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Animacy and threat influence location memory in adults

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Abstract

A substantial body of research indicates that fitness-relevant entities (e.g., animate and threatening entities) are more readily recalled than nonfitness-relevant entities (e.g., inanimate and nonthreatening entities). However, little research has examined whether these effects persist when memory for their spatial location is tested even though this is an important issue for the ultimate explanation of these biases. To address this issue further, two experiments were conducted to examine whether animates (Experiment 1) and threats (Experiment 2) could benefit from a processing advantage in location memory. In both experiments, adults were asked to play Memory games (concentration games) on a digital tablet. The number of errors made in matching pairs of cards was recorded, as was the mean Euclidean distance between the location of the correct card and the location of the selected card in cases of error. We also investigated the extent to which the emotional dimensions of the stimuli (i.e., arousal, valence, and emotional intensity) could act as potential proximate mechanisms underlying the effects of animacy and threat on location memory. Consistent with the adaptive memory view (Nairne, 2016), our findings indicated that both animacy and threat enhanced location memory in adults. Furthermore, emotional intensity emerged as a valuable emotional variable for further investigation, as it consistently correlated with free-recall scores for both the animacy and threat effects.

Keywords Animacy · Threat · Location memory · Evolutionary psychology · Emotions

Introduction

Just as evolution has shaped our physical characteristics, it has also sculpted our cognitive systems to promote adaptive behavior (e.g., Nairne, 2010; Tooby & Cosmides, 2005). Specifically, evolutionary psychologists argue that our memory systems have been shaped by natural selection to be tuned to retain information that is relevant to survival and reproduction more effectively than information that is not (i.e., the adaptive memory view; Nairne, 2014, 2016; Nairne & Pandeirada, 2008; Nairne et al., 2017). Information related to animate entities – living things capable of self-propulsion (Bonin et al., 2015) – has been particularly crucial for survival and reproduction in our distant past and even today, and thus animates should have a special status in cognitive processing. Much work in recent years suggests that this is indeed the case, revealing a processing advantage for animates over inanimates. For example, animates are detected faster than inanimates in change detection paradigms (Altman et al., 2016; New, Cosmides et al., 2007) and in inattentional blindness tasks (Calvillo & Jackson, 2014). Furthermore, the animacy advantage has been found in free-recall tasks with explicit (e.g., Gelin et al., 2017; Nairne et al., 2013) or incidental encoding instructions (e.g., Komar et al., 2023b), as well as in recognition tasks (e.g., Bonin et al., 2014; Félix & Pandeirada, 2024), cued recall tasks (e.g., VanArsdall et al., 2015) and, more recently, in an incidental paired-associate learning task (Lhoste et al., 2024). This mnemonic advantage for animate entities is known as the animacy effect in memory. This mnemonic phenomenon is not the only memory bias that supports the adaptive view of human memory cognition. Indeed, a substantial number of studies also suggest that threatening, survival-relevant stimuli, benefit from a processing advantage. Several studies have found that dangerous items are detected more quickly and held attention longer than nondangerous ones (Blanchette, 2006; Brosch & Sharma, 2005; Flykt, 2005; LoBue & DeLoache, 2008, 2010; Öhman et al., 2001; Yorzinski et al., 2014; but see Zsidó et al., 2024). Threatening stimuli also appear to be better remembered than nonthreatening entities (e.g., Leding, 2019; Meyer et al., 2015). Moreover, while

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much of the research cited above used evolutionary threatening entities as stimuli, modern threats have also been shown to benefit from a processing advantage over nonthreatening stimuli (e.g., Brosch & Sharma, 2005; Fox et al., 2007; Subra et al., 2017). These findings suggest that while the human cognitive system may have evolved to prioritize the detection and processing of ancient threats, biases for modern threats can also emerge through experience (LoBue, 2012; Sulikowski, 2022).

Biases for fitness-related information in location memory

While the "what" of the animacy and the threat superiority effects provide strong support for the adaptive memory view, it is worth considering whether simply having a better memory of the item, without contextual information such as spatial details, is sufficient to be deemed adaptive – "the where." Indeed, to what extent is it relevant to survival and reproduction to remember encountering a snake or another human if that memory lacks context? In the great struggles of life, knowing the "where" seems as crucial as knowing the "what."

There is evidence in the literature that supports the existence of cognitive biases for fitness-relevant information in spatial memory. For example, locations of high-calorie foods (which represent energy-dense resources) have been shown to be better remembered than locations of low-caloric foods (de Vries et al., 2020; New, Krasnow et al., 2007). More broadly, emotional information, which is considered as a fitness-relevant cue (Talmi et al., 2019), seems to improve location memory (D'Argembeau & Van der Linden, 2004; Mather & Nesmith, 2008; Nashiro & Mather, 2011; Schmidt et al., 2011). However, this topic is still under debate due to conflicting results (Maddock & Frein, 2009; Mather et al., 2006), suggesting that the effect of emotional information on source memory may be highly dependent on various methodological factors (e.g., material used, encoding conditions).

The influence of animacy on location memory

Few studies have investigated the effects of animacy or threat on location memory (Gelin et al., 2018; van Buren & Scholl, 2017). Gelin et al. presented participants with animate and inanimate words displayed on a computer screen divided into four locations. These words appeared in one of the four locations and had to be categorized as either animate or inanimate. After a distraction phase, a surprise recognition test was administered in which participants had to determine whether the presented word had been encountered before and, if so, to indicate the location where the word had been displayed. An animacy advantage was found not only for word recognition, but also for location memory. Participants were better at remembering the screen locations of words referring to animates than those referring to inanimates (see also Mieth et al., 2019, for a replication using an intentional learning condition and a process-pure source memory measure[1]). Along the same lines, van Buren and Scholl (2017) provided further evidence for the effect of animacy on spatial memory. In their study, four experiments were conducted in which participants played a matching game (also known as the "Memory" game) with cards depicting shapes that were perceived as either animate or inanimate. Participants had to memorize each card location in order to match all pairs of identical cards in the fewest number of trials. Locations of animate shapes were consistently better remembered, suggesting that animacy does indeed enhance location memory.

