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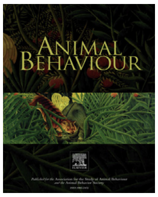

The effect of metabolism on cognitive performance varies with task complexity in common minnows, *Phoxinus phoxinus*

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Cognitive abilities are crucial for survival and adaptation, enabling animals to navigate their environment, recognize predators and remember the location of food resources. However, underlying factors related to learning and memory can be energetically demanding and thus may vary depending on an individual's metabolism or aerobic capacity, potentially affecting individuals' cognitive performance. In this study, we explored the link between cognitive performance and whole-body metabolic traits, including aerobic scope (AS), maximum metabolic rate (MMR) and standard metabolic rate (SMR). European minnows, *Phoxinus phoxinus*, were trained over 20 days to locate a food reward in a maze. Individuals were trained in either a simple (two-door) or a complex (four-door) maze. Fish in the simpler maze had consistently higher success and a lower latency to reach the reward, suggesting the two-door maze was less cognitively challenging. We found a correlation between metabolic traits and cognitive performance traits (i.e. success and latency to reach the reward) at the end of training. However, this relationship varied depending on maze complexity. In the two-door maze, individuals with higher MMR and SMR had higher success and a lower latency to reach the reward. However, in the more complex maze, fish with lower metabolic rates (MMR and SMR) had higher success and lower latency to reach the reward. AS followed similar patterns but mostly affected the success to reach the reward. In simpler environments, having a higher metabolism may be more beneficial for cognitive performance, whereas in complex environments, having a lower metabolism may be more beneficial as it could be associated with a slower but more thorough exploration and learning process.

Cognitive performance relates to a range of ecologically imperative tasks including foraging (Kendall & Wikenheiser, 2022), predator avoidance (Griffin, 2004; Griffin et al., 2001) and mate choice (Szabo et al., 2022). In environments where food is patchy but consistent, for example, memory of food sources and appropriate adjustment of foraging strategies can reduce search time and associated predation risk (Warburton, 2003). Despite the benefits of learning about and remembering the location of items, individuals within a species differ in their cognitive performance, which may have consequences for fitness and survival (Dukas, 2004). However, the diversity of factors that influence cognitive performance can make measuring it challenging and lead to an ambiguous relationship with fitness (Rowe & Healy, 2014). Interindividual variation in cognitive performance has been extensively documented in humans (Carroll & Maxwell, 1979), but is increasingly observed in other taxa (Boogert et al., 2018; Thornton & Lukas, 2012), from invertebrates (Lucon-Xiccato et al., 2024) to vertebrates, such as mammals (Mazza et al., 2018), birds (Brucks et al., 2022) and fish (Agrillo & Bisazza, 2018; Lucon-Xiccato & Bisazza, 2017). Differences in cognitive performance among individuals can be attributed to a range of factors, including age (Watowich et al., 2020), sex (Wallace et al., 2020), social environment (Boogert et al., 2018; Dunbar, 1998), as well as consistent individual variation in other behaviours (Lucon-Xiccato & Dadda, 2017; Sih & Del Giudice, 2012). Despite these known factors, unexplained variation in cognitive performance among individuals remains.

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Important yet understudied factors that may influence cognitive performance are metabolism and energetics. Metabolism could be directly related to cognitive performance due to the energetic cost of cognitive functioning (Ames, 2000). The expensive tissue hypothesis posits that there are potential trade-offs between investing in brain tissue and other energy-consuming processes and organ systems because brain tissue is energetically demanding to produce and maintain. Indeed, guppies, *Poecilia reticulata*, artificially selected for large brains relative to body size performed better on cognitive tests but also developed smaller guts, as predicted by the expensive tissue hypothesis (Kotrschal et al., 2013). Research in humans has shown that diet and metabolic disfunctions can affect cognition (Farruggia & Small, 2019; Gomez-Pinilla & Tyagi, 2013). Metabolism may also indirectly influence cognition due to effects on behaviours related to cognition. For example, from studies in humans and rodents, it is known that exercise improves sleeping (Kredlow et al., 2015), with benefits for cognition (Raven et al., 2018). Less is known about the links between metabolism and cognition in an ecological context, despite metabolic rate being related to a range of behaviours and personality traits in several species (Mathot et al., 2019).

Generally, individuals that tend to live a ‘slower pace’ of life are less active, bold and exploratory and have correspondingly lower metabolic requirements compared to ‘fast-paced’ individuals (Careau & Garland, 2012). These traits may in turn influence cognitive performance; for example, individuals that are ‘fast-paced’ and thus more exploratory, may encounter learning opportunities more often and thus appear better at learning than less exploratory ‘slow-paced’ individuals (Sih & Del Giudice, 2012; but see Watrobska et al., 2023). Similarly, the cognitive styles hypothesis proposes that there is a trade-off between speed and accuracy in cognition that also varies along the slow–fast continuum; ‘fast-paced’ individuals should make decisions faster but with less accuracy than ‘slow-paced’ individuals (Sih & Del Giudice, 2012). Alternatively, individuals with a higher maximum metabolic rate (MMR) or aerobic scope (AS; i.e. the difference between the maximum metabolic rate (MMR) and the baseline or standard metabolic rate (SMR)) may have a higher capacity to use energy for simultaneous aerobic functions. Those individuals may thus have generally higher cognitive performance (i.e. be both faster and more accurate at problem solving) compared to individuals with a lower AS or MMR. Metabolic rate may also influence motivation to engage in cognitive tasks, as individuals with higher metabolic rates may require more food (Killen et al., 2023), so foraging-related tasks and accurate learning and memory may have more importance to those individuals. However, the relationship between metabolic rate and behaviour, including cognitive performance, may only be revealed in specific contexts, such as during food deprivation or absence of shelter (Killen et al., 2013).

Several studies have shown how variation in environmental factors may reveal changes in the relationship between metabolic rate and behaviour. For instance, the link between SMR and activity may only be revealed at a specific temperature (Careau & Garland, 2012), while the relationship between routine metabolic rate and risk-taking behaviour may only be revealed under hypoxia (Killen et al., 2012). Additionally, the relationship between SMR and social tendency disappear under food deprivation conditions (Killen et al., 2016). Therefore, the relationship between metabolic rate and behaviour may be more apparent under stressful or challenging conditions (Killen et al., 2013). Similarly, potential relationships between metabolic rate and cognitive performance may only be revealed if the task is challenging enough that individuals exhibit sufficient variation in their ability to complete the task, such that differences in metabolic rate are meaningful for their success (Jones et al., 2023; Rowe & Healy, 2014). The link between metabolic rate and variation in cognitive performance, however, has not been extensively studied in any context.

We studied the relationship between metabolic rate and cognitive performance in European minnows, *Phoxinus phoxinus*, using an arena maze. European minnows are small-bodied freshwater fish (<12 cm) that live in complex environments; they can be found in a variety of river systems and generally experience variation in vegetation, shelter, food availability and temperature throughout their life (Raffard et al., 2019). In addition, minnows have been demonstrated to be able to engage in spatial navigation tasks (Závorka et al., 2020) and associative learning tasks (Jones et al., 2023). Fish were trained individually, once per day, for 20 days in a spatial learning task where they had to locate a food reward in a set amount of time. After all learning trials were complete, we measured individual oxygen consumption rate using intermittent-flow respirometry to estimate SMR, MMR and AS of each fish. If fish with higher MMR and AS have more capacity to use available energy in energetically expensive cognitive tasks or are more motivated to engage in the task, then fish with high metabolic rates should both reach the reward quicker and be more accurate in locating the reward. However, if there is a trade-off between speed and accuracy in making decisions as per the cognitive styles hypothesis (Sih & Del Giudice, 2012), then we would predict that individuals with higher metabolic rates should make decisions faster but be less accurate. To determine whether the relationship between metabolic rate traits and cognitive ability is only present when the task is more complicated, half of the fish were tested with two potential locations (two doors) for the food reward and half were tested with four potential locations (four doors).

