

# Stressfulness of the Design Influences Consistency of Cognitive Measures and Their Correlation With Animal Personality Traits in Wild Mice (*Mus musculus*)

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## Research Article

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# Abstract

Individual variation in cognition is being increasingly recognized as an important evolutionary force but contradictory results so far hamper a general understanding of consistency and association with other behaviors. Partly, this might be caused by external factors imposed by the design. Stress, for example, is known to influence cognition, with mild stress improving learning abilities, while strong or chronological stress impairs them. Also, there might be intraspecific variation in how stressful a given situation is perceived. We investigated two personality traits (stress coping and voluntary exploration), spatial learning with 2 mazes and problem-solving in low- and high-stress tests with a group of 30 female wild mice. For each test, perceived stress was assessed by measuring body temperature change with infrared thermography. None of the learning measures were significantly repeatable between the 2 stress conditions, indicating that the stress level impacts learning. We found correlations between learning and personality traits; however, they differed between the 2 stress conditions and between the cognitive tasks suggesting that different mechanisms underlie these processes. These findings could explain some of the contradicting findings in the literature and argue for very careful design of cognitive test setups to draw evolutionary implications.

## Introduction

Since the past decade, we observe a growing interest in animal cognition in multiple biological disciplines. This young field aims to study the whole processes from the acquisition of information in the environment (perception), to the processing of that information (learning), its storage (memory) and later use (decision-making)<sup>1</sup>. Cognitive traits may influence the ecology and evolution of populations as some traits have been shown to be directly related to fitness<sup>2</sup>. The evolutionary potential relies on the heritability of a trait and its consistency over time and contexts<sup>3</sup>. Consistency in cognition is so far often neglected and has only been demonstrated recently. A meta-analysis from <sup>4</sup> shows both temporal ( $R = 0,18$ ) and contextual consistency ( $R = 0,20$  to  $0,27$ ) in various animal cognitive abilities<sup>4</sup>. Nevertheless, the demonstrated consistency in cognitive traits is lower than that found for other behavioral traits ( $R$  usually varying between  $0,29$  and  $0,41$ )<sup>5-7</sup>. Whether this low consistency is an inherent biological phenomenon or caused by the low number of empirical studies and methodological heterogeneity, is not yet known.

Contrasting results are also often reported in the literature regarding associations between cognition and personality traits, so-called "cognitive syndromes", although such associations are predicted by several hypotheses<sup>8-10</sup>. Shared underlying risk-reward trade-offs are hypothesized to lead to predictable associations between personality and cognitive traits<sup>10</sup>. Through these trade-offs, personality and cognitive traits may even be integrated with life history<sup>11</sup>. The pace-of-life syndrome hypothesis states that many different biological traits (life history, physiology and behavior) could be correlated to form a "fast-slow" pace-of-life gradient. Fast individuals should express a more "proactive" behavior (bold, fast explorers, etc.) and should also be better learners in new cognitive tasks. On the contrary, slow individuals are expected to be more "reactive" (fearful, slow explorers, etc.) and perform better in a reversal learning

task<sup>8,11,12</sup>. For example, an association between associative learning and exploration has been found in the black-capped chickadee<sup>13</sup>. Nevertheless, no such correlation was reported in a related species, the great tit<sup>14</sup>. On the other hand, exploration was positively correlated with social learning in great tits<sup>15</sup>. Also on great tits, Titulaer et al (2012) found a relation between exploration and reversal learning, but only in the most difficult test and in a sex-dependent way<sup>16</sup>.

To achieve a better understanding of the ecological and evolutionary impact of individual differences in cognitive abilities, we therefore need a better understanding of the processes underlying consistency in cognition and correlations with personality traits, which is probably way more complex than we might think (for a full discussion, see<sup>17</sup>). One important step in this process is studying the effects of potential confounding factors on both consistency and cognitive syndromes<sup>18</sup>.

An important factor which is known to influence cognitive performance is stress. However, the relations between stress and learning performance are complex. In Pavlovian conditioning, acute stress has been found to lead to a linear increase in learning abilities<sup>19</sup>. However, for some other learning abilities such as spatial learning, this relation has been found to resemble an inverted U-shape<sup>19,20</sup>. In these cognitive tasks, mild stress should improve learning abilities while strong or chronic stress would impair it<sup>21</sup>. Therefore, cognitive tasks that differ in the stress they induce are expected to influence learning performances differently<sup>22,23</sup>.

In addition to that, all individuals do not cope the same way with stress. Some factors such as the age, sex<sup>21</sup> and personality can be linked with how stressful a situation is perceived and how that situation is dealt with (coping styles)<sup>24</sup>. Across taxa, ample evidence shows associations between personality traits such as boldness, exploration, activity, sociability and stress measures such as glucocorticoid level and anxiety-like behaviors<sup>25–30</sup>. Assuming an inherent relationship between cognition and personality, these individual differences in sensibility to stress may influence the way that stress influences cognition. During a cognitive test, stress-sensitive individuals would be better learners in a low-stress situation, but they would be more easily overwhelmed by stress in a stressful task and consequently be the worse learners (and vice versa)<sup>20,31</sup>. Accordingly, we expect to find no consistency between cognitive performance in different stress conditions, and the strength and/or sign of correlations between personality and cognition to depend on how stressful the test situations are experienced and/or how they are dealt with.

In this study, we want to investigate how the stress induced by the experimental design of both, cognitive and personality tests influence a) the consistency cognitive traits and b) the personality-cognition relationships. Therefore, we tested descendants of wild mice (*Mus musculus domesticus*) in multiple cognitive tasks. We used 2 mazes to measure spatial learning performances and 4 different problem-solving (PS) tasks. Despite the high variability in consistency found in the literature these cognitive traits were generally found to be repeatable in mice both on a temporal and contextual point of view<sup>32</sup>. Half of our tests have been designed to be more stressful for the mice (1/2 mazes and 2/4 PS). The stress was

directly induced by the test itself and was simulated as biologically relevant as possible. We also tested the mice with 2 commonly used personality tests. We chose the novel environment to investigate exploration and an open field to study stress coping, 2 personality traits that have already been linked to problem-solving and/or spatial learning abilities<sup>20,33</sup>.

