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Article

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Abstract

While the interaction between emotions and cognition is relatively well known in humans, it remains to be explored in non-human primates, whose dedicated studies are carried out on a limited diversity of species, preventing us from discussing the evolutionary origin of this interaction. Here, we explored this cognition-emotion interaction in the grey mouse lemur (Microcebus murinus), often described as possessing ancestral characteristics, allowing us to better comprehend if this link appears soon in the phylogeny of primate.

We tested whether emotions could modify the learning performance of 60 mouse lemurs during a visual discrimination task. In this task, individuals had to learn to discriminate between two platforms using emotionally valued visual stimuli and to jump on the target platform. Our results showed that individuals learning performance improved when distractors had an emotional valence compared to when they were neutral. Opposite, individuals had impaired learning performance when targets had an emotional valence compared to when they were neutral. These results are consistent with the cognitive avoidance pattern for negative stimuli reported in other studies. This study is the first to explore emotion in mouse lemurs and to demonstrate that the emotion-cognition interaction is already present in a lemur's species.

1. Introduction

In humans, an important interaction exists between cognitive abilities and emotions. Indeed, several studies have shown that emotions can affect most cognitive processes such as judgments, attention, memory, reasoning, decision making, learning (de Houwer & Hermans, 2010; Lemaire, 2021; Robinson et al., 2013). For example, performance in a working memory task is better when images to memorize have an emotional value (positive or negative) than when they are neutral (Lindström & Bohlin, 2011). The emotional Stroop Task is commonly used in human psychology to assess attentional biases induced by emotion. In this task, human participants are instructed to name the colors in which emotionally loaded words are written. Participant's attention tends to be drawn to emotionally relevant stimuli (see Williams et al., 1994 for review) resulting in slower and less accurate responses when the words are negative, such as death or accident (Bar-Haim et al., 2007; McKenna & Sharma, 2004).

Thus, while the links between emotion and cognition are relatively well known in humans, they remain to be explored in other primates in order to understand when this link appears in the phylogeny of primates. For non-human primates, an increasing number of dedicated studies show that in some haplorrhine's species (Guinea baboons, chimpanzees, bonobo, Japanese macaques, rhesus macaques, capuchins, gorilla), cognitive processes can be modulated by the emotional value of stimuli. For example, in a visual search task, Japanese macaques (*Macaca fuscata*) are faster to detect threatening stimuli (snakes) than neutral stimuli (flowers) (Shibasaki & Kawai, 2009) and show preferential engagement of attention to snakes (Masataka et al., 2018). This attentional prioritization of threatening stimuli (snake in this study) may be explained from an evolutionary perspective: individuals prone to detect threats would have a survival advantage (Lacreuse et al., 2013). In a dot-probe task (a dot appears at the same location as one

of the stimuli, the distribution of attention is measured by the time taken to respond to the dot), rhesus macaques (*Macaca mulatta*) detect targets presented in the same locations as social stimuli more quickly when the faces of conspecifics are threatening rather than neutral (Lacreuse et al., 2013). Several studied also use a modified version of the emotional Stroop task uses in humans. Developed by Allritz and al., 2016, this task has only recently been used in 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 emotionally valent stimuli (images) would interfere with the performance (accuracy and response time) of individuals in a color discrimination task (i.e., emotionally loaded pictures were presented with different colored borders, one of which gave a reward. The response time and accuracy to select the right color was measured). These studies show tendencies of longer response time for emotion-associated stimuli (Allritz et al., 2016; Laméris et al., 2022; Vonk et al., 2022) or decreased accuracy (i.e. proportion of correct response) (Hopper et al., 2021). These effects can be attributed to the fact that participants' attention is drawn to emotionally relevant stimuli. In addition, a study on Guinea baboons (*Papio papio*) demonstrated that the emotional value of mental representations, in the absence of physical stimuli, can also impact individuals' cognitive abilities (Blanchette et al., 2017). In this study, baboons were asked to memorize the location of two targets of the same color, presented with a distractor of a different color, in a short-term memory task. As a result of long-term conditioning in the group of baboons involved in this study, one of the colors (green) was associated by individuals with a negative emotion (the green color is used as a signal of an incorrect response during their routine touch screen tests). The results showed that individuals were slower and less accurate when the targets were negative compared to when they were neutral. In contrast, subjects were faster and more accurate when the distractors were negative than when they were neutral. These results support the hypothesis of the cognitive equivalent to the phenomenon of avoidance of negative stimuli, showed in several studies (e.g., chimpanzee, rhesus macaques) (e.g., Hopkins & Bennett, 1994; Lacreuse et al., 2012; Machado et al., 2009; Murray & Fellows, 2021; Nelson et al., 2003; Sinnott et al., 2012; Thompson, 1954). For example, an eye-tracking study documented sustained avoidance of negative images (threatening picture of conspecifics) in stressed rhesus macaques (Bethell et al., 2012).

