



Locating calories: Does the high-calorie bias in human spatial memory influence how we navigate the modern food environment?

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ABSTRACT

Human memory appears to be adaptively “biased” towards remembering the locations of (fitness-relevant) high-calorie nutritional resources. It remains to be investigated whether this high-calorie bias in human spatial memory influences how individuals navigate the modern food environment, and whether it is proximally associated with attentional processes. 60 individuals completed computer-based food eye-tracking and spatial memory tasks in a lab setting, as well as a food search and covert food choice task in an unfamiliar supermarket. The high-calorie spatial memory bias was replicated, as individuals more accurately recalled locations of high-calorie relative to low-calorie foods, regardless of hedonic evaluations or familiarity with foods. Although individuals were faster at (re)locating high-calorie (versus low-calorie) items in the supermarket, the bias did not predict a lower search time for high-calorie foods, or a higher proportion of high-calorie food choice. Rather, an enhanced memory for high-calorie food locations was associated with a lower perceived difficulty (i.e. greater ease) of finding high-calorie items in the supermarket, which may potentiate later choice of a high-calorie food. The high-calorie spatial memory bias was also found to be expressed independently of the amount of visual attention individuals allocated to high-calorie versus low-calorie foods. Findings further substantiate the notion that human spatial memory shows sensitivity to the caloric content of a potential resource and automatically prioritizes those with greater energy payoffs. Such a spatial mechanism that was adaptive for energy-efficient foraging within fluctuating ancestral food environments could presently yield maladaptive “obesogenic” consequences, through altering perceptions of food search convenience.

1. General introduction

A growing body of evidence proposes that the human mind was functionally shaped by evolutionary selection pressures to maximize fitness, much like physical traits were (Tooby & Cosmides, 1992; Tooby & Cosmides, 2005). That is, our present cognitive architecture is thought to harbour inbuilt mechanisms that were optimized for solving specific fitness-relevant “adaptive” problems encountered within the ancestral environments in which we evolved (Tooby & Cosmides, 1992; Tooby & Cosmides, 2005). One such cognitive mechanism that could have evolved as an adaptation for foraging within harsh ancestral food settings is a prioritization (or bias) in human memory for the locations of high-calorie foods (Allan & Allan, 2013; New et al., 2007; de Vries et al., 2020a; de Vries et al., 2020b). Indeed, a comparable foraging-related cognitive mechanism has been documented in various (non-human)

primate species (Cunningham & Janson, 2007; Janmaat et al., 2014; Janson, 1998). However, empirical research on the existence of such a “high-calorie bias” in human spatial memory, and particularly whether (or in what manner) it influences how individuals navigate the modern obesogenic food environment, is currently limited.

A recurring adaptive problem faced by all species is the efficient attainment of nutritional resources (Schoener, 1971). For a substantial portion of human evolutionary history, the acquisition of food was characterized by extensive hunting-gathering activities within a fluctuating landscape, where food supply varied along both temporal and spatial dimensions (Adler et al., 2006; Stiner & Bar-Yosef, 2005; Stiner & Kuhn, 2009). The survival and reproductive success of an individual were therefore a function of the energy-efficiency of foraging bouts, such as the fluency with which a forager could identify and (re)locate high-quality resources, as they became available or valuable over time

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(MacArthur & Pianka, 1966; Schoener, 1971). It follows that a cognitive adaptation that could have evolved to support energy-efficient foraging, is one that automatically assesses the profitability of potential food resources and prioritizes in memory the locations of those higher in caloric quality (Krasnow et al., 2011; New et al., 2007; de Vries et al., 2020a; de Vries et al., 2020b). In a series of recent investigations, we obtained evidence consistent with the existence of such an implicit high-calorie bias in human spatial memory for foods: Across sensory modalities (e.g. vision and olfaction) and experimental paradigms, we found that individuals more accurately recalled locations of high-calorie (relative to low-calorie) food stimuli – independently of hedonic food evaluations, personal familiarity with foods, encoding time, or encoding conditions (i.e. incidental versus intentional learning) (de Vries et al., 2020a; de Vries et al., 2020b).