To determine the stress level of the different tests and individual differences in immediate stress response, infrared thermography has been used. The acute temperature increase of the eyes during a test situation such as the open field has been recently shown to be correlated with behavioral measures of stress in rodents and has been then proposed to be a reliable, non-invasive way to measure physiological stress<sup>34</sup> (for a review on multiple endothermic taxa, see<sup>35</sup>).

## Material And Methods

### Animals and housing

Thirty female wild mice (*Mus musculus domesticus*) ~6–7 months of age at the start of experiments were used in this study. They were kept in sister pairs, with food (Altromin 1324, Germany) and water *ad libitum*. Housing cages were standard type III (24 x 40 x 14 cm) laboratory cages littered with wood chips. Cages always included a shelter made of egg carton and nesting material such as toilet paper. In addition, mice received various physical enrichment changed every 2–4 weeks. The room temperature varied seasonally between 16°C and 24°C and the animals received artificial light in addition to natural light from a large window from 8:00 am to 4:30 pm. The home cage could be connected to the experimental setups with a tube through a hole made in the cage, thus, allowing the mouse to enter and leave voluntarily without handling. Except during experiments, the tube was closed by a sliding door.

### Behavioral and cognitive tests

We measured stress coping using an open field test (OF) and voluntary exploration using a novel environment test (NE). Every individual was tested twice in order to estimate repeatability. Learning performance was assessed with two mazes and four problem-solving tasks, half of which have been designed stressful for the mice while the others were designed in a non-stressful way (see in the detailed descriptions). Half of the individuals started with the high-stress test and the other half with the low-stress test.

### Physiological stress measure

Before and after each test, the home cage was opened and put in a black box where multiple live traps were placed. To avoid any stress of handling, we waited until the focal mouse had entered one of the traps voluntarily. Since the mice were used to this method, this usually only took 1–3 minutes. The live traps were covered with a wire mesh. Then, 3 pictures were taken with an infrared thermography camera (FLIR T860) focusing on the eyes of the mouse from a distance of about 40 cm. The increase in

temperature was measured as the difference between the average temperature of the eyes after the test minus the average temperature of the eyes before the test.

## Personality

For the OF, the individual is released in the center of an empty white box (60x60 cm). Its behavior is directly recorded for 5 minutes. The total distance covered, and the time spent in the central area (a square of 30x30 cm in the middle of the arena) are calculated by the software VideoMot2 (TSE systems). The test takes place in a brightly illuminated room that the individuals do not know, they are forced to enter the experimental setup, and have no place to hide, which makes this a more stressful situation.

On the contrary, for the NE, the home cage with one animal inside is placed in a white box (60x60 cm) covered with bedding and containing objects the individual does not know. The mouse is then free to leave the cage and explore the novel environment through the opening in the cage wall. If it leaves the cage within 5 minutes after the test has started, the behavior is recorded for 5 additional minutes, if not, the test is stopped. The behavioral measures are the latency to leave the cage the first time, the time spent actively exploring the NE, and the number of times it is going back to its cage (i.e., the number of exploration trips). This test takes place in the room where the individuals are housed, the box is poorly illuminated, and the individuals have access to their own cages at any time of the test, which makes it as stress-free as possible for the mice.

## Mazes

Spatial learning performance was measured with two mazes, following a similar protocol. The mouse is placed in a small black box (15 x 10 cm) connected to one end of the maze and is free to leave this box in order to reach the reward to the other end (its own cage). Each individual has 5 trials (1 trial/day). The latency to enter the maze, the time spent in the maze and the number of mistakes is measured for each trial. The learning measures are defined as a) the difference between the initial number of errors and the least number of errors, b) the number of the trial with the least number of errors (i.e. how fast the individual learned to navigate the maze), c) the difference between the time spent during the first trial and this trial, and d) the number of errors at trial 3. For this last measure, trial 3 has been chosen for multiple reasons. It is the first trial for which the percentage of error is significantly below 50% (therefore different from random chance) and the first trial in which one individual could reach the end of the maze without any mistake. In addition to that, this trial is exactly at the halfway of the experiment and shows therefore the state of the learning of the different individuals in the middle of the learning process.

The Low-Stress Maze (LSM) takes place in the room where the individuals are housed. The maze is dark gray, poorly illuminated, smaller (154cm long), with narrow corridors (5cm) and has a lid, thus, giving the animals the feeling of being in a narrow corridor. On the other hand, the second maze (High-Stress Maze; HSM) takes place in a room the animals do not know. The maze has white walls, wide corridors (15cm), is larger (540cm) and is brightly illuminated, making it more stressful.

## Problem-solving

Four different tests have been used (2 low-stress and 2 high-stress).

For the low-stress PS task, the mice are first habituated to the experimenter opening the cage and putting a plate containing a mealworm inside the cage during two consecutive days. Then, the easiest PS is conducted the following day and the hardest one, one day after. The easy PS task consists of pushing/lifting a dome (here after LSPS1 (Low-Stress Problem-Solving 1)) and in the hard PS task, the mouse has to slide a tab (LSPS2), in order to access the mealworm hidden below. Both tests take place in the mouse's own cage and the animal could voluntarily decide to participate or stay hidden in its shelter. They are conducted as follows. The opened apparatus is put in the cage with a mealworm inside. After the mouse has eaten the mealworm, a second is put in and the apparatus is closed. The test ends when the mouse solves the problem-solving task (max 15 min). The behavior of the mouse is recorded for the whole test. Whether or not the problem has been solved in 15 min, the latency to solve and the time spent exploring the apparatus are the 3 learning measures. In addition to that, two other behaviors are measured: the latency to eat the first mealworm (motivation) and the latency to approach the apparatus (exploration).

The two high-stress tests include escaping an unknown brightly illuminated box by pulling (1) a door (HSPS1 (High-Stress Problem-Solving 1)) or (2) a lever (HSPS2), in order to get back to its own cage. Half of the individuals were randomly selected to start with the door test (1) and the other half started with the lever test (2). The second test is done the following day. As for the low-stress PS, the individuals have 15 minutes to solve the PS task and the same learning measures are taken. In addition to this, one other behavior is measured (latency to approach the apparatus, exploration).

All experimental setups are cleaned with alcohol between each test.

## Ethics

Animal facilities are approved and controlled regularly for keeping of wild mice by the local veterinary office. All animal procedures are in accordance with European and German animal protection laws and were carried out under licence V244-19227/2019(43 - 4/19) granted by the MELUND (Ministerium für Energiewende, Landwirtschaft, Umwelt, Natur und Digitalisierung des Landes Schleswig-Holstein).