Finally, none of these studies, exploring the relationship between emotion and cognition, have focused on primates more distant from humans from a phylogenic point of view, such as strepsirrhines. In particular, to our knowledge, no studies explored the relationship between emotion and cognition in 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 (Scheumann et al., 2007). They provide important models to explore the origin of primate behavior (Scheumann et al., 2007). Thus, the aim of the present study is to evaluate the interaction between emotion and cognition in a small nocturnal Strepsirrhini, the grey mouse lemur (*Microcebus murinus*). This will be, to our knowledge, the first study to evaluate this relation in a lemur species and will allow us to learn more about the evolutionary origin of this interaction, of which little is known. Grey mouse lemurs are often described as primates who have retained several primitive features (e.g. small size, arboreal and nocturnal lifestyle, omnivorous diet) characteristic of the primate ancestors (Charles-

Dominique & Martin, 1970; Ho et al., 2021; Radespiel & Zimmerman, 2001). Weighing between 60 and 120 g and with an average height of 25 cm from head to tail (Languille et al., 2012), it is one of the smallest primates in the world. During the day, the mouse lemur sleeps in holes on tree that he covers with leaves to build a nest. These nests are important resources for this nocturnal primate since they allow it to increase its chances of survival against predators (e.g. raptors, snakes, fossas) and to have a better thermoregulation by insulating them and creating a favorable microclimate (Radespiel et al., 1998; Schmid, 1998). Efforts of field biologists provided detailed analyses of many aspects of their behavior and ecology (Radespiel, 2000; Radespiel et al., 1998; Radespiel & Zimmerman, 2001; Schliehe-Diecks et al., 2012; Schmid & Kappeler, 1998). In captivity, the grey mouse lemur is a model of choice for various domains of biology, mainly aging (e.g., Joly et al., 2006, 2014; Languille et al., 2015; Schmidtke et al., 2020; Wittkowski et al., 2021; See Languille et al., 2012 for a review on the benefits of mouse lemurs as a model for aging studies), and nutrition (e.g., Dal-Pan et al., 2010; Marchal et al., 2012; Pifferi et al., 2015, 2018; Royo et al., 2018; Vinot et al., 2011). They are also models of choice for studies assessing the ontogeny of behavior (e.g., Boulinguez-Ambroise et al., 2019, 2020; Leonard et al., 2020) and the evolutionary origins of behavior in primates (e.g., Reghem et al., 2011; Toussaint et al., 2013, 2015). Very few studies have also assessed the personality in these primates and provided tools for its evaluation (Thomas et al., 2016; Verdolin & Harper, 2013; Zablocki-Thomas et al., 2018, 2019 and in the wild: Dammhahn, 2012; Dammhahn & Almeling, 2012). Although mouse lemurs are established models, no study to date has been conducted on their emotions, which therefore remains unexplored. Thus, the present study has a twofold objective: to advance on the understanding of the evolutionary origin of the interaction between emotion and cognition by studying it in a primate close to the common ancestor, and to improve the knowledge of mouse lemurs' emotions, which could allow in the longer term to improve and optimize their well-being in captivity.

We conducted a learning test in which individuals have to discriminate two platforms (only one giving access to a reward) using visual cues. Visual stimulus can be used since vision has been identified as a key modality for prey detection in captive born mouse lemurs (Piep et al., 2008). The visual discrimination task has already been used as a classic cognitive task (with emotionally neutral stimuli) in various cognitive studies on mouse lemurs (Gary et al., 2019; Hozer & Pifferi, 2020; Picq et al., 2015; Royo et al., 2018). This task has several advantages such as a fast habituation time and understanding of the apparatus, a possibility to easily manipulate the stimuli and to repeat the learning endlessly, provided stimuli are changed. Moreover, this task is adapted to the arboreal nature of mouse lemurs since it requires them to jump to make a choice. The present study will be the first to develop such an ecological task for the study of cognition and emotion interaction, adapted to small arboreal primate species and to species for which the use of a touchscreen requires too much training time and/or is not accessible. In our task, mouse lemurs had to discriminate two platforms, using visual stimuli with supposed emotional or neutral value, and to jump on one of the platforms.

We hypothesized that the emotional nature of the stimuli, depending on whether they are target (associated with the correct platform) or distractor (associated with the incorrect platform), would modify the learning performance of grey mouse lemurs in this visual discrimination task. Specifically, we

hypothesized that individuals would exhibit cognitive avoidance, characterized by the inhibition of processing threatening information (Blanchette et al., 2017; Günther et al., 2022). This will result in better performance when the negative stimulus is the distractor and poorer performance when it is the target. We expected the contrary for the positive stimuli, with an approach tendency. Finally, we also expected differences between individuals. Indeed, in humans, highly anxious individuals show an attentional bias for threatening stimuli (Bar-Haim et al., 2007). Anxious humans are also more likely to have their attention captured by negative stimuli and to have difficulty to disengaging attention from the threat (Yiend & Mathews, 2001). In non-humans' animals, "shy" individuals (generally slow explorer, non-aggressive, anxious) tend to take longer time to make choices but are more accurate (Sih & del Giudice, 2012) which could result in better learning compared to "bold" individuals (generally fast explorer, aggressive). To test these individuals' differences, we conducted two behavioral tests that have been previously validated as variables reflecting personality in grey mouse lemurs (Verdolin & Harper, 2013; Zablocki-Thomas et al., 2018).