The influence of threat on location memory

Wilson et al. (2011) found that the locations of threatening evolutionary-relevant items (e.g., dangerous animals) were better remembered than the locations of modern threats (e.g., weapons) in a matching game paradigm. Results showed that participants committed fewer location errors when matching pairs of evolutionary threatening items than when matching pairs of modern threats. Furthermore, when errors were made, the selected card was closer to the target for evolutionary stimuli. However, a comparison between threatening and nonthreatening stimuli was not examined in this study. Gallup (2022) provided more insight into this issue. Participants were presented with a set of nine pictures and had to remember the locations of the pictures within 10 s. In a first experiment, pictures of snakes, lions, and impalas were presented. The locations of pictures representing snakes were remembered significantly better than those representing lions and impalas. In a second experiment, no superior location memory was found for snakes or spiders compared to mushrooms. However, a third experiment showed a significant difference in location memory for spiders and snakes compared to cockroaches, which are generally perceived as significantly more unpleasant but equally arousing. According to Gallup, these results suggest that the observed differences in location memory are predominantly influenced by the threat level rather than arousal or negative valence. Given the contradictory nature of the above findings, further research is warranted to test whether there is a mnemonic advantage for the location of threatening entities.

[1] The process-pure source memory measure used by Mieth et al. (2019) allows for the separation of source memory from item recognition, providing an uncontaminated assessment of source memory.

The present study

Evidence for animacy and threat superiority effects in location memory is still scarce, and the findings reported above need to be replicated and clarified in further studies. Therefore, our overall goal was to investigate whether the locations of animate (Experiment 1) or threatening (Experiment 2) entities would be better remembered than those of inanimate or nonthreatening entities, respectively. Another goal was to examine the extent to which emotional dimensions might influence the location memory for both animate and threatening entities. As mentioned above, although some conflicting results were found, some studies have shown that emotional variables such as valence (Costanzi et al., 2019) or arousal (Gobin et al., 2017; Zsidó, 2024) can influence location memory (e.g., Mather & Nesmith, 2008). In addition to the arousal and valence dimensions, we thought it would be interesting to explore the role of "emotional intensity" in both animacy and threat memory biases. Emotional intensity corresponds to the strength with which an emotion is experienced, regardless of the type of emotion and its valence (Reisenzein, 1994).

Emotional variables, particularly arousal, have been proposed as a proximate mechanism to explain the animacy advantage in memory (Meinhardt et al., 2018) and the bias in favor of threatening entities (Schimmack, 2005). Although the arousal account of animacy effects in memory has been rejected (Félix et al., 2019; Meinhardt et al., 2018; Popp & Serra, 2018), it should be noted that the majority of studies examining the role of arousal in evolutionary biases have used normative ratings provided by external participants (but see Meinhardt et al., 2018, Experiment 1). Thus, arousal was not rated by the very participants whose memory was being tested. To avoid individual difference effects, it may be more appropriate to ask actual participants to rate the emotional variables (Popp & Serra, 2018). Therefore, to our knowledge, our study is the first to be conducted from an evolutionary perspective in which participants were asked to rate stimuli across three emotional dimensions (valence, arousal, and emotional intensity).

Two experiments were designed to investigate the aforementioned research questions using a paradigm similar to that employed by Wilson et al. (2011), namely the Memory game. Previous studies have already used the Memory game to investigate location memory (e.g., McBurney et al., 1997; Thibodeau et al., 2021; Washburn et al., 2007), thus validating this experimental approach. Following Wilson et al., we measured the mean number of location errors made to match the pairs (assessment of accurate location memory) and the mean Euclidean distance between the location of the correct card and the location of the selected card in the case of an error (assessment of approximate location memory or "gist-based spatial memory"; Siegel & Castel, 2018). It is worth stressing that Wilson et al. did not provide a clear definition of location memory errors. As a poor operationalization of this variable could potentially affect the results, we sought to address this methodological limitation by providing precise definitional criteria: An error could only occur if the participant had previously flipped over the target card and thus seen where its location was. In addition, we also computed free-recall scores by including a surprise free-recall test in each experiment: At the end of the Memory game, participants had to recall all the pictures they remembered from the games on an Excel spreadsheet. This free-recall task was used to confirm the well-established animacy and threat superiority effects with our stimuli.

In the first experiment, participants had to complete four Memory games in which cards depicted either animate entities (i.e., humans and animals) or inanimate entities (i.e., manufactured objects and vehicles). In contrast to previous studies (Gelin et al., 2017; Mieth et al., 2019), we used colored drawings as stimuli because drawings are much more ecological than words (Kindt & Brosschot, 1999). In line with the functional view of human memory, we posited that the locations of animates would be better remembered than those of inanimates. With respect to free recall, animates should be better remembered incidentally than inanimates (e.g., Bonin et al., 2014; Komar et al., 2023b).

In the second experiment, participants had to perform three Memory games. Two games involved the presentation of threatening entities, including dangerous animals and natural threats, or nonthreatening entities, such as harmless animals and natural elements. These games allowed for a comprehensive comparison between threatening and nonthreatening stimuli. In addition, another game included cards depicting natural threats (e.g., a tsunami) or modern threatening objects (e.g., a gun). Given that natural forces are hypothesized to have played an essential role in shaping the "prehistoric evolution of human behavior" (Lowder & Gordon, 2015), it is reasonable to infer that adaptations to natural threats are "at least as possible as adaptations to predation, if not more likely" (Shapouri et al., 2023). Thus, the latter comparison was conducted to gain further insight into whether this type of inanimate evolutionary threat could also benefit from a processing advantage over modern threats.

Preliminary study

To ensure that the images selected for the Memory games were appropriate for our research goals, a preliminary study was conducted to assess several variables related to these drawings and the names of the entities depicted. Three variables were rated online by adult participants: name agreement (i.e., the agreement between the drawings and their respective names), animacy, and dangerousness. Animacy and dangerousness ratings were used to confirm that our a priori classification of the stimuli (animate vs. inanimate for Experiment 1, and dangerous vs. nondangerous for Experiment 2) was correct, and to control for dangerousness in Experiment 1 and animacy in Experiment 2. Additional control variables were obtained from the French database Lexique.org (New et al. 2004), in particular the frequency of occurrence of the names of the selected stimuli in printed material.

Method

Participants

Three groups of adults rated the entire set of images used in Experiments 1 and 2, with each group rating either name agreement, animacy, or dangerousness. The groups consisted of 31 adults (M_{age} = 20.7 years, SD = 2.75), 29 adults (M_{age} = 21.1 years, SD = 5.1), and 30 adults (M_{age} = 20.0 years, SD = 4.05), respectively. Participants were students at the Université Bourgogne Europe, recruited via email, and all were native French speakers. None were taking any medication known to affect the central nervous system. All experiments reported in this paper, including this preliminary assessment study, were approved by a local ethics committee (N° UBFC-2023-12-12–059).