## Statistics

The statistical analysis has been done with the software R version 4.1.1.

First, we checked for each category of tests (personality, maze and problem-solving) whether there were differences in the temperature increase or in the behavior to verify the assumed difference in stressfulness induced by the tests. Linear mixed models (lmer() function from lme4 package) have been used to compare the temperature increase, with individual ID as random effect and with the test as fixed effect. For the mazes, we included in addition the interaction trial\*test. For the behavior in the maze, it has been tested whether there was an effect of the test, the trial and their interaction on the latency to enter the maze with a glmm (glmer() function from lme4 package, Poisson distribution, individual ID as

random effect). Model assumption of the normality of the residuals and heterodasticity were checked. However, in the case of the latency to approach the set-up in the PS task, model assumption were not fulfilled and we instead used a non-parametric test (aovperm() from permuco package, with ID as random effect and test as fixed effect).

Repeatability has been assessed for the different behavioral measures in order to see which could be considered as personality traits, and for the different learning measures to test for consistency between the low- and high-stress conditions (i.e. contextual repeatability). The function rpt() from rptR package was used to test for the repeatability (with arguments family = "Poisson" for the traits that followed a Poisson distribution (Time spend in the center (OF), Latency to leave the trap (NE), Number of exploration sessions (NE), Difference between the time spend in the maze during the first and the best trial (HSM and LSM), Number of mistakes at trial 3 (HSM and LSM), Latency to solve (PS) and Time spend exploring the setup (PS)) or family = "Binary" for one learning measure in the PS tasks (solved or not)).

Before checking for the presence of correlations between the temperature increase, personality traits and learning in the different conditions, we simplified the correlation table. First, only repeatable, i.e., personality traits have been considered, and the mean value across both trials for each individual was used for the calculation of correlations. Regarding the learning measures, they have all been kept for the mazes. For the PS tasks, only the learning measures from LSPS1 have been used for the low-stress condition, because too few animals solved the LSPS2 task (4/22). For the high-stress condition, the mean between the learning measures from both tasks was used since they were found to be repeatable. The correlations have then been calculated with the rcorr() function from the Hmisc package (with argument type="spearman" as some of the measures do not follow a normal distribution). In addition to the significant correlations, we also took biologically relevant correlations into consideration. We defined a biologically relevant correlation as any correlation whose coefficient is above 0,3 or below -0,3. We chose this value following the meta-analysis from Bell et al.<sup>5</sup> estimating the mean repeatability of a behavior around 0,37, following the one from Cauchoux et al.<sup>4</sup> that calculated the repeatability of cognitive traits between 0,18 and 0,27, and the meta-analysis from Garamszegi et al.<sup>36</sup> that found a mean effect size for correlations between different personality traits between 0,074 and 0,566. In order to find significance with such a correlation, we would have needed a group size of 85 individuals (according to a power analysis with the function pwr.r.test() from the package pwr with arguments r = 0,3, sig.level = 0,05, power = 0,8). We therefore preferred to keep a smaller group size for ethical reasons but to still consider them.

## Results

### Differences between tests (perceived stressfulness of the tests situations)

For all the categories of tests (personality, maze and problem-solving), the increase in temperature was significantly higher in the condition we assumed to be more stressful (personality ( $p = 0,034$ ); maze ( $p =$

0,0011); PS: effect of the test ( $p = 0,0011$ ), LSPS1 – HSPS2 ( $p = 0,048$ ), LSPS2 – HSPS2 ( $p = 0,048$ ); Fig. 1). All together, the mean increase in temperature in the low-stress condition was  $+ 0,38 \pm 0,84^\circ\text{C}$ , while it was of  $+ 0,71 \pm 0,92^\circ\text{C}$  in the high-stress condition. Trial or the interaction between the test and the trial were never significant.

In the mazes, the effect of the interaction between test and trial on the latency to enter the maze was highly significant ( $p = 0,00041$ ). The latency to enter the maze on the first trial was comparable in both mazes, but it was rapidly decreasing in the LSM, while it stayed constant in the HSM (Fig. 2a). For the PS tasks, the test has a significant effect on the latency to approach the experiment set-up ( $f = 3,4$ ;  $p$  (parametric) = 0,021;  $p$  (permutation) = 0,012). The latency to approach the set-up was lower in the high-stress condition compared to the low-stress condition (Fig. 2b).

## Repeatability

### Temperature

We wanted to know if the temperature increase is a consistent individual characteristic. Therefore, we tested its repeatability across the different tests and trials (with the test and the trial as explanatory factor). We found that the increase in temperature was indeed consistent, even if the repeatability estimate was very low ( $R = 0,070$ ;  $p = 0,00072$ ). However, the repeatability of the temperature increase was higher when only including the high stress conditions measurements in the analysis ( $R = 0,116$ ; suppl. mat. S1). In addition to that, we also found that the basal temperature (temperature before the test) was consistent over time ( $R = 0,17$ ;  $p = 1,13*10^{-10}$ ).

### Learning

For the mazes, contextual consistency wasn't found for any of the learning measures between the high- and low-stress condition (Number of the best trial ( $p = 1$ ),  $\Delta$  number of mistakes between the first and the best trial ( $p = 0,246$ ),  $\Delta$  time spend in the maze between the first and the best trial ( $p = 0,255$ ), number of mistakes at trial 3 ( $p = 1$ )).

To investigate consistency in problem-solving performance, repeatability has first been estimated pooled across all PS tests (except LSPS2, which had too few solvers). In this situation, none of the learning measures were found to be repeatable (whether the task has been solved or not ( $p = 0,15$ ), latency to solve the task ( $p = 0,5$ ), time spend exploring the set-up ( $p = 0,45$ )). However, when repeatability was assessed by testing pairwise between and within conditions (Fig. 3), we observed that learning performance were generally consistent within the high-stress condition (HSPS1 – HSPS2: solved or not ( $R = 0,93$ ;  $p = 0,00052$ ), latency to solve ( $R = 0,51$ ;  $p = 0,01$ ), exploration time ( $R = 0,35$ ;  $p = 0,083$ )). On the contrary, repeatability between high- and low-stress conditions was never significant.

