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RESEARCH

Remembering the Orchard: Evolutionary Biases in Spatial Memory for Forageable Plants

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Abstract
Prevailing psychological perspectives support the view that human memory operates independently of content. However, evolutionary psychologists contend that memory may exhibit adaptive biases, prioritizing information that enhanced ancestral survival and reproductive success. This study examines spatial memory for forageable plants, drawing upon the concept of adaptive memory to understand how certain characteristics—such as calorie density, ripeness, size, perishability, and availability during scarcity—may influence mnemonic biases. We aimed to investigate how the spatial memory of humans is influenced by the evolutionary salience of various fruit and vegetable attributes. Sixty Iranian individuals completed a series of mnemonic tasks online. Participants viewed arrays of fruit and vegetable images, categorized by calorie density, ripeness, size, availability during scarcity, and perishability, and were asked to recall their locations. The results indicated an adaptive bias in human spatial memory in some attributes. Individuals demonstrated enhanced recall for higher-calorie fruits and vegetables, supporting the hypothesis that memory systems evolved to prioritize nutritionally dense resources. Women exhibited no significant differences in spatial memory. Contrary to expectations, larger fruits and vegetables did not yield better relocation scores than smaller ones. While no significant differences were found in the recall of ripe, unripe, or perished products, a trend suggesting higher retention of locations for highly perishable fruits and plant resources available during scarcity was observed. This study provides some empirical evidence for adaptive memory biases in the spatial recall of forageable plant attributes, reinforcing the concept that evolutionary pressures have shaped human memory systems to favor the retrieval of information crucial for ancestral survival.

Keywords Adaptive memory · Spatial memory · Forageable plants · Calorie density · Perishability · Fruits and vegetables

Introduction

The mainstream perspective in psychology supports the notion that human memory is a domain-general, content-independent faculty (Baddeley, 2012; Postle, 2006). However, evolutionary psychologists challenged this view, arguing that the mind and its underlying architecture have been sculpted by the selective pressures human ancestors encountered during human evolutionary history, particularly Pleistocene era (Cosmides & Tooby, 1997). During this time, adaptive problems that required information processing for their solutions such as detecting predators, avoiding pathogens, and foraging for food shaped cognitive mechanisms, including memory. The concept of adaptive memory suggests that our memory has been shaped by natural selection to prioritize information that has recurrently affected the survival and reproduction of our ancestors (Nairne & Pandeirada, 2016; Thiebaut et al., 2021). Memory can be viewed as a suite of domain-specific systems, each finely tuned to encode, retain, and recall survival and reproduction-relevant information (Nairne & Pandeirada, 2008; Nairne et al., 2008). Empirical findings substantiate this viewpoint; for instance, people better detect and recall the location of

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images of snakes than non-threatening stimuli such as mushrooms or flowers (Gallup, 2022; Gallup & Meyers, 2021); individuals exhibit superior recall of objects that have been touched by sick persons (Fernandes et al., 2017, 2021; Gretz & Huff, 2019; Thiebaut et al., 2022); they relocate a nutritionally rich than poor food resource (Dunbar, 2004); they possess a higher ability to remember words presented in a survival scenario in which they imagine themselves stranded in grassland where they need to protect themselves from predators than scenarios where they ought to rate words according to their pleasantness or where they have to move to a foreign land (Nairne et al., 2007).

Certain spatial memory biases likely evolved to meet the specific demands of foraging behavior in the hominin lineage, as they were hunter-gatherers for roughly two million years and foragers for several million years beforehand. During the epoch of hominin evolution, flora played a crucial role in dietary regimes (Ungar & Teaford, 2002). An individual's fitness directly depends on how efficiently one acquires energy. The necessity to consistently locate stationary widely dispersed vegetative entities with varying nutritional values imposed selective pressures that favored biases in spatial memory—the ability to recall the location of resources—critical for efficient foraging (New et al., 2007; Silverman & Eals, 1992). For example, remembering where fruit trees or edible plants are located would have reduced energy expenditure and increased the likelihood of survival. These locative preferences aided in detecting and accumulating valuable plant resources, distinct from the spatial skills necessary for hunting (Adler et al., 2006; Eaton, 2006; New et al., 2007).