Material

A total of 84 drawings were selected: 48 in Experiment 1 and 36 in Experiment 2 (see Online Supplementary Material for a complete list of the picture labels used, English translations of the picture labels are also provided). In Experiment 1, 24 pictures depicted animate entities, and 24 pictures depicted inanimate entities. In Experiment 2, 12 pictures of dangerous entities and 12 pictures of nondangerous entities were selected for the dangerous/nondangerous comparison. In addition, six pictures of natural threats and six pictures of modern threatening objects were selected to specifically compare these categories of threatening entities. The colored drawings used in the studies were created by the same graphic artist who contributed to IMABASE (Bonin et al., 2020). Twenty-eight images for Experiment 1 and ten images for Experiment 2 were drawn from this database.

Procedure

The assessment questionnaires were created using Limesurvey (www.limesurvey.com) and completed online by the participants individually. Participants gave informed consent on the first page of the questionnaire, and then demographic information (age, gender, level of study, native language, possible dyslexia and medication) was collected on the second page. On the third page, participants were given instructions, followed by the full set of images to be rated (see Online Supplementary Material for detailed rating instructions). Ratings were made on a 7-point Likert scale (1: no name agreement/inanimate/harmless; 4: moderate name agreement/moderately animate/moderately dangerous; 7: full name agreement/fully animate/fully dangerous).

Results

This study used t-tests to compare images preclassified by the authors as depicting animate or inanimate entities in Experiment 1, and dangerous or harmless, natural or modern threats in Experiment 2. When the distribution did not conform to normality (as indicated by Shapiro–Wilk tests, with $ps < .05$), Wilcoxon tests (W values) were used. To anticipate the results, and as reported below, in the few cases where a difference was found between the relevant categories of images for an examined variable, there were never significant correlations between this variable and the relevant dependent variables measured in our experiments, namely the number of location errors and the free-recall scores.

Animate versus inanimate entities in Experiment 1

As expected, animacy ratings were higher for animates (M = 6.45, SD = 0.9) than for inanimates (M = 2.24, SD = 0.9), $W = 435$, $p < .001$, $r = 1.00$. There was no reliable difference in name agreement ratings between animates (M = 6.68, SD = 0.42) and inanimates (M = 6.65, SD = 0.53), W = 157, p = .89, r = –0.03. In addition, each category had a percentage of name agreement greater than 80%, $ps < .001$. Regarding the dangerousness ratings, inanimate stimuli (M = 2.63, SD = 0.6) were perceived as more dangerous than animate stimuli (M = 2.18, SD = 0.8), W = 73, p = .001, r = –0.68. However, this dimension was not correlated with our two main dependent variables (i.e., number of location errors and free-recall scores), $ps > .102$.

Finally, animate and inanimate entities were found to be matched on other variables. No significant difference was found in the number of syllables (p = .200) and letters (p = .094) of the picture names, nor in their respective objective frequencies of occurrence in printed material (p = .558, see New et al., 2004). They were also matched on visual complexity, $t(46) = –0.49$, $p = .628$, $d_z = –.14$ (as measured by the number of bytes in JPEG format, expressed in 10^3 bytes; see Bonin et al., 2020).

Dangerous versus nondangerous entities in Experiment 2

As expected, dangerous entities were rated as more threatening (M = 5.78, SD = 0.78) than nondangerous entities (M = 2.30, SD = 0.66), $t(29) = 21.8$, $p < .001$, $d_z = 3.97$.

There was no significant difference in dangerousness ratings between natural ($M = 5.69$, $SD = 0.79$) and modern ($M = 5.62$, $SD = 0.89$) threats, $W = 202.5$, $p = .287$, $r = .25$. There was no reliable difference in name agreement ratings between dangerous ($M = 6.44$, $SD = 0.65$) and nondangerous entities ($M = 6.48$, $SD = 0.60$), $t(30) = –0.765$, $p = .450$, $d_z = –0.14$. Each category of items showed a percentage of name agreement above 80%, $ps < .001$. Regarding the animacy ratings, we found no reliable difference between dangerous ($M = 5.45$, $SD = 0.80$) and nondangerous entities ($M = 5.41$, $SD = 0.92$), $t(28) = .341$, $p = .736$, $d_z = .06$. Interestingly, natural threats ($M = 4.21$, $SD = 1.34$) were rated as more animate than modern threats ($M = 1.72$, $SD = 0.99$), $t(28) = 8.95$, $p < .001$, $d_z = 1.66$. However, the correlations between animacy ratings and free-recall scores or mean number of location errors were not significant, $ps > .27$.

The mean number of syllables and letters did not differ between the picture names of the dangerous or nondangerous entities, natural or modern threats, $ps > .10$. Furthermore, the respective objective frequencies of occurrence of the names of the natural or modern threats did not differ, $p = .89$. However, the objective frequency for the dangerous entity names was significantly lower than for nondangerous entities, $p = .039$, but this variable did not correlate with the number of location errors or free-recall scores, $ps > .296$. Finally, the mean visual complexity of the images was significantly lower for nondangerous entities and modern threats than for dangerous entities and natural threats respectively, $ps > .008$, but again, this variable did not correlate with our dependent variables in all cases, $ps > .421$. In summary, this preliminary study confirmed our a priori classification of images into those depicting animate or inanimate entities, and those depicting dangerous or nondangerous entities. Finally, the findings unexpectedly revealed an interesting result, which will be commented on in the final discussion, suggesting that natural (inanimate) threats were perceived as more animate events than modern (inanimate) threats.

Experiment 1: Location memory of animate versus inanimate entities

Method

Participants

A group of 39 adults (32 females, $M_{age} = 20.8$, $SD = 2.6$) participated in the study. They were students at the Université Bourgogne Europe and received course credit for their participation. All participants were native French speakers, and none were taking any medication known to affect the central nervous system or had dyslexia. To determine the required sample size, a power analysis was performed using G*Power (Faul et al., 2007) based on the results of Gelin et al. (2018). These authors reported an effect size of $d_z = .42$. With such an effect size, 37 participants were needed to obtain an effect of a similar size with a power of .80. Two additional willing participants were also included.

Material

The four Memory games were run on Lenovo M10 tablets. In each game, participants were presented with a grid comprising 12 pairs of cards, resulting in a total of 24 cards per game arranged in a 6 × 4 configuration. Of the total of 48 pictures, 24 pictures represented a variety of animate entities (12 humans in specific occupations and 12 were nondangerous animals), and 24 pictures represented a variety of inanimate objects (12 were vehicles and 12 were manufactured objects). Figure 1 provides examples of images from each category. Two games opposed nondangerous animals to either vehicles or manufactured objects (six animals/six vehicles; six animals/six manufactured objects), and two others opposed humans in specific occupations to either vehicles or objects (six humans/six vehicles; six humans/six manufactured objects). The same picture never appeared in two different games.