METHODS

Experimental Overview

The current experiment was carried out using the same fish used in a previously published study (Jones et al., 2023). The data set collected for Jones et al. (2023) was extended with respirometry measurements for the current study. As described in Jones et al. (2023), adult European minnows of undetermined sex were collected from the river Kelvin (Glasgow, 55°52′42″N, 004°17′03″W) in September 2021 with hand-nets and minnow traps and immediately brought to laboratory aquaria facilities. Here, fish were kept in 42-litre tanks ($N = 50$ fish per tank) at a constant temperature of 14 °C (i.e. average temperature of the river Kelvin at the time and location where fish were caught) with a 12:12 h light:dark cycle (LD). Fish were fed bloodworms twice a day ad libitum. After 2 weeks of laboratory acclimation, fish were anaesthetized and tagged with two visible implant elastomers (Northwest Marine Technologies, Anacortes, WA, U.S.A.) to identify individuals. Following the tagging procedure, we allowed the fish to recover for 2 weeks, then moved 39 individuals to two 27-litre aerated tank (18 individuals in one tank and 21 in the other) containing ‘natural’ mixed colour pea gravel and three plastic plants, maintained at the same temperature (14 °C) and photoperiod (LD 12:12 h). The experiment was conducted outside the breeding season, which occur in April–June (Frost, 1943; Griffiths et al., 2014); however, fish that showed any sign of breeding colour or aggression towards other fish in the tank were excluded from the trials to control for potential sex-related effects (4 fish excluded, 3 from one tank and 1 from the other); the remaining fish were either females or males that did not take on breeding colours.

Individual fish were then trained once a day for 20 consecutive days to locate a food reward (bloodworm) in a maze. Two rounds of training were conducted; the first cohort started 21 days post-tagging ($N = 15$ individuals) and the second cohort started 41 days post-tagging ($N = 20$ individuals), after the first cohort was done. We tested two maze complexities, two-door and four-door choice mazes, where each door opened into a prechamber connected to an interior chamber containing the reward (Fig. 1). However, in the design of both mazes, the interior reward chambers were only accessible by one prechamber; all other options were blocked by mesh doors (see methods in Jones et al., 2023 for more detailed description of the maze design, which was based on Závorka et al., 2020). Each fish was assigned pseudorandomly to a specific maze complexity (two- or four-door choice) and a specific accessible reward chamber location. The accessible reward chamber was indicated by a landmark (an artificial plant) placed outside of the open door of the prechamber. An individual was always trained in the same maze and with the same location of accessible reward chamber. A total of 35 individuals were trained, of which 19 were trained in the two-door choice maze (cohort $1 = 9$; cohort $2 = 10$ individuals) and 16 in the four-door choice maze (cohort $1 = 6$; cohort $2 = 10$ individuals). During training, fish were only fed once a day, at the end of each day of training. One month after the end of the 20 days of training, we estimated fish metabolic rates from measures of oxygen consumption over time using intermittent-flow respirometry (see 'Metabolic rate measurements' below for more details; $N = 33$, because one fish from each cohort was euthanized for husbandry reasons after completing training but prior to respirometry). Metabolic rate was measured after learning trials in order to minimize any potential stress-related effect associated with the metabolic measure. Due to repeatability of metabolic rate measurements over brief periods (i.e. <10 weeks; Norin & Malte, 2011), we considered metabolic rates measurements obtained 1 month after the end of training in the same condition as a proxy of metabolic rate during training.

Ethical Note

This experiment was conducted under the approval of the University of Glasgow Animal Welfare and Ethical Review Board and U.K. Home Office project licence PB94DAA0. To minimize fish stress, we implemented several measures. We minimized air exposure during capture, transport and release, and we handled the fish gently, avoiding unnecessary chasing. When catching wild fish, we deployed traps for ca. 1 h, maintained low fish density in holding buckets (never exceeding 5% of water volume) and closely monitored and controlled temperature and oxygen levels, minimizing variation through the use of coolers and portable aerators. To tag fish with visible implant elastomer (VIE), we followed a standard operating procedure that included temporary anaesthesia (10 ml of a stock solution of benzocaine diluted in 1 litre of water). A combination of two VIE tags of eight different colours (blue, green, orange, violet, yellow, pink, red, white) were injected subcutaneously on the dorsal area of each individual. After tagging, fish were measured (mass and total length) and immediately returned to an aerated bucket for recovery (tagging and measurement procedure lasted less than 1 min). Recovery was visually assessed by continuous monitoring, and fish were returned to their holding tank once they resumed routine swimming behaviour. All fish recovered from the procedure. Additionally, we provided holding tanks with 'natural' mixed colour pea gravel and three plastic plants for shelter. As previously mentioned, these tanks were kept at a temperature matching that of the Kelvin River at the time of capture (14 °C) and followed a 12:12 h light:dark cycle to imitate natural environmental conditions.

Spatial Learning Procedure

Details about the training procedure are given in Jones et al. (2023); briefly, three mazes were used to test three individuals simultaneously (one individual per maze). Because individuals from both maze designs were tested at the same time, in each trial, two individuals were tested in one maze complexity and one individual was tested in the other maze complexity. Each maze was filled with 14 °C fresh water, which was changed between each trial. Trials lasted for 20 min; 5 min of acclimation in a start chamber, which was remotely opened with a pully system from behind a black curtain, followed by 15 min of maze exploration. Each trial was recorded with a video camera (GoPro 4 or 7, at 25 frames/s) set-up ~1 m above each maze. All videos were manually scored to determine two key measures. First, we assessed whether the fish reached the reward chamber as their first choice (i.e. no other prechamber was entered before the fish entered the reward chamber), defined as 'success to reach the reward'. This measure was used to obtain the success probability. Second, we calculated the latency to reach the reward chamber after leaving the start chamber. Note that latency is only applicable to fish that successfully reached the reward chamber during the trials. Singular trials where the fish never reached the reward chamber (unrewarded trials) were excluded from this measurement, which represented about 24% of the total trials. Despite some individuals not reaching the reward in multiple trials, the unrewarded trials were

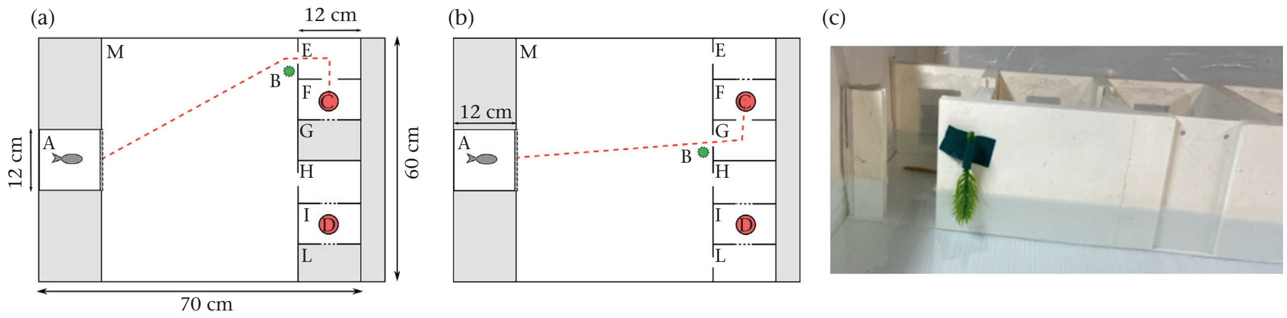

Figure 1. Arena set-up for the (a) two-door and (b) four-door choice maze. Each arena included a starting chamber (A) where a door was remotely lifted with a pully system after the acclimation period in order to allow the fish to freely swim into an open arena (M) connected by doors to either two or four prechambers (two-door choice: E, H; four-door choice: E, G, H, L) but only one of them allowed access to the food reward (two-door choice: E; four-door choice: G). In each arena there was also a plant landmark (B) that indicated the right path (shown by the red dashed line) to the reward chamber (F) containing the food reward, i.e. a bloodworm (C). An additional food reward (D) was placed in a closed reward chamber (I), i.e. a chamber not accessible by the fish because it was blocked by mesh doors in order to control for visual and olfactory cues. All prechambers that did not allow access to the reward had a mesh door to block access to either the reward chamber or the closed reward chamber (two-door choice: I; four-door choice: E, H, L). (a, b) Illustrate possible configurations, however, in actual trials, any of the prechambers could be the open path but the open path was consistent for a fish across all trials. (c) Shows the two-door choice three-dimensional printed maze with a fish exploring the maze. Figure adapted from Jones et al. (2023).

distributed among 30 different individuals (i.e. 85% of individuals), and we observed no effect of maze complexity on the number of unrewarded trials (Fig. 2a, b, Appendix, Table A1). Since individuals may have failed to complete the trials for various reasons, such as not leaving the start box or having actively explored the maze without entering the reward chamber, interpreting these results would be ambiguous. Therefore, the latency analyses were conducted only for individuals who effectively completed the trial. Finally, videos from the last day of training (day 20) were also analysed with Ethovision XT 15 to obtain the distance that individuals moved over the full duration of videorecording (15 min) as a proxy of fish activity.