2. Methods

2.1 Subjects

Sixty adult male (28) and female (32) grey mouse lemurs (*Microcebus murinus*) aged 2-5 years, born and raised in the laboratory colony of UMR 7179 (CNRS/MNHN, Brunoy, France), were involved in this study. The animals were kept alone or in groups in their usual cages of variable size, provided with branches, leaves, various enrichments and a wooden nestbox, 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 day length (14:10 light:dark) and winter-like short day length (10:14 light:dark). In this study, all individuals involved were in summer. The mouse lemurs were fed *ad libitum* with fresh fruits and vegetables and a mixture of cereals, gingerbread, yogurt, egg, 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 (Rotarod test). This allowed us to exclude the possibility that the results were due to impaired motor skills and/or physical condition. The animal's eyes were also checked by a veterinary ophthalmologist.

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

2.2 Cognitive task

2.2.1 Apparatus

The experiments were conducted in an isolated cognition room containing the apparatus. The apparatus was a handmade rectangular parallelepiped (height = 150 cm) composed of plywood walls (Figure 1). The apparatus was completely closed to prevent, as much as possible, 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 center 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, 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 cm x 30 cm). If the animal did not jump within 30 seconds, starting stand was progressively tilted downward using the wire and slow back and forth movements were performed to increase the motivation to jump. If the animal jumped onto the incorrect platform, the platform swung down and the mouse lemur fell into the bottom of the apparatus on a wide soft pillow to avoid any risk of injury. One side of the device could open to allow the experimenter to take back the mouse lemur and put it back on the starting platform, passing again through the trapdoor, for another trial.

If the animal jumped onto the correct platform, it could pass through one of the 3 openings of an opaque Plexiglas screen to access its nestbox. The opaque screen prevented mouse lemur from jumping directly to the opening of the nestbox. The reward consisted in allowing the mouse lemur to reach its nest and then to be "home safe" for 2 minutes. This reward (to enter and stay in the wooden nest) is particularly effective in mouse lemurs as they are very keen to find their nestbox, due to their habit in their natural environment to make use of tree holes as vital means to evade predation and ensure thermoregulation. The placement of the correct platform was chosen randomly, trial by trial, with the condition that the same side could not be chosen for more than three consecutive trials. If the animal jumped on the same side 3 times in a row, the random alternation of location was temporarily suspended, and the correct platform was placed on the opposite side until the individual jumped there. This avoids reinforcing a side bias.

2.2.2 Stimuli

The aim was to test whether learning performance of mouse lemur in this discrimination task could be altered by emotions. Visual stimuli with supposed emotional values were chosen to discriminate the platforms. A glove was chosen as a negative stimulus. Grey mouse lemur involved in this study are regularly handled with gloves that causes them stress. For the positive stimulus, laurel leaves, with which our mouse lemurs make their nests, were chosen. Supposedly neutral stimuli (cardboard stars, which are not part of the mouse lemurs' daily life) were also used as controls. To avoid bias, stimuli were created to have the same surface area as possible. Each stimulus could either be associated with the correct platform or with the incorrect platform. In the first case, the stimulus was referred to as the target and in the second as the distractor, the goal of the task being to learn the location of the correct platform. By combining the three types of stimuli with the two types of platforms, six experimental groups were created (Figure 2 - see legend for a description of the groups). A seventh group with target and neutral distractors is used as a control.

2.2.3 General procedure

This visual discrimination test was conducted over 3 days. The first day was for the habituation phase and the other two days to the learning phase. The learning phase was conducted on two days to allow the animal to consolidate its learning during the night.

2.2.3.1 Habituation phase

The habituation phase was designed to familiarize the mouse lemur with the apparatus and to teach it to jump on the landing platforms. The habituation was composed of seven phases of eight trials each. During phases n°1 and n°2, a central landing platform was attached between the two landing platforms, just below the nestbox opening. On phases n°3 and n°4, an opaque Plexiglas screen was added above the middle of the landing platform masking the nestbox opening. The mouse lemur had to jump onto the central landing platform then to pass through one of the 3 openings of the screen to access its nestbox. For the last three phases, the central landing platform was removed and a single landing platform was placed alternately to the left or to the right of the nestbox opening, which was still masked by the opaque screen. For each phase, 8 trials were possible. A failed trial was recorded if the animal jumped elsewhere than on the platforms or did not jump after 5 minutes. If the animal failed all 8 trials in a phase, the habituation was stopped and repeated the next day.

2.2.3.2 Learning phase

During the learning phase, the mouse lemurs were given each day a session of a maximum of 30 trials. On each trial, the animal had to choose between one of two platforms on which were placed the positive, negative or neutral emotionally valent stimuli. A trial was considered successful when the animal jumped onto the correct platform. A trial was considered unsuccessful when the animal jumped onto the incorrect platform. Also, a trial was marked as a refusal if the animal jumped elsewhere than on the platforms or did not jump after 5 minutes. After 5 consecutive refusals, the test session was interrupted. The session could also be interrupted if the animal reached the success criterion, i.e., if it successfully completed 8 out of 10 consecutive trials. Each stimulus was associated with a platform at the beginning of the session, depending on which group the individual belonged to, and remained associated with it until the end of the two sessions. The goal was for the mouse lemur to learn the location of the correct platform using the visual stimulus.