Fig. 1 Examples of images from each category used in Experiment 1 (from left to right an illustration of an item taken from the categories of animals [cow], humans [doctor], manufactured objects [basket], and vehicles [car])

Procedure

Participants were tested in a quiet room. They first gave informed consent, and then demographic information was collected (age, gender, level of study, native language, possible dyslexia and use of neuroleptics).

Game phase: Before starting the experiment, the experimenter reminded the participants of the rules of the Memory game and made sure that they were well understood. At the beginning of each game, all pictures were displayed face down on the digital tablet. Participants were asked to touch one card at a time to reveal its image, and then select a second card to find the corresponding match. If the images matched, both cards became inactive and flipped to dark luminance. Otherwise, they were turned over again after a short interval. The game continued until all pairs were successfully matched. The primary goal was for participants to remember the location of each picture in order to match all pairs in the fewest number of trials. Across the participants, the location of the pictures for each game was randomized, as was the order in which the four games were presented.

As in the Wilson et al. (2011) study, two dependent variables were calculated to assess location memory. The first variable was the number of location errors per participant per item. The second variable was the mean Euclidean distance between the location of the correct card and the location of the selected card in the case of an error (see Online Supplementary Material for a description of the error cases).

Free-recall task: After the game session (which lasted less than 5 min), a surprise free-recall test was administered. Participants were given 5 min to recall and list all the pictures they could remember from the games, on an Excel spreadsheet. They were instructed to describe the images they had in mind as accurately as possible. Their responses were matched to the labels provided in the naming task to determine the corresponding reference, meaning that exact label matches were not required.

Rating task: Following the free-recall task, participants were presented, in a randomized order, with 5.5 ×5.5 cm cards depicting the pictures they had seen earlier in the game session and were given four rating tasks. They were asked to perform a naming test and to rate the emotional valence, arousal, and intensity of the pictures. Participants viewed one card at a time and completed the naming test and rating tasks sequentially (see Online Supplementary Material for instructions on rating emotional variables). Thus, for each item, they first wrote the name of the picture on an Excel sheet and then rated the emotional variables on the same sheet, presented in a randomized order across participants. The goal of the naming task was to ensure that the pictures used in the games were correctly identified. If the participant provided the correct label or the label that corresponded to the superordinate category of the item (e.g., "boat" instead of "sailboat"), a score of "1" was assigned. If the given label was incorrect, the response was assigned a value of zero. All adults correctly labeled all pictures. For the rating tasks, participants were asked to rate each item on a 7-point Likert scale ranging from calm/relaxed to excited for the arousal dimension (e.g., Bonin et al., 2018), from not emotionally intense at all to emotionally intense for the emotional intensity dimension (e.g., Aragón, 2017), and from negative to positive emotional state for the valence dimension (e.g., Grühn & Scheibe, 2008). Emotional arousal and intensity were both assessed as they may not refer to the same concept (see Picard et al., 2016). For example, severe depression is considered a low arousal state, even though it is an intense emotional state characterized by sadness and hopelessness (Moratti, 2012). Thus, in some cases, the intensity of emotion works in opposition to arousal.

Results

For each dependent variable, a comparison was made between animate and inanimate entities by grouping the scores obtained for the animal and human categories, and the scores obtained for the vehicle and manufactured object categories. It was beyond the scope of this research to break down the results by subcategory. To analyze the data, we used either *t*-tests or Wilcoxon tests when the distribution did not conform to normality (Shapiro–Wilk test, $p_s < .05$). One-tailed tests were used to analyze location memory and free-recall scores.

Location memory for animate versus inanimate entities

Two dependent variables were used to assess location memory, the mean total number of location errors per participant for each entity category and the mean total Euclidean distance between the location of the correct card and the location of the selected card in case of an error.

Figure 2A shows that the mean total number of location errors was lower for animates ($M = 20.74$, $SD = 14.26$) than for inanimates ($M = 24.31$, $SD = 17.81$), $W = 235$, $p = .015$, $r = -.40$. Participants had a more accurate location memory for animates than for inanimates. As shown in Fig. 2B, the mean total Euclidean distance was also smaller for animates ($M = 6.18$, $SD = 2.79$) than for inanimates ($M = 7.24$, $SD = 2.36$), $t(38) = -2.59$, $p = .007$, $d_z = -.42$. Participants were, on average, closer to the correct card when making errors for animates than for inanimates.

Incidental recall memory for animate versus inanimate entities

Importantly, because the number of exposures is known to influence subsequent recall (Ebbinghaus, 1964), we checked

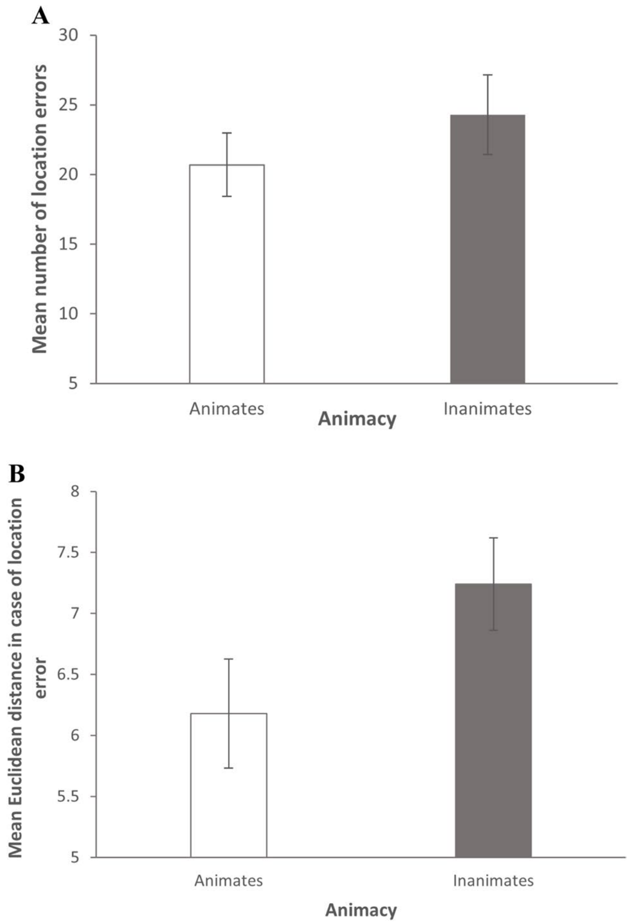

Fig. 2 **A** Mean total number of location errors. Error bars represent standard errors of the mean. **B** Mean total Euclidean distance in case of location error. Error bars represent standard errors of the mean

whether participants had seen images from each category an equal number of times during the game phase. A significant difference was found between the occurrence of animates and inanimates, $W = 195$, $p = .030$, $r = -0.41$. Pictures of inanimates occurred more frequently ($M = 109.1$, $SD = 21.16$) than pictures of animates ($M = 104.8$, $SD = 16.84$), which is understandable since participants made more errors with inanimates. Despite this difference in favor of inanimates, the proportion of correctly recalled animate pictures ($M = 0.38$, $SD = 0.13$) was higher than that of inanimate pictures ($M = 0.28$, $SD = 0.1$), $t(38) = 5.40$, $p < .001$, $d_z = .86$. Overall, the number of intrusions was very low, with only six participants incorrectly recalling one picture each. Animate stimuli ($M = 0.08$, $SD = 0.27$) did not yield more intrusions than inanimate ones ($M = 0.08$, $SD = 0.27$).

