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Cognitive performance of grey mouse lemurs (*Microcebus murinus*) during a discrimination learning task: Effect of the emotional valence of stimuli

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Abstract

Emotions are omnipresent in many animals' lives. It is a complex concept that encompasses physiological, subjective, behavioural and cognitive aspects. While the complex relationship between emotion and cognition has been well studied in humans and in some nonhuman primates, it remains rather unexplored for other nonhuman primate species, such as lemurs. In our study, we evaluated the performance of $N = 48$ grey mouse lemurs (*Microcebus murinus*) in a discrimination learning task using visual emotional stimuli. We tested whether the type of visual stimulus (positive, negative or neutral) influenced the cognitive performance of mouse lemurs. Individuals had to learn to discriminate between two platforms according to the associated visual stimuli and to jump to the target platform (leading to a reward). Our main finding was that emotional stimuli, whether positive or negative in valence, impaired cognitive performance when used as a target. Specifically, the lowest success rate occurred when the target was associated with the emotional stimuli, and the highest success rate occurred when it was associated with neutral stimuli. Our results show a similar pattern to that found in other primate species and support the adaptive role of emotion. Our results also support that individual differences could be a factor impacting the relation between emotion and cognition. This study is the first to explore how emotions interfere with the cognitive abilities of a lemur species and highlights the importance of acknowledging emotion in mouse lemurs as well as studying the emotion-cognition interaction in a wider range of primate species.

KEYWORDS

cognition, emotional stimuli, learning, lemurs, visual discrimination

Abbreviations: D⁺, positive distractor; D⁻, negative distractor; D^N, neutral distractor; EMs, estimated marginal means; GLMM, generalized linear mixed model; LC, learning criterion; T⁺, positive target; T⁻, negative target; T^N, neutral target.

E. Pouydebat and F. Pifferi contributed equally to this study.

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1 | INTRODUCTION

The central role of emotion in human life is clear. Emotion induces physiological and behavioural changes and influences perceptions and reactions to a given situation, as well as social interactions. Emotion can also considerably affect cognitive abilities; hence, considerable attention has been devoted to the interaction of emotion and cognition. Indeed, numerous human studies have shown that emotions can affect cognitive processes such as attention, memory, reasoning, decision-making, and learning (De Houwer & Hermans, 2010; Lemaire, 2021; Robinson et al., 2013). To explore this interaction, some studies induced a positive or negative mood by showing the participants videos or images before performing a cognitive task. Those studies highlight that mood induction modifies cognitive task performance. For example, in a problem-solving task, participants in a positive mood performed better than participants in a negative mood, while the participants in a neutral mood performed better than both of these groups (Jung et al., 2014). Instead of generating an emotional state before the task, other researchers manipulated the emotional content of stimuli involved in the cognitive task, such as pictures or words with emotional valence. For example, the emotional Stroop task is commonly used in human psychology studies to assess attentional biases induced by emotion. In these tasks, human participants are instructed to name the colours in which emotionally loaded words are written or name the colour of a border of a picture with emotional valence. Participants' attention tends to be drawn to emotionally relevant stimuli (see Williams et al., 1996 for review), resulting in slower and less accurate responses when the words have negative associations, such as death or accident (Bar-Haim et al., 2007; McKenna & Sharma, 2004). Indeed, attention is likely to be focused on the emotional content and diverted from the other stimulus dimensions, resulting in impaired performance (Kensinger & Corkin, 2003). An opposite theory posits that this attention prioritization leads to preferential processing of emotional content and could lead to enhanced performance (Kensinger & Corkin, 2003). For instance, Lindström and Bohlin (2011) found that working memory performance increased when positive or negative pictures were used as targets compared with neutral pictures.

In nonhuman primates, emotion was more recently acknowledged to be omnipresent in their daily life, for example during social interactions. Being able to correctly read facial expressions associated with specific emotions and to provide appropriate responses is an essential skill in primates and for all social animals (Ferretti & Papaleo, 2018; Nieuwburg et al., 2021). As in humans, emotion can lead to measurable physiological changes. For example, a study with rhesus macaques showed that temperatures in the nasal region decreased during negative emotional states (Kuraoka & Nakamura, 2010). Emotion can also lead to specific behavioural changes, such as behavioural avoidance of negative stimuli, as shown in a study in rhesus macaques that documented sustained avoidance of threatening pictures of conspecifics (Bethell et al., 2012).

The impact of emotion on cognitive abilities has also been investigated in nonhuman primates but to a much lesser extent than in humans. An increasing number of studies have shown that in some haplorhine species (Guinea baboons, chimpanzees, bonobos, macaques, capuchins, and gorillas), cognitive processes can be modulated by the emotional value of stimuli.

For example, in a visual search task, Japanese macaques (*Macaca fuscata*) were faster in detecting threatening stimuli (snakes) than neutral stimuli (flowers) (Shibasaki & Kawai, 2009) and showed preferential allocation of attention to snakes (Masataka et al., 2018). This attentional prioritization of threatening stimuli may be explained from an evolutionary perspective: individuals prone to detecting threats would have a survival advantage (Lacreuse et al., 2013). In a dot-probe task (a task in which a dot appears at the same location as one of the stimuli, and the distribution of attention is measured according to the time taken to respond to the dot), rhesus macaques (*Macaca mulatta*) spotted targets presented in the same locations as social stimuli faster when the faces of conspecifics were threatening compared to not threatening (Lacreuse et al., 2013).

Several studies have also used a modified version of the emotional Stroop task typically used in humans. Developed by Allritz et al. (2016), this task has recently been performed with chimpanzees, gorillas, Japanese macaques, and bonobos (Allritz et al., 2016; Hopper et al., 2021; Laméris et al., 2022; Vonk et al., 2022). This emotional Stroop task explores whether images with emotional valence interfere with the performance (accuracy and response time) of individuals in a colour discrimination task. More precisely, two identical, emotionally loaded images are presented with borders in different colours, and only one of the colours was rewarded. The response time and accuracy of selecting the rewarded colour were measured and compared based on the emotional valence of the images. These studies revealed a decrease in accuracy (i.e., a lower proportion of correct responses; Hopper et al., 2021) or a longer response time for emotion-associated stimuli (Allritz et al., 2016; Laméris et al., 2022; Vonk et al., 2022). Emotionally relevant stimuli seem to draw participants' attention and to divert it from other information (in this case, the coloured borders). A study on working memory performance in rhesus macaques (Zarei et al., 2019) found that the performance of individuals in a delayed-matching-to-sample task was better when the images to match were neutral rather than emotional. Their findings support a scenario that suggests that emotional stimuli are likely to capture individuals' attention to further process emotional content (Ohman et al., 2001). This leaves limited cognitive resources for performing the task and leads to impaired performance.