2.3 Behavioral coding

The behavior of individuals was considered through two tests described below: agitation score and emergence time. Only 52 individuals out of 60 were tested because 8 animals died before testing or colony constraints prevented testing them. In this study, these tests could only be performed once but have already been validated as variables reflecting personality 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 lemurs based on their behavior during a manipulation. We followed the same protocol as described in Verdolin and Harper (2013). In brief, the test consisted in grabbing the animal and scoring its reaction: urinating (1 point), defecating (1 point), screaming (1 point), struggling (2 points), and biting (3 points). According to this protocol, 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 nestbox and lasted 45 seconds.

2.3.2 Emergence time

The second test was to measure 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 nestbox. We placed the wooden nestbox 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 from the manipulation. The test consisted in opening the trap door and recording the latency for the animal to escape from the nestbox and return to its home cage. The test lasted 5 min maximum. Individuals that never left the nestbox within this 5 min were given a score of 300s.

2.4 Statistical analysis

All statistical analyses were performed using R software (version 4.2.1). For all analyses, we considered an effect to be statistically significant when $P < 0.05$.

To test our hypotheses, we examined three measures obtained during the cognitive tests: the percentage of success corresponding to the number of successful trials (trials during which the individual jumped on the correct platform) divided by the total number of trials; the percentage of errors corresponding to the number of failed trials (trials during which the individual jumped on the incorrect platform) divided by the total number of trials; and finally, the refusal rate corresponding to the number of refusals (the individual did not jump or jumped anywhere other than on the platforms) divided by the total number of trials. Our aim was to find out whether the emotional valence of the target and distractor stimuli (i.e. the group) influenced these performance parameters. We performed analysis of covariance (ANCOVA) with the performance variables (success, error and refusal rate) as independent variables and with age, sex, group and behavioral data as dependent variables. These ANCOVA were performed with the Anova() function of the "car" package (*cran.r-project.org/web/packages/car*). In order to select the best model for our data, we used the AIC (Akaike Information Criterion) index by using the stepAIC() function of the "MASS" package (*https://cran.r-project.org/web/packages/MASS/index.html*). The application requirements were met for the success and error percentages. For the percentage of refusals, we had to transform our data with a LOG transformation. In case of significant effects, post-hoc tests were performed (adjustment method:

Bonferroni) via the tukeyhsd() function of the "rstatix" package (*https://cran.r-project.org/web/packages/rstatix/index.html*).

3. Results

We hypothesized that performance in the learning task would be modified by the nature of the target and distractor stimuli. As the age of the animals was consistent between the groups (Kruskal-Wallis's test: P = 0.133), we did not take it into account in the models. This also applies to the weight of individuals.

3.1 Success rate

Analysis of covariance (ANCOVA) showed significant effects of group on success rate (P < 0.001; Table 1). Post-hoc tests comparing the success rate of each group show a significant difference between group + TND (35.87%) and group NT + D (69.5%) (p.adj = 2.06e-02) ; between groups + TND and NT-D (77.75%) (p.adj = 1.68e-03) ; between groups NT + D and -TND (31.12%) (p.adj = 5.08e-03) ; between groups NT + D and -T + D (18.89%) (p.adj = 5.10e-05) ; between groups NT + D and NTND (31.9%) (p.adj = 3.43e-03) ; between groups -TND and NT-D (p.adj = 3.44e-04) ; between groups -TND and + T-D (62.75%) (p.adj = 4.40e-02) ; between groups NT-D and -T + D (p.adj = 2.32e-06) ; between groups NT-D and NTND (p.adj = 1.91e-04) ; between groups + T-D and -T + D (p.adj = 6.54e-04) ; between groups + T-D and NTND (p.adj = 3.45e-02) (Fig. 3a). For the other explanatory variables tested (gender, behavior), the ANOVA did not show a significant influence on the percentage of success.

3.2 Non-success rate (errors and refusals)

3.2.1 Errors rate

ANCOVA also showed significant effects of group on error rate (P < 0.001, Table 1). Post-hoc tests show a significant difference in error rate between group + TND (60.5%) and group NT + D (26.37%) (p.adj = 7.38e-03) ; between groups + TND and NT-D (19.38%) (p.adj = 6.45e-04) ; between groups NT + D and -TND (62%) (p.adj = 4.48e-03) ; between groups NT + D and NTND (59.8%) (p.adj = 5.11e-03) ; between groups -TND and NT-D (p.adj = 3.71e-04) ; between groups NT-D and NTND (p.adj = 3.73e-04) (Fig. 3b). Error rate for groups + T-D and -T + D were 31.86% and 43.11%, respectively.

3.2.2 Refusals rate

Finally, ANCOVA showed significant group effects on the refusals rate (P < 0.001, Table 1). Post-hoc tests show a significant difference in the refusal rate between group -T + D (38%) et group + TND (3.75%) (p.adj = 1.59e-02) ; between groups -T + D and NT + D (4.12%) (p.adj = 1.18e-02) ; between groups -T + D and -TND (6.75%) (p.adj = 0.05) ; between groups -T + D and NT-D (2.87%) (p.adj = 1.02e-03) ; between groups -T + D and + T-D (1.87%) (p.adj = 4.32e-03) et between groups -T + D and NTND (8.3%) (p.adj = 1.92e-02) (Fig. 3c). Finally, the analysis revealed an effect of the agitation score, attributed to each individual, on the refusals rate during the learning task (P = 0.02).