Role of emotional variables

We examined whether our selection of animate and inanimate entities differed in the ratings of emotional variables and, if so, whether these variables influenced the preceding results.

No significant difference was found between animate ($M = 4.07$, $SD = 0.39$) and inanimate entities ($M = 3.99$, $SD = 0.49$) in arousal ratings, $t(38) = 0.97$, $p = .341$, $d_z = .16$. Furthermore, the correlations between arousal ratings and the mean number of location errors or free-recall scores were not significant, $ps > .674$. On the valence dimension, animate entities ($M = 4.73$, $SD = 0.56$) were rated more positively than inanimate entities ($M = 3.93$, $SD = 0.77$), $t(38) = 6.99$, $p < .001$, $d_z = 1.12$. However, the correlations between valence ratings and the number of location errors or free-recall scores were not reliable, $ps > .130$. Finally, pictures of animate entities were rated as more emotionally intense ($M = 3.94$, $SD = 0.94$) than pictures of inanimate entities ($M = 3.19$, $SD = 1.05$), $t(38) = 6.25$, $p < .001$, $d_z = 1.00$. There was no significant correlation between emotional intensity ratings and the number of location errors, $r(46) = -.198$, $p = .177$. The accuracy of location memory was not influenced by emotional intensity ratings. However, a significant positive correlation was found between free-recall scores and emotional intensity ratings, $r(46) = .31$, $p = .034$. Thus, the more emotionally intense the pictures were, the more likely participants were to recall them.

Experiment 2: Location memory of dangerous versus nondangerous entities

Method

Participants

A total of 34 adults participated in the experiment (28 females, $M_{age} = 19.68$, $SD = 1.80$). We conducted an a priori power analysis using G*Power (Faul et al., 2007) to estimate the required sample size based on data from Gallup's (2022) Experiment 1. To do this, we calculated the data for dangerous animals (lions and snakes) and compared them to the data for nondangerous animals (impalas). We obtained a d_z of .61. With such an effect size, a total of 19 participants was needed to obtain an effect of similar size with a power of .80. Preferring more power than minimally necessary, we decided to collect data from at least 30 participants to detect a medium effect size ($d_z = .5$; Cohen, 1988). Participants had the same characteristics as those in Experiment 1, but none had been previously involved.

Material and procedure

As in Experiment 1, the Memory games were run on Lenovo M10 tablets, and participants were presented with 24 cards arranged in a 6×4 grid for each game. However, unlike

Experiment 1, participants were asked to play three games instead of four. Two games were designed to pit dangerous entities against nondangerous ones. In one game, participants were presented with six pictures of dangerous animals (e.g., a snake) and six pictures of harmless animals (e.g., a penguin). In another game, six pictures depicted natural threats (e.g., an erupting volcano) and six pictures depicted nonthreatening natural elements (e.g., a tree). Figures 3 and 4 provide examples of images from each category. Finally, the third game included two categories of dangerous entities, either natural threats (e.g., a storm) or threatening modern objects (e.g., a gun). The total number of items used in this study was 36.

The procedure was the same as in Experiment 1.

Results

First, we compared the scores (location errors, mean Euclidean distance errors, free-recall scores) obtained for dangerous entities and nondangerous entities by grouping the scores obtained for the categories of dangerous animals and natural threats and the scores obtained for the categories of nondangerous animals and nondangerous natural elements. Then, natural (ancestral) threats and modern threatening objects were compared, using the scores obtained in the game with these two categories. As in Experiment 1, paired *t*-tests were used for these comparisons, and Wilcoxon tests when the distribution did not conform to normality. One-tailed tests were used to analyze location memory and free-recall scores for the comparison between dangerous and nondangerous entities. Two-tailed tests were used to compare natural and modern threats, as previous research has yielded mixed findings regarding a potential advantage of one over the other.

Location memory for dangerous versus nondangerous entities, for modern versus natural threatening entities

As illustrated in Fig. 5A, the mean total number of location errors was significantly smaller for dangerous (M = 8.91,

Fig. 4 Examples of images from each category in games that compare natural threats (fire) to threatening modern objects (gun)

SD = 8.20) than for nondangerous entities (M = 10.65, SD = 8.75), W = 171, p = .040, r = –.35, suggesting that participants had more accurate location memory for the former than for the latter. Furthermore, as shown in Fig. 5B, participants were on average closer to the correct card when making errors for dangerous entities (M = 2.63, SD = 1.70) compared to nondangerous entities (M = 3.44, SD = 1.56), $t(33)$ = –2.50, p = .009, d_z = –.43. No significant difference was found between natural or modern threats in either the mean total number of location errors or the mean total Euclidean distance between the selected and the correct cards, ps > .099.

Incidental recall memory for dangerous versus nondangerous entities, for modern versus natural threats

We first tested whether the frequency of exposure during the game phase was equivalent between the different categories of entities. A significant difference was found between the occurrence of dangerous (M = 51.2, SD = 10.12) and nondangerous entities (M = 53.2, SD = 9.85), $t(33)$ = –2.17, p = .037, d_z = –.37. Pictures of nondangerous entities occurred more frequently than pictures of dangerous entities, which was certainly due to the greater number of location errors made with the former. However, the proportion of correctly recalled pictures was higher for pictures of dangerous entities (M = 0.45, SD = 0.19) than for pictures of nondangerous