A recent study involving capuchins (*Sapajus apella*), a platyrrhine species, also revealed that individuals tended to perform worse in a delayed matching-to-sample task following a negative experience (Webster & Brosnan, 2021). This study suggests that emotions may influence cognitive performance, even when they are not integrated into the task. Additionally, a study on Guinea baboons (*Papio papio*) demonstrated that the emotional

importance of mental representations (i.e., colours) can also impact individuals' cognitive abilities (Blanchette et al., 2017). The results showed that individuals were slower and less accurate when the targets were negative than when they were neutral. The opposite was observed for the distractors. The authors suggested that the results were due to cognitive avoidance, with individuals tending to avoid processing threatening information, equivalent to the behaviour avoidance of negative stimuli.

The relationship between emotion and cognition has not received as much attention in strepsirrhines. In particular, no studies have been published on Malagasy lemurs, which belong to the most ancient extant primate radiation (Yoder & Yang, 2004) and show the largest variation in body sizes, activity, feeding patterns, locomotion styles, and sociality patterns among the strepsirrhine species (Scheumann et al., 2007). The present study aims to explore in what extent emotion can interfere with the cognitive abilities of a Strepsirrhini primate, the grey mouse lemur (*Microcebus murinus*). Mouse lemurs are arboreal and nocturnal primates and are one of the smallest primates in the world (weighing between 60 and 120 g and with an average height of 25 cm from head to tail, Languille et al., 2012). During the day, mouse lemurs sleep in tree holes that they cover with leaves to build a nest. These nests are important resources for this primate since they improve thermoregulation by insulating this species, create a favourable microclimate (Radespiel et al., 1998; Schmid, 1998), and increase its chances of survival against predators. Because of their small body size, mouse lemurs face high predation pressures (Scheumann et al., 2007), with at least 14 predator species documented to prey on them (e.g., raptors, snakes, fossas; Sündermann et al., 2008). Predation likely influenced the evolution of the mouse lemurs. For instance, predator-naïve mouse lemurs showed specific behavioural reactions to predator odours, suggesting that the ability to recognize olfactory cues of predators is innate (Sündermann et al., 2008). In addition to eluding predators, finding food and a sleeping site are nightly concerns of mouse lemurs. These activities require cognitive skills to complete, and as highlighted in the studies mentioned above, emotional states could influence the cognitive abilities needed to properly complete these tasks. For instance, during a foraging activity, an individual could smell a potential predator nearby. The emotional state triggered by this stimulus might distract the lemur from the ongoing task, increasing the chances of survival. Thus, emotion is likely to play an important role in the nightly life of mouse lemurs and lead to adaptive responses. However, no study to date has investigated the emotion-cognition interaction in this species.

To assess to what extent emotion may interfere with the cognitive abilities of mouse lemurs, we used a visual discrimination learning task. This task has been used in various cognitive studies on mouse lemurs (Gary et al., 2019; Hozer & Pifferi, 2020; Picq et al., 2015; Royo et al., 2018). In this task, individuals learn to discriminate between two platforms, with only one providing access to their nest (hereafter, the target platform). To manipulate the emotions, we modified the task by associating the platforms with emotional visual stimuli. Visual stimuli can be used since vision has

been identified as a key modality for prey detection in captive-born mouse lemurs (Piep et al., 2008). Moreover, we used real objects rather than 2D images to enhance the ecological realism of the task.

We expected that emotional stimuli would capture and retain mouse lemurs' attentional resources and cognitive abilities, leaving limited cognitive resources (Kensinger & Corkin, 2003; Zarei et al., 2019). This could lead to impaired performance when the emotional stimuli are associated with the target platform. According to cognitive avoidance theory, performance would be impaired when negative emotional stimuli were associated with the target platform and improved performance when these stimuli were associated with the other platform (distractor platform).

When studying the emotion-cognition interaction, it is crucial to characterize influential factors such as the personality traits of individuals. For example, in humans, anxious individuals are more likely to have their attention captured by negative stimuli and to have difficulty disengaging attention from the threat (Yiend & Mathews, 2001). In nonhuman animals, "shy" individuals (generally slow explorers, nonaggressive, anxious) tend to have longer reaction times and better accuracy (Sih & Del Giudice, 2012), which could result in better learning compared to "bold" individuals (generally fast explorers, aggressive). In baboons, the cognitive performance of individuals with a higher proportion of negative behaviours tends to be more affected by the emotional value of the target stimuli (Blanchette et al., 2017), suggesting that individual differences may influence the impact of emotions. Few studies have assessed the personality traits of mouse lemurs and provided tools for their evaluation (in captivity: Thomas et al., 2016; Verdolin & Harper, 2013; Zablocki-Thomas et al., 2018, 2019; in the wild: Dammhahn & Almeling, 2012; Dammhahn, 2012). To consider the potential influence of individual personality traits on the emotion-cognition interaction, we conducted two behavioural tests suitable and validated for assessing personality traits in grey mouse lemurs (Verdolin & Harper, 2013; Zablocki-Thomas et al., 2018).

2 | METHODS

2.1 | Animals

Forty-eight (23 males, 25 females) adult grey mouse lemurs (*M. murinus*) aged two to 5 years, born and raised in the laboratory colony of UMR 7179 (CNRS/MNHN, Brunoy, France), were involved in this study. The animals were kept in social groups in their cages, provided with branches, leaves, various enrichment objects and a wooden nest box, at constant temperature (24–26°C) and relative humidity (55%), mimicking the conditions of Madagascar. The mouse lemurs were exposed to a seasonal alternation of the light/dark cycle consisting of summer-like long days (light:dark ratio of 14 h:10 h) and winter-like short days (light:dark ratio of 10 h:14 h). In this study, all individuals were tested in summer. The mouse lemurs were fed ad libitum with fresh fruits and vegetables and a mixture of cereals, gingerbread, yogurt, eggs, milk and water prepared daily in the laboratory.

To ensure that all animals tested were in a suitable physical condition to perform the task, we also performed a motor coordination and endurance test using an accelerating rotating cylinder (the rotarod test, Nemoz Bertholet, 2003). This allowed us to exclude the possibility that the results were due to impaired motor skills and/or physical condition. The animals' eyes were also checked by a veterinary ophthalmologist.

All experimental procedures were noninvasive and approved by the ethical committee "Comité d'éthique Cuvier n°68" under authorization n°12992-2018011613568518 v4.