Table 1
Summary table of ANCOVA results testing which variables (age, sex, groups, agitation score, exploration time) affect performance parameters (success, error, and refusal rates). Models represented in this table are best fit models according to the AIC index. Variables in bold significantly influence performance (α = 0.05).

Dependent variables	Independent variables	Df	F	P
Success rate	**Group**	6	12.7579	2.746e-08
	Emergence time	1	1.0672	0.3071
Errors rate	**Group**	6	5.9828	1.237e-04
	Emergence time	1	0.5069	0.4802576
Refusals rate (log)	**Group**	6	9.0148	1.972e-06
	Agitation score	1	5.1148	0.02872

4. Discussion

While the interaction between emotions and cognition is relatively well known in humans, it remains to be explored in non-human primates, whose dedicated studies are carried out on a limited diversity of species, mostly haplorrhines, preventing us from discussing the evolutionary origin of this interaction. Our goal was to explore this interaction between emotion and cognition in a lemur species, the grey mouse lemur (*Microcebus murinus*), a strepsirrhine often described as possessing ancestral characteristics. We tested whether emotions could modify the learning performance of mouse lemurs in a visual discrimination task. In this task, individuals had to learn, by trial-and-error, to discriminate between two platforms using emotionally valent visual stimuli (supposedly positive, negative, or neutral) and to jump onto the correct platform giving access to their nestbox.

Our results showed that the learning performance of mouse lemurs are modified by the emotional value of stimuli. In line with our prediction, mouse lemurs were less successful (low success rate and high error rate) on the learning task when the targets were negative and the distractors neutral (group -TND). In contrast, subjects were more successful (high success rate and low error rate) when the distractors were negative and the targets neutral (group NT-D). In short, relative to neutral stimuli, negative targets impaired performance and negative distractors improved performance, resulting in a more efficient learning. These results are consistent with previous study on the effect of negative stimuli on short term memory (Blanchette et al., 2017) or on the effect of negative stimuli on an emotional stroop task (Hopper et al., 2021). They can be explained by the phenomenon of cognitive avoidance, where the individual will avoid processing threatening information (Blanchette et al., 2017; Günther et al., 2022). This effect is analogous to the basic behavioral avoidance of negative stimuli (Blanchette et al., 2017). This avoidance led to impaired performance when the negative stimuli is the target. In contrary, avoidance of the negative stimuli, when it is the distractor, can result in less interference with the target processing and thus improve

learning performance. Our result added to the existing literature on the effect of negative stimuli on primates' cognition (Allritz et al., 2016; Blanchette et al., 2017; Lacreuse et al., 2013; Masataka et al., 2018; Shibasaki & Kawai, 2009) and demonstrated that this effect is present in a lemur species with ancestral characteristics (Charles-Dominique & Martin, 1970; Ho et al., 2021; Radespiel & Zimmerman, 2001).

In contrast to our prediction, positive target stimuli did not improve mouse lemurs' performance. Indeed, the same pattern observed with negative stimuli was also observed with positive stimuli: positive targets and neutral distractors (group + TND) impaired performance and positive distractors and neutral targets (group NT + D) improved performance. In short, relative to neutral stimulus, positive targets impaired learning performance and positive distractors improved learning performance. These results could be explained by the fact that what we assumed to be positive (laurel leaves) is not perceived as positive for the mouse lemur. Indeed, while it is rather easy to generate negative emotions, it is more challenging to generate positive emotions in mouse lemurs and in nonhuman species in general which is highlighted by the lack of study on positive emotions (Webster & Brosnan, 2021). However, we know that the glove and the laurel leaves generate different types of reactions in individuals. Indeed, when the emotional stimuli were opposed to each other's, performance were better when the positive stimulus was the target, and the negative stimulus was the distractor (group + T-D) than the other way around (negative target and positive distractors (group -T + D). This shows a gradient in the stimuli used, with stronger effect for the negative stimulus (glove). Our results with positive stimuli can also be explained by the fact that positive stimuli, compared to neutral stimuli, do not necessarily improve the cognitive performance of individuals. A study on capuchins monkey finds that, in a working memory task, positive experience did not facilitate performance compared to control condition (Webster & Brosnan, 2021), though 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 nullified by subjects' frustration when the apparatus was removed.

This shows, once again the challenge of evaluating positive emotion. Another study using the modified emotional Stroop task for non-humans' primates (Hopper et al., 2021) find that the individuals made more errors in selecting the correct square when it contained positive or negative photographs compared to neutral images, indicating that their cognitive ability was disrupted by emotional stimuli compared to neutral.

Moreover, when the two emotion-related stimuli were presented together (group + T-D & -T + D), we observed significant difference in success rate but not in error rate. This is because in the group where the target is negative and distractor positive, individuals refused a lot to jump on the platforms. It's in fact the only group with a high rate of refusal. One explanation is that individuals avoid the glove, as observed in other groups. However, individuals also tend to avoid laurel leaves, as also observed in the other groups. Here, the leaves are additionally associated with the negative platform resulting in a double negative effect. This combination of negative effects leads to a total stop of the learning, the animals not wanting to perform the task anymore and either staying on the departure platforms or jumping on the side walls of the apparatus.