### Personality

For the OF test, only the distance covered was repeatable ( $R = 0,55$ ;  $p = 0,00045$  – time spent in the center:  $p = 0,24$ ). For the NE test, the number of explorations was repeatable ( $R = 0,35$ ;  $p = 0,045$ ) and the

latency to enter the novel environment tended to be repeatable ( $R = 0,29$ ,  $p = 0,063$ ) but not the time spent exploring ( $p = 0,116$ ). Three personality measures were kept for the correlation analyses: the distance covered (OF), the number of explorations (NE) and the latency to enter the novel environment (NE).

## Correlations

### Learning – learning

Within cognitive tasks, the different measures used to assess learning performance were almost all positively correlated, although not always significantly (see Fig. 4 1st column). Correlations within high-stress correlated on average with  $R = 0,36 \pm 0,29$  while correlations within the low-stress situations correlated on average with  $R = 0,29 \pm 0,30$ . We found no statistical difference in the strength of correlations with a paired t-test;  $t = 0,21$ ;  $df = 7$ ;  $p = 0,83$ .

Across cognitive tasks within either high or low stress condition, the learning measures were also in general positively correlated in the high-stress condition (average  $R = 0,14 \pm 0,27$ ). On the other hand, learning measures between the maze and the PS task in the low stress conditions were not correlated (average  $R = 0,01 \pm 0,18$ ) (Fig. 4 2nd column). The strength of the correlations was significantly lower in the latter (paired t-test;  $t = 2,71$ ;  $df = 11$ ;  $p = 0,02$ ).

Across cognitive tasks of different stress conditions, the only positive correlation found is between learning in the problem-solving task in the high and low stress conditions (average  $R = 0,24 \pm 0,18$ , with 1 significant and 3 biologically relevant positive correlations out of 9). No other correlations have been found between learning performance in the high- and low-stress situations (Fig. 4 3rd column).

### Learning – personality/temperature

The only clear correlation between learning performance and measures (behavior or stress level) in the personality tests is a positive correlation between learning in the HSM and the increase in temperature in the OF (average  $R$  across learning measures =  $0,20 \pm 0,23$ , with 2 significant positive correlations; Fig. 5). This indicates that individuals with a higher temperature increase in the OF were better or faster learners in the HSM. In addition to this, the correlations suggest two other associations between learning in the LSPS and the NE measures. The first one is a positive correlation between learning performance in the LSPS and a proactive behavior in the NE (average  $R = 0,15 \pm 0,14$ , with one biologically relevant positive correlation; Fig. 5)). And the second one may be a positive correlation between learning in the LSPS and a steeper temperature increase in the NE (average  $R = 0,13 \pm 0,23$ , with one significant positive correlation; Fig. 5)). It indicates that the best learners in a low-stress PS task are also the fastest explorers and/or the most sensitive to stress in a NE test, albeit these relations are weaker compared to correlations among high-stress situations.

All the observed correlations are summarized on Fig. 6.

## Discussion

With this study, we wanted to investigate whether the experimental design, particularly the stress it induces, would influence the consistency of learning performances in cognitive tasks and their associations with personality traits. We therefore designed both low- and high-stress versions for each test. Across all tests, we observed a significantly higher temperature increase during the tests that have been designed to be more stressful compared to the low-stress tests. Moreover, the difference in temperature increases with the duration of the tests in a high-stress test while it remains constant in a low-stress situation (suppl. mat. S3). In addition to that, some behaviors also indicated that the high-stress situations were really experienced as more stressful. In the mazes, the latency to enter decreased by the 2nd trial in the low-stress situation, indicating a quick habituation. On the contrary, in the high-stress condition, the latency to enter stays steady across all five trials. In the PS tasks, the latency to approach the setup seems higher in the low-stress condition, potentially indicating a higher motivation to get access back to their home cage in the HSPS. However, the different approach latencies could also indicate a difference in perception and/ or attention rather than indicating a difference in stress. All together, the physiological and behavioral results show that the tests that were designed more stressful were also perceived as more stressful by the mice.

In addition to the measure of the stressfulness of the design, infrared thermography could be used as a measure of individual sensibility to stress. This method has been proposed to be a new non-invasive measure of stress in a couple of studies<sup>35</sup>. In mice, for example, differences in temperature increase have been linked with some personality and behavioral traits<sup>34,37</sup>. In this study, the temperature increase was consistent over quite a substantial time period (ca. 6 months) and across contexts, revealing consistent inter-individual differences in this physiological trait.

We did not find consistency between learning performances in low- and high-stress conditions although in general, wild mice exhibit consistency in the problem-solving tasks we used<sup>38</sup> and we found problem-solving to be consistent when only considering the high-stress situations. Furthermore, we found that the personality-cognition correlations differ between the high and low stress conditions. This shows that the design-induced stress can have an impact on both trait consistency and cognitive syndromes.

## Stress and cognition: absence of consistency

In the meta-analysis from Cauchoix et al.<sup>4</sup>, cognition was generally found to be repeatable across time and contexts. Despite the high variability in consistency between species and cognitive tasks, problem-solving and spatial learning were always found to be repeatable in adult rodents (including *Mus musculus*) except some species of the genus *Sciurus*<sup>4,9,39</sup>. While problem-solving was also repeatable in *Mus musculus* (even of the same population as used in this study) and in *Apodemus agrarius* using the same problem-solving test setups as in our low-stress situation<sup>38,40</sup>, here, we could not find consistency across the high- and low stress situation.

Stress is already known to influence behavior in such a way that it impacts the repeatability of personality traits. For example, acclimation time has been shown to influence the repeatability of activity

in guppies<sup>41</sup>. The methodology is then expected to also influence results in cognitive experiments. Different spatial learning testing set-ups have already been shown to induce different stress levels<sup>22</sup> and influence memory retention and working memory<sup>42</sup>. Nevertheless, the influence of stress varies from one context to the other: while strong or chronic stress is expected to impair cognitive performances, mild fear could have the opposite effect<sup>21,43</sup>. Additionally, perceived stress will be different from one individual to the other, which will modulate the effect of stress on cognitive performance by displacing or changing the shape of the relations stress-cognition. For example, it has been suggested that the inverted U-shape of the cognitive abilities could be moved along the stress axis following the personality of an individual. This means that the “optimal stress” (i.e., the stress level at which learning performances are the highest) could vary from one individual to the other<sup>20</sup>. In such a situation, stress-sensitive individuals would be better learners in a low-stress situation but the worse learners in a more stressful task, and vice versa, explaining the lack of consistency found in this study. A couple of studies tend to support this statement<sup>20,31,44</sup> while some other studies do not<sup>33,45,46</sup>, however, the lack of control for the stress level of the task in the latter makes it difficult to interpret the generality and importance of this phenomenon.