2.2 | Cognitive task

2.2.1 | Apparatus

The experiments were conducted in an isolated cognitive assessment room containing the apparatus. The apparatus was a handmade rectangular box (height = 150 cm) composed of plywood walls (Figure 1). The apparatus was completely closed to prevent the animal from being disturbed by our presence. The interior of the apparatus was illuminated by a light bulb attached to the ceiling of the cage, in the right corner. To observe the animal, a camera was placed in the centre of the ceiling, allowing us to have an overall view

of the apparatus. The lemur was placed inside the apparatus via a trapdoor opening from the outside. This trapdoor opened onto the starting platform and connected to the outside by a wire. In each trial, the animal had to jump from the starting platform onto one of the two landing platforms (15 × 30 cm). If the animal did not jump within 30 s, the starting platform was progressively tilted downwards using the wire, and slow back and forth movements were performed to increase the animal's motivation to jump. If the animal jumped to the incorrect platform, the platform swung downward, and the mouse lemur fell into the bottom of the apparatus, landing on a wide soft pillow placed to prevent any injury. One side of the device could open to allow the experimenter to take the mouse lemur and return it to the starting platform, passing back through the trapdoor, for another trial. The same procedure was applied if the individual jumped anywhere else than the platform or did not jump after 5 min. If the animal jumped to the correct platform, it could pass through one of 3 openings in an opaque Plexiglas screen to access its nest box. The opaque screen prevented the mouse lemur from jumping directly to the opening of the nest box. The mouse lemur's reward on correct trials was allowing it to reach its nest and rest safely inside for 2 min. This reward (to enter and stay in the wooden nest) is particularly effective in mouse lemurs, as they are highly motivated to return to their nest box. The correct platform location was chosen at random in each trial using a simple R code, provided that the same

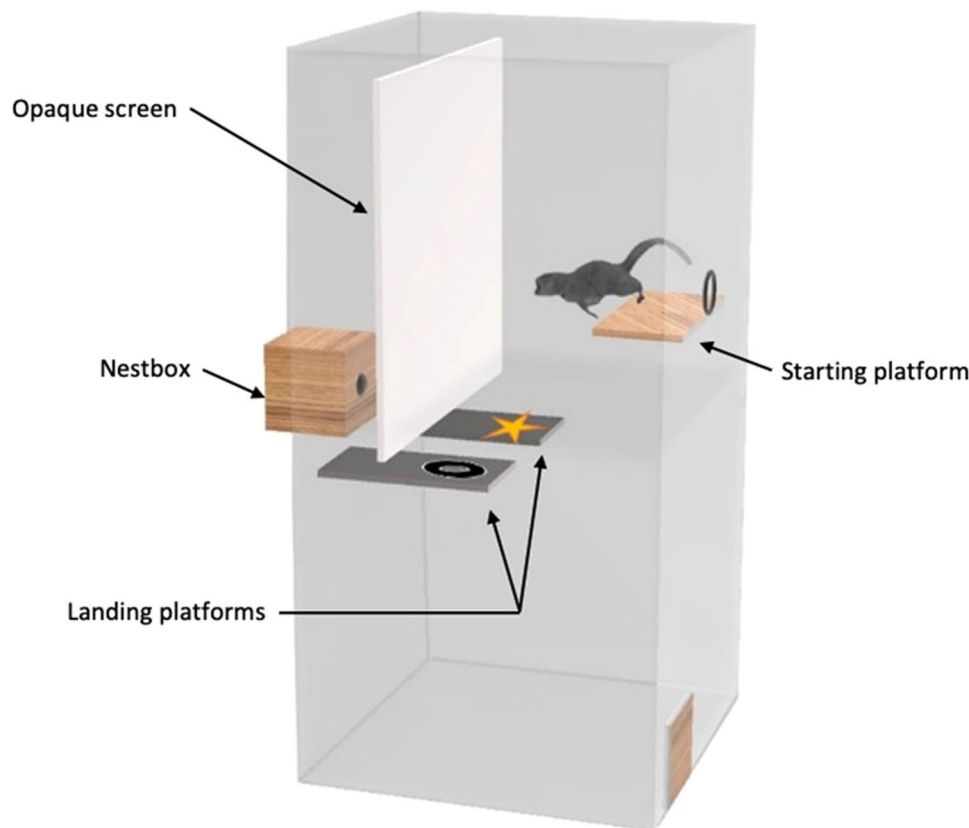


FIGURE 1 Visual discrimination apparatus for grey mouse lemurs. The mouse lemur must jump from the starting platform onto one of two landing platforms. One of the platforms leads to the nest box, while the other tilted downward if landed on, making the animal fall. (The stimuli shown here are for illustrative purposes only. See Figure 2 for the actual stimuli used).

side was not chosen on more than three consecutive trials. If the animal jumped to the same side 3 times in a row, the random selection of location was temporarily suspended, and the correct platform location was set to the opposite side until the individual jumped there. This was designed to avoid reinforcing a side bias.

2.2.2 | Stimuli

Visual stimuli with potential emotional valence were chosen to discriminate the platforms. A glove was considered a negative stimulus since the grey mouse lemurs involved in this study were regularly handled with gloves. Handling can induce stress, so avoidance and aggression are often observed towards these gloves. We assumed that laurel leaves were a positive stimulus, as they are enrichment objects included in the mouse lemurs' environment, and the mouse lemurs use them to make their nests. Finally, we used a cardboard star as a neutral stimulus, since it is an unknown object that is not part of the mouse lemurs' daily life (e.g., Hopper et al., 2021; Zarei et al., 2019). Moreover, it is one of the stimuli used in visual discrimination tasks routinely performed with mouse lemurs (e.g., Picq et al., 2015). To avoid bias, stimuli were created to have a similar surface area to the extent possible. Each stimulus could be associated with the correct platform (i.e., the target stimulus) or with the incorrect platform (i.e., the distractor stimulus). The goal of the task was to learn the location of the correct platform. By

combining the three types of stimuli with the two types of platforms, six experimental conditions were created (Figure 2 - see the legend for a description of the conditions). Individuals were randomly assigned each of the experimental conditions, controlling age and sex homogeneity between conditions, with each mouse lemur participating in only one group. This approach ensured that the lemurs were naïve to the task, as we aimed to examine the influence of emotionally valenced stimuli on a learning task.

2.2.3 | General procedure

This visual discrimination test was conducted over 3 days. The first day was the habituation phase, and the other 2 days were the learning phase, corresponding to the testing phase. The learning phase was conducted over 2 days to allow the animal to consolidate the learned information during the night (Samson et al., 2019).

The protocol for the two following phases is the one described in paragraph 2.2.1.