If human spatial memory is indeed attuned to optimal foraging within erratic ancestral food habitats, this begs the question of what the behavioural implications of the high-calorie spatial memory bias are within a modern (food abundant) foraging context. The (once adaptive) high-calorie bias in spatial memory may presently confer maladaptive obesogenic effects, by directly enhancing the ease with which high-calorie items are located and acquired within a heterogeneous food environment (Allan & Allan, 2013; de Vries et al., 2020b). However, the evidence is currently inconclusive: Allan & Allan (2013) observed that an improved location memory for high-calorie snack foods (relative to low-calorie fruits and vegetables) predicted a greater BMI in women. de Vries et al. (2020b) similarly reasoned that the high-calorie spatial memory bias may promote unhealthy high-calorie food choice, but did not find any systematic relationships between the expression of the cognitive bias and eating-related parameters. Given that previous efforts were limited to either distal (anthropometric) markers of dietary intake or controlled food choice measures in lab settings, finer-grained effects of the high-calorie spatial memory bias on an individual's eating behaviour could have gone undetected. Therefore, the current study represents a more powerful and ecologically valid test of the potential behavioural implications of a high-calorie bias in human spatial memory, by examining its relation to proximate foraging-related outcomes (i.e. food search and food choice) within a real-world food environment.

Similarly, it remains to be elucidated what processes are proximally associated with the high-calorie bias in human spatial memory, as evolved cognitive mechanisms often have a neurophysiological basis (Cosmides et al., 2021). These insights would be especially relevant for health interventions aiming to directly alter the expression of the bias. With regards to candidate proximal mechanisms, it is reasonable to expect that a bias in attention for high-calorie (relative to low-calorie) food cues may facilitate an enhanced memory for locations of high-calorie foods. Namely, evidence has accumulated for the phenomenon of “object-based spatial attention”, in which individuals make use of objects to guide attentional processing to specific locations in the visual field, such as the spatial region an object occupies (Arrington et al., 2000). As such, one can assume that a greater attentional allocation to high-calorie foods could similarly lead to an enhanced attentional processing of (and later superior memory for) the locations of those items. An additional justification stems from research suggesting that high BMI (overweight/obese) individuals display a visual attention bias for high-calorie foods, and the magnitude of the high-calorie spatial memory bias has been previously linked to a higher BMI (Allan & Allan, 2013; Castellanos et al., 2009; Hendrikse et al., 2015; Werthmann et al., 2011). Indeed, spatial memory performance for gatherable foods (e.g. fruit) has been shown to improve with the amount of attention deployed to them, particularly in situations of “item-specific” motivation (i.e. when a forager encounters a valuable high-calorie gatherable resource; Krasnow et al., 2011). Direct examination of the relationship between food-related attention biases and the high-calorie spatial memory bias is thus warranted, especially in light of the fact that associations between attention and (episodic) memory faculties vary depending on the exact information that is attended to and later recalled (e.g. Allan et al., 2012;

Becker et al., 2005).

In sum, the aim of the present study was twofold. Our primary research objective was to investigate the potential implications of a high-calorie bias in human spatial memory on the food search and food choice of individuals navigating a real-world food environment. Secondly, we examined the extent to which high-calorie biases in visual attention are related to the high-calorie bias in spatial memory. We hypothesized the following outcomes:

H_{1A} : The high-calorie bias in spatial memory predicts a faster localization of (i.e. lower search time for) high-calorie relative to low-calorie foods.

H_{1B} : The high-calorie bias in spatial memory predicts a higher proportion of high-calorie food choice.

H_2 : An attention bias for high-calorie foods will be positively associated with the high-calorie spatial memory bias.

2. Methodology

2.1. Design

The study had a repeated measures design with *Caloric Density* (High versus Low) as a within-subjects factor. Each participant completed a series of lab-based computer tasks (i.e. eye-tracking and spatial memory tasks) and a supermarket-based food search and (covert) food choice task in two test sessions separated by a delay of at least one day. The hypotheses, experimental design, and data analysis plan were preregistered and are available with study data on the Open Science Framework database (Project URL: <https://osf.io/7hmwf/>).