Metabolic Rate Measurements (SMR, MMR and AS)

Fish metabolic rates (SMR, MMR) were measured using intermittent-flow respirometry (details in Appendix, Table A2; Killen et al., 2021; Svendsen et al., 2016). Fish aerobic scope (AS) was calculated as the difference between MMR and SMR.

Prior to metabolic rate measurements, fish were fasted for 24 h. For MMR, fish were manually chased with a plastic stick in an elliptical tank containing freshwater for 2 min (Chrétien et al., 2021), then immediately transferred into the intermittent-flow respirometry set-up to measure oxygen consumption rate as a proxy of MMR (Norin & Clark, 2016). Fish SMR was measured overnight. The minnows were left in the respirometry chambers for ~14 h, with cycles of 2 min of flushing of oxygenated freshwater and 8 min for closed phases, during which fish oxygen consumption was recorded, resulting in an average of 73 slopes of oxygen uptake rate. Background microbial oxygen uptake rate was measured in the empty respirometry chambers before and after fish metabolic measurements. Immediately after metabolic measurements, we recorded fish mass and total length (mean ± SD: mass: 1.54 ± 0.49 g; total length: 58.52 ± 6.01 mm).

We calculated the slope of oxygen depletion over time during the closed phases (Svendsen et al., 2016) as the change in dissolved oxygen in each chamber's water over time. During MMR measurements, the open phases were suspended, and oxygen depletion was measured for a minimum of 6 min (and up to 10 min). We determined MMR as the slope with maximum decline in oxygen obtained for rolling regressions of 2 min length, starting every 2s over the total time of MMR measurements. The maximum decline in oxygen typically occurred in the first 4 min of measurements. We calculated SMR as the average of the lowest 20th percentile of the overnight measures, calculating one slope per closed phase (Chabot et al., 2016; see Appendix, Table A2 for more details) using the FishResp R package (Morozov et al., 2019). We calculated oxygen uptake rates for each fish by multiplying these slopes by the volume of the respirometry chamber after subtracting fish volume and background microbial respiration, where changes in background respiration over time were modelled linearly.

Statistical Analyses

All analyses were performed in R (R version 4.3.1) using the following packages: ‘tidyverse’ (Wickham et al., 2019), ‘lme4’ (Bates et al., 2015), ‘lmerTest’ (Kuznetsova et al., 2017), ‘piecewiseSEM’ (Lefcheck, 2016) and ‘Rmisc’ (Hope, 2013). Before analysing the effect of metabolic traits on cognitive performance traits (success and latency to find the reward), we assessed whether fish improved their performance over time (learning rate). We fitted a generalized linear mixed model to explore the effects of maze complexity (categorical variable of two levels: two- versus four-door) and trial number (continuous variable) on the success to reach the reward as a first choice (binomial), a measure of performance accuracy (Appendix, Table A3). Using a generalized linear mixed model with gamma (link = log) distribution, we investigated the role of trial number and maze complexity on the latency to reach the reward (continuous variable), a proxy of performance speed (Appendix, Table A4). In both models, we included fish mass as a covariate and included fish identity (ID), maze ID (1, 2 or 3), reward position (central or edge) and round of training (1 or 2) as random intercepts. The interaction between trial number and maze complexity was initially included and subsequently removed if nonsignificant according to the likelihood ratio test (LRT) and Akaike's information criterion (AIC).

To explore whether metabolic rate affected performance accuracy, we ran generalized linear models with a binomial distribution, where success to reach the reward as the first choice at the start of training (first 5 days) or the end of training (last 5 days) were used as response variables. We also explored the effect of metabolic rate on time to find the reward within a trial by fitting a linear mixed effect model with latency to reach the reward at the start of training or at the end of training as response variables. In all models, the explanatory variables were fish mass, metabolic rate (SMR, MMR or AS, run separately due to correlations between variables) and the interaction of both mass and metabolic rate with maze complexity (Appendix, Tables A5–16). Trial number, maze ID, reward position

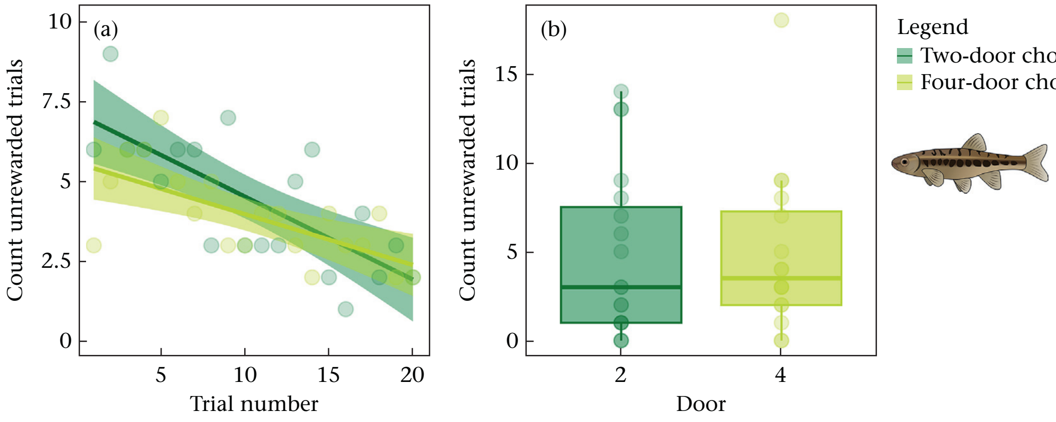

Figure 2. (a) Change in the number of unrewarded trials, i.e. singular trials in which the fish did not reach the reward chamber, over time and (b) differences in numbers of unrewarded trials across treatments. The lines show the decrease of unrewarded trials over the course of trials (1 trial per day over 20 days of training) in two different configurations of complexity arenas: two-door choice and four-door choice. Shadows indicate 95% confidence intervals. In (a), each data point is the sum of unrewarded trials per day. In (b), each data point is the number of unrewarded trials of a single individual.

and round of training were included as random intercepts. All model residuals were checked by visual inspections to ensure normality and homoscedasticity. The latency to reach the reward was log-transformed to meet model residuals assumptions.

Finally, we correlated fish metabolic traits (SMR, MMR, AS) with the distance moved on the last day of training, in order to understand whether any relationship between metabolic rate and activity could help explain potential improvement in cognitive performance. To do this, we fitted linear mixed models with distance moved as the response variable and fish mass, metabolic rate (SMR, MMR or AS, run separately due to correlations between variables) and the interaction of both mass and metabolic rate with maze complexity (Appendix, Tables A17–19) as explanatory variables. Maze ID, reward position and round of training were included as random intercepts. The distance moved was log-transformed to meet model residuals assumptions.

RESULTS

The success to reach the reward as the first choice improved as training progressed and differed between maze complexities (Fig. 3a, Appendix, Table A3). The overall success probability for fish in the four-door maze was lower than in the two-door maze (Appendix, Table A3). Latency to reach the reward decreased over time and was longer in the four-door maze, especially at the start of training (Fig. 3b, Appendix, Table A4). By the end of training, the time to reach the reward was similar between the two- and four-door mazes (Fig. 3b). This result suggests that the four-door maze was more challenging than the two-door maze. As expected, we observed a higher number of unrewarded trials at the start of the experiment, but this effect was observed regardless of maze complexity (Fig. 2a, Appendix, Table A1).