Our results did not reveal individual differences, regarding behavioral traits, in success and error rates. They did highlight individual differences with a significant effect of agitation score on the refusal rate. However, these results should be taken with great caution. Indeed, even though the tests we used have been validated as reflecting personality traits in mouse lemurs in different studies (Verdolin & Harper, 2013; Zablocki-Thomas et al., 2018), we did not perform the tests several times. Moreover, due to deaths or other constraints, we could not perform these tests on all the animals (only 52 out of 60 were tested). Additionally, refusal rate was high for only one group, which leads to difficulties in interpreting the results showing an effect of agitation scores on refusal rates. Still, the individuals with the higher agitations score are the ones with the lowest refusal rates. In previous studies, agitation score was considered to reflect shyness or anxiety in mouse lemurs (Verdolin & Harper, 2013) with greater agitation reflecting a shy personality and thus lower agitation a bold one. Therefore, the individuals with the lowest refusal rates are potentially the individual with a shy personality, which could be explained by a greater motivation to join their nest. Future research will have to further test the mouse lemurs' personality in order to draw conclusions on the effect of personality on the emotion-cognition relation.

To further interpret these results, it would be interesting for future research to conduct a new learning test with several stimuli per group. Indeed, multiplying the stimuli for each category can ensure that the observed results are due to emotions and not to an object-specific effect. Also, to further improve our study, modifications of the apparatus could be necessary. Indeed, it would be interesting to consider the reaction time of individuals (in our study it would be the time to jump) to determine if the attention of mouse lemur in this task was drawn by emotional stimuli, as observed in other studies (Allritz et al., 2016; Lacreuse et al., 2013; Masataka et al., 2018; Shibasaki & Kawai, 2009). This will require automation of the starting platform, as the way it is moved is experimenter dependent. We could also observe the direction of the gaze of individuals to allow us to see the attention paid by individuals to different stimuli. It would be necessary to place a camera in front of the individuals. The positioning of the body of the individual may also give an indication, as mouse lemurs tended to approach the edge of the side from which they were jumping and to bend over several times before jumping. Another ideal, but time-consuming modification, would be for individuals to perform this learning task completely independently. We could for example imagine placing a device inside the home cage of the individuals. This would remove entirely the bias due to our presence. Indeed, even if we tried to reduce the effect of the experimenter as much as possible, the mouse lemurs are very sensitive to the human presence. A study from our team (DiFrancesco et al., 2023) showed extremely high ECG values as soon as a human was present in a room near the lemurs. This consistently high level of stress may have caused bias in our test and masked potentially significant individual differences on performance parameters (e.g., success and error rate, learning efficiency).

To our knowledge, this preliminary study is the first to demonstrate that the interaction between emotion and cognition is already present in a lemur species: we showed that the emotional value of target or distractors modified learning performance of mouse lemurs, suggesting a cognitive avoidance of emotional stimuli (Blanchette et al., 2017; Günther et al., 2022). The implication for this study is double. First, this allow us to develop our knowledge on the emotions of the grey mouse lemur, since no study to

date has been conducted on this subject. The grey mouse lemur being an emerging model, it is necessary to develop our knowledge on their emotions and to develop tools to assess their well-being. Second, this brings some new data concerning the evolutionary origins of the emotion-cognition interaction which remains poorly known. In the future, comparative studies exploring the interaction between emotion and cognition in different primate species, representative of the phylogeny, will be needed to learn more about the evolution of this interaction.

Declarations

Author contributions

E.M and F.P designed the cognitive experiments, E.M and C.N executed the experiments, E.M conducted data analyses, E.M wrote the manuscript, F.P and E.P supervised the experiments and analyses and reviewed the manuscript, D.B reviewed the manuscript, F.P, E.P and D.B supervised the whole project.