2.2. Participants

60 healthy university students (73% female; $M_{\text{Age}} = 24.6$ years, $SD = 3.2$) took part in the research. The majority of participants had a Caucasian background (82% Caucasian; 8% Asian; 8% Latino; 2% Other) and were postgraduate students (80% postgraduates; 20% undergraduates). The sample size was determined *a priori* via a power calculation on our primary research objective (see pre-registration link). Participants were limited to the BMI range of 18.5 – 30 kg/m² ($M = 22.8$ kg/m², $SD = 2.4$), to minimize ceiling effects (for BMI values > 30 kg/m²) and floor effects (for BMI values < 18.5 kg/m²) on food-related attention bias measures (Castellanos et al., 2009; Giel et al., 2011). Moreover, we included only individuals who were sufficiently unfamiliar with the test supermarket environment (i.e. did not habitually grocery shop there, did not visit the supermarket in the month before testing, and self-reported a store familiarity score lower than 50 mm on a VAS ranging from 0 (“Not At All”) to 100 (“Very Much”) mm), in order to circumvent potential ceiling effects on food search performance (O'Neill, 1992). Finally, individuals were not included when reporting a dietary restriction to specific foods (e.g. meat), a medical history of eating or psychiatric disorders, or participation in previous related studies. All participants provided written informed consent prior to testing and were financially compensated. This study received ethical approval from the Social Sciences Ethics Committee of Wageningen University.

2.3. Apparatus and stimuli

2.3.1. Food stimuli in computer tasks

Standardized images of (sweet/savoury) high- and low- calorie foods were obtained from the *Food Pics* database (Blechert et al., 2014). High-calorie items were defined as those that contained at least 225 – and low-calorie items at most 60 – kcal per 100 g of food (de Bruijn et al., 2017; World Cancer Research Fund/American Institute for Cancer Research, 2007). For the spatial memory task, a set of 12 (unbranded) food pictures was chosen for each caloric density group, encompassing fruits and vegetables for the low-calorie condition, and baked and fried goods as

high-calorie variants (de Vries et al., 2020b). For the eye-tracking task, a subset of 10 high- and low-calorie food stimuli from that of the spatial memory task was used (see *Food Pics Catalogue Numbers* in the Supplemental Material). Importantly, an equal number of taste (i.e. sweet and savoury) options were included across caloric density categories, as working and spatial memory faculties are documented to process tastes differently (Meule et al., 2012; de Vries et al., 2020b).

In both tasks, high- and low-calorie images differed on caloric density, total energy content, perceived caloric content, and perceived healthiness (see Table S1 in the Supplemental Material). Furthermore, high- and low-calorie stimuli were matched on nutrient balance (i.e. protein to carbohydrate and fat ratios; Simpson et al., 2003), pertinent image characteristics (e.g. colour, size, brightness), recognizability, and subjective complexity ratings (see Table S1) (Graham et al., 2011; Werthmann et al., 2011).

2.3.2. Free-viewing eye-tracking task

The eye-tracking paradigm was adapted from Graham et al. (2011) and Werthmann et al. (2011). The task was created with Tobii Pro Lab (Tobii Technology, Danderyd, Sweden) and run on a Windows laptop (screen size: 15.6 in.; resolution: 1920 × 1080) with a Tobii X2-60 eye-tracker mounted on the computer screen. Participants were seated approximately 65 cm away from the screen and placed their heads on a chin-rest. A five-point calibration procedure was conducted prior to recording.

The eye-tracking task comprised a total of 120 trials: 80 critical trials and 40 filler trials. Critical trials consisted of 20 high- and low-calorie food image pairs, and each pair was presented four times. High- and low-calorie foods occurred equally frequently on the left and right sides of an image pair. Filler trials consisted of 10 pairs of non-food images (e.g. tools and office supplies), each also presented four times. All trials began with a central fixation cross that was displayed for 2000 ms, whereas trials were shown for 3000 ms. During recording, participants were instructed to look at presented images freely – as if they were watching television – and to focus on the fixation cross displayed between trials. The order of critical and filler trials was randomized differently for each participant.

Unknown to participants, the computer screen was divided into a left, middle, and right Area of Interest [AOI]. Only visual fixations – defined as eye movements that are maintained for at least 100 ms – directed to the left or right AOI during critical trials were extracted for further analyses (Werthmann et al., 2011).