Habituation phase

The habituation phase was designed to familiarize the mouse lemur with the apparatus and the action of jumping to the landing platforms. The habituation phase was composed of seven stages of eight trials each. During stages 1 and 2, a central landing platform was attached between the two landing platforms, just below the nest

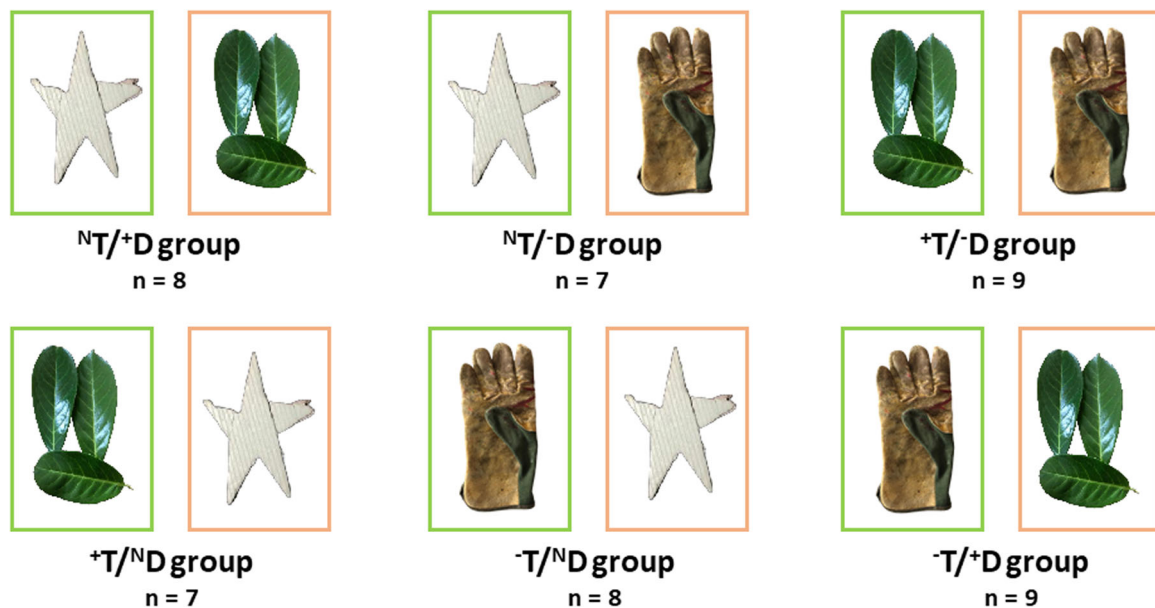


FIGURE 2 The six experimental conditions created by combining the two types of platforms with the three types of stimuli: laurel leaves were a positive stimulus, the glove was a negative stimulus, and the cardboard star was a neutral stimulus. The green rectangle indicates the target/correct platform. The red rectangle indicates the distractor/incorrect platform. **^NT/⁺D group**: Neutral (N) stimulus on target (T) platform and positive (+) stimulus on distractor (D) platform ($n = 8$). **⁺T/^ND group**: Positive stimulus on target platform and neutral stimulus on distractor platform ($n = 7$). **^NT/⁻D group**: Neutral stimulus on target platform and negative (-) stimulus on distractor platform ($n = 7$). **⁻T/^ND group**: Negative stimulus on target platform and neutral stimulus on distractor platform ($n = 8$). **⁺T/⁻D group**: Positive stimulus on target platform and negative stimulus on distractor platform ($n = 9$). **⁻T/⁺D group**: Negative stimulus on target platform and positive stimulus on distractor platform ($n = 9$).

box opening, creating a single large landing platform. Those two stages aimed to teach the lemur to jump from the starting platform to the single large landing platform to reach directly his nest box. In stages 3 and 4, an opaque Plexiglas screen was added above the middle of the landing platform, masking the nest box opening. The mouse lemur had to jump to the single large landing platform and then pass through one of the three openings of the screen to access its nest box. Those phases were designed to instruct the lemur to pass through the opaque screen and to familiarize him with the concept that the nest box was located just beyond it. Stages 1 and 2 are identical, as are stages 3 and 4. We repeat those stages twice to ensure thorough understanding by the mouse lemurs. The final stages were intended to train the lemur to jump on a smaller landing platform located on either the left or right side, depending on the specific phase. For each stage, eight trials were possible. The chosen number of trials for this experiment was determined during the development of this task, eight trials being both necessary and sufficient for the mouse lemur to learn the task. It has first been published in Picq et al., 2015 and repeated several times since (e.g., Hozer & Pifferi, 2021; Royo et al., 2018). Trials were recorded as failures if the animal jumped anywhere other than to the platform or did not jump after 5 min. If the animal failed all eight trials in a stage, the habituation phase was stopped and repeated the next day.

Testing phase

During the testing phase, the mouse lemurs completed a maximum of 30 trials in each session; one session was administered per day during 2 days (total of 2 sessions and 60 trials). In each trial, the animal had to choose between one of two platforms containing the positive, negative or neutral stimuli. A trial was considered successful when the animal jumped to the correct platform. A trial was considered unsuccessful when the animal jumped to the incorrect platform. A trial was marked as a refusal if the animal jumped anywhere other than the platform or did not jump after 5 min. After five consecutive refusals, the test session was interrupted. The session was also interrupted if the animal reached the success criterion, that is, if it successfully completed 8 out of 10 consecutive trials. Each stimulus was associated with the correct or incorrect platform at the beginning of the session, depending on the experimental group that the individual belonged to, and remained associated with it until the end of the two sessions. The goal was for the mouse lemur to find the correct platform using the visual stimulus.

2.3 | Behavioural coding

The behaviour of individuals was evaluated through two tests described below, yielding an agitation score and emergence time. One individual did not perform these behavioural tests due to colony constraints that prevented us from testing her. These test variables have been validated as reflecting personality traits in mouse lemurs (Verdolin & Harper, 2013; Zablocki-Thomas et al., 2018).

2.3.1 | Agitation score

The first test consisted of assigning an agitation score to each mouse lemur based on its behaviour during handling. We followed the same protocol as described in Verdolin and Harper (2013). In brief, the test consisted of holding the animal in our hand and scoring its reaction: urination (1 point), defecation (1 point), screaming (1 point), struggling (2 points), and biting (3 points). Animals could score a minimum of 0 (no agitation) and a maximum of 8 (high agitation). The scoring started directly after extraction of the animal from its nest box and lasted 45 s.

2.3.2 | Emergence time

The second test measured the emergence time of individuals, according to the protocol used in Zablocki-Thomas et al. (2018). We caught animals directly in their cage and placed a single individual in the wooden nest box. We placed the wooden nest box at the entrance of the home cage of the individual. We then waited at least 2 min so that the animal could habituate and calm down after being handled. The test consisted of opening the trap door and recording the latency for the animal to escape from the nest box and return to its home cage. The test lasted a maximum of 5 min. Individuals who never left the nest box within this 5 min period were given a score of 300 s.