Some factors other than stress are known to influence learning performance and might consequently decrease consistency if not accounted for in experimental designs. For example, previous experience of a task has been shown to increase performance in a similar task<sup>47,48</sup>. However, this has been controlled for in this study by splitting our set of animals into 2 groups which started either with high- or low-stress tests and our results show that there is no influence of the sequence of the test on the different learning measures (see Suppl mat S5). Motivation is another important factor that can influence performance in a cognitive test<sup>47</sup>. We tested the effect of motivation in the LSPS tasks by measuring the latency to eat the first mealworm. Despite a trend of the latency to eat the mealworm to influence the latency to solve the PS, the 2 other learning measures were not influenced by motivation (see Suppl mat S5) in accordance with previous results on wild mice<sup>38</sup>. This result suggests that, at least for the LSPS task, motivation did not influence learning performances.

Another factor explaining the lack of consistency is that some tasks that appear very similar to us could in fact rely on different mechanisms<sup>4</sup>. For example, an experiment of Troisi et al.<sup>49</sup> showed that learning was not consistent in a spatial and a reversal learning task between 2 different spatial scales. They hypothesize that this could be due to differences in the cognitive mechanisms implied at different spatial scales (allo- vs egocentric navigation and cue use)<sup>49</sup>. This could contribute to the lack of consistency we observe between the high- and the low-stress maze, as one of the differences between them is their size. However, in their study, for both the spatial learning and the reversal learning tasks, the smaller scale test took place in the individual’s cage, while the larger scale tests happened in another room. We showed that such a difference in design leads to a different perceived stress for the animals, both, behaviorally and physiologically, while the stress level was not controlled for in the study of Troisi et al.<sup>49</sup>. Furthermore, a scale difference may only explain a lack of consistency in the mazes while all the problem-solving setups were of approximately the same size but still lacking in consistency. Nevertheless, this example shows

that experimental setups and their intended effects on animals need to be designed very rigorously and several potential confounding factors need to be considered.

## Underlying mechanisms

For both the maze and PS, correlations between learning measures and personality were different in high- and low-stress conditions. Learning performances in the HSM were linked with individual sensitivity to stress in the OF, while we found no personality-learning correlations with the LSM. On the contrary, learning in the HSPS tasks wasn't linked with any personality measure but learning in the LSPS task was linked with the behavior and the temperature increase in the NE.

Correlations between different biological traits can result from shared underlying trade-offs<sup>10</sup>. For example, an active and bold individual is expected to explore a task faster, find cues easily and react to them more quickly than a shy individual. However, in this study, different correlations between personality and cognition are found following the stress level of the task, suggesting that these relations might be more complex than imagined<sup>17</sup>. As suggested for the lack of consistency, this could also be due to different underlying mechanisms. In an experiment on great tits (*Parus major*), Titulaer et al (2012) found personality-learning correlations only in the most difficult reversal learning task. They hypothesize that easy and hard tasks might be differently perceived for example by the attention that is paid to the cues. These context differences could then reveal mechanisms that underlie cognition<sup>16</sup>. Specifically, it is known that different neurobiological mechanisms are involved in low- and high-stress cognitive tests<sup>19</sup>. It has been shown in a spatial learning task that the memory-related protein ERK2 was activated during learning in the amygdala, a brain region linked to fear, in a high-stress situation, but not in a low-stress one<sup>50</sup>. Similarly, stress-related hormones such as glucocorticoids can bind to their respective receptors in the brain and affect cognitive performances<sup>51</sup>. In rats, corticosterone blockade in a stressful situation decreased learning performances in a spatial learning task, while corticosterone enhancement in a low-stress situation increased them<sup>52</sup>. This could easily explain both the lack of consistency found between the HSM and the LSM and that learning performances in a high-stress situation such as the HSM are correlated with stress-sensitivity. On the other hand, exploration is often linked with cognitive performances<sup>8</sup>, and especially aspects of problem-solving<sup>33,53</sup>. This explains that learning in a low-stress condition such as the LSPS task was correlated with personality in the NE. The involvement of these different physiological reactions following the stress context indicates that the cognitive performances are strongly influenced by the design of the experiment, while personality remains relatively consistent, hence, leading to different personality-learning associations. In addition, correlations between cognitive measures appeared stronger in high-stress conditions compared to the low stress conditions. It is suggesting that some of the mechanisms involved in the stressful situation are common to multiple learning tasks, while the different cognitive tasks in the low-stress situation are more independent or more strongly influenced by external factors.

Additionally, the lack of consistency between the two stress conditions suggests that cognitive traits may be particularly flexible. On an evolutionary point of view, the flexibility of the underlying mechanisms of

cognition can be adaptive, as the optimal cognitive phenotype can be different in different stress contexts. Indeed, multiple trade-offs are involved in the determination of cognitive abilities and the optimal outcome can be different following the situation. The first one is the trade-off costs-benefits of cognition<sup>4</sup>. Advantages provided by learning are sometimes counteracted by direct (time and energy demand) and indirect (correlations with other traits such as personality) costs<sup>54</sup>. Secondly, the speed-accuracy trade-off describes the compromise between the precision/accuracy during a task and the time necessary to perform it<sup>55</sup>. The stakes of low- and high-stress situation are intrinsically different, as the individual's life is supposedly more at risk in a stressful situation. This can influence the energy allocation and the importance given to speed and/or accuracy in a cognitive task<sup>55,56</sup>. Acting distinctively on cognitive performances in low- and high-stress situation would allow for a better fine-tuning of these traits.

However, we also find some differences between learning tasks. Cognitive syndromes are only present in the low-stress condition in the PS tasks, but we only find personality-learning correlations in the high-stress condition in the maze. In addition, while learning performances in the mazes are drastically different between the 2 stress conditions, it is much less strong in the PS tasks. Indeed, even if consistency could not be found between the learning measures from LSPS and HSPS, they still tended to be positively correlated. In the same way as consistency in cognition<sup>4</sup>, our results suggest that the effect of stress on cognitive performances and its strength are highly dependent on the cognitive task. Different mechanisms are probably involved in the different learning tasks and, therefore, they are differentially mediated by the stress level of the test. More cognitive abilities should be tested in order to have a broader view on the influence of stress on cognitive performances.