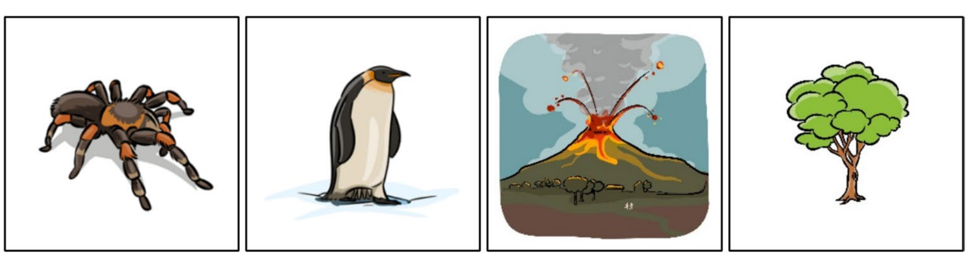

Fig. 3 Examples of images from each category in games that compare dangerous and nondangerous entities (from left to right an illustration of an item taken from the categories of dangerous animals [tarantula], nondangerous animals [penguin], natural threats [volcano] and natural elements [tree])

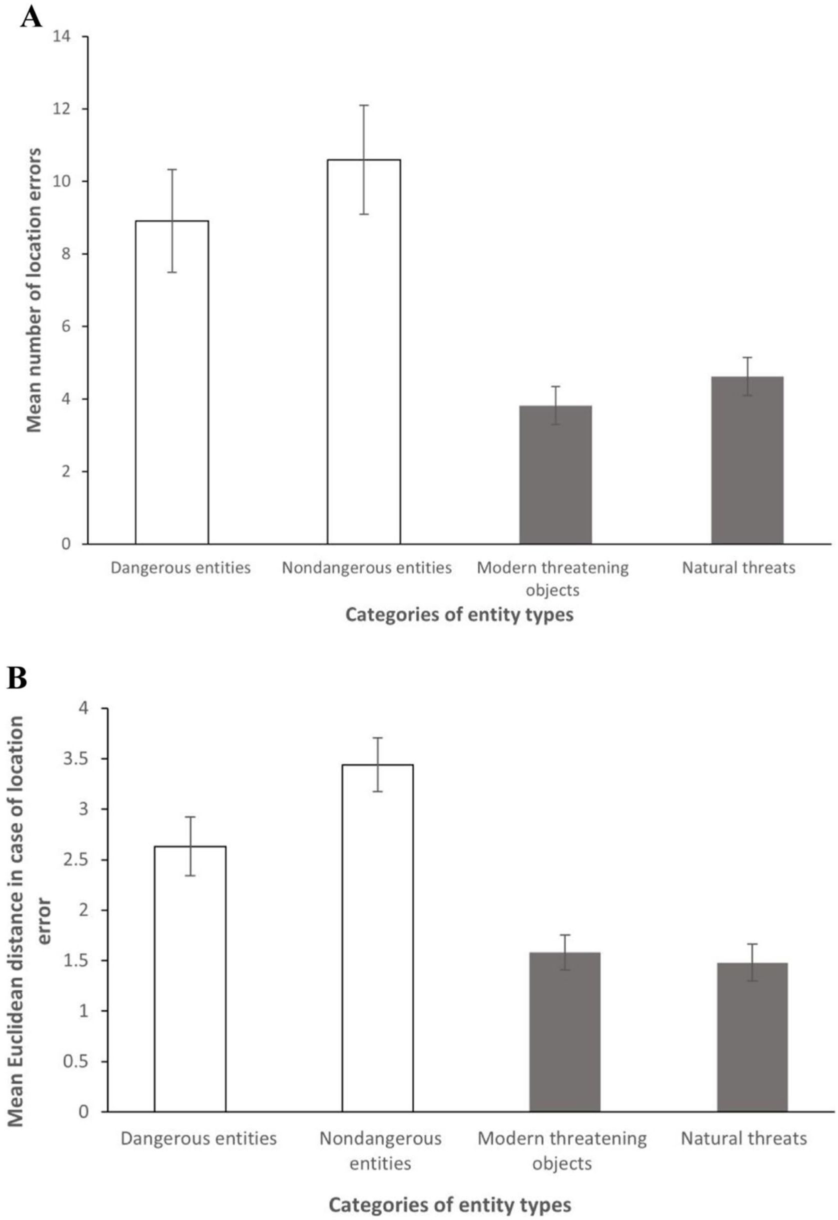

Fig. 5 **A** Mean total number of location errors for each of our two comparisons. Error bars represent standard errors of the mean. **B** Mean total Euclidean distance in the case of location error for each of our two comparisons. Error bars represent standard errors of the mean

entities ($M = 0.40$, $SD = 0.17$), $t(33) = 1.75$, $p = .045$, $d_z = .30$. Although modern threats ($M = 24.7$, $SD = 3.75$) were seen more frequently during the game than natural threats ($M = 25.9$, $SD = 3.72$), $p = .028$, no difference was found in the proportion of correctly recalled pictures between natural threats ($M = 0.26$, $SD = 0.21$) and modern dangerous objects ($M = 0.31$, $SD = 0.20$), $t(33) = –1.28$, $p = .209$, $d_z = –.22$. As in Experiment 1, the number of intrusions was very low, with only seven participants incorrectly recalling one picture each. Dangerous stimuli ($M = 0.09$, $SD = 0.29$) did not yield more intrusions than nondangerous ones ($M = 0.12$, $SD = 0.33$).

Role of emotional variables

As in Experiment 1, we examined the influence of emotional variables. Data from two participants were removed due to a technical problem.

In terms of arousal, pictures depicting dangerous entities were rated significantly more arousing ($M = 5.45$, $SD = .58$) than pictures depicting nondangerous entities ($M = 2.96$, $SD = .73$), $t(31) = 17$, $p < .001$, $d_z = 3.03$. The correlation between arousal ratings and the mean number of location errors per item was negative but not significant, $r(22) = –.39$, $p = .063$. There was no correlation between arousal ratings and the total number of pictures correctly recalled in the surprise recall task, $r(22) = .24$, $p = .264$. Natural threats were rated as more arousing ($M = 5.37$, $SD = .70$) than modern threats ($M = 4.98$, $SD = .63$), $t(31) = 3.42$, $p = .002$, $d_z = .604$, but these arousal ratings were not reliably correlated with either location errors or free-recall scores, $ps > .59$.

Nondangerous entities ($M = 5.52$, $SD = .66$) were rated more positively than dangerous entities ($M = 3.20$, $SD = 1.02$), $t(31) = -10.5$, $p < .001$, $d_z = -1.86$. However, valence ratings did not correlate significantly with the number of location errors, $r(22) = .37$, $p = .08$. They did not correlate at all with the free-recall scores, $r(22) = -.007$, $p = .975$. There was no difference in valence ratings between natural threats ($M = 2.89$, $SD = 1.03$) and modern threats ($M = 2.84$, $SD = .73$), $t(31) = 0.31$, $p = .761$, $d_z = 0.05$. In addition, there was no correlation between these ratings and the number of location errors or free-recall scores, $p_s > .53$.