There was no effect of metabolic traits (AS, MMR, SMR) or mass on the probability of success at the start of training (Appendix, Tables A5, A9, A13); however, success to reach the reward as the first choice at the end of training was affected by both mass and metabolic rate (AS, MMR, SMR), but the effect was different depending on maze complexity (Appendix, Tables A7, A11, A15). Fish with higher metabolic rate (in AS, MMR and SMR) had a higher success probability in the two-door maze while the opposite relationship was observed in the four-door maze, where success probability decreased with increasing AS, MMR and SMR (Fig. 4a, c, e, Appendix, Tables A7, A11, A15). We also observed an interaction between fish body mass and maze complexity on the success to reach the reward; larger fish tended to have lower success in simpler mazes; however, larger fish in more complex mazes (with four doors) had higher success to reach the reward than smaller fish (Appendix, Tables A7, A11, A15).

Similarly, there was no effect of metabolic traits or mass on the latency to find the reward at the start of training (Appendix, Tables A6, A10, A14); however, the latency to find the reward at the end of training was affected by both mass and metabolic traits depending on maze complexity (especially MMR and SMR: Appendix, Tables A8, A12, A16). The effect of metabolic traits on the latency to find the reward was opposite to their effect on the success to reach the reward. Fish with higher MMR and SMR had a lower latency to find the reward in the two-door maze, while in the four-door maze, latency to reach the reward tended to increase as a function of SMR and MMR (Fig. 4d, f, Appendix, Tables A12, A16). The effect of AS followed the same trend but was not significant at $P < 0.05$ (Fig. 4b, Appendix, Table A8). Note, however, that although the larger range of SMRs relative to body mass in fish assigned to the two-door maze was mainly driven by one individual, the patterns of both success and latency to reach the reward as a function of SMR were maintained even when the analyses were repeated without that individual. This result suggests that metabolic traits may be important for cognitive performance in different ways depending on the complexity of the task. Similarly to the effects observed on the success to reach the reward, there was an interaction between mass and maze complexity on the latency to reach the reward: larger fish tended to have higher latency when in the two-door maze compared to smaller fish; however, when in the four-door maze, the larger fish had a lower latency to reach the reward compared to the smaller fish (Appendix, Tables A12, A16).

There was no correlation between individual metabolic rates (AS, MMR, SMR) and distance moved in the maze on the last day of training (Appendix, Tables A17–A19).

DISCUSSION

Overall, the results indicate that baseline energy demand (represented by SMR), the maximal rate of aerobic metabolism (MMR) and the physiological capacity for simultaneous aerobic processes above maintenance (AS) are related to performance in a cognitive task, but that the direction of the effects depend on task complexity. In the simpler two-door maze, fish with higher metabolic rates and aerobic capacities were more successful and faster at finding the reward than fish with lower metabolic rates, as

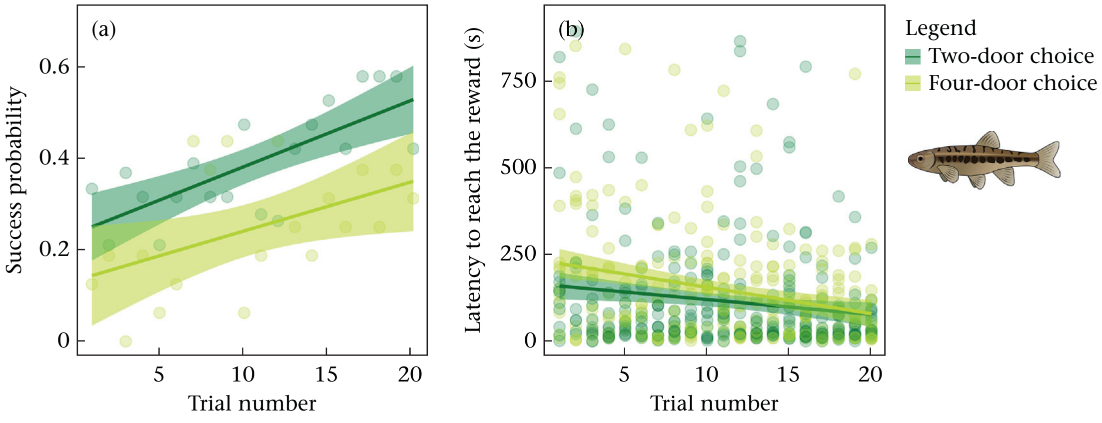

Figure 3. Learning rate of European minnows in terms of (a) success probability, i.e. success to reach the reward as a first choice, and (b) latency to reach the reward after leaving the start chamber. The lines show the progression in performance over the course of trials (1 trial per day over 20 days of training) in two different configurations of complexity arenas: two-door choice ($N = 19$ individuals) and four-door choice ($N = 16$ individuals). Shadows indicate 95% confidence intervals. Fig. 3a is based on the same data presented in Jones et al. (2023) and graphically represented in Fig. 4c.