## Evolution of cognition

For the two studied cognitive tasks, learning performances have been shown to be not consistent across different stress contexts and the correlations between the measured learning and personality traits were different. Controlling for these conditions would be very important to unravel when cognitive syndromes may affect fitness and what are their underlying mechanisms are. There are 3 important conditions for a trait to be subject to evolution<sup>2,57</sup>. The first one, the presence of inter-individual variation in a population, seems to be generally verified for cognition<sup>4</sup>. Secondly, the cognitive traits should be heritable. Even if not completely clear, multiple clues tend to indicate that at least some of these traits are transmitted to the next generation<sup>2,58</sup>. Finally, the inter-individual differences should lead to differences in fitness. A causality between cognition and fitness is hard to determine, but several correlations have been found<sup>2,4,54</sup> suggesting that such a relationship exists. In addition to that, some studies found differences in cognition between populations or related species with different ecology that could be adaptive<sup>38,59</sup>. These results imply that cognitive traits probably under selection pressure. It also means that if cognition is correlated with some other traits, they won't evolve in isolation<sup>8,57</sup>. Then, evolutionary changes in one of these traits would lead to concurrent changes in correlated traits even if these are not under direct selection<sup>60,61</sup>. The differences found in learning performances and their correlations with personality

between stressful and non-stressful conditions shows the importance of taking stress into account when designing a cognitive experiment, as it could drastically bias and induce misleading conclusions on the underlying mechanisms and therefore also on the evolution of cognition.

## Declarations

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## Author contributions

M.D. and A.G. planned the study. M.D. collected the data. M.D. analyzed the data. M.D. and A.G. wrote the paper.

## Additional information

## Competing interests

The authors declare no competing interests.

## ARRIVE guidelines

This study has been reported following the recommendations of the ARRIVE guidelines

## Data availability

Raw data and R code is available: See attached files

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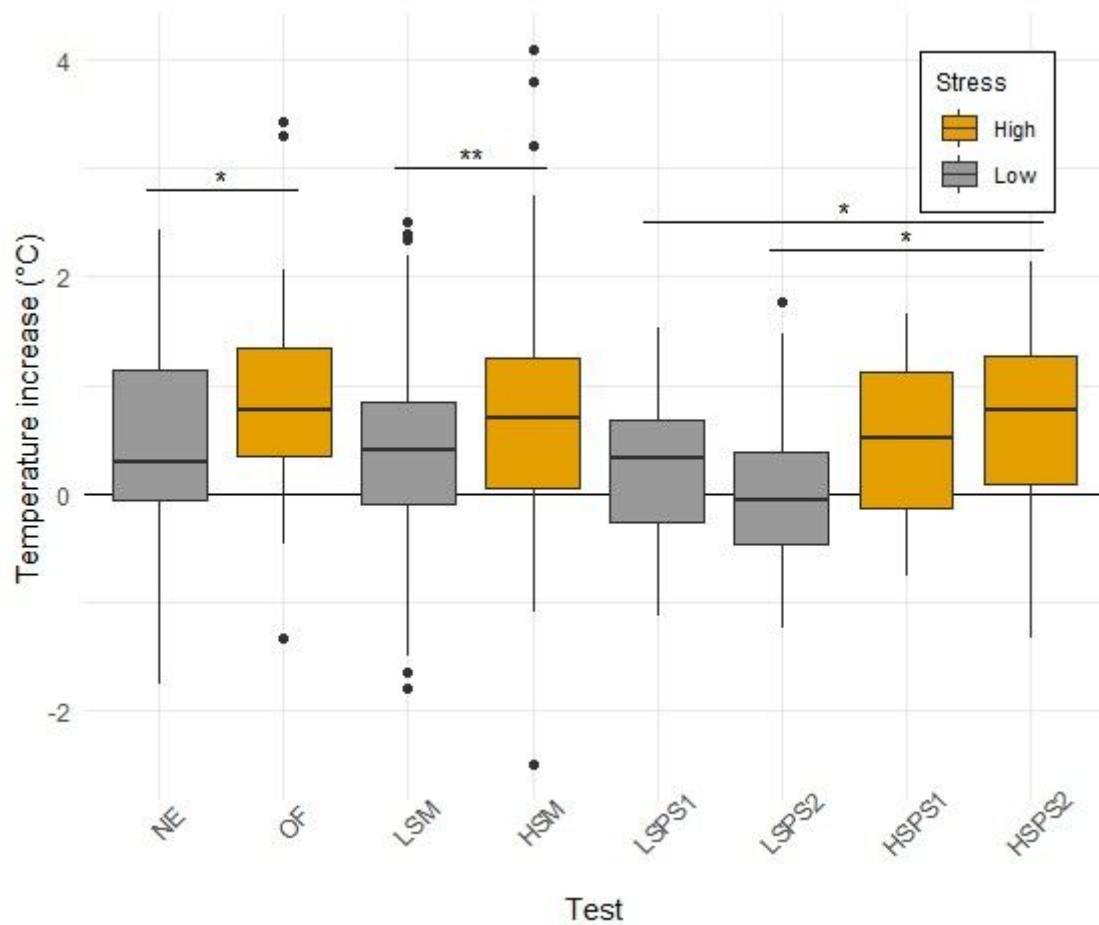
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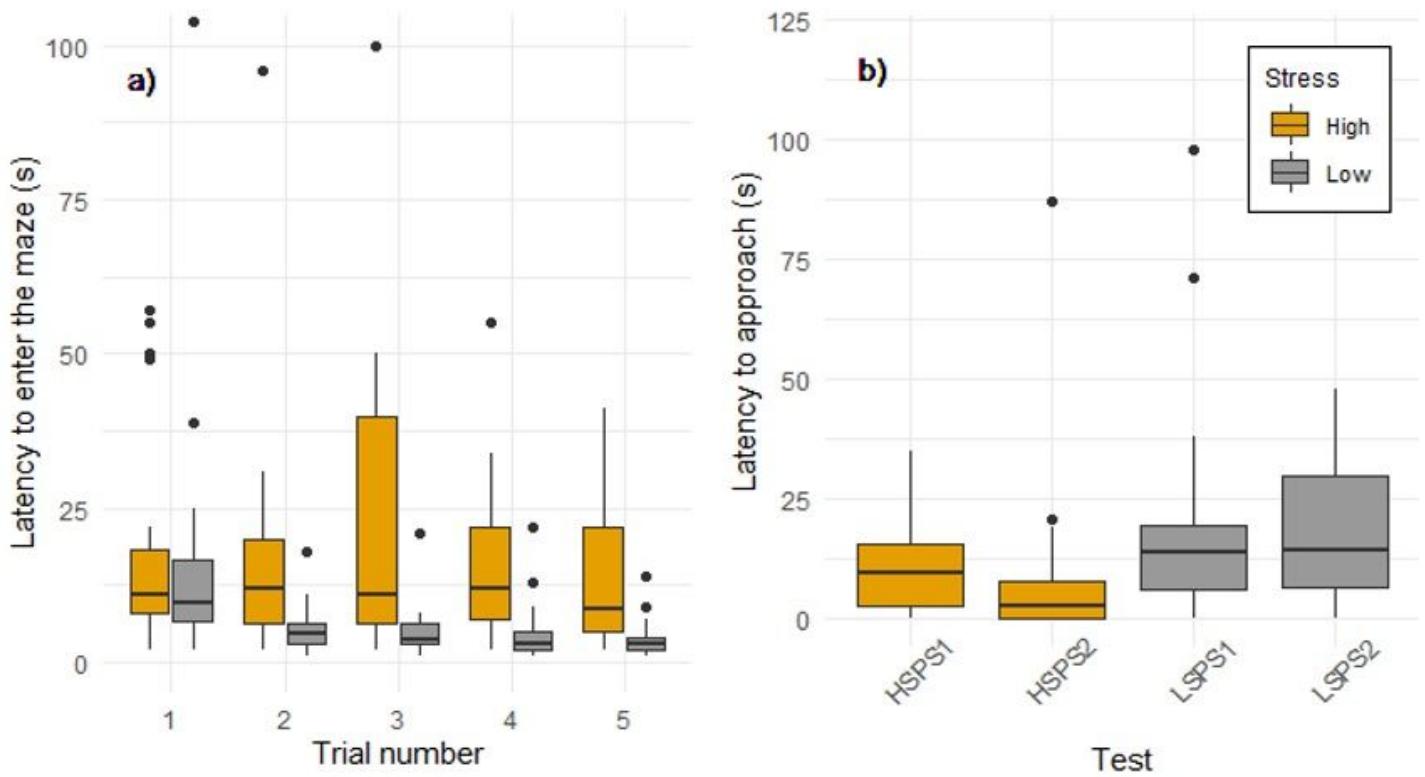
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## Figures