2.4 | Statistical analysis

First, to compare the proportions of correct and incorrect trials among experimental conditions, we included only trials in which individuals made a choice (hereafter, response) and excluded trials in which individuals refused to participate (hereafter, refused trials). Then, we compared the proportions of refused and response trials among experimental conditions. Finally, we compared the proportions of individuals that reached the learning criterion (LC) among experimental conditions as well as the number of trials taken to reach this LC. Each analysis is described in detail below. The age ranges for each condition are summarized in the Supplementary Table S1.

We performed all analyses using R software (version 4.3.1) in the integrated development environment RStudio (RStudio Team, 2023). For all analyses, we considered a difference to be statistically significant when the p value (hereafter, p) was lower than 0.05.

The data that support the findings of this study and the R code are available from the corresponding author upon reasonable request.

2.4.1 | Success & refusal rates

To highlight cognitive performance differences among experimental conditions, we fitted a generalized linear mixed model (GLMM) with

binomial error structure and logit link function (using the `glmmTMB` function from the R package `glmmTMB`). We chose a binomial structure because our response variable was a categorical variable with two levels: 1 for a correct trial and 0 for an incorrect trial. We included as random factors the identity of the individuals and the trial number (ranging from 1 to 60), which we standardized (z-transformed). We added as fixed factors the experimental group, the sex and age of the individuals, and the behavioural variables (agitation score and emergence time). Before running the model, we verified the absence of heteroscedasticity and overdispersion with the package `DHARMA`. To test the effect of each factor on the response variable, we conducted type II Wald Chi-square tests. When a categorical fixed factor had a significant effect on the response variable, we followed the analysis with pairwise comparisons between groups using estimated marginal means (EMMs) with the Sidak method for *p*-value adjustment (`emmeans` function from the R package `emmeans`). When a continuous fixed factor had a significant effect on the response variable, we followed the analysis with a visualization of the model predictions using the function `ggpredict` from the R package `ggeffects`. We used `ggplot2` and `graphics` packages to generate the figures. We used the same method to highlight differences in the refusal rate among experimental conditions. Our response variable was a categorical variable with two levels: 1 for a refused trial and 0 for a response trial. We included as random factors the identity of the individuals and the trial number (ranging from 1 to 60), which we standardized (z-transformed). We added as fixed factors the experimental group, the sex and age of the individuals, and the behavioural variables (agitation score and emergence time). We performed the same verification and analysis as described for the success rate. The description of those two models can be found in the Supplementary Table S2.

2.4.2 | Learning criterion

To highlight learning performance differences among experimental conditions, we ran two models: one to compare the number of individuals reaching the LC per group and one to compare the number of trials before the LC was reached.

We fitted a GLMM with a binomial error structure and logit link function (using the `glmmTMB` function from the R package `glmmTMB`). We chose a binomial structure because our response variable was a categorical variable with two levels: 1 when the individual reached the LC and 0 when the individual did not reach the LC. To compare the number of trials before the individual reached the LC, we only included individuals that eventually reached the LC. Then, we fitted a GLMM with a Gaussian error structure and logit link function (using the `glmmTMB` function from the R package `glmmTMB`). For both of these models, we included as the identity of the individuals as a random factor, and we added the experimental group as a fixed factor. We verified the absence of heteroscedasticity and overdispersion with the package `DHARMA`. To test the effect of each factor on the response variable, we conducted type II Wald

Chi-square tests. When a categorical fixed factor had a significant effect on the response variable, we followed the analysis with pairwise comparisons between groups using estimated marginal means (EMMs) with the Sidak method for *p* value adjustment (`emmeans` function from the R package `emmeans`). We used the `ggplot2` package to generate figures. The description of the model can be found in the Supplementary Table S2.

3 | RESULTS

3.1 | Success rate

Analysis of the data revealed a significant interaction between the success rate and the experimental group (Wald $\chi^2 = 44$, $p < 0.001$). Visualization (Figure 3) revealed that the two groups with the neutral target platform had the highest success rate. In contrast, the group with the negative target platform and the positive distractor platform tended to have the lowest success rate. The other groups were intermediate, with a higher success rate for the groups with the positive target platforms.

Pairwise comparison revealed significant differences between the $^+T/^ND$ and $^NT/^+D$ groups ($p = 0.004$), between the $^+T/^ND$ and $^NT/^D$ groups ($p = 0.008$), between the $^NT/^+D$ and $^-T/^ND$ groups ($p < 0.001$), between the $^NT/^+D$ and $^-T/^+D$ groups ($p < 0.0001$), between the $^-T/^ND$ and $^NT/^D$ groups ($p < 0.001$), between the $^NT/^D$ and $^-T/^+D$ groups ($p < 0.0001$) and between the $^+T/^D$ and $^-T/^+D$ groups ($p = 0.001$) (Figure 3). Pairwise comparison revealed a tendency for significant differences between $^+T/^ND$ and $^-T/^+D$ ($p = 0.056$). Comparisons between the other groups did not reveal significant differences: $^+T/^ND$ and $^-T/^D^N$ ($p = 0.936$); $^+T/^ND$ and $^+T/^D$ ($p = 0.893$); $^NT/^+D$ and $^NT/^D$ ($p = 0.999$); $^NT/^+D$ and $^+T/^D$ ($p = 0.146$); $^-T/^ND$ and $^+T/^D$ ($p = 0.235$); $^-T/^ND$ and $^-T/^+D$ ($p = 0.169$); $^NT/^D$ and $^+T/^D$ ($p = 0.078$). The mean success rate for each group can be found in the Supplementary Table S5.

In addition, analysis revealed a significant interaction between the age of individuals and the success rate (Wald $\chi^2 = 4.8$, $p = 0.028$). Visualization revealed a tendency towards a lower success rate in older individuals (Figure S1). Analysis also revealed a significant interaction between emergence time and the success rate (Wald $\chi^2 = 5.7$, $p = 0.017$). Visualization revealed a tendency towards a higher success rate in individuals that took longer to emerge (Figure S2).

Finally, the analysis revealed no significant relationship between sex and success rate, nor between agitation score and success rate.

3.2 | Refusal rate

Analysis of the data revealed a significant relationship between the refusal rate and experimental group (Wald $\chi^2 = 16.4$, $p = 0.006$). Visualization (Figure S3) revealed that the group with the negative target platform and the positive distractor platform had a higher refusal rate than the other groups.