Finally, pictures depicting dangerous entities ($M = 4.88$, $SD = 1.03$) were rated as more emotionally intense than those depicting nondangerous entities ($M = 3.97$, $SD = 1.29$), $W = 483$, $p < .001$, $r = .83$. Similarly, pictures representing natural threats ($M = 4.89$, $SD = 1.13$) were rated as more emotionally intense than pictures representing modern threats ($M = 3.96$, $SD = 1.29$), $t(31) = -4.72$, $p < .001$, $d_z = -0.83$. No significant correlations were found between the mean number of location errors per item and emotional intensity in these two comparisons, $ps > .330$. However, we found a significant positive correlation between free recall and emotional intensity, $r(22) = .56$, $p = .005$, for the dangerous/nondangerous entities comparison, suggesting that the more emotionally intense the pictures were rated, the better participants were able to remember them. The correlation between emotional intensity and free-recall scores did not reach significance for the natural/modern threat comparison, $r(10) = -.04$, $p = .891$.

Discussion

Although a substantial body of evidence supports the effects of animacy (e.g., Bonin et al., 2014; Félix et al., 2019; Nairne et al., 2013) and threat (e.g., Blanchette, 2006; Brosch & Sharma, 2005; Flykt, 2005; LoBue & DeLoache, 2008, 2010) on human memory, the question of whether these dimensions influence location memory remains to be investigated in depth due to its significant importance within the theoretical framework of adaptive memory (Nairne, 2014, 2016; Nairne & Pandeirada, 2008; Nairne et al., 2017). As stated by Nairne et al. (2012), “in some sense, location memory is the sine qua non of adaptive memory” (p. 499). Thus, the primary objective of the present research was to investigate the effects of animacy and threat on location memory, using a digital Memory game. The second goal was to examine the role of some emotional variables in these effects. As detailed below, the main findings suggest that: (1) both animacy and threat enhance location memory in adults, (2) the emotional dimensions of the items do not seem to have an impact on location memory in adults with regard to both the animacy and threat effects, and (3) emotional intensity correlates positively with free recall for both the animacy and threat superiority effects suggesting that it is a valuable variable to investigate further from an evolutionary perspective.

The locations of animates were remembered better than those of inanimates. In Experiment 1, participants made fewer errors in matching pairs of animates and were closer to the correct card when they did commit errors. These results are consistent with previous studies on location memory (Gelin et al., 2018; Mieth et al., 2019; van Buren & Scholl, 2017) and are the first to demonstrate that this animacy advantage in location memory can be obtained with pictures. In fact, the Gelin et al. study used words, and the van Buren and Scholl study used shapes, but not pictures of real animate or inanimate entities. It is important to emphasize that the demonstration of animacy effects with pictures, and not just with words, is crucial to support an evolutionary interpretation of this memory phenomenon. Our results are also consistent with studies showing that animates selectively enhance recollection, as demonstrated using the remember-know-guess paradigm (Bonin et al., 2014; Rawlinson & Kelley, 2021) and the process-dissociation procedure (Komar et al., 2023a). These findings suggest that animates are associated with richer contextual details compared to inanimates. Furthermore, the results of Experiment 2 also clearly revealed a threat superiority effect in location memory in adults. Indeed, not only did participants make fewer errors in matching pairs of pictures depicting dangerous entities, but they were also more accurate in matching these cards in the case of error. Thus, our findings replicate those of Gallup’ (2022) Experiment 3 and extend them to a variety of dangerous entities. Importantly, the data obtained in both of our experiments are in line with the predictions of an ultimate explanation of the animacy and the threat superiority effects. Knowing the “where” seems to be as fundamental as knowing the “what.”

Moreover, with regard to free recall, the results obtained in Experiment 1 corroborate those of previous studies indicating an animacy effect in incidental encoding conditions (Bonin et al., 2014; Félix et al., 2019; Gelin et al., 2017; Komar et al., 2023b). Similarly, consistent with the findings of previous studies, we also found that dangerous entities were better remembered than nondangerous ones (Leding, 2019; Meyer et al., 2015). Taken together, the free-recall results thus reinforce our experimental approach.

With respect to the opposition between ancestral (natural) and modern threats, we found no significant difference in either location error, distance in case of error, or free-recall scores. Thus, our results do not support the predictions of a "strong" version of the evolutionary perspective, which would predict a prioritization of evolutionary threats over modern threats (Subra et al., 2017). It should be noted that the literature comparing modern and evolutionary threats in location memory is sparse. To our knowledge, the only study to address this issue is that of Wilson et al. (2011), which found an advantage for evolutionary over modern threats. Our findings differ from those of Wilson et al., but as mentioned above, Wilson et al. did not clearly define what they considered to be location memory errors. Thus, it is difficult to determine whether our results truly contradict those of Wilson et al. or whether the apparent discrepancy is due to the way location errors were operationalized. More generally, studies that have used attentional paradigms to compare modern and evolutionary threats have yielded mixed results. Our findings are consistent with those reporting no reliable processing differences between modern and evolutionary threats (e.g., Brosch & Sharma, 2005; Fox et al., 2007). However, they are not consistent with other studies that have demonstrated a processing advantage for evolutionary threats compared to modern threats (e.g., Zhang & Guo, 2019) or even a superiority effect for modern threats (e.g., Subra et al., 2017; Zsidó et al., 2019). It is important to emphasize that our study differs from the studies cited above because, as far as we know, all studies comparing modern and evolutionary threats have used animate stimuli to represent evolutionary threats, introducing a potential confounding effect between threat and animacy (Grossi, 2014; Leding, 2019; Sulikowski, 2022). Thus, further studies are needed to better understand whether evolutionary threats are indeed treated differently from modern threats.