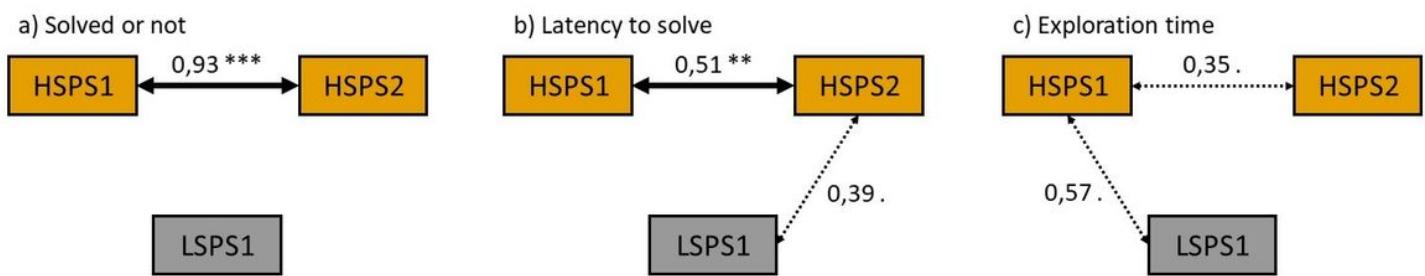
**Figure 1**

Increase in temperature related to physiological stress for each test. NE = novel environment, OF = open field, LSM = low-stress maze, HSM = high-stress maze, LSPS = low-stress problem-solving, HSPS = high-stress problem-solving. The high stress tests are represented in orange and the low-stress test in grey. The significant differences are shown by stars (\*: 0,01 < p < 0,05; \*\*: 0,005 < p < 0,01; \*\*\*: p < 0,005).



**Figure 2**

Differences in behavior between the high and low stress conditions in cognitive tests. a) Latency to enter the maze for each trial, b) latency to approach the PS set-up for each test. High-stress condition is represented by the orange color and low-stress condition by the grey color. Note: 22/290 values above 120 are not visible on fig. a) (of which 4 are from the LSM and 18 from HSM) and 4/108 above 120 on fig. b) (all from LSPS).



**Figure 3**

Repeatability estimates found between the learning measures of the different PS tasks: (a) whether the task has been solved or not (b) the latency to solve the task (c) the time spent exploring the set-up before solving. Solid arrows show a significant repeatability (\*:  $0,01 < p < 0,05$ ; \*\*:  $0,005 < p < 0,01$ ; \*\*\*:  $p < 0,005$ ) and dotted arrows an almost significant repeatability (. :  $0,05 < p < 0,1$ ). The high stress tests are

represented in orange and the low-stress test in grey. Numbers above arrows show repeatability estimates.

		WITHIN A TEST			WITHIN A CONDITION			BETWEEN CONDITIONS		
		HSM			HSM			HSM		
HIGH-STRESS	LOW-STRESS	HSM			HSM			HSM		
		$\Delta e$	e3	$\Delta D$	#t	$\Delta e$	e3	$\Delta D$	#t	$\Delta e$
HIGH-STRESS	HIGH-STRESS	0,40	HSM	0,54	0,00	0,49	HSM	0,25	0,35	-0,20
						0,46	HSM	0,19	0,41	-0,14
HIGH-STRESS	LOW-STRESS					s	HSPS	0,15	0,09	-0,10
							ex	0,94	0,35	-0,29
LOW-STRESS	HIGH-STRESS	LSM			LSM			LSM		
		$\Delta e$	e3	$\Delta D$	#t	$\Delta e$	e3	$\Delta D$	#t	$\Delta e$
LOW-STRESS	HIGH-STRESS	0,46	LSM	0,62	-0,08	-0,13	LSM	0,21	-0,02	-0,05
				0,24	0,44	-0,08		0,16	0,22	0,12
LOW-STRESS	LOW-STRESS					s	LSM	0,05	0,06	0,01
							ex	0,64	0,16	-0,04
HIGH-STRESS	LOW-STRESS	LSPS			LSPS			LSPS		
		$\Delta e$	e3	$\Delta D$	#t	$\Delta e$	e3	$\Delta D$	#t	$\Delta e$
HIGH-STRESS	LOW-STRESS	0,40	LSPS	0,32	0,47	-0,13	LSPS	0,00	0,12	-0,01
				0,16	0,47	-0,08		0,18	0,47	-0,04
HIGH-STRESS	HIGH-STRESS					s	ex	0,22	0,06	-0,04
							ls			