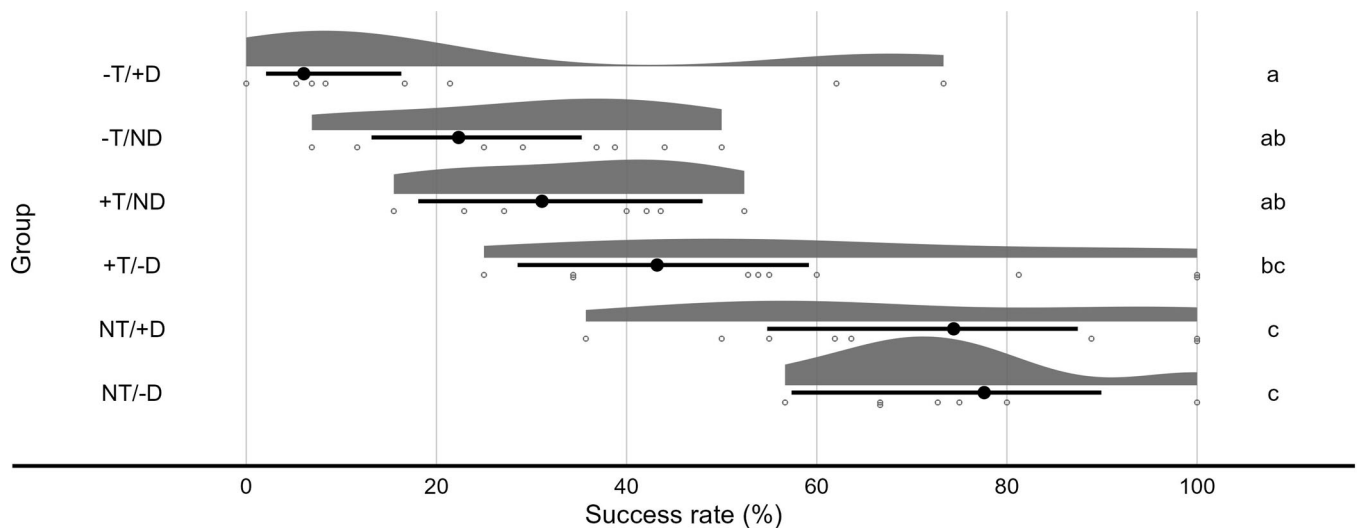


FIGURE 3 Success rate of each group in the discrimination learning task. The grey slab represents the distribution of raw success rates for each group, calculated with the raw mean success rate for each individual (grey points). Black points represent the estimated marginal means (Model 1), and black lines represent the associated 95% confidence level. Letters indicate results from pairwise comparisons (Tukey): if two or more groups share the same letter, they were not significantly different (but were not identical either). Groups are sorted from the lowest success rate to the highest.

Pairwise comparison revealed significant differences between the $^+T/^ND$ and $^-T/^+D$ groups ($p = 0.0012$), between the $^NT/^+D$ and $^-T/^+D$ groups ($p = 0.013$), between the $^-T/^ND$ and $^-T/^+D$ groups ($p = 0.004$), between the $^NT/^+D$ and $^-T/^+D$ groups ($p = 0.04$) and between the $^+T/^D^-$ and $^-T/^+D$ groups ($p = 0.006$) (Figure S3). Pairwise comparisons between the other groups did not reveal significant differences: $^+T/^ND$ and $^NT/^+D$ ($p = 0.9762$); $^+T/^ND$ and $^-T/^ND$ ($p = 0.6039$); $^+T/^ND$ and $^NT/^D^-$ ($p = 0.9322$); $^+T/^ND$ and $^+T/^D^-$ ($p = 0.8207$); $^NT/^+D$ and $^-T/^ND$ ($p = 0.9808$); $^NT/^D^+$ and $^NT/^D^-$ ($p = 0.9997$); $^NT/^+D$ and $^+T/^D^-$ ($p = 0.9982$); $^-T/^ND$ and $^NT/^D^-$ ($p = 0.9996$); $^-T/^ND$ and $^+T/^D^-$ ($p = 0.9994$); $^NT/^D^-$ and $^+T/^D^-$ ($p = 1.0000$). The mean refusal rate for each group can be found in the Supplementary Table S8.

In addition, analysis revealed a significant relationship between the agitation score and the refusal rate (Wald $\chi^2 = 4.4$, $p = 0.03$). Visualization revealed a tendency towards a higher refusal rate in individuals with higher agitation scores (Figure S4).

Finally, the analysis revealed no significant relationship between sex and refusal rate, age and refusal rate or emergence time and refusal rate.

3.3 | Learning criterion

Analysis of the data did not reveal a significant relationship between the number of individuals who reached the learning criterion (LC) and the experimental group (Wald $\chi^2 = 4.1$, $p = 0.54$). However, we found a significant relationship between the number of trials needed to reach the LC and the experimental group (Wald $\chi^2 = 23.9$, $p < 0.001$).

Pairwise comparison revealed significant differences between the T^+/D^N and T^N/D^- groups ($p = 0.023$), between the T^N/D^+ and

T^-/D^N groups ($p = 0.021$) and between the T^-/D^N and T^N/D^- groups ($p = 0.01$) (Figure 4). The mean number of trials for each group can be found in the Supplementary Table S12.

4 | DISCUSSION

Emotion is a complex concept that encompasses cognitive, behavioural, physiological, and subjective components. On a day-to-day basis, ecological and social stimuli trigger emotions, inducing physiological and behavioural reactions along with modifications in cognitive performances. While the complex relationship between emotion and cognition is well studied in humans, it has yet to be explored in lemurs. Our study evaluated the effect of the emotional valence of stimuli on performance in a cognitive task that involved learning. Our main finding was that emotional stimuli, regardless of valence, impaired cognitive performance.

The results showed that the cognitive performance of individuals was impaired when the target platform was associated with emotional stimuli rather than neutral stimuli. These results are consistent with findings in other studies, for example, on bonobos (Lam ris et al., 2022), chimpanzees (Hopper et al., 2021) and rhesus macaques (Zarei et al., 2019). For example, in Hopper et al. (2021), individuals made more errors in selecting the correct square when it contained positive or negative photographs rather than neutral images, indicating that their cognitive ability was disrupted by the presence of emotional stimuli compared to neutral stimuli.