2.3.3. Spatial memory task

The spatial memory task was previously validated as an instrument to measure food location memory accuracy in the target population (Allan & Allan, 2013; de Vries et al., 2020b). The task was run on E-Prime 2.0 using computers standardized across screen size (19.3 in.) and resolution (1280 × 1024). Participants were asked to imagine that an international food market with 24 food stalls was taking place on a (unfamiliar) university campus. Participants were then shown 12 images of either high-calorie foods or low-calorie alternatives, followed by an image of a university campus map showcasing all possible stall locations (N = 24), at a duration of three seconds each. After, the location of the stall selling each food item (N = 12) was indicated one-by-one on the campus map by a green crosshair. During the location viewing process, participants were instructed to rate each food item on desirability and familiarity. Following a two-minute break, participants completed a series of 12 spatial memory tests in which they were randomly presented with one of the previous food images and required to specify (via mouse-click) its correct corresponding stall location on the campus map. The total number of possible stall sites was displayed anew each recall round, and a stall location could be selected more than once although assigned locations did not overlap between foods. The order of stimulus presentation and the stimuli itself (i.e. food-location pairs) were randomized differently for each participant. Furthermore, the order in which

participants performed the spatial memory task between caloric density conditions was counterbalanced.

2.3.4. Food search task

The food search task was carried out using EyeQuestion software (Logic8 B.V., Elst, Gelderland, the Netherlands). A set of 16 food products (N = 8 per caloric density group) sold at the test supermarket (i.e. *Jumbo Verberne Wageningen*) was selected for the task. Chosen high- and low-calorie products (e.g. High-calorie: Chocolate cookies and Potato chips; Low-calorie: Oranges and Eggplant; see Table S2 in the Supplemental Material) had an equal number of sweet and savoury items, were matched on spatial distributions within the supermarket (i.e. floor sections and vertical height) as closely as possible, and were piloted to verify correct caloric content and healthiness perceptions.

For the encoding phase of the task, participants were first walked through all supermarket aisles by the experimenter and instructed to observe their surroundings as they moved. The order in which supermarket aisles were explored was counterbalanced across participants, ensuring that (target) high- and low-calorie aisles were encountered equally often at the beginning and end of a walking sequence. Individuals were then provided with a tablet and presented with a sequence of images of target food products, which they had to (re)locate as quickly as possible within the supermarket. Upon finding a product, participants had to rate how difficult it was to find, product familiarity, and product attractiveness. Participants also had to rate how eye-catching they found the respective product aisle, before proceeding on to the next food item. The presentation order of food products during the search (recall) portion of the task was randomized differently per participant.

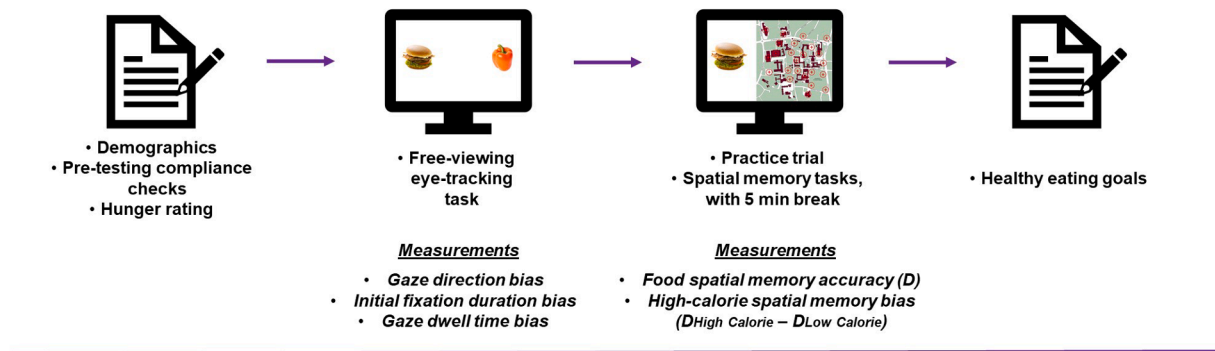
2.4. Procedure

Participants were informed that the experiment aimed to investigate how people perceive and (cognitively) process foods typically found in the modern food environment. They were also told that they would be rewarded with paid-for groceries at the end of the study as part of their compensation. Hunger states were standardized before sessions by instructing individuals to consume their habitual meals or snacks no later than two hours – and no sooner than 45 min – before testing. Test sessions were scheduled around typical breakfast and lunch times to facilitate compliance to pre-testing requirements, as well as outside of peak supermarket hours to ensure relatively calm surroundings for the food search task.