Research illustrates predilections in spatial skills directed toward the recollection of food resources, which have evolved due to nutritional variances, resulting in better retention and retrieval of resources with higher than lower caloric values (de Vries et al., 2020b, 2021; de Vries et al., 2020a; New et al., 2007). Evidence includes remembering the location of energy-dense sessile resources in market settings (New et al., 2007), as well as utilizing visual and olfactory cues through technological simulations (e.g., de Vries et al., 2020b). This suggests that humans demonstrate selective memory dynamics based on the calorie density of resources (de Vries et al., 2020a, 2020b, 2021; New et al., 2007; Pravosudov & Roth, 2013). A greater preference for caloric food implicitly assumes that larger food items should be better retained than smaller food items, as they could potentially provide more calories per unit of effort in locating and harvesting them; however, this prediction has never been tested. Plant resources also have varying caloric values at different developmental stages, peaking once ripe (e.g., Phillips et al., 2021). Preferential recall of ripe fruits is only implicitly examined in a study on teaching botany, in which Prokop and Fančovičová (2014) showed that participants exhibited a higher retention rate of red and black fruit species, indicating ripeness, in comparison with green fruit species. Such retrieval discrimination was also evident in toxic species which are more relevant to survival than non-toxic species (Fančovičová et al., 2020; Prokop & Fančovičová, 2019). Differential relocating abilities for caloric values have yet to be exclusively investigated regarding plant resources.

Higher scores in spatial tasks among women who exhibit elevated recall of object placements may stem from sex-based foraging differences dating back to the Pleistocene epoch (Silverman & Eals, 1992). Indeed, women excelled at gathering immobile plant resources more than men (Laiacona et al., 2006) due to evolutionary pressures that favored a sexual division of foraging labor, which encouraged fruit and plant collection by females (Krasnow et al., 2011). In visual detection tasks, where participants were instructed on the names of plants and their toxicity, women responded faster to plant images and demonstrated greater accuracy in identifying plant species than men (Prokop & Fančovičová, 2019). Most studies on the recall locations of foods with varying calories did not examine gender differences at all (de Vries et al., 2020a, 2020b, 2021), leaving gender differences in retaining food sources understudied. This is also the case for the intensity of sex biases in the retention of the favorable over less favorable plant location, as selective pressures have been stronger for women given their ancestral gathering roles, which remain unexplored.

The availability and longevity of plants can yield different payoffs. The susceptibility of fruits and vegetables to environmental stressors, such as drought or extreme temperatures, can impact productivity. Some may thrive during periods of scarcity, and their ability to survive adverse environments ensures a more reliable food source for hunter-gatherers and horticulturists when other edible plants may be non-existent. This suggests that such unfavorable conditions should trigger cognitive processes prioritizing their locations. Additionally, fruits and vegetables vary in perishability; while some are durable, others are highly perishable and must be gathered and consumed before spoiling. Therefore, more perishable fruits and vegetables should be prioritized in cognitive tasks over less perishable ones. To our knowledge, these hypotheses have not yet been tested. Studies on non-human primates, such as howler monkeys and chimpanzees, demonstrate that these species utilize spatial memory to locate fruits during food shortages (and not food prosperity) when alternative food resources are limited indicating a reliance on remembering the locations of critical food sources (Ban et al., 2016; Janmaat et al., 2014; Janson, 1998; Milton, 1981). Given the dynamic nature of fruit tree productivity, frugivorous primates may gain a significant advantage by accurately recalling the locations of fruit trees. Failure to do so could result in unnecessary travel to more distant trees, thereby increasing energy expenditure and vulnerability to predators (Cunningham & Janson, 2007). Similarly, food-caching animals like grey squirrels (*Sciurus carolinensis*) exhibit sophisticated spatial memory, prioritizing the locations of scarce food items (Hadj-chik et al. 1996). Evidence implicates bias in spatial memory use according to food perishability. For example, when grey squirrels, *Sciurus carolinensis*, were presented with acorns differing in perishability from two oak subspecies, they consumed the highly perishable acorn and cached the low-perishable one (Hadj-chik et al. 1996).

In this study, we investigated the influence of specific fruit and vegetable characteristics on human spatial memory and its biases, within the framework of adaptive memory outlined above. Hypotheses one, three, and four seek to investigate biases in the relocation of vegetation according to their caloric value, replicating previous research and extending it to further findings. The fifth and sixth hypotheses are supposed to explore the role of fruit availability, scarcity, and longevity on human mnemonic predilections for fruit and vegetable reso1.ces. The second hypothesis examines gender differences in spatial memory.

1. Participants will exhibit a higher rate of spatial recall for high-calorie fruits and vegetables compared to low-calorie ones.
    2. a. Women exhibit superior spatial memory in comparison with men.
    b. The bias in remembering plants with more favorable than less favorable attributes will be more pronounced in women than men.
3. Participants demonstrate a preferential capacity to relocate ripe plants as opposed to their unripe counterparts. Additionally, due to nutritional value and prospective consumption, unripe fruits and vegetables enhance spatial memory compared to perished ones.
4. Heavier fruits and vegetables may be more easily remembered than lighter ones.
5. Participants will show improved spatial memory for fruits and vegetables that are available during times of scarcity, compared to those that are unavailable during scarcity.
6. People are hypothesized to more readily relocate high-perishable fruits and vegetables compared to low-perishable ones.