Our results could be explained from an adaptive perspective. Emotional stimuli capture an individual's attention, leading to further processing, and thus limit the cognitive resources available for the task. This attention prioritization for emotional stimuli is crucial for

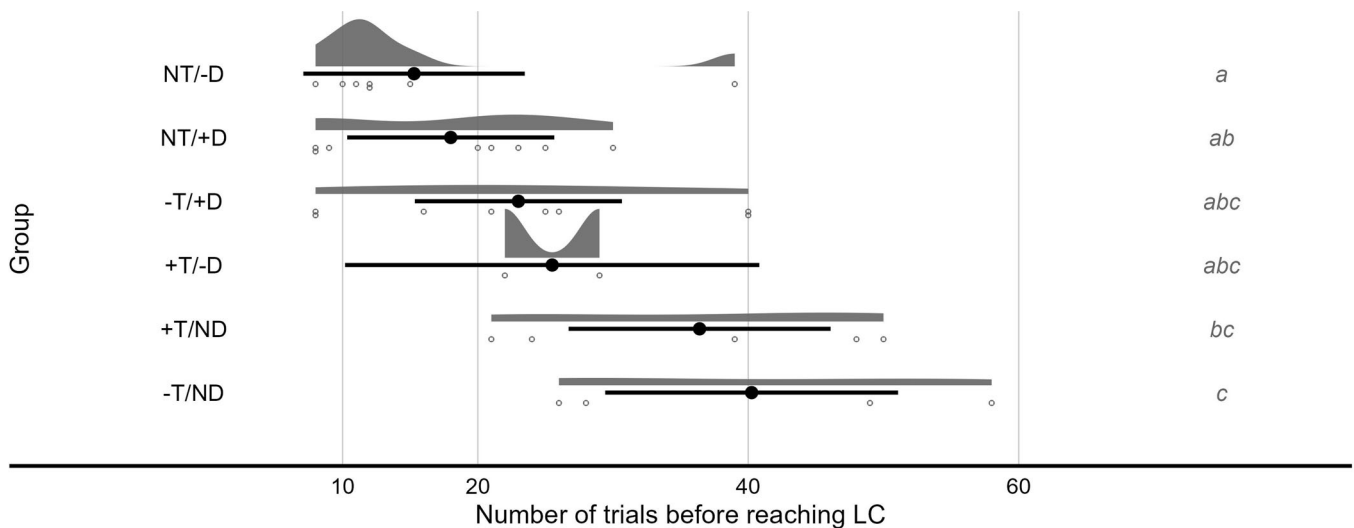


FIGURE 4 Number of trials before the individual reached the learning criterion (LC) for each group in the discrimination learning task. The grey slab represents the distribution of the number of trials before the LC was reached for each group, calculated with the raw mean max trial for each individual (grey points). Black points represent the estimated marginal means (Model 4), and black lines represent the associated 95% confidence level. Letters indicate results from pairwise comparisons (Tukey): if two or more groups share the same letter, they were not significantly different (but were not identical either). Groups are sorted from the lowest number of trials to the highest.

survival: the cost of ignoring potential threats is much greater than the cost of expending energy attending to benign stimuli (Haselton & Nettle, 2005). Based on this theory, we might expect an even higher success rate when the task involves two neutral stimuli since no emotion will interfere with task completion. Alternatively, a study on humans reported a better memory for events associated with emotional information (MacKay & Ahmetzhanov, 2005). Undoubtedly, humans tend to retain more emotionally salient memories than memories that are not associated with strong emotions. This contrasting finding might be due to the difference in mnemonic processes that support episodic and working memory functions (Kensinger & Corkin, 2003). Another factor that could explain this long-term memory enhancement is that emotion may serve as a cue to retrieval, thereby making retrieval of emotional information easier than retrieval of neutral information (Kensinger & Corkin, 2003).

One could contend that our findings might also be interpreted through the lens of an avoidance of the emotional valence stimuli. Indeed, our results indicate that lemurs performed significantly better than chance level in groups where the target stimuli were neutral. Conversely, in groups with emotional valence target stimuli, lemurs consistently performed below chance level. This suggests that lemurs could decide to avoid the emotional valence stimuli. However, if we follow this rationale (i.e., expecting the individual to consistently choose the platform associated with neutral stimuli to avoid the emotional ones), we would expect a success rate nearing 100% for groups with emotional valence distractors and close to 0% for groups with emotional valence targets. However, our results do not align with this expectation, indicating that lemurs do engage with platforms associated with emotional stimuli. An additional theory that can explain our results is the cognitive avoidance theory which

posits that individuals avoid processing threatening information, similar to the behavioural avoidance of threats (Blanchette et al., 2017; Günther et al., 2022). Blanchette et al., suggested that baboons exhibiting lower success rates with negative targets could be attributed to cognitive avoidance of the threat. This theory could similarly elucidate the low success rates observed for groups with negative targets in our study. Furthermore, our results might suggest that this cognitive avoidance may extend to positive targets as well, indicating a general avoidance of emotional stimuli. The current results do not enable us to definitively favour one theory over another. However, these theories are not mutually exclusive. Indeed, an individual may further process emotional stimuli, which could lead to an adaptive response of emotional stimuli avoidance. Furthermore, both cognitive avoidance and behavioural avoidance could operate simultaneously, notably for the groups where the two platforms have emotional valence stimuli. Individuals might avoid processing the emotional target also avoiding jumping onto the emotional distractor. This could explain the high refusal rate observed in the group with the negative target and the positive distractor.

Our results indicated that the negative stimuli impaired the success rate even more than the positive stimuli. This is consistent with other studies employing positive stimuli in humans (Jung et al., 2014) and in capuchins (Webster & Brosnan, 2021). However, this last study also highlights that the positive condition (i.e., familiar puzzle apparatus with access to a preferred food reward) was most likely not perceived as positive by the individuals or that this positive aspect was nullified by subjects' frustration when the apparatus was removed. This shows the challenge of generating and evaluating positive emotion, which could also explain the bias towards negative rather than positive emotions in the literature.

Although our results, which indicated altered capacity for emotional stimuli compared with neutral stimuli, are in line with previous findings, only a few studies have included positive stimuli in research on nonhuman primates (Hopper et al., 2021; Laméris et al., 2022; Vonk et al., 2022; Webster & Brosnan, 2021; Zarei et al., 2019), preventing us from being confident about our hypothesis on positive stimuli. Moreover, in humans, some studies have found opposite results, with positive emotion improving cognitive abilities compared to neutral emotion (Lindström & Bohlin, 2012; Yang et al., 2012). This might call into question whether our stimuli induced the assumed emotional state in the mouse lemurs. However, gloves are associated with handling, and our lemurs systematically presented defence and attack behaviour in their presence, thus indicating the presence of negative emotions. Laurel leaves were a relevant candidate for generating positive emotions since they are used to build nests, especially by mothers. However, it is difficult to confirm that the leaves generated positive emotions. It is also possible that the subjects considered that jumping on leaves could be dangerous. Indeed, it is not natural for mouse lemurs to jump on leaves, which would cause them to fall, rather than on branches. This highlights the fact that emotional valence is not the only variable influencing individual behaviour and that the emotional valence of stimuli can change according to the context, situation and experience of individuals. For the neutral stimulus, we used a plastic star, as it is the stimulus classically used in this task with mouse lemurs (Picq et al., 2015). We considered this stimulus to be neutral because it was something that mouse lemurs had never seen, as classically done in studies involving other primates' species. Indeed, images considered neutral are those of objects that primates have never seen before and/or are not part of their environment, such as ping-pong tables, chairs, books, and mugs (e.g., Hopper et al., 2021; Zarei et al., 2019). However, the true valence of such stimuli remains unknown. Moreover, we cannot completely exclude a potential colour effect since the three stimuli have different colour. It is however important to note that all of stimuli have colour that are visible for the mouse lemurs and that their colours are part of their intrinsic characteristic. Nevertheless, ideally, each of the stimuli would have been the same colour to control for a potential colour effect.