Role of emotional variables

An additional goal of our research was to investigate the extent to which emotional variables might influence location memory for animate and threatening entities. Our first experiment on animacy failed to show significant correlations between location errors and the three emotional dimensions (i.e., arousal, valence, intensity). Similarly, the results of the second experiment, although less clear, also failed to find significant correlations between the emotional variables and location memory. Interestingly, however, we found a significant positive correlation between free-recall scores (item-related information) and emotional intensity ratings in both of our experiments. How can we explain this different pattern of results between free recall and location memory? A deeper understanding of this discrepancy can be achieved by closely examining the cognitive processes underlying these two tasks. Location memory relies on the interaction between the ventral visual stream (i.e., the "what" pathway; Goodale & Milner, 1992), which encodes item-related information, and the dorsal visual stream (i.e., the "where" pathway), which processes item-spatial-related information (Eichenbaum et al., 2007; Washburn et al., 2007), with the involvement of the hippocampus, which plays a critical role in supporting object-to-location binding by integrating information from the "what" and "where" pathways (Postma et al., 2008). Interestingly, recent evidence suggests that the emotional dimensions of an item may differentially affect the cognitive and neuroanatomical processes involved in remembering item-related versus item-context-related information. Indeed, some studies (e.g., Ritchey et al., 2019) have proposed that the emotional dimensions of an item primarily affect brain activity involved in item encoding (i.e., the "what") rather than context encoding. More specifically, according to the emotional binding account (Yonelinas & Ritchey, 2015), the amygdala is thought to support item-emotion associations by binding the emotional response elicited by the item to its representation in the perirhinal cortex. Once established, these "amygdala bindings" support recollection of the item itself. This mechanism may account for the observed positive correlation between emotional intensity and free-recall scores, as item-related memory benefits directly from the effects of emotional dimensions. In contrast, we could hypothesize that location memory, which depends on the integration of the hippocampal "what" and "where" pathways, may be less sensitive to the emotional dimensions of the item. This may explain the lack of significant correlations between location memory scores and emotional intensity in our study.

Our study is the first to distinguish emotional intensity from arousal in investigating the proximal mechanisms of evolutionary biases. As previously highlighted by Reisenzein (1994) and Frijda et al. (1992), emotional intensity has been relatively understudied in the existing literature. The majority of research examining the impact of emotion on cognition is based on the circumplex model of affect (also known as pleasure-arousal theory; Russell, 1980), which proposes that all emotional experiences can be represented within a two-dimensional framework defined by emotional valence (ranging from positive to negative emotions) and arousal (ranging from high to low levels). This model does not explicitly address emotional intensity as a construct that is separate from arousal, which may explain why researchers using this framework often use the terms "arousal" and "emotional intensity" as if they were interchangeable concepts. However, although emotional intensity and arousal can be thought of as correlated, there are instances where this is not the case. According to Reisenzein (1994), emotional intensity is more accurately gauged by the sum of the absolute values of valence and arousal, rather than solely by arousal (for a review of theoretical conceptions of emotional intensity, see Goto & Schaefer, 2017). Thus, it seems valuable to consider emotional intensity when studying the effects of emotional dimensions on cognition from an evolutionary perspective, as it may operate in a different way than arousal. Our results support this claim, since that, as mentioned above, emotional intensity ratings were positively correlated with free-recall scores in both of our studies. However, it should be noted that we obtained only a weak correlation in Experiment 1, warranting a cautious interpretation of the relationship between free-recall scores and emotional intensity in this study. Furthermore, while we suggest that incorporating this dimension into the study of evolutionary biases may provide valuable insights into the proximate mechanisms underlying these biases, we acknowledge that emotional intensity alone does not reveal the specific nature or quality of the emotion experienced. Further research should also explore how the nature of the emotion, beyond intensity, might interact with the animacy and the threat superiority effects to provide a more complete understanding of their underlying mechanisms.

Animacy dimension of natural threats

Although it was not a focus of our research, we would like to discuss an interesting finding regarding the animacy dimension of natural threats. We used natural threats to represent evolutionary threatening entities in order to avoid a potential confounding effect between threat and animacy. However, the results of the animacy rating task indicated that natural threats were rated as more animate than modern threats. Therefore, natural threats were perceived as having an animacy dimension. Although natural threats can be classified as inanimate from a semantic perspective, it is not entirely unexpected that participants tended to ascribe an animacy dimension to them. Indeed, natural threats exhibit behaviors that are more akin to those of animate entities, as they are capable of initiating movement and occasionally causing damage. From a theoretical perspective, our results are consistent with the work of VanArsdall and Blunt (2022), who argue that animacy is not a simple binary distinction (living vs. nonliving), but rather a multidimensional construct that includes both physical (e.g., movement likelihood) and mental (e.g., goal-directedness) dimensions. Because natural threats have both a high likelihood of movement and apparent goal-directedness, they may engage both the physical and mental animacy dimensions. This may explain why natural threats fall in an intermediate region of the animate-inanimate spectrum (Lubbe & Castillo Alfonzo, 2024) and why people tend to attribute anthropomorphic characteristics to these natural phenomena (Lowder & Gordon, 2015). Although the correlational analysis indicated that the animacy dimension of natural threats did not influence the results of our study, it may be worthwhile to investigate this aspect of the stimuli more comprehensively. To begin with, it would be particularly valuable to establish animacy norms (see Félix et al., 2023; Mahjoubnavaz et al., 2024) and test whether the animacy dimension of natural elements affects cognitive processes in a similar way to animate entities.

Study limitations and future directions of research

Several limitations of our experiments are worth mentioning. First, most of the participants involved in our study were female. Several studies have reported different patterns of results of the effect of fitness-relevant entities on cognition depending on the gender of the participants (New, Krasnow, et al., 2007; Sulikowski, 2022). Their results were not consistent, but their very existence encourages a more balanced gender ratio to broaden the scope of our findings. Second, increasing the number of games used in our studies may contribute to more robust results. The decision to present four games in Experiment 1 and three games in Experiment 2 was made with the intention of extending the same paradigm to young children. To ensure sustained engagement with the tasks, it was necessary to limit the number of trials.[2] Another potential limitation of our study is that we used colored drawings rather than realistic images as stimuli. It is widely accepted that pictures are more effective than words in conveying emotional meaning (Pereira et al., 2023). The use of realistic images rather than drawings may be a more ecologically valid approach to examine the effects of fitness-relevant entities on location memory, as well as the involvement of emotional dimensions. Moreover, as noted above, further research is also needed to elucidate the proximate mechanisms underlying the effects of threat and animacy on location memory. The use of physiological measures may provide further insight into the role of emotional dimensions in the effect of fitness-relevant entities on cognition (Zsidó et al., 2020). In addition to these considerations, future studies should build on the current findings by examining the relative effects of animacy and threat on location memory within the same experiment, similar to the approach used in previous research (Leding, 2019, 2024) with words. Examining their combined effects and interactions would provide valuable insights into how these factors influence memory and cognition.

[2] The data concerning the children's study are currently being collected.

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Availability of data and materials The datasets generated and analyzed during the current study are available via the Open Science Framework at https://osf.io/7xj5e/?view_only=8456c52f54e3483ea0009af852c10657

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethics approval Before conducting the current experiments, the authors obtained approval from the ethics committee of the Université Bourgogne Franche-Comté (N° UBFC-2023-12-12-059).

Consent to participate Informed consent was obtained from all individual participants included in the study.

Consent for publication Participants were made aware that their data would be used for publication.

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