Method

Participants

A total of $N = 60$ individuals completed anonymous online surveys at their convenience, using G*Power 3.1 software (Faul et al., 2007). For a medium effect size (Cohen's $f = 0.25$, corresponding to $\eta^2 = 0.06$), an alpha coefficient of 0.05, a power of 0.90, and a repeated measures ANOVA, within-between interactions, the required sample size was calculated at 16 for part 1 (3 within-subject factors, 1 between-subject factor, and 12 measurements) and 30 for part 2 (1 within-subject factor, 1 between-subject factor, and 4 measurements). Sixty individuals (mean age = 37.00, SD = 10.58) were recruited: 28 women (mean age = 38.00, SD = 10.23) and 32 men (mean age = 36.12, SD = 10.96).

The research was administered online, using Porsline, an Iranian survey platform. The link was shared through social media services such as Telegram, as well as Divar, an Iranian Persian classified ads and E-commerce mobile app. Data collection took place in 2024. All participants were Iranian, and they completed the questionnaire in Persian. The participants were briefed on the study's objectives and were assured the right to withdraw from the study. Because there were several images in any single array, and they might not have been observable on the phone screen one at a time, participants were informed not to use their smartphones and use their laptops, tablets, or home computers instead. Having answered a few demographic questions (age, sex, civil status, and educational level), the participants were directed to the mnemonic task.

Materials and Procedures

Part 1

Using a 2 within-subject (calorie density: high vs low) by 3 within-subject (ripeness: ripe vs unripe vs perished) by 2 within-subject (size: large vs small) repeated measures design, 24 species of fruit and vegetables were selected, and corresponding colorful photographs were generated by Bard, a large language model from Google AI, 2024 Google (2024). Using AI to create images rather than relying solely on database-derived pictures can offer several advantages. AI-generated images were customized to meet specific research needs, that is, controlling for lighting, background color, size, and perspective. Other advantages include the ease of reproducibility of AI-generated images, high accuracy and consistency of images, and high detail and resolution, capturing nuances. The items were divided into four groups based on their calorie density and weight, each encompassing one corresponding condition. A list of fruit and vegetable names along with their calorie

Table 1 Twenty-four commonly consumed fruits and vegetables based on their calorie density (high vs. low) and weight classification (light vs. heavy). The data presented include the average weight of each fruit and vegetable and the corresponding calorie content per 100 g. For the purpose of this research, fruits and vegetables heavier than 100 g and lighter than 50 g were considered large and small, respectively

Name (smaller fruits)	Calories (Kcal per 100 g)	Average weight (gr)[a]	Name (larger fruits)	Calories (Kcal per 100 g)	Average weight (gr)
Date	277	16	Avocado	160	236
Single grape	70	5	Coconut	359	1722
Fig	74	39	Pomegranate	83	319
Olive	116	3	Banana	89	120
Hazelnut	628	2	Sweet potato	103	156
Walnut	654	15	Butternut squash	82	2143
Mulberry	43	2	Watermelon	30	8347
Raspberry	52	2	Cantaloupe	34	1222
Plum	46	47	Quince	47	215
Sour cherry	50	8	Pumpkin	26	2380
Strawberry	32	21	Zucchini	17	197
Apricot	48	41	Peach	39	128

Fig. 1 A sample 3 × 3 array from the first part of the study. Each image represents one condition of the three categories (calorie-density, ripeness, and size). The location of images was randomized for each array. Participants were given 30 s to study each array

density[1] and size category used in the current research is presented in Table 1. In order to measure the predilection in relocating vegetation resources with respect to ripeness, calorie density, and size, images of 24 plant species varying in calorie density and size were generated. And accounting for three states of ripe, unripe, and perished, a total of 72 images were presented to the participants in six successive arrays, with only one image from each category positioned in the same array in a random order (see Fig. 1). Images had the same brightness and contrast, had white backgrounds, their size was standardized (1.9 × 1.9 in), and they were randomly presented to the participants. Images of single fruits were presented for fruits such as grapes and sour cherries that grow in bunches. Using images of individual fruits

[1] Food Data Central download: https://fdc.nal.usda.gov/

rather than entire bunches enhances standardization, focuses on individual characteristics, reduces complexity, and facilitates easier perception and control over variables in the study.

