Once the bird completed two test sessions, it was returned to the home cage with food and water ad libitum.

Response variables of interest, including (1) task participation, (2) latency to choice and (3) learning performance, were measured and recorded during the test phase. Task participation was based on the number of individuals that successfully participated in the associative learning test and chose a feeder at least once (outcome: 1 = choice; 0 = no choice), regardless of whether the choice was correct or not. Latency to choice was the average time (s) until the subject had chosen a feeder over two sessions. Learning performance outcome was scored as correct (0.5), incorrect (−0.5) and inactive/no choice made (0) in each test session. The scores for the two test sessions were combined to acquire an overall performance. The scores had five levels: both sessions correct (1), one incorrect and one inactive (−0.5), both inactive or one correct and one incorrect (0), one correct and one inactive (0.5), both sessions correct (1).

We used cumulative link mixed models (CLMM) to analyse the performance outcome. CLMM models correctly treat the ordered categorical data which provide a flexible regression framework for analyses (Christensen, 2019). The model included fixed effects of Origin, Rearing, Latency, Sex, Age at testing, Start time and the interaction between Origin and Rearing.
Start time was transformed by centring when the models suggested rescaling of the variables due to a large eigenvalue ratio. BoxPair and ColourPair were included as random effects.

RESULTS

Task Participation

Individuals reared in the variable condition had a significantly higher participation rate than those reared in the stable condition (70% versus 58%; Table 1, Fig. 3). There was also a borderline significant effect of the interaction between the Origin and the Rearing conditions (Table 1). Post hoc analysis on the effect of this interaction carried out separately for each Rearing condition showed that individuals from the Stable—Variable group made a choice significantly faster than those of the Variable—Variable group (EMMs: estimate = −2.58 ± 1.26, t98.8 = −2.05, P = 0.04; Fig. 4). Individuals that originated from stable or variable conditions did not differ in latency when both were reared under stable conditions (EMMs: estimate = 0.82 ± 1.33, t82.2 = 0.61, P = 0.54; Fig. 4). Individuals that were tested later in the day chose a feeder more quickly (Table 2).

Learning Performance

Birds that participated in the task had an average outcome score of 0.63, which is significantly different from 0 (one-sample t test: t132 = 13.86, P < 0.001), where 0 would indicate the lack of learning about which was the rewarded colour. There were no effects of the experimental conditions or their interaction (Table 3). Individuals with a shorter latency to choice performed better (Table 3) and the effect was consistent in all groups (Fig. 5). Sex, Age at testing and Start time were removed from the model because they did not affect learning performance.

DISCUSSION

We generated conditions in which developing zebra finches were exposed to day-to-day environmental variability and a change in the environmental stability experienced at hatching. Our main finding is that juveniles that experienced this short- and long-term environmental variability were more active in the associative learning test. Specifically, birds that were reared in the variable conditions and that also experienced a change in environmental stability at the time of hatching clearly had the highest participation rate in the test (ca. 70%; Stable—Variable group, Fig. 3) and the
shortest latency to perform the task (Fig. 4). Individuals that chose more quickly also performed significantly better than slower ones (Fig. 5). However, contrary to our expectations, we found no effect of temperature variability on the performance outcome of the associative learning test. In the discussion below, we first consider juvenile task participation and latency to choice in relation to individual differences in activity, and then the learning performance itself.

**Task Participation and Latency to Choice**

Task participation is essentially the latency measured as a threshold value below or above our observation cutoff time of 10 min. Our results showed that juveniles from the Stable—Variable group participated in the associative learning test significantly more than the other groups (Fig. 3), indicating that the variability of environmental conditions experienced by the juveniles increased their activeness or willingness to forage and to choose one of the feeders. How could variable ambient temperature affect activity and performance in the learning task? Theoretically, variable conditions could prepare the juveniles to cope better with hunger. In this case, the short-term fasting that was used to increase motivation for the test would have had different effects depending on the experimental treatment. That was not the case: participation in the test was higher and latency to choice was shorter for birds tested later in the day for all groups (see the effect of Start time in Tables 1, 2), but the effect of test start time did not interact with our temperature treatments. Variable conditions could also make the birds forage more actively, and that is what we see in our results. This effect was specific to juveniles that were cross-fostered from the stable to the variable condition, that is, those that experienced the greatest environmental change during their ontogeny. Greater activity might be favoured in a variable environmental condition as it promotes more versatile responses to the unpredictable resource limitation. Moreover, the natural environment of zebra finches is characterized by a wide range of temperature (Mariette & Buchanan, 2016; Zann & Bamford, 1996). So variable temperature may potentially be perceived as the more favourable condition. Note that the variable conditions experienced by our juveniles resemble their natural environment more than the stable conditions usually applied in captivity (Griffith et al., 2017). Thus, variability in ambient temperature could act as an environmental enrichment that promotes greater activity, motivation for foraging and the cognitive mechanisms responsible for more versatile behaviours through brain functions (Grimberg-Henrici et al., 2016; Salvanes et al., 2013; Zentall, 2021). However, previous studies on the effects of environmental enrichment consist of clear differences between the treatment groups such as a bigger enclosure or the addition of various stimulating items. The potential for the variability in temperature to act as an environmental enrichment requires further investigation.