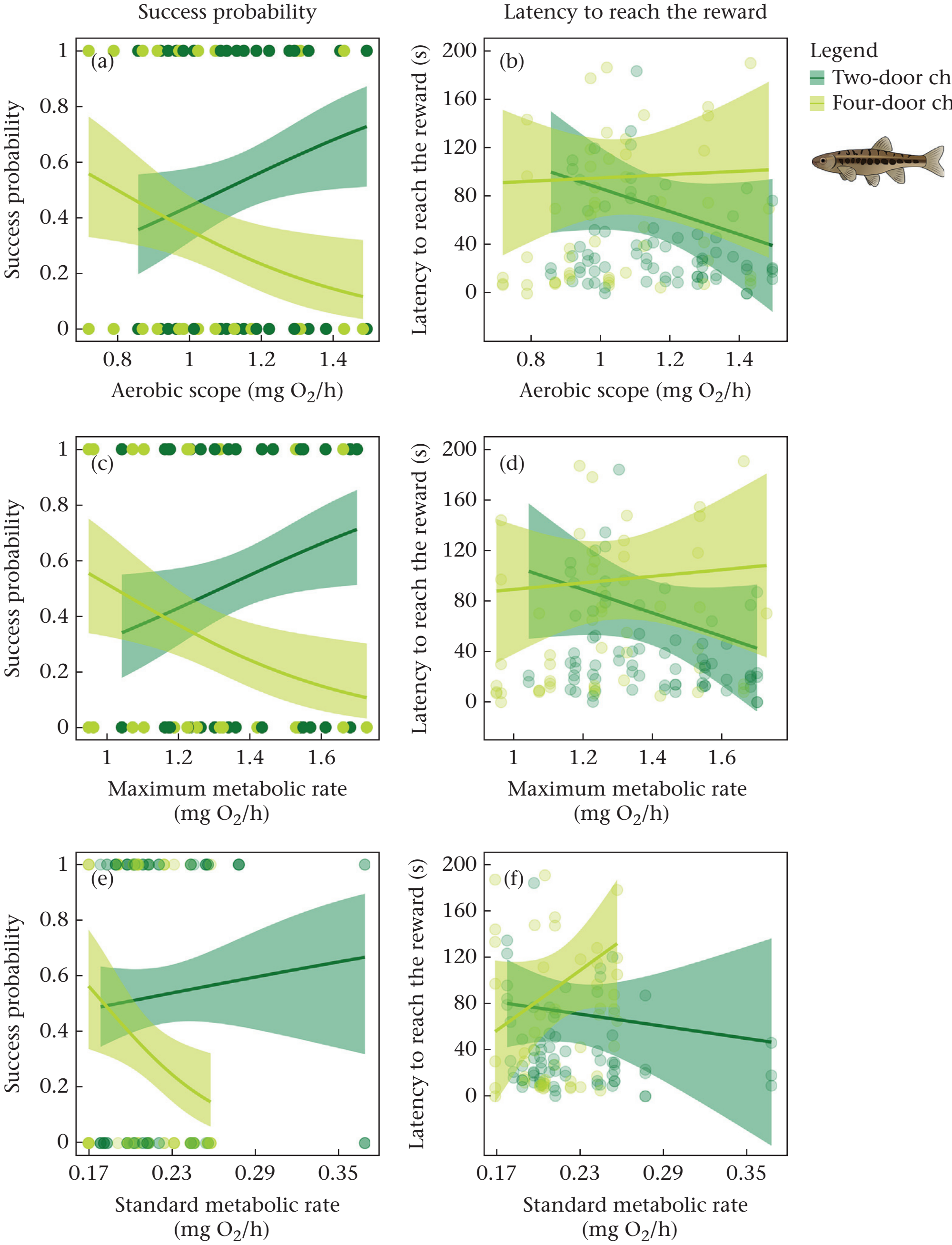

Figure 4. Effects of metabolic traits on minnows' cognitive performance at the end of training in two-door (N = 18 individuals) and four-door (N = 15 individuals) choice mazes. Effects of (a) aerobic scope, (c) maximum metabolic rate and (e) standard metabolic rate on the probability of successfully reaching the reward chamber as a first choice. Effects of (b) aerobic scope, (d) maximum metabolic rate and (f) standard metabolic rate on the latency to reach the reward after leaving the start box. Shadows indicate 95% confidence intervals. Values of metabolic rates were adjusted to the overall mean body mass of fish used in this study (i.e. 1.54 g) for graphical representation due to the strong relationship between metabolic rate and body mass (Clarke & Johnston, 1999).

predicted. However, the pattern of success and time to reach the reward reversed in the more complex four-door maze, suggesting context-specific costs and benefits of metabolic traits associated with cognitive abilities.

In the simple two-door maze, fish with higher SMR, MMR and AS were better learners. Fish with higher metabolic rates may be better at relatively simple spatial tasks because they are hungrier and therefore more motivated to find food rewards. AS and feeding rate are often correlated in fish since fish with higher AS have a greater aerobic capacity to accommodate the energetic costs of digestion (Killen et al., 2023). Because fish were kept under a controlled feeding schedule in our study, those with higher metabolic rates may have been more motivated to find food (Killen et al., 2011). Although individuals with high metabolic rates can also be more active (Careau & Garland, 2012), we observed no correlation between metabolic rate and distance moved over the duration of trials on the 20th day of training, suggesting that fish with high metabolic rates reached the reward faster because of factors other than activity alone.

In the more complex maze, when fish had the choice between four options, the cognitive performance patterns shifted. When the task was more challenging, fish with a lower standard metabolic rate (SMR), lower maximum metabolic rate (MMR) and lower capacity for simultaneous aerobic processes (AS) were both more successful and slightly faster at finding the reward than fish with higher metabolic rates and aerobic capacity. The cognitive styles hypothesis (Sih & Del Giudice, 2012) proposes that bolder and more active individuals (with potentially higher metabolic rates) should make decisions faster but be generally less accurate (fast-style learners), compared to less active individuals, which should make decisions slower but be more accurate (slow-style learners). Fast-style learners are also predicted to have a shallow spatial map compared to a more complex spatial map for slow-style learners (Sih & Del Giudice, 2012). There is empirical support for the cognitive styles hypothesis across many species. For example, bolder and more active bank voles, *Myodes glareolus*, were faster at associative learning tasks but less flexible in a reversal learning task compared to shy and inactive individuals (Mazza et al., 2018). Similarly, more exploratory great tits, *Parus major*, were less flexible to changes in a discrimination task (Guillette et al., 2011). Similar connections between individual behavioural differences and cognitive performance have been found in a range of fish species (Lucon-Xiccato & Bisazza, 2017). For example zebrafish, *Danio rerio*, exhibited interindividual differences in discrimination tasks with clear accuracy trade-offs: some fish made slower, more accurate decisions, while others made faster, less accurate choices (Wang et al., 2015). In other fish species, such as Panamanian bishop, *Brachyrhaphis episcopi*, the more exploratory individuals were faster at learning cues that predicted access to food (DePasquale et al., 2014). Similarly, banded archerfish, *Toxotes jaculatrix*, that spent more time in the open (bolder individuals) were faster to learn simple associations between targets and respective food rewards (Jones et al., 2021). Our results suggest that, in simple environments (as in the two-door maze), individuals with a faster metabolism have an advantage in spatial learning tasks, potentially because the relative simplicity of the maze benefits individuals that spend less time making decisions and instead rapidly move through the arena. However, as environments get more complex (as in the four-door maze), it is beneficial to have a slower metabolism and cognitive style because spending more time developing a detailed understanding of the maze layout and reward location ultimately results in superior performance. The idea that complexity is important for detecting differences in learning styles is not new; in spotted archerfish, *Toxotes chatareus*, for example, individuals that shot quicker at targets in a discrimination task were less successful than individuals that took longer to shoot, but only when the number of targets to choose from was greater than two (Jones et al., 2020). However, the results here are the first evidence that the link between metabolism and cognitive performance depends on task complexity.

Fish learned in both two- and four-door mazes (i.e. the success to reach the reward as the first choice increased and the latency to reach the reward decreased over consecutive days of testing), but levels of success were consistently higher in the simpler maze, until the end of training. This suggests that the two-door maze was easier for fish to complete. At the beginning of training (i.e. the first 5 days), there was no relationship between metabolic traits and either latency to find the reward or the probability of success. In the final 5 days, however, there was a relationship between metabolic rate and both latency to find the reward and probability of success. This change in relationship between the first 5 days and the last 5 days suggests that metabolic rate did not influence initial success in a novel maze but did influence an individual's ability to improve cognitive performance over time with repeated exposure to the task. Note that, in our study, by chance, fish assigned to the four-door maze had a lower range of SMRs relative to their body mass compared to fish assigned to the two-door maze (i.e. ranges of SMR and body mass were similar, but no individuals had a high SMR relative to their body size). Therefore, while results concerning the effects of SMR on both latency to find the reward and probability of success followed similar patterns as those of AS and MMR, the specific effects of SMR at the higher end of its range relative to body mass should be interpreted carefully due to the lack of data in the higher end of the SMR range. However, across multiple different analyses, at the end of training, maze complexity was important for revealing differences in the relationship between cognitive performance and metabolic rates. Our results also revealed an interacting effect of mass and maze complexity on the latency to find the reward and probability of success. Those effects may be linked to variation in the body mass–metabolism relationship across maze complexities. Indeed, in the two-door maze, fish with a higher metabolism performed better, but larger fish did not. In contrast, in the four-door maze, fish with a lower metabolism performed better but so did larger fish. The interacting effect observed in this study can partially help to understand some of the unexplained variation around the effect of metabolism.

Overall, our results illustrate the important role of metabolic traits and the importance of task complexity for understanding among-individual variation in cognitive performance. It also underscores the importance of carefully considering the design of cognitive tasks (Jones et al., 2023). For example, individuals that perform well in one task or maze design may not perform relatively well in another task (Rowe & Healy, 2014). It is important to consider the trade-offs associated with high performance in a task and, without more detailed study, only draw conclusions for specific experimental contexts. Still, beginning to understand when having a high versus low metabolic rate is beneficial for learning about the location of food resources or other ecologically relevant information is an important step for predicting how environmental factors may impact cognitive performance. For example, in ectotherms, metabolic rate and aerobic capacity are associated with a variety of other environmental factors, including temperature, oxygen availability and feeding history (Clarke & Johnston, 1999), and in a simple T-maze, the spatial learning rate of zebrafish was higher at a higher temperature (Babkiewicz et al., 2021). An exciting future direction will be to understand how environmental factors influence interactions among energy demand, aerobic capacity and cognition (Maille & Schradin, 2017).

Author Contributions

Daphne Cortese: Writing - review & editing, Writing - original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Amelia Munson**: Writing - review & editing, Writing - original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Zoe Storm**: Writing - review & editing, Investigation. **Nick A.R. Jones**: Writing e review & editing, Conceptualization. **Shaun S. Killen**: Writing - review & editing, Supervision, Funding acquisition, Conceptualization.