Fruits and vegetables are, in general, considered low-calorie food products (de Vries et al., 2020a, 2020b). However, as they vary in calorie density, for the purpose of this research, fruits and vegetables exceeding 70 cal per 100 g were considered higher-calorie, while the ones below 60 cal per 100 g were considered lower-calorie. We are aware of the fact that high- and low-calorie food do not have universally agreed-upon definitions and may be arbitrarily defined. However, we tried to hinder this limitation by relying on statistically significant differences in the relative means of these categories. In this research, for the first part, we used vegetation resources that are ecologically existent and familiar to the participants. Although the human line originated from African Savannah hundreds of thousands of years ago, recent studies suggest that human evolution has been multiregional in Africa (e.g., Lahr, 1996), and combining it with out-of-Africa dispersal roughly 50–70 thousand years ago, it is evident that there were not many fruits and vegetables that our ancestors encountered across many generations. Consequently, we predicted that rather than having mnemonic biases for ancestral vegetation, humans have design features that assist them in exploiting the flora that exists in their local environments. Hence, plants that are available in Iran and familiar to people were selected.

The model utilized Google's extensive dataset to train and validate the production of high-quality images. The AI model was specifically trained to discern between ripe, unripe, and perished fruits and vegetables by focusing on key visual indicators associated with each condition. The model was trained to distinguish between ripe and unripe fruits primarily by analyzing color variations and texture patterns. It learned to identify the rich, vibrant cues typical of ripe fruits and the smoother or more uniform textures that contrast with the irregularities found in unripe ones. Unripe fruits were generated based on the criteria of less saturated colors and firmer textures. In contrast, the model was trained to recognize characteristic signs of perished fruits such as browning, the presence of black spots, and the development of wrinkles, which indicate decay. People show higher recall for pathogen-relevant stimuli, among which are decaying food supplies that can be detected by cues such as mold and are moderated by the feeling of disgust. To minimize the effect of the disgust-eliciting motif for perished items, the model was instructed to identify the absence of mold as a necessary criterion for classifying a fruit as perished. To determine the content validity of the AI-generated images, using the Content Validity Index (CVI), a panel of five experts in biology and agriculture rated the images according to their relevance on a 4-degree Likert scale (4 = completely relevant, 1 = completely irrelevant). The ratings were above 0.80 for every item, and the average rating was 0.98, 0.98, and 0.97 for ripe, unripe, and perished fruits, respectively. A separate group of ten unspecialized individuals categorized the images into three groups according to their ripening stage. All categorization corresponded with the generated images. A Cronbach alpha of 0.944 was obtained for the category of the ripening stage.

A random sample of a dozen fruits was weighed and averaged for each fruit species, and the results can be seen in Table 1. The same panel of five experts investigated the relevance of the weight-based categorization and rated them on a 4-point Likert scale. CVIs were higher than 0.80 for all heavy and light categories.

Participants were instructed to look at each array carefully for 30 s. Subsequently, the array disappeared, and they were asked to relocate each image using numbers ranging from 1 to 12. Each number should have been used once. After each recall task, they were directed to the next array, and this procedure recurred for the rest of this part.

Part 2

Having dealt with the six arrays, participants were given a 30-s break and then moved to the next part of the study. Perishability refers to the tendency of a product or good to deteriorate or spoil over time due to factors such as microbial growth, enzymatic breakdown, and oxidation (Roberta & Alejandra, 2018). Information concerning the perishability of vegetation resources is available in general guidelines, which vary owing to different subspecies and extrinsic factors such as temperature and humidity (Barth et al., 2009). The same applies to availability during scarcity. As selecting specific fruit species based on these criteria seemed infeasible, a slightly modified experiment was designed using a 2 within-subject (availability during scarcity: available vs unavailable) by 2 between-subject (perishability: high vs low) mixed design to test the fifth and sixth hypotheses. Participants were divided into two groups and were presented with AI-generated images of 12 unfamiliar edible fruits (ecologically non-existent edible plants were chosen to avoid the unwanted effect of familiarity and calorie density on retention). The AI tool was trained with the same instructions used in part 1, except that only ripe fruits were generated for this part. The images and the task were assessed and validated by the panel of experts. Six images were instructed to belong to fruits, which are resilient to harsh environments and existent during times of scarcity, while the other subsequent six images belong to fruits less resilient to environmental stress and unavailable during scarcity (Table 2).

Before the image presentation, participants were primed with the following text: "Imagine you are stranded in a tropical grassland in which your survival partly depends on foraging plants. You will be shown a number of nutritious fruits and you have to relocate them." Divided into two groups, further information for one group was about plants' high perishability: "Such fruits rot shortly after the ripening stage, should be consumed within a day and have higher urgency for gathering due to their shorter time of consumption," whereas the additional descriptions for the other group concerned lower rates of perishability. After reading the descriptions, a 4 × 2 array was displayed with one image of a plant in a random location. The remaining squares were blank (see Fig. 2). We presented a single fruit image within an array of blank squares to minimize the effect of distraction and other confounding variables such as visual clutter or interference effects. Participants were shown each plant for 5 s. After the images of the first six plants unavailable during scarcity were displayed (the description concerning these plants consisted of their availability throughout the year, but not at the time of scarcity, such as drought or cold winters), they were asked to identify the location within the array where they had seen each plant. Responses ranged from 1 to 8, corresponding to the positions within the array. This procedure recurred for the subsequent six images of fruits and vegetables available during times of scarcity. (In our study, such vegetation referred to those more resilient to environmental stress, such as drought or cold, and available during plant resource scarcity.) Participants were informed that the task measured memory capacity, yet the study's main purpose was not explicitly emphasized.