A possible way to reduce the above doubts concerning the stimuli and thus the potential associated biases would be to use several stimuli per group, as is typical in studies in humans and other haplorrhines. Potential choices for negative stimuli are pictures of predators or specific predator parts (or visual stimuli mimicking those specific parts), such as the eyes. Eyes are a cue used by individuals to identify potential danger (i.e., aposematic signalling). For instance, a study compared the approach of green monkeys (*Chlorocebus sabaues*) to predators, nonpredators, and nonpredators with predator eyes. Once near the images, the individuals were less likely to reach for peanuts near the predator's eyes than those near the nonpredator eyes (Burns-Cusato et al., 2016). In this sense, future studies in mouse lemurs could test a stimulus mimicking owl eyes to generate negative emotions and to investigate the impact on cognitive performance.

Another possibility could be to investigate the impact of other sensory modalities. Indeed, in the present study, we chose to test the emotion-cognition interaction using emotionally loaded visual stimuli. Vision is a key modality for prey detection in captive-born mouse lemurs (Piep et al., 2008). However, the olfactory sensory organs (olfactory bulbs) of mouse lemurs are particularly developed (Smith et al., 2007). This is attributed to their environment in the wild; mouse lemurs evolved in dense forests and are active at night. They also rely on chemical signals for social interaction. Social communication relies for instance on chemical signals, actively dispersed by mouse lemurs through specific behaviours such as urine washing (Schilling & Perret, 1987). Reproduction in these primates also relies on pheromones. Thus, testing the use of olfactory stimuli to induce emotion might be interesting and ecologically relevant. Mouse lemur communication also relies on acoustic signals, with ten call types previously described (Zimmermann, 2010a, 2018). The acoustic modality could also be a relevant modality to elicit specific emotions, especially since emotions play a role in social interactions. Indeed, the mouse lemur uses acoustic signals to coordinate social interaction, and results suggest that these vocalizations express the emotional state of a signaller reliably when linked to the respective individualized context (Zimmermann, 2010b). In addition, even if we assume that our cues were processed in the visual modality, this does not rule out the possibility that their olfactory aspects also influenced the animals' behaviour. Laurel leaves have a specific odour, and although the glove was washed, it still had a strong smell. Moreover, a study demonstrated that detection performance in mouse lemurs increases with the number of sensory modalities available (Piep et al., 2008). It would be interesting to consider the individual and joint influence of various modalities on emotion generation and cognitive performance in a single task.

To consider potential individual differences, we measured the individuals' personality traits. The results showed that individuals with a longer emergence time tended to have better cognitive performance, with a higher success rate (Figure S2). This shows, once again, the importance of personality traits in the relationship between emotion and cognition and highlights the need to take this parameter into account. In mouse lemurs, emergence time is used as an index of exploration (Zablocki-Thomas et al., 2018), and longer emergence times reflect slow explorers. Slow exploration is often characteristic of a shy personality (Koolhaas et al., 1999; Réale et al., 2007), and shy individuals tend to have longer reaction times and better accuracy (Sih & Del Giudice, 2012). In the present study, we suggest that shy individuals took more time to decide. Taking more time before answering may allow a better assessment of the task, resulting in fewer errors.

Our results also highlighted the age effect on cognitive abilities. The success rate tended to decrease with age (Figure S1). This age effect is consistent with classic findings as well as most of the studies on the age effect on the cognitive abilities of mouse lemurs (Chaudron et al., 2021). This cognitive impairment effect was found in all six experimental conditions. It is noteworthy that there were differences in the average age per group (Table S1). However, the

mean ages of all experimental conditions were between 2.5 and 3.5 years. This is not a major difference in mouse lemurs, as this age falls within the young adult category and, more importantly, below the midpoint of the lifespan of captive mouse lemurs (5 years). In addition, a study of the impact of age on the cognitive abilities of mouse lemurs on the same discrimination task (with neutral stimuli) showed no difference in performance between young (3.3 years) and old (7.5 years) subjects (Picq et al., 2015). The only difference observed between the young and old groups was in the long-term retention of visual discrimination.

Emotions are ubiquitous in mouse lemurs' environments, generated for instance by high predation pressure (Scheumann et al., 2007; Sündermann et al., 2008) or social interactions (Zimmermann, 2010b). However, mouse lemurs' emotions have been overlooked. The present study sheds new light on the importance of considering grey mouse lemur emotions. Indeed, mouse lemurs are models of choice for various domains of biology, such as neurobiology, including research on ageing (Languille et al., 2012) and nutrition (Pifferi et al., 2018). They are also often considered to possess the characteristics of primate ancestors (small size, arboreal and nocturnal lifestyle, omnivorous diet; Charles-Dominique & Martin, 1970; Ho et al., 2021; Radespiel & Zimmermann, 2001) and thus are often used in studies exploring the origins of primate behaviour (e.g., Toussaint et al., 2015). It is crucial to take into account the mouse lemur emotions in cognitive studies to avoid interpretation bias since our data demonstrate that, compared to neutral stimuli, emotional stimuli modify the cognitive response of mouse lemurs in a discrimination task. Moreover, mouse lemurs are pertinent models to explore the origin of primate behaviours (Scheumann et al., 2007). Exploring in what extent emotion interacts with cognition in this species, allows us to advance our understanding of the evolution of this interaction in primates, but also in animal species in general.

5 | CONCLUSION

This study is the first to explore how emotions can interfere with the cognitive abilities of mouse lemurs. Our results suggest a similar interaction between emotion and cognition to that reported in other primate species and support an adaptive role of emotion. More studies on a wider diversity of primate species are needed to fully elucidate the emotion-cognition interaction and to deepen our understanding of the origin and evolution of this interaction.

AUTHOR CONTRIBUTIONS

E. Mortessagne: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing—original draft (lead); Writing—review & editing (equal). **D. Bovet:** Writing—review & editing (equal). **C. Nozières:** Data curation (equal). **E. Pouydebat:** Conceptualization (supporting); Funding acquisition (equal); Methodology (supporting); Project administration (equal); Resources (equal); Supervision (equal);

Validation (equal); Writing—review & editing (equal). **F. Pifferi:** Conceptualization (supporting); Funding acquisition (equal); Methodology (supporting); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Writing—review & editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study and the R code are available from the corresponding author upon reasonable request.

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