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Figures

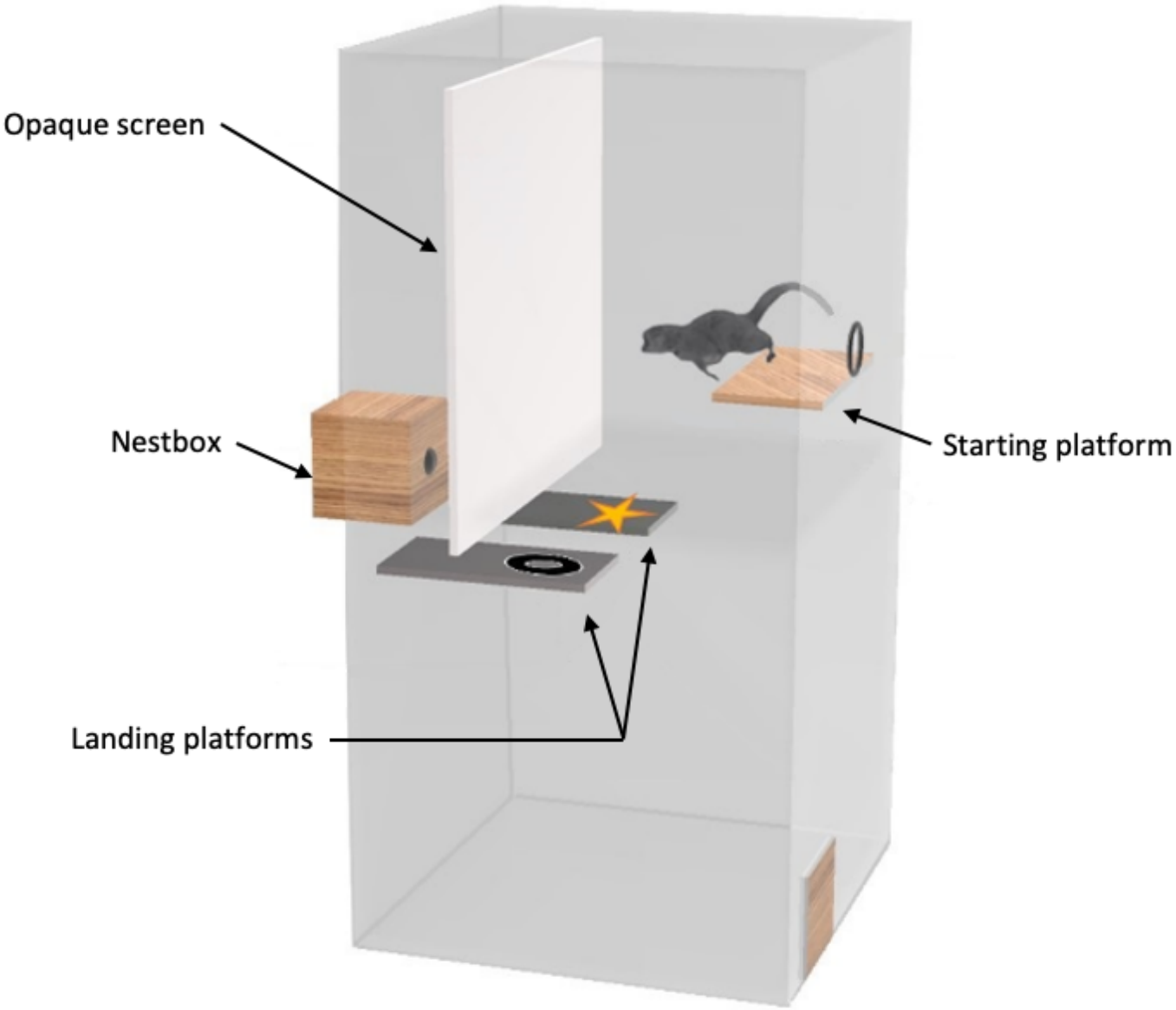

Figure 1

Visual discrimination apparatus for grey mouse lemurs.

The mouse lemur must jump from the starting platform onto one of two landing platforms. One of them leads to the nestbox while the other one topples over and makes the animal fall. (The stimuli shown here are only illustrative, see figure 2 for a representation of the stimuli used).

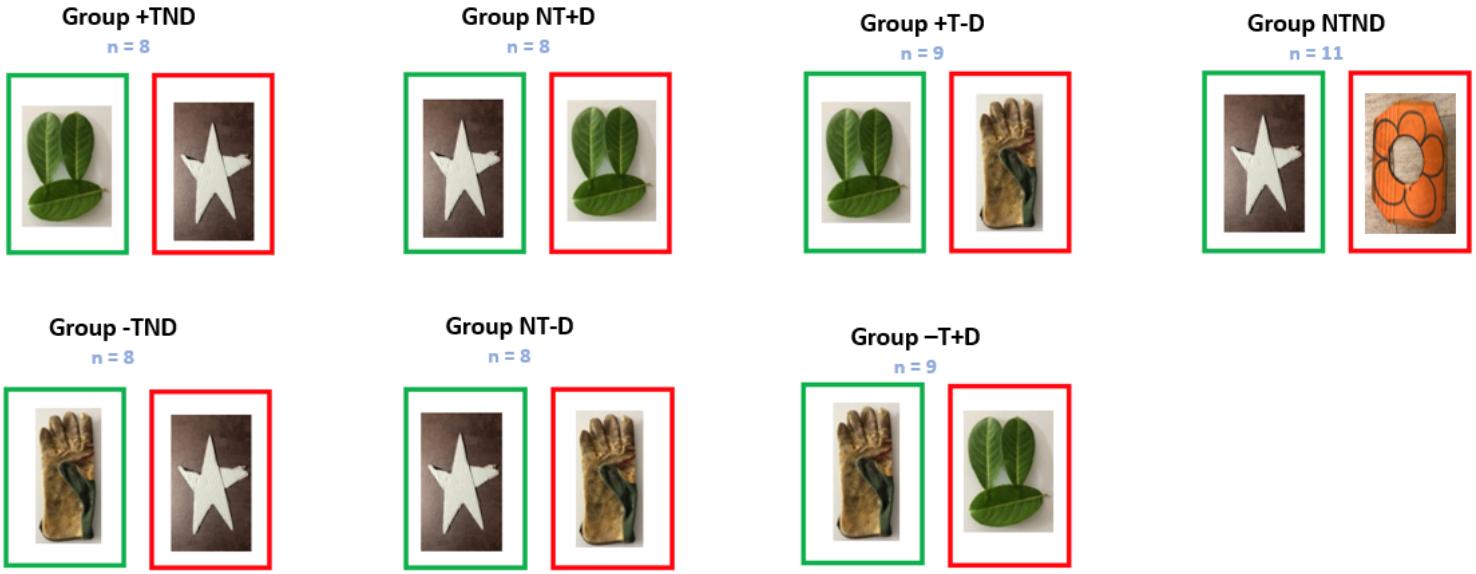

Figure 2

Seven experimental groups, created by combining the two types of platforms with the three types of stimuli: laurel leaves as a positive stimulus, a glove as a negative one, and a cardboard star as a neutral one. The green rectangle represents the target/correct platform. The red rectangle represents the distractor/incorrect platform.