Statistical Analyses

The proportion of correct answers was calculated for each category. After applying descriptive statistics, a mixed-design ANCOVA was conducted to test hypotheses one, two, three, and four. Calorie density, ripeness, and size were entered as within-subject factors, gender as a between-subject factor, age as a covariate, and the proportion of correct location responses was considered the dependent variable.

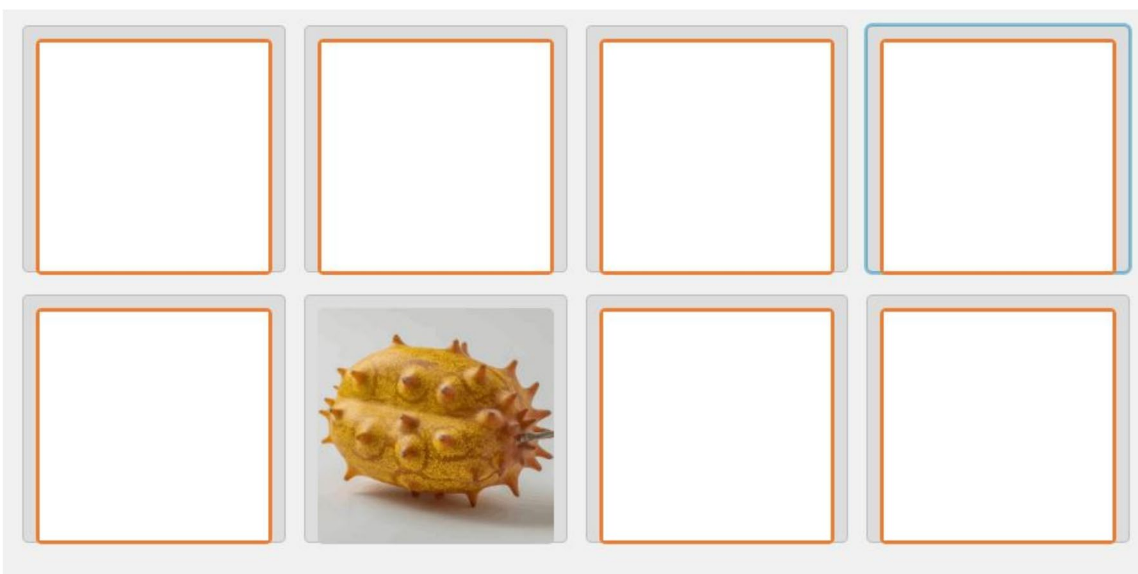

Fig. 2 A sample 4× 2 array from the second part of the study, which represents a kiwano and seven other blank squares. Participants were informed that they had 6 s to look at each array

Table 2 Twelve species of fruits unfamiliar in Iran, varying in availability during scarcity

Name		Name	
Rambutan	Unavailable during scarcity	Cherimoya	Available during scarcity
Mangosteen		Feijoa	
Longan		Kiwano	
Tamarillo		Jaboticaba	
Durian		Fingered citron	
Lychee		Cupuacu	

Table 3 Descriptive statistics of the correct proportion of answers in relocating the items related to the study variables: gender, calorie density, ripeness, size, availability during scarcity, and perishability

Variable	Mean	SD	Minimum	Maximum
Men	0.408	0.202	0.111	1.000
Women	0.431	0.207	0.166	0.820
High calorie	0.436	0.215	0.028	1.000
Low calorie	0.402	0.209	0.083	1.000
Ripe	0.410	0.218	0.000	1.000
Unripe	0.417	0.200	0.083	1.000
Perished	0.430	0.227	0.000	1.000
Heavy	0.404	0.209	0.029	1.000
Light	0.438	0.209	0.083	1.000
Available during scarcity	0.639	0.302	0.000	1.000
Unavailable during scarcity	0.503	0.297	0.000	1.000
Highly perishable	0.622	0.267	0.000	1.000
Lowly perishable	0.526	0.263	0.000	1.000

Table 4 Descriptive statistics of the correct proportion of answers in relocating the items regarding the study variables for men and women