For the first test session in the lab, participants were seated in isolated testing booths fitted with a computer. Data on demographics and hunger state were first recorded via a questionnaire. Participants then had to complete the free-viewing eye-tracking task. Following a brief intermission, participants performed the spatial memory task for both caloric density conditions: Individuals were first exposed to a practice trial involving the encoding and recall of (non-food) object locations to familiarize themselves with the protocol. After, they completed the actual spatial memory task with (high- and low-calorie) food images, with a five-minute break between conditions. Upon finishing, participants answered questions on healthy eating goals. The first test session took approximately 60 minutes (Fig. 1).

At least one day later, participants arrived at the test supermarket. After providing preliminary ratings (i.e. Hunger), participants performed the food search task and rated their general sense-of-direction upon completion. As part of the covert food choice measure, they were then given a budget of 10 euros and 10 min to freely shop for food items within the supermarket, the receipts of which were handed over to the experimenter. The second test session took an average of 30 minutes (Fig. 1).

Test Session 1 - Lab



Test Session 2 - Supermarket

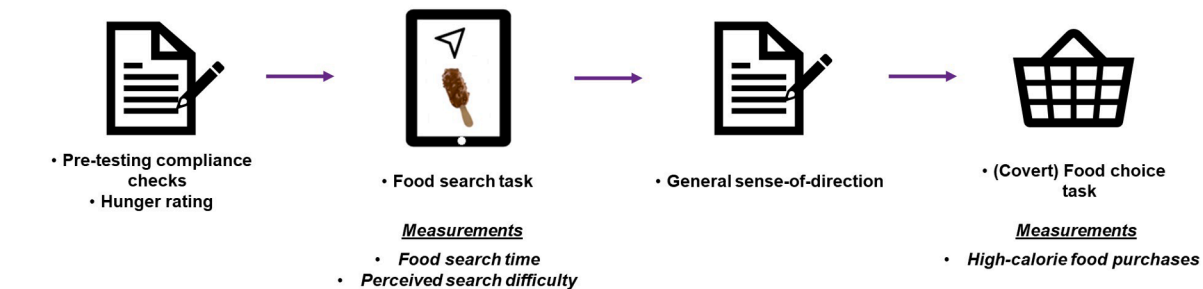


Fig. 1. Experimental procedure. Participants completed a series of tasks in a lab and (unfamiliar) supermarket setting, on two separate occasions.

2.5. Measurements

2.5.1. Primary outcome variables

Food search performance was operationalized as the time (in seconds) required to (re)locate a target food product in the food search task, from the onset of stimulus presentation. Perceived search performance was also gauged by asking participants to rate how difficult it was to find a food product on a 100 mm VAS (anchored from “Not At All” to “Very Much”), as an alternative to (objective) search time. A similar (subjective performance) VAS scale was employed in earlier studies and shown to accurately covary with individuals’ actual task performance (de Vries et al., 2020b). Search times and difficulty ratings were averaged per caloric density category.

The number of high-calorie food products bought from the (rewarded) groceries of each participant, expressed as a proportion of the total number of purchased food items, was taken as a covert measure of high-calorie food choice.

2.5.2. Predictor variables

Spatial memory accuracy for high- and low-calorie foods was calculated as the average ‘pointing error’ or Euclidian distance (D) between true and indicated stall locations of each food type (cf. Allan & Allan, 2013; de Vries et al., 2020b). Consequently, lower D scores denote a higher accuracy in food spatial memory. The difference in spatial memory accuracy for high- and low-calorie foods ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) was taken to represent the high-calorie bias in spatial memory. Accordingly, negative values indicate an enhanced spatial memory for high-calorie foods.

Three eye movement metrics that reflect different temporal components of attention were measured to directly assess attention biases for high-calorie foods (Castellanos et al., 2009; Graham et al., 2011; Werthmann et al., 2011):

The gaze direction bias is an index of biases in initial attentional orientation. It was calculated as the number of critical trials in which the

first fixation was directed to a high-calorie food, as a proportion of the total number of critical trials in which first fixations were observed. A proportion higher than 0.5 indicates an orientation bias towards high-calorie foods; a proportion lower than 0.5 indicates an orientation bias towards low-calorie foods.