In the analysis of latency, the interaction effect between the treatments indicated that the juveniles that experienced greatest changes in conditions (Stable—Variable) at hatching chose a feeder more quickly than the other groups (Fig. 4). Our findings suggest the possibility that the juveniles themselves may be able to compensate for the variable environment during development by

**Figure 4.** Differences in the square root latency to choice between the four treatment groups (Stable-Stable; Stable-Variable; Variable-Stable; and Variable-Variable) estimated by the LMEM. Least squares means from the model are represented by the centre line, SEs are represented by the outer box and 95% confidence intervals are represented by the whiskers (N = 133 individuals). Circles represent data points in each group.

**Table 2**

Results of the linear mixed-effect model (LMEM) estimates with the sqrt latency to choose as the response variable.

| Fixed effects       | Estimate | SE    | df  | t     | P        |
|---------------------|----------|-------|-----|-------|----------|
| (Intercept)         | 15.19    | 1.85  | 57.49 | 8.22   | <0.001   |
| Origin              | -0.82    | 1.32  | 73.17 | -0.62  | 0.54     |
| Rearing             | -1.98    | 1.29  | 127.05 | -1.54  | 0.13     |
| Start time          | -0.12    | 0.00  | 71.99 | -2.52  | 0.01     |
| Origin*Rearing      | 3.40     | 1.75  | 118.64 | 1.93   | 0.06     |

Random effects:

| Variance | SD   |
|----------|------|
| BoxPair  | 1.04 | 1.02 |
| ColourPair | 1.24 | 1.12 |
| Residual | 24.32| 4.93 |
being more active in foraging. This is similar to the findings of Krause et al. (2017) in which the change in the nutritional condition experienced after independence affected the hopping activity of zebra finches. The authors found that the individuals from the mismatched treatment condition were more active than those from the matched condition.

**Learning Performance**

Learning performance did not differ between our treatment groups, but we found that the outcome of the tests was better when individuals were quicker to choose (Fig. 5). Latency to complete a task has been viewed as an indication of the ability to learn (Kozlovsky et al., 2015; Roth et al., 2010). However, the speed-accuracy trade-off (SAT) is one of the implied constraints of learning, where individuals completing the task slower and with more information should have greater accuracy (Chittka et al., 2009). David et al. (2011) revealed the SAT related to foraging success in zebra finches by assessing the food detection probability. Interestingly, the negative relationship we found between latency and performance indicates the opposite of the SAT (Table 3, Fig. 5). Rojas-Ferrer and Morand-Ferron (2020) also found no evidence for the SAT in their zebra finch study, which investigated the learning performance of juveniles that experienced and learned with predictive cues. The agreement between the latter study, which was performed on 3-month-old birds, and ours may suggest that the SAT is not manifested in young birds. This hints at the possibility that SAT increases with age, but, so far, there are too few studies on juvenile learning to make a firm conclusion.

The lack of direct effects of our experimental treatment on learning could also stem from the fact that the individuals in the Variable conditions had mixed signals, as ambient temperature fluctuated daily but the food and water availability remained the same. This may have weakened the effects of our experimental treatment on the performance because the temperature variability was not accompanied by variability in other resources.