	Men		Women	
Variable	Mean	SD	Mean	SD
High calorie	0.434	0.214	0.438	0.220
Low calorie	0.383	0.215	0.425	0.205
Ripe	0.394	0.209	0.427	0.230
Unripe	0.417	0.204	0.418	0.199
Perished	0.414	0.224	0.448	0.234
Heavy	0.388	0.210	0.421	0.209
Light	0.431	0.206	0.446	0.215
Available during scarcity	0.661	0.343	0.613	0.253
Unavailable during scarcity	0.521	0.299	0.482	0.299

Gender was used to compare the ability of forageable plant relocation across genders and to determine the intensity of biases in remembering plants with more favorable than less favorable attributes across genders. A two-way mixed-design ANOVA was conducted to test the fifth and sixth hypotheses, taking availability during scarcity as a within-subject factor, perishability as a between-subject factor, and the proportion of correct responses as the dependent variable. Given that the data for part 2 did not meet the normality assumption, non-parametric tests (Wilcoxon signed-rank test for availability during scarcity and the Kruskal–Wallis test for perishability) were also reported. We considered effect sizes of approximately 0.01 for small, 0.06 for medium, and 0.14 for large (Bakker et al., 2019; Cohen, 2013). All statistical tests were performed with SPSS ver. 26 (IBM Corp, 2019).

Results

Participants' descriptive statistics are shown in Tables 3 and 4.

Calorie Density

The calorie category had a significant main effect (F (1, 57) = 6.376, P = 0.014, partial η^2 = 0.101). As predicted, the locations of high-calorie fruits and vegetables were retained at a higher proportion, compared with low-calorie ones, supporting hypothesis one.

Gender Differences

Women showed a statistically similar relocation rate to men (F (1, 57) = 0.329, P = 0.568, η^2 = 0.006).

Contrary to our expectations, men exhibited higher biases concerning high-calorie versus low-calorie and small versus large fruits and vegetables. However, the two-way interactions of our mixed-designed ANCOVA showed that the differences were insignificant for the interaction of calorie-gender (F (1, 57) = 1.097, P = 0.299, η^2 = 0.019) and size-gender (F (1, 57) = 0.746, P = 391, η^2 = 0.013).

Ripeness

Although perished vegetation slightly elicited a higher proportion of correct answers than unripe plants, which, in turn, were remembered slightly better than ripe fruits, none of these differences turned out to be statistically significant (F (2, 114) = 2.174, P = 0.118, partial η^2 = 0.037), and the third hypothesis was rejected.

Size

Contrary to the hypothesis that individuals would possess a higher capacity to relocate larger than smaller fruits and vegetables, larger fruits indeed evoked no significantly higher rate of correct relocation (F (1, 57) = 0.003, P = 0.957, partial η^2 = < 0.001). Hypothesis 4 was not supported.

No two-way interactions were significant. However, the calorie-ripeness-size three-way interaction was statistically significant (F (2, 114) = 4.350, P = 0.015, η^2 = 0.071). Pairwise comparisons are not reported, as they were beyond the scope of this article.

Availability During Scarcity and Perishability

No significant interaction was found concerning the relocation of plants according to availability during scarcity and perishability (F (1, 58) = 0.876, P = 0.353, η^2 = 0.015). Participants showed higher performance regarding the spatial recollection of edible vegetation with higher availability during scarcity (F (1, 58) = 14.653, P = < 0.001, η^2 = 0.202). Aligning with our fifth hypothesis, individuals remembered a larger proportion of fruit and vegetable locations available during scarcity. Forageable plants with higher perishability demonstrated a higher but insignificant main effect (F (1, 58) = 1.955, P = 0.167, η^2 = 0.033). The Wilcoxon signed-rank test also showed a significant result for availability during scarcity (Z = −3.553, p = < 0.001). According to Kruskal–Wallis test results, individuals did not differ in retention of highly versus lowly perishable edible plants (H (1) = 1.463, P = 0.226).

Discussion

Human memory is intricately designed through evolution to enhance survival and reproduction. It exhibits mnemonic predilections for adaptively relevant situations, such as the heightened recall of evolutionarily dangerous stimuli like snakes or spiders. Using an online task, we found support for some evolutionary-informed hypotheses concerning cognitive biases in retaining vegetative sources in humans. As predicted, participants located high-calorie fruits and vegetables at higher rates than low-calorie ones. They also exhibited a bias in the relocation of vegetation available during scarcity over those unavailable during scarcity. In contrast to our hypotheses, participants did not prioritize large or ripe fruit and vegetable items over small or non-ripe fruit and vegetable items, and there were no gender differences in spatial memory. Finally, experimentally induced conditions of perishability did not enhance spatial memory for fruits and vegetables.