Group +TND: Positive (+) stimulus on Target platform and Neutral stimulus on Distractor platform

Group NT+D: Neutral stimulus on Target platform and Positive stimulus on Distractor platform

Group -TND: Negative (-) stimulus on Target platform and Neutral stimulus on Distractor platform

Group NT-D: Neutral stimulus Target platform and Negative stimulus on Distractor platform

Group +T-D: Positive stimulus on Target platform and Negative stimulus on Distractor platform

Group +T-D: Negative stimulus on Target platform and Positive stimulus on Distractor platform

Group NTND: Neutral stimulus on Target platform and Neutral stimulus on Distractor platform

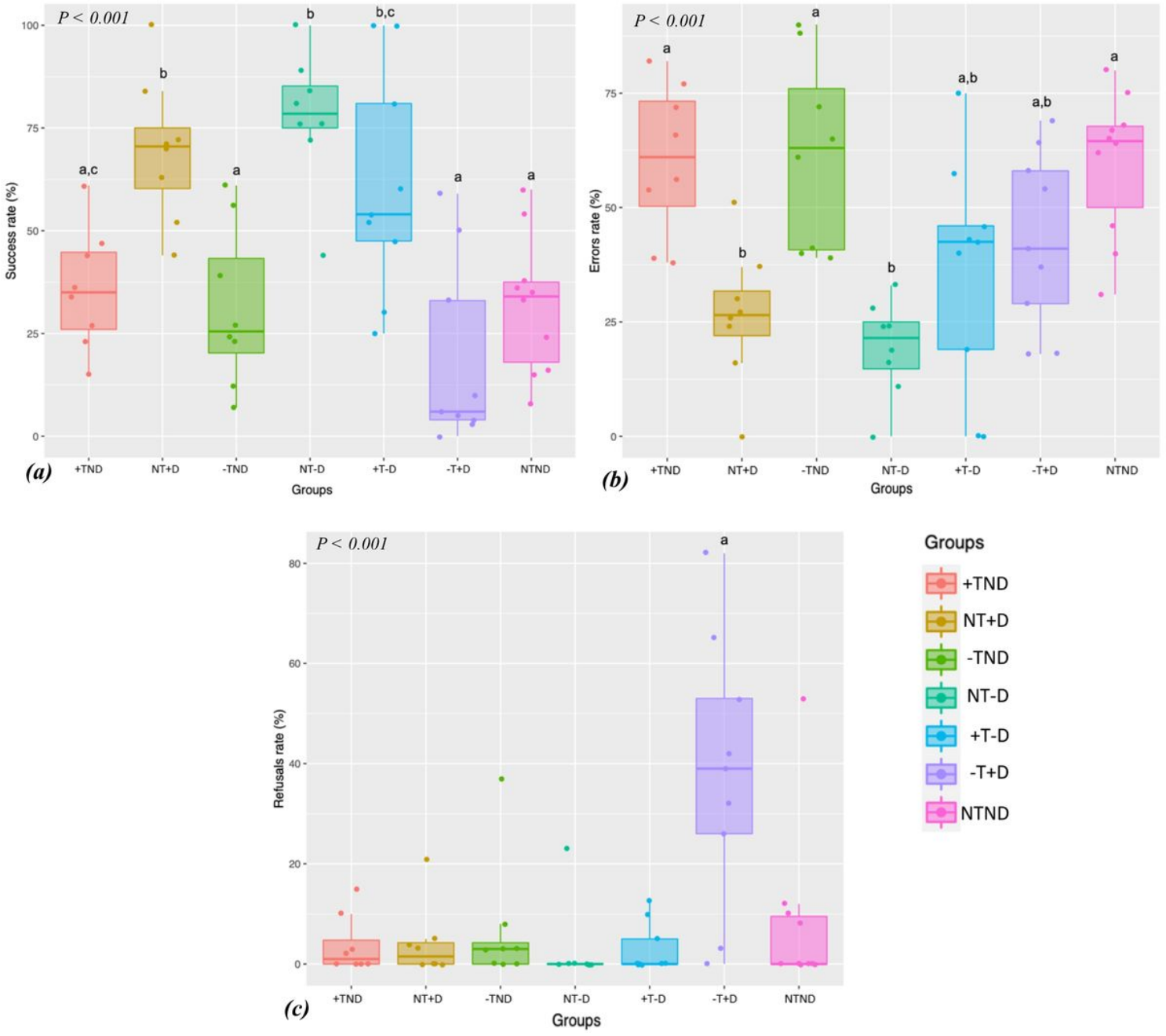

Figure 3

Performance parameters of mouse lemurs in the learning task according to experimental groups. (a) Success rate; (b) Errors rate; (c) Refusals rate.

Letters represent significant differences between groups (Tukey test, Bonferroni correction).