Contrary to our expectation, we did not see any prehatching maternal effects influencing the juveniles’ learning performance. Likewise, in another zebra finch study in which the two generations experienced different early nutritional conditions, the authors did not find any interaction between the matched and mismatched parental and offspring environments (Krause & Naguib, 2014). This may indicate that it may not be beneficial for parents to program their offspring to the matching condition in an unpredictable environment. However, we found maternal effects acting on activeness, with juveniles originating from the stable condition

**Table 3**

| Fixed effects | Estimate | SE  | z    | P    |
|---------------|----------|-----|------|------|
| Origin        | -0.46    | 0.64| -0.72| 0.47 |
| Rearing       | -0.64    | 0.60| -1.06| 0.29 |
| Latency       | -0.004   | 0.002| -2.62| 0.009|
| Origin*Rearing| 1.09     | 0.81| 1.34 | 0.18 |

| Random effects | Variance | SD  |
|----------------|----------|-----|
| BoxPair        | 0.81     | 0.90|
| ColourPair     | 0.25     | 0.50|

**Figure 5.** Relationships between the learning performance (expressed as the combined score over two test sessions, each session scored as correct (0.5), incorrect (−0.5) and inactive/no choice made (0)) and the latency to choice in the four treatment groups (Stable-Stable; Stable-Variable; Variable-Stable; and Variable-Variable). The regression lines are represented by the solid lines and the SEs are represented by the shaded areas (N = 133 individuals).
being more active when reared in the variable condition and this might indirectly affect the learning performance.

Our results also showed a difference in participation rate between the treatment groups, which may have influenced our further interpretation of the learning performance. Task participation and latency have often been documented as proxies of animal personality traits such as neophobia, exploratory behaviour or boldness (Careau & Garland, 2012; Tuliozi et al., 2018). Our results hint at the importance of considering personality bias when conducting experiments for cognitive functions. Individuals that did not participate could have equally obtained the associative learning ability but their performance was not captured by our tests. Indeed, individual differences in personality traits have been found to affect both task participation and cognitive performance in primates: openness of individuals was positively related to participation but their performance was not captured by our tests. Indeed, not participate could have equally obtained the associative learning ability but their performance was not captured by our tests. Indeed, not participate could have equally obtained the associative learning ability but their performance was not captured by our tests.

**Supplementary Material**

Supplementary material associated with this article can be found online at https://doi.org/10.1016/j.anbehav.2022.01.010.

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ChuChu Lu: Methodology, Investigation, Formal analysis, Writing—Original Draft, Writing—Review & Editing, Visualization.

Maelle Lefeuvre: Writing—Review & Editing, Investigation.

Joanna Rutkowska: Conceptualization, Methodology, Investigation, Resources, Writing—Review & Editing, Supervision, Funding acquisition.

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APPENDIX 1

We formed 44 pairs in the Stable and 44 pairs in the Variable condition. Of these, there were 40 pairs that started breeding (laid at least one egg) in the Stable and 43 pairs in the Variable condition.

Around the time of hatching, nests were monitored several times a day. We aimed to track which hatching came from which eggs and hatchlings were marked according to the egg number (egg 1: hatching A; egg 2: hatching B, etc.).

For cross-fostering, we matched pairs from the two conditions for D. This cross-fostering was possible between 25 pairs in the Stable condition. Of these, there were 40 pairs that started breeding (laid at least one egg) in the Stable and 43 pairs breeding in the Variable condition. There were 237 chicks involved in cross-fostering. Of these, 214 embryos were used.

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APPENDIX 2

To analyse the colour of the feeders, we used a JAZ spectrophotometer (range 300–700 nm) with the PX Lamp (Ocean Optics, Dunedin, FL, U.S.A.) and bifurcated probe 7 × 400 μm, equipped with a permanently attached 3 mm long black collar. Before the measurements, we took a calibration measurement of the Spectralon

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white standard (Ocean Optics). We collected five measurements per feeder, with the probe held at 90° to the feeder’s wall surface. Obtained spectra were further processed (averaged and smoothed) in the package pavo (see Fig. A1; Maia et al., 2019). Final combinations were chosen by selecting the spectra that were farther apart from the other based on the results (Figs A1, A2). Burgundy, red and purple, which were similar to one another, did not form any combination.

Colour feeder combinations were as follows: (1) blue/burgundy; (2) blue/purple; (3) blue/graphite; (4) blue/red; (5) burgundy/blue; (6) burgundy/green; (7) burgundy/pear; (8) graphite/pear; (9) graphite/yellow; (10) green/burgundy; (11) pear/graphite; (12) purple/blue; (13) red/blue; (14) yellow/graphite.

Figure A1. Illustration of the averaged spectra for the colour feeders.

Figure A2. Representation of the feeders’ colours in the avian tetrahedral colour space. Each of the vertices denotes maximum stimulation of a given cone type.