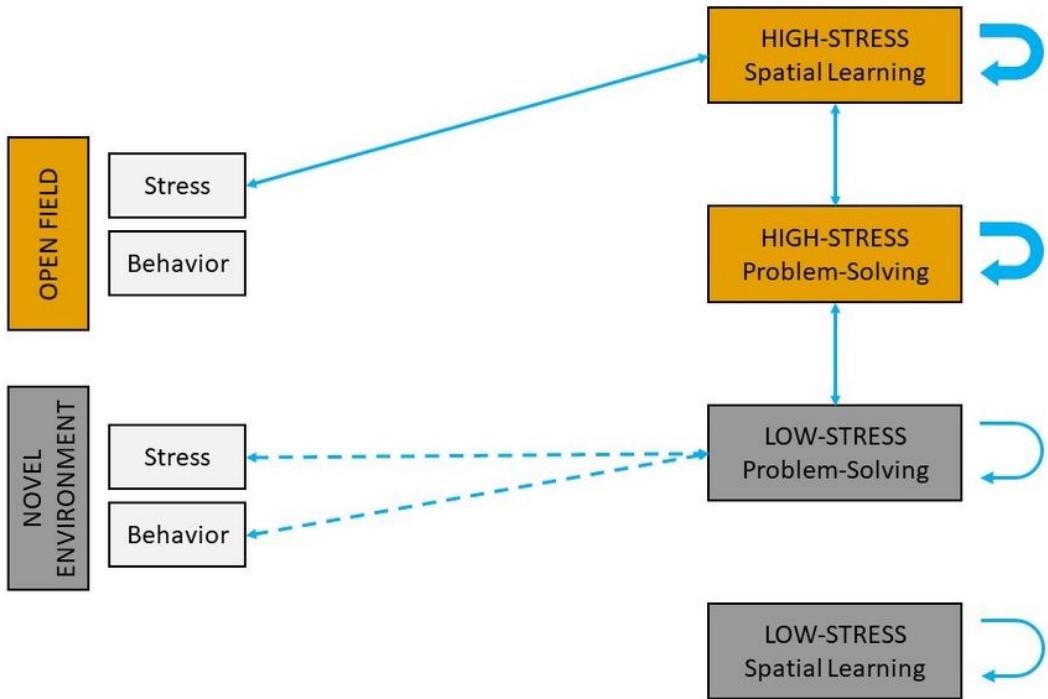
Figure 4

Table of the correlations between the learning measures in the cognitive tests. Positive coefficients are displayed in blue and negative coefficients in red. The cell is also colored in light blue or red when the correlation is biologically relevant (above 0,30 or below -0,30) and in bright blue or red when the correlation is statistically significant. Learning measures of the maze:  $\Delta e$  = difference in the number of errors between the first and the best trial, e3 = number of errors at trial 3,  $\Delta D$  = difference in the duration of the test between the first and the best trial, #t = number of the best trial. Learning measures of the PS: ex = time spend exploring the set-up before solving, ls = latency to solve, s = solved or not.

		HIGH-STRESS				LOW-STRESS				
OPEN FIELD	Stress	Spatial learning		Problem-solving		Spatial learning		Problem-solving		
		$\Delta e$	e3	$\Delta D$	#t	ex	ls	s		
NOVEL ENVIRONMENT	Stress	0,00	0,04	0,07	0,12	-0,02	0,15	-0,43	0,38	
	$\Delta T_1$	0,64	0,44	0,26	0,02	0,34	0,26	0,22	-0,04	
NOVEL ENVIRONMENT	Behavior	d	-0,13	-0,01	-0,20	0,23	-0,27	-0,03	-0,28	0,09
	#ex	-0,01	0,24	0,02	0,15	0,18	0,36	-0,32	-0,25	
NOVEL ENVIRONMENT	Stress	-0,29	-0,03	-0,22	-0,01	0,27	-0,01	-0,05	-0,35	
	$\Delta T_1$	-0,29	-0,12	0,02	-0,07	-0,08	-0,03	-0,21	0,23	
NOVEL ENVIRONMENT	Behavior	le	0,22	0,19	-0,21	0,11	0,33	0,29	-0,02	-0,22
	#ex	0,22	0,19	-0,21	0,11	0,34	0,06	0,18	-0,17	0,46

Figure 5

Table of the correlations between learning measures in the cognitive tests and stress and behavioral measures from the personality tests. Positive coefficients are displayed in blue and negative coefficients in red. The cell is also colored in light blue or red when the correlation is biologically relevant (above 0,30 or below -0,30) and in bright blue or red when the correlation is significant. Learning measures of the maze:  $\Delta e$  = difference in the number of errors between the first and the best trial, e3 = number of errors at trial 3,  $\Delta D$  = difference in the duration of the test between the first and the best trial, #t = number of the best trial. Learning measures of the PS: ex = time spent exploring the set-up before solving, ls = latency to solve, s = solved or not. Behavioral measure in the OF: d = distance. Behavioral measure in the NE: #ex = number of exploration sessions, le = latency to emerge in the NE. Stress measures:  $\Delta T_1$  = Increase in temperature during trial 1,  $\Delta T_2$  = Increase in temperature during trial 2.



**Figure 6**

Summary of the observed correlations between learning measures and with personality traits. Positive correlations are shown in blue. Thick arrows represent stronger correlations and dashed arrows uncertain correlations.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Curiosity.csv
- DelacouxandGuentherStressCognitionSupplementarymaterial.docx
- DelacouxandGuentherStressCognitionstatisticsR.rmd
- IranBehaviors.csv
- IraniansALL.csv
- Learningmaze.csv
- MazeALL.csv
- Openfield.csv
- Probsol.csv
- Temperatures.csv