Data Availability

The data are available on Zenodo (https://doi.org/10.5281/zenodo.10846021).

Declaration of Interest

None.

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Appendix

Table A1
Generalized linear model (GLM) structure and output of the effect of maze complexity and trial on the number of unrewarded trials ('NA'; singular trials in which the fish did not reach the reward) and generalized linear mixed model (GLMM) structure and outputs of the effect of maze complexity on the number of unrewarded trials per fish ID

Model structure	Model outputs						
GLM: Count NA ~ Complexity+Trial	Fixed effects	Estimate	SE	*z*	*P*	R^2	
	Intercept Complexity(four-door) Trial	1.9781 −0.1206 −0.0514	0.162 0.156 0.014	12.218 −0.776 −3.723	<0.001 0.438 <0.001	0.591	
GLMM: Count NA (per fish ID) ~ Complexity+(1|maze)+(1|position)+(1|round)	Fixed effects	Estimate	SE	*z*	*P*	mR^2	cR^2
	Intercept Complexity(four-door)	1.5163 0.0946	0.233 0.156	6.517 0.608	<0.001 0.543	0.007	0.282

Table A2
Detailed information of the static intermittent-closed respirometry set-up and measures of maximum metabolic rate (MMR) and standard metabolic rate (SMR) of fish (list from Killen et al., 2021)

Criterion number	Criterion and category	Description
Equipment, materials and set-up		
1	Fish body mass	1.54 ± 0.49 g (mean ± SD)
2	Volume of empty respirometer	58.36 or 81.98 ml (depending on fish size)
3	To achieve chamber mixing	Peristaltic pump (Masterflex L/S; Cole-Parmer, Vernon Hills, IL, U.S.A.)
4	Ratio of net respirometer volume to animal body mass	~37.8–53.2
5	Material of tubing used in mixing circuit	PVC
6	Volume of tubing in mixing circuit	9.38–14.79 ml
7	Declare whether volume of tubing in mixing circuit was included in calculations of oxygen uptake	Yes
8	Material of respirometer	Glass
9	Type of oxygen probe and data recording	FireStingO_2; Pyro Science GmbH, Aachen, Germany
10	Sampling frequency of water oxygen concentration	2 s
11	Placement of oxygen probe	In recirculation circuit, specifically in a flow-through chamber connected by a 2–3 cm tube to the actual respirometer chamber
12	Flow rate during flushing and recirculation, or confirm that chamber returned to normoxia during flushing	About one chamber volume/min; chambers returned to normoxia during flushing
13	Flush/closed cycles	2/8 min
14	Wait (delay) time excluded from closed measurement cycles	60 s for SMR measurements
15	Describe frequency and method of probe calibration (for both 0 and 100% calibrations)	0% at start of experiment and 100% every day of measurements
16	Mention whether software temperature compensation was used during recording of water oxygen concentration	Yes, it was used
17	Temperature during respirometry	14.00 ± 0.05 ℃ (mean ± SE)

(*continued on next page*)

Table A2 (*continued*)

Criterion number	Criterion and category	Description
18	How was temperature controlled?	Thermostat (TMP-REG; Loligo Systems, Viborg, Denmark) controlled a pump that directed water through a heat exchange coil within a heated reservoir whenever temperature within the bath dropped below the setpoint
19	Photoperiod during respirometry	~LD 3:12 h (light:dark)
20	Describe if ambient water bath was cleaned and aerated during measurement of oxygen uptake and, if so, how this was done (e.g. filtration, periodic or continuous water changes)	Continuously aerated during measurement (aeration within the bath)
21	Provide volume of ambient water bath and any associated reservoirs	40 litres
22	Minimum water oxygen level or concentration reached during closed phases	During SMR measurements: 8.0 mg/litre (or 80% air saturation), exceptionally reached 6.6 mg/litre during MMR measurements
23	Describe whether chambers were visually shielded from external disturbance	Yes, shielded with a black plastic bag
24	Number of fish that were measured during a given respirometry trial	15
25	Were fish able to see each other during measurements?	No
26	Duration of animal fasting before placement in respirometer	24 h
27	Duration of all trials combined (number of days to measure all animals in the study)	3 days of measures (1 day for measurement of fish from trial 1 and 2 days separated by 1 day for measurement of fish from trial 2)
28	Acclimation time to the laboratory before respirometry measurements	3 and 4 months for the first and second round of fish, respectively
Background respiration		
29	Method used to measure background respiration (if measured)	Before and after SMR with empty respirometry chamber
30	Background respiration: number and duration of slopes measured	Three slopes of 8 min each before fish went in for MMR and three slopes of 8 min each after fish were removed on the morning after SMR measurements. The average of all three slopes before fish went in for MMR was used for MMR while the first slope before fish went in for MMR and the first slope after fish were removed were used to model a linear change in background respiration overnight for SMR
31	How were changes in background respiration modelled over time?	Linearly
32	Level of background respiration (e.g. as a percentage of SMR)	~6%
33	Method and frequency of system cleaning	The system was cleaned with bleach after every trial after fish were removed, and with ultraviolet (UV) lamps during trials, i.e. during metabolic rate measurements
Standard metabolic rate		
34	Time to reach beginning of metabolic rate measurements after introduction of fish to the chamber	About 2 h
35	Duration over which metabolic rate was estimated	~ 15 h
36	State what value was taken as SMR	Lowest 20% Calculates quantile value of the slope distribution using the parameter *p* (see Appendix S1 in Chabot et al., 2016)
37	Total number of slopes measured and used to derive metabolic rate	62–82 (depending on the day)
38	State whether any time periods were removed from calculations of SMR	~1 h
39	Provide r^2 threshold for slopes used for SMR	0.95
40	Proportion of data removed due to being outliers below r^2 threshold	1.6 ± 4.3% (mean ± SD)
Maximum metabolic rate		
41	When was MMR measured in relation to SMR?	Before
42	Method used	Manual chase to exhaustion (~2 min)
43	State what value was taken for MMR	Highest oxygen uptake rate (rolling slopes of 2 min)
44	Length of activity challenge used for estimated MMR	2 min
45	Was air exposure added after exercise?	No
46	Time until transfer to chamber after exhaustion and time to start of oxygen uptake recording	Immediately (likely few seconds)
47	Duration of slopes used to calculate MMR	2 min
48	Slope estimation method for MMR	Rolling regression
49	How was absolute aerobic scope calculated?	Using the difference of raw MMR and SMR
Data handling and statistics		
50	Sample size	35
51	How were oxygen uptake rates calculated?	FishResp R package (Morozov et al., 2019)
52	Confirm that volume (or mass) of the animal was subtracted from respirometer volume when calculating oxygen uptake rate	Yes
53	Specify whether variation in body mass was accounted for in analyses and describe any allometric body mass correction or adjustment	Metabolic rate was adjusted by fish body mass by including body mass as a covariate in the model. When the model included an interaction between metabolic rate and maze complexity, the interaction of maze complexity and body mass was also included to allow MR to be adjusted for mass in a door-specific way

Table A3
Generalized linear mixed model structure, selection and outputs of the effect of maze complexity on cognitive performance accuracy (success to reach the reward as a first choice)

Model selection

Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	9	779.76	820.15	−380.88	761.76	0.015	0.903
2	8	777.77	813.67	−380.89	761.77		

Model outputs

Fixed effects	Estimate	SE	*z*	*P*	mR^2	cR^2
Intercept	−1.0342	0.578	−1.789	0.074	0.094	0.241
Mass	−0.1498	0.361	−0.415	0.678		
Complexity(four-door)	−0.8740	0.359	−2.434	0.015		
Trial	0.0757	0.016	4.721	<0.001		

Model 1: Success to reach the reward as a first choice ~ Mass+Complexity∗Trial+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Success to reach the reward as a first choice ~ Mass+Complexity+Trial+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 2). Abbreviations: npar = number of parameters; AIC = Akaike information criterion; BIC = Bayesian information criterion; LogLik = log likelihood; χ^2 = chi-square statistic, calculated as the difference between the deviance of model 1 and model 2; *P* value = *P* value associated with the chi-square statistic; mR^2 = marginal R^2, which describes the proportion of variance explained by the fixed factors alone; cR^2 = conditional R^2, which describes the proportion of variance explained by both fixed and random factors.