Edible plants have differential adaptive value, and an ancestral psyche with a bias for recalling plants suitable for more efficient foraging could have conferred a reproductive advantage to their bearers in comparison to those with no such biases. Previous studies have investigated the role of memory in the effortless biased relocation of high-calorie food items (e.g., de Vries et al., 2020a, 2020b; New et al., 2007). In these studies, the focus has been on food sources in general. In one study, in which plants were the most prevalent stimuli, other gatherable items such as honey and olive oil were also encompassed (New et al., 2007). To our knowledge, no prior studies have exclusively focused on such attributes regarding forageable plants. Our research successfully replicated previous findings. It appears that the use of an online task among the non-WEIRD contemporary Iranian sample fully supports ancestral preferences for high-calorie foods. Our findings provide indirect support for previous research indicating that high-calorie foods stimulate visual-associative cortical brain regions more intensely than low-calorie control items (Becker et al., 2016). In a world where one could have been surrounded by numerous plants with high variability in fitness value, ancestral hominins whose memory propelled them to preferably remember the location of higher-calorie plants could have had a reproductive advantage over those without such psychological discriminative capacity (Krasnow et al., 2011).

Our second hypothesis, postulating that women would excel in the ability to relocate images of fruits and vegetables was not supported. Women showed a superior but insignificant spatial ability over men. According to the hunter-gatherer theory of sex differences, women's cognition has been adapted to the gathering demands (Krasnow et al., 2011; Panter-Brick, 2002). Several previous studies have found a better recall in females for recognizing the place where they had seen a given object. Still, no former study, to our knowledge, investigated sex differences in spatial memory exclusively with respect to forageable plants. Although several studies have found a significant difference in mnemonic function across sexes (e.g., New et al., 2007; Prokop & Fančovičová, 2019; Silverman & Eals, 1992), some studies found insignificant female excel (e.g., Prokop & Fančovičová, 2014). It is noteworthy that the differences between genders in our study appeared to favor women. Therefore, further replications using a more diverse sample might reveal more substantial differences. Small gender differences may also be attributed to cognitive flexibility and plasticity of the human mind. Modern environments require different demands for acquiring food sources, potentially diminishing the selective pressures that drove the gender gap in spatial memory.

The lack of more pronounced biases in women may be explained by the fact that men possess approximately 61% more total muscle mass than women and have a higher daily energy intake (Bennett et al., 2018; Lassek & Gaulin, 2009). Enhanced spatial memory for high-calorie foodstuffs has predicted higher BMI (Allan & Allan, 2013). We hypothesize that men's higher biases for localizing high-caloric and large fruits and vegetables are driven by their substantial food intake requirements. Conversely, women invest more resources in reproduction through pregnancy, lactation, and subsequent maternal care. It is possible that having dependent offspring would augment women's memory for large food items. However, we lack additional data to support this prediction.

Our data did not support our third hypothesis positing that individuals better recall the location of ripe fruits and vegetables. The participants did not differ in the proportion of correct answers regarding ripe, unripe, or perished fruits and vegetables. There is a variation in calorie richness throughout a vegetation's developmental stage, which peaks during ripeness (e.g., Phillips et al., 2021).

However, the lack of prioritization for ripe fruits can be explained by the fact that unripe fruits, despite their lower nutritional value, need a longer time for mental retention than ripe fruits, and there may be a compromise between calorie density and the amount of time needed for retention before harvest. Although previous work suggested that, in comparison to green fruits, red coloration could be a sign of ripeness and enhances the rate of recall (Prokop & Fančovičová, 2014), such memory enhancement may be due to the fact that conspicuous colorations are used in aposematic signaling, which is a type of animal advertising, suggesting that the animal is dangerous, toxic, or venomous and may deter the predator from attacking (Lev Yadun & Ne'Eman, 2004). Participants showed no bias in remembering the location of perished fruits compared to the other two categories, despite the presentation of mold-free stimuli. It can be proposed that knowing the location of rotten food sources may have had an adaptive advantage, irrespective of their disgust-evoking effect, seeing that they may be accompanied by pathogens, and such upregulation could avoid the possible consequential infection. Further research is indeed warranted to explore the psychological conflict surrounding the retention of edible versus toxic foods, particularly in relation to fruits and vegetables. For example, functional imaging data collected from participants who visually focused on edible and non-edible foods revealed greater activation in the extrastriate visual cortex when processing inedible items compared to edible ones. This suggests that the human brain is particularly responsive to visual cues linked to potential dangers, such as contamination from spoiled or rotten foods (Becker et al., 2016).