Table A4
Generalized linear mixed model structure, selection and outputs of the effect of maze complexity on cognitive performance speed (latency to reach the reward)

Model selection

Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	10	5901.1	5943.3	−2940.5	5881.1	0.018	0.893
2	9	5899.1	5937.1	−2940.5	5881.1		

Model outputs

Fixed effects	Estimate	SE	*z*	*P*	mR^2	cR^2
Intercept	5.1660	0.256	20.193	<0.001	0.032	0.076
Mass	0.0108	0.153	0.071	0.944		
Complexity(four-door)	0.3120	0.153	2.038	0.042		
Trial	−0.0487	0.008	−5.764	<0.001		

Model 1: Latency to reach the reward ~ Mass+Complexity∗Trial+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Latency to reach the reward ~ Mass+Complexity+Trial+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 2). Abbreviations as in Table A3.

Table A5
Generalized linear mixed model structure, selection and outputs of aerobic scope (AS) and maze complexity effects on cognitive performance accuracy (success to reach the reward as a first choice) at start of training.

Model selection

Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	10	174.49	205.49	−77.244	154.49	1.243	0.537
2	8	171.73	196.53	−77.865	155.73		

Model outputs

Fixed effects	Estimate	SE	*z*	*P*	mR^2	cR^2
Intercept	−0.8316	0.680	−1.224	0.221	0.109	0.109
Mass	−0.7125	0.938	−0.760	0.447		
Complexity(four-door)	−1.1947	0.471	−2.536	0.011		
AS	0.8608	0.915	0.941	0.347		

Model 1: Success to reach the reward as a first choice ~ Mass∗Complexity+AS∗Complexity+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Success to reach the reward as a first choice ~ Mass+Complexity+AS+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 2). Abbreviations as in Table A3.

Table A6

Linear mixed model structure, selection and outputs of aerobic scope (AS) and maze complexity effects on cognitive performance speed (latency to reach the reward) at start of training

Model selection							
Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	11	219.69	249.19	−98.844	197.69	1.145	0.564
2	9	216.83	240.97	−99.416	198.83		
Model outputs							
Fixed effects	Estimate	SE	*df*	*t*	*P*	mR^2	cR^2
Intercept	1.8431	0.261	12.53	7.075	<0.001	0.031	0.203
Mass	−0.0324	0.292	99.35	−0.111	0.912		
Complexity(four-door)	0.2260	0.128	98.12	1.769	0.080		
AS	0.0623	0.289	93.96	0.215	0.830		

Model 1: Latency to reach the reward ~ Mass∗Complexity+AS∗Complexity+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Latency to reach the reward ~ Mass+Complexity+AS+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 2). Abbreviations as in Table A3.

Table A7

Generalized linear mixed model structure, selection and outputs of aerobic scope (AS) and maze complexity effects on cognitive performance accuracy (success to reach the reward as a first choice) at the end of training

Model selection							
Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	10	230.15	261.21	−105.08	210.15	8.237	0.016
2	8	234.39	259.24	−109.19	218.39		
Model outputs							
Fixed effects		Estimate	SE	*z*	*P*	mR^2	cR^2
Intercept		0.4809	0.749	0.642	0.521	0.125	0.134
Mass		−1.6277	1.031	−1.579	0.114		
Complexity(four-door)		−4.0958	1.599	−2.562	0.010		
AS		1.8661	1.284	1.454	0.146		
Mass:Complexity(four-door)		5.3276	1.954	2.726	0.006		
AS:Complexity(four-door)		−4.6178	1.858	−2.485	0.013		

Model 1: Success to reach the reward as a first choice ~ Mass∗Complexity+AS∗Complexity+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Success to reach the reward as a first choice ~ Mass+Complexity+AS+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 1). Abbreviations as in Table A3.

Table A8

Linear mixed model structure, selection and outputs of aerobic scope (AS) and maze complexity effects on cognitive performance speed (latency to reach the reward) at the end of training

Model selection							
Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	11	251.35	283.86	−114.67	229.35	4.730	0.094
2	9	252.08	278.68	−117.04	234.08		
Model outputs							
Fixed effects	Estimate	SE	*df*	*t*	*P*	mR^2	cR^2
Intercept	1.6782	0.172	47.12	9.729	<0.001	0.012	0.034
Mass	−0.1407	0.233	136.28	−0.603	0.547		
Complexity(four-door)	0.1311	0.103	130.22	1.268	0.207		
AS	0.0762	0.226	116.07	0.337	0.737		

Model 1: Latency to reach the reward ~ Mass∗Complexity+AS∗Complexity+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Latency to reach the reward ~ Mass+Complexity+AS+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 2). Abbreviations as in Table A3.

Table A9
Generalized linear mixed model structure, selection and outputs of maximum metabolic rate (MMR) and maze complexity effects on cognitive performance accuracy (success to reach the reward as a first choice) at start of training

Model selection

Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	10	174.35	205.35	−77.174	154.35	1.239	0.538
2	8	171.59	196.39	−77.794	155.59		

Model outputs

Fixed effects	Estimate	SE	*z*	*P*	mR^2	cR^2
Intercept	−0.8720	0.664	−1.313	0.189	0.111	0.111
Mass	−0.8624	1.018	−0.847	0.397		
Complexity(four-door)	−1.1925	0.472	−2.527	0.012		
MMR	0.9201	0.909	1.012	0.311		

Model 1: Success to reach the reward as a first choice ~ Mass∗Complexity+MMR∗Complexity+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Success to reach the reward as a first choice ~ Mass+Complexity+MMR+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 2). Abbreviations as in Table A3.

Table A10
Linear mixed model structure, selection and outputs of maximum metabolic rate (MMR) and maze complexity effects cognitive performance speed (latency to reach the reward) at start of training

Model selection

Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	11	219.93	249.44	−98.967	197.93	0.891	0.641
2	9	216.82	240.96	−99.412	198.82		

Model outputs

Fixed effects	Estimate	SE	*df*	*t*	*P*	mR^2	cR^2
Intercept	1.8417	0.257	12.22	7.154	<0.001	0.031	0.201
Mass	−0.0415	0.321	99.65	−0.129	0.897		
Complexity(four-door)	0.2268	0.128	98.35	1.772	0.080		
MMR	0.0630	0.284	96.26	0.222	0.825		

Model 1: Latency to reach the reward ~ Mass∗Complexity+MMR∗Complexity+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Latency to reach the reward ~ Mass+Complexity+MMR+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 2). Abbreviations as in Table A3.

Table A11
Generalized linear mixed model structure, selection and outputs of maximum metabolic rate (MMR) and maze complexity effects on cognitive performance accuracy (success to reach the reward as a first choice) at the end of training

Model selection

Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	10	227.77	258.83	−103.89	207.77	10.603	0.005
2	8	234.38	259.22	−109.19	218.38		

Model outputs

Fixed effects	Estimate	SE	*z*	*P*	mR^2	cR^2
Intercept	0.3575	0.754	0.474	0.635	0.149	0.159
Mass	−1.9815	1.148	−1.727	0.084		
Complexity(four-door)	−4.3408	1.657	−2.620	0.009		
MMR	2.0545	1.259	1.631	0.103		
Mass:Complexity(four-door)	6.7469	2.227	3.029	0.002		
MMR:Complexity(four-door)	−5.3597	1.882	−2.848	0.004		

Model 1: Success to reach the reward as a first choice ~ Mass∗Complexity+MMR∗Complexity+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Success to reach the reward as a first choice ~ Mass+Complexity+MMR+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 1). Abbreviations as in Table A3.