Contrary to our hypothesis 4 that individuals would remember the location of larger edible plants in a higher proportion, it turned out that smaller fruits and vegetables elicited higher but insignificant recall. However, the difference was insignificant. The compromise in retaining larger versus smaller fruits and vegetables may be interpreted by the fact that smaller plants are generally easier to carry and transport, which means they can be harvested and moved more frequently. This increased interaction with smaller plants could lead to more frequent encoding of their locations into memory. The frequency of an environmental challenge, and not its severity, is the determinant of recollection ability (Soldati et al., 2024). Smaller fruits and vegetables may have been more frequent in the past than larger ones, which arose more recently as a result of the cultivation and domestication of plants. Furthermore, the aggregate tree or bush vegetation could have a higher evolutionary payoff. Consequently, remembering the location of the whole plant may be favored rather than single fruits. One more possible explanation is that there might be perceptual biases at play where smaller objects are more easily remembered due to their relative size contrast. This could be related to how the human visual system processes and prioritizes information.

Our last two hypotheses regarding availability during scarcity and perishability in plant relocation were supported. While perishability showed insignificant bias, availability during scarcity significantly influenced memory retention. Availability during scarcity and perishability can be indicative of resource scarcity and urgency for immediate gathering and consumption. Notwithstanding the zoological evidence that some animals prioritize the retention and utilization of scarce fruits (Hadj-chik et al., 1996; Vander Wall, 1990), no human studies have so far investigated this phenomenon in human populations. Our results, indicating that there is a priority for retention of the whereabouts of highly perishable fruits and vegetables, are in contrast with those of food-caching animals that had an inclination for immediate consumption of highly perishable resources and instead employ their memory for the location of lowly perishable foods.

Limitations and Future Research

In the current study, we employed AI-generated stimuli. Although the images are reproducible and offer advantages in control, they might not fully capture the real-world visual complexities and nuances of fruits and vegetables. Future research would benefit from examining the effects of both AI-generated and real-world images of fruits and vegetables to better capture the visual complexities and nuances present in natural settings. The present study focused on immediate recall and did not assess long-term memory retention. Understanding how these memory biases persist over time could provide additional insights into the adaptive nature of memory. Even though individuals exhibited biases in relocating fruits and vegetables with high perishability and availability during scarcity, it can be inferred that such preferences may reflect a more domain-general mnemonic mechanism that pertains to adaptive memory in survival contexts. This is because in the vignettes, participants were primed with an ancestrally mundane scenario, in which their hypothetical survival depended on their ability to detect the location of forageable plants varying in specific characteristics. As each array could only include images of relatively small size to fit the screen, including fruits and vegetables according to their real-world size did not seem feasible. This was because smaller items would have appeared too small and undetectable. As a result, the fruits and vegetables were presented in the same size. This may not have captured the bias in the relocation of larger vegetation. Food scarcity should be manipulated in future studies using more ecologically valid elicitors. For example, hunger levels significantly influence human behavior (Montmayeur and Coutre, 2009), and this factor can be leveraged to investigate spatial memory. Our study was outlined in the adaptive memory framework, according to which memory comprises domain-specific mechanisms. However, we acknowledge that the debate on the domain-general domain-specific dichotomy remains unresolved. Some evidence suggests that memory operates more flexibly, depending on the nature of the challenges confronted (Henriques da Silva et al., 2019; Moura et al., 2021; Sandry et al., 2013). The current study does not rule out the possibility of domain-general cognitive mechanisms for foraging-related spatial memory. Future research can shed light on whether or not domain-specific mechanisms govern such biases. Additionally, our research adopted arrays of stimuli rather than focusing on a store layout or locating objects on a map. We acknowledge that real-world experiments may have greater ecological validity, but they can have lower control than an array, as the memory retrieval may be influenced by the distance between the items and participant familiarity with certain parts within a given place, such as the campus. At the same time, we admit that seeing objects in the same visual field may be perceived as a simulation of a within-patch model; future research can benefit from explicitly distinguishing between within- and between-patch vegetative spatial representations. This may strengthen the generalizability of plant recollection abilities in real-world settings. Moreover, the current scenario provided by task 2 may not explicitly capture ecological harshness and scarcity, and there can be a mismatch between more resilient food items and environmental stressors. Future studies should incorporate a more explicit manipulation of the environmental scarcity to better correspond with the inherent qualities and adaptive traits of fruits and vegetables.

Conclusion

This study offers some evidence for adaptive memory biases in the spatial recall of forageable plant attributes. It reinforces the idea that evolutionary pressures have shaped human memory systems to prioritize the retrieval of information essential for ancestral survival. These biases have implications for understanding how memory works and provide insight into the evolutionary mechanisms that underlie human cognition.

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Data Availability Data are attached as supplementary material.

Declarations

Ethics Approval and Consent to Participate All participants provided their informed consent at the beginning of the questionnaire. This research was approved by the Ethical Committee of Department of Psychology at Shahid Beheshti University.

Conflict of interest The authors declare no competing interests.

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