Table A12

Linear mixed model structure, selection and outputs of maximum metabolic rate (MMR) and maze complexity effects on performance speed (latency to reach the reward) at the end of training

Model selection							
Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	11	249.53	282.04	−113.76	227.53	6.514	0.039
2	9	252.04	278.64	−117.02	234.04		
Model outputs							
Fixed effects	Estimate	SE	*df*	*t*	*P*	mR^2	cR^2
Intercept	1.8127	0.215	36.65	8.445	<0.001	0.060	0.113
Mass	0.4824	0.349	121.80	1.384	0.169		
Complexity(four-door)	0.2074	0.404	134.42	0.513	0.609		
MMR	−0.7456	0.378	130.65	−1.972	0.051		
Mass:Complexity(four-door)	−1.1971	0.576	133.87	−2.080	0.039		
MMR:Complexity(four-door)	1.3284	0.505	131.30	2.629	0.010		

Model 1: Latency to reach the reward ~ Mass∗Complexity+MMR∗Complexity+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Latency to reach the reward ~ Mass+Complexity+MMR+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 1). Abbreviations as in Table A3.

Table A13

Generalized linear mixed model structure, selection and outputs of standard metabolic rate (SMR) and maze complexity effects on cognitive performance accuracy (success to reach the reward as a first choice) at the start of training

Model selection							
Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	10	175.26	206.26	−77.632	155.26	1.076	0.5841
2	8	172.34	197.14	−78.169	156.34		
Model outputs							
Fixed effects		Estimate	SE	*z*	*P*	mR^2	cR^2
Intercept		−1.174	0.729	−1.611	0.107	0.099	0.099
Mass		−0.256	0.736	−0.348	0.728		
Complexity(four-door)		−1.191	0.463	−2.572	0.010		
SMR		2.881	5.539	0.520	0.603		

Model 1: Success to reach the reward as a first choice ~ Mass∗Complexity+SMR∗Complexity+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Success to reach the reward as a first choice ~ Mass+Complexity+SMR+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 2). Abbreviations as in Table A3.

Table A14

Linear mixed model structure, selection and outputs of standard metabolic rate (SMR) and maze complexity effects on performance speed (latency to reach the reward) at the start of training

Model selection							
Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	11	220.3	249.8	−99.171	198.34	0.451	0.798
2	9	216.8	240.9	−99.396	198.79		
Model outputs							
Fixed effects	Estimate	SE	*df*	*t*	*P*	mR^2	cR^2
Intercept	1.8232	0.255	11.73	7.124	<0.001	0.031	0.196
Mass	−0.0057	0.285	88.25	−0.020	0.984		
Complexity(four-door)	0.2268	0.128	98.15	1.766	0.081		
SMR	0.2148	1.987	94.67	0.108	0.914		

Model 1: Latency to reach the reward ~ Mass∗Complexity+SMR∗Complexity+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Latency to reach the reward ~ Mass+Complexity+SMR+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 2). Abbreviations as in Table A3.

Table A15

Generalized linear mixed model structure, selection and outputs of standard metabolic rate (SMR) and maze complexity effects on cognitive performance accuracy (success to reach the reward as a first choice) at the end of training

Model selection							
Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	10	229.26	260.32	−104.63	209.26	8.902	0.012
2	8	234.17	259.01	−109.08	218.17		
Model outputs							
Fixed effects		Estimate	SE	*z*	*P*	mR^2	cR^2
Intercept		0.2859	0.752	0.380	0.704	0.136	0.136
Mass		−0.9605	0.784	−1.225	0.221		
Complexity(four-door)		−0.7921	1.282	−0.618	0.537		
SMR		5.8336	5.814	1.003	0.316		
Mass:Complexity(four-door)		4.1847	1.481	2.826	0.005		
SMR:Complexity(four-door)		−30.7845	11.574	−2.660	0.008		

Model 1: Success to reach the reward as a first choice ~ Mass∗Complexity+SMR∗Complexity+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Success to reach the reward as a first choice ~ Mass+Complexity+SMR+(1|ID)+(1|maze)+(1|position)+(1|round).Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 1). Abbreviations as in Table A3.

Table A16

Linear mixed model structure, selection and outputs of standard metabolic rate (SMR) and maze complexity effects on performance speed (latency to reach the reward) at the end of training

Model selection							
Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	11	246.89	279.40	−112.44	224.89	9.122	0.010
2	9	252.01	278.61	−117.01	234.01		
Model outputs							
Fixed effects	Estimate	SE	*df*	*t*	*P*	mR^2	cR^2
Intercept	1.8306	0.209	89.90	8.757	<0.001	0.071	0.085
Mass	0.1010	0.244	95.20	0.414	0.680		
Complexity(four-door)	−0.4653	0.346	133.97	−1.344	0.181		
SMR	−2.0326	1.701	123.67	−1.195	0.234		
Mass:Complexity(four-door)	−0.8360	0.406	131.26	−2.060	0.041		
SMR:Complexity(four-door)	8.7041	3.074	135.55	2.832	0.005		

Model 1: Latency to reach the reward ~ Mass∗Complexity+SMR∗Complexity+(1|ID)+(1|maze)+(1|position)+(1|round). Model 2: Latency to reach the reward ~ Mass+Complexity+SMR+(1|ID)+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 1). Abbreviations as in Table A3.

Table A17

Linear mixed model structure, selection and outputs of aerobic scope (AS) and maze complexity effects on distance moved at the end of training

Model selection							
Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	10	570.85	585.82	−275.43	550.85	2.831	0.243
2	8	569.68	581.65	−276.84	553.68		
Model outputs							
Fixed effects	Estimate	SE	*df*	*t*	*P*	mR^2	cR^2
Intercept	1050.269	784.10	9.09	1.339	0.213	0.020	0.210
Mass	589.121	902.09	28.34	0.653	0.519		
Complexity(four-door)	113.939	399.90	28.03	0.285	0.778		
AS	−374.534	846.80	28.03	−0.442	0.662		

Model 1: Distance moved ~ Mass∗Complexity+AS∗Complexity+(1|maze)+(1|position)+(1|round). Model 2: Distance moved ~ Mass+Complexity+AS+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 2). Abbreviations as in Table A3.

Table A18

Linear mixed model structure, selection and outputs of maximum metabolic rate (MMR) and maze complexity effects on distance moved at the end of training

Model selection							
Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	10	571.68	586.64	−275.84	551.68	2.076	0.354
2	8	569.75	581.73	−276.88	553.75		
Model outputs							
Fixed effects	Estimate	SE	*df*	*t*	*P*	mR^2	cR^2
Intercept	1087.055	771.98	8.71	1.408	0.194	0.183	0.207
Mass	545.789	983.36	28.46	0.555	0.583		
Complexity(four-door)	115.571	400.89	28.03	0.288	0.775		
MMR	−292.365	840.88	28.11	−0.348	0.731		

Model 1: Distance moved ~ Mass∗Complexity+MMR∗Complexity+(1|maze)+(1|position)+(1|round). Model 2: Distance moved ~ Mass+Complexity+MMR+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 2). Abbreviations as in Table A3.

Table A19

Linear mixed model structure, selection and outputs of standard metabolic rate (SMR) and maze complexity effects on distance moved at the end of training

Model selection							
Model	npar	AIC	BIC	LogLik	Deviance	χ^2	*P*
1	10	74.608	89.573	−27.304	54.608	1.650	0.438
2	8	72.258	84.230	−28.129	56.258		
Model outputs							
Fixed effects	Estimate	SE	*df*	*t*	*P*	mR^2	cR^2
Intercept	2.9010	0.457	5.336	6.347	0.001	0.035	0.345
Mass	−0.4814	0.415	27.881	−1.160	0.256		
Complexity(four-door)	0.1034	0.209	27.386	0.494	0.625		
SMR	3.5200	3.054	27.954	1.152	0.259		

Model 1: Distance moved ~ Mass∗Complexity+SMR∗Complexity+(1|maze)+(1|position)+(1|round). Model 2: Distance moved ~ Mass+Complexity+SMR+(1|maze)+(1|position)+(1|round). Model selection was performed using the likelihood ratio test (LRT) and Akaike information criterion (AIC) in order to test the significance of the interaction between maze complexity and trial number and identify the best-fit model (model 2). Abbreviations as in Table A3.