The initial fixation duration bias is a proxy for biases in early attentional maintenance. It represents the duration of the first fixation directed to a particular image type (i.e. the first fixation to occur on an image following the onset of a critical trial), and was calculated as the difference between the average duration of initial fixations on high- and low-calorie foods (across all critical trials per participant). A positive score denotes a longer initial attentional maintenance on high- versus low-calorie foods.

The gaze dwell time bias is informative of biases in maintained attention. It was calculated by subtracting the average fixation time (i.e. using the sum of individual fixations across critical trials) on low-calorie food images from the average fixation time on high-calorie food images. A positive score suggests a longer maintained attention on high-calorie foods.

At the conclusion of testing, eye movements were detected on an average of 98.9% of critical trials and all participants had sufficient fixation data recorded (i.e. at least 80% of critical trials). Gaze direction bias scores were not found to correlate with either initial fixation duration ($r_s = 0.04$), $p = .757$, or gaze dwell time bias measures ($r_s = 0.19$), $p = .152$. Similarly, the (relative) amount of time individuals initially fixated on high-calorie food items did not correlate with the overall time individuals fixated on high-calorie versus low-calorie food images ($r_s = 0.12$), $p = .359$, suggesting that the three bias scores indeed reflect different underlying components of visual attention.

2.5.3. Control measures

To eliminate confounding influences of food ‘wanting’ on spatial memory accuracy, we required participants to rate a food item’s Desirability on a 100 mm VAS (anchored from “Not At All” to “Very

Much”) in the spatial memory task (de Vries et al., 2020a; de Vries et al., 2020b). Furthermore, individual exposure to a food type was documented using a five-item Familiarity scale (Tuorila et al., 2001) in both spatial memory and food search tasks. Choice options of the Familiarity scale reflect behaviourally-meaningful differences relevant to individual experiences with a food (e.g. having tasted versus not tasted a specific item; Tuorila et al., 2001), and both Desirability and Familiarity measures were shown to effectively capture additional variation in spatial memory performance not attributable to a food’s nutritional properties (de Vries et al., 2020a; de Vries et al., 2020b).

To specifically control for extraneous effects on food search performance, we required participants to record the Attractiveness of (target) food products, how Eye-catching a product aisle was, and Familiarity with the test supermarket on a 100 mm VAS (anchored from “Not At All” to “Very Much”). We adopted a “continuous” VAS format for these controls, as opposed to an “ordinal” forced-choice alternative such as a Likert scale, to better detect subtle deviations in these measures between individuals and respective products (McCormack et al., 1988). Individuals were additionally asked to quantify their General Sense-of-Direction on a seven-point scale ranging from “Poor” to “Good”, as self-reports of this measure are shown to correlate with field measures of navigational ability in unfamiliar environments (Kozłowski & Bryant, 1977; New et al., 2007).

As an individual’s explicit nutritional intentions were found to significantly predict eating behaviour in previous studies (de Vries et al., 2020b), a Healthy Eating Goals measure was administered with two items (*In my daily life, I strive to eat healthy; It is important to me to eat healthy foods*) rated on a seven-point scale anchored from “Strongly Disagree” to “Strongly Agree” (de Vries et al., 2020b). Finally, demographic characteristics (e.g. Sex, Age, Ethnicity) and Hunger states (100 mm VAS anchored from “Not At All” to “Very Much”) at the onset of each test session were recorded.

2.6. Data analysis

Data were analysed using IBM SPSS Statistics 25 with statistical significance defined as $p < .05$. The first statistical analysis was of an exploratory nature, in order to firstly confirm the existence of the high-calorie bias in human spatial memory prior to assessing its behavioural and attentional correlates. Remaining statistical models represent confirmatory analyses that correspond to our preregistered hypotheses.

2.6.1. Caloric density and spatial memory accuracy (Exploratory)

To explore whether human spatial memory is indeed biased for high-calorie foods, we formulated a random intercept linear mixed model with main and interaction effects of *Caloric Density* and *Taste* as fixed factors, *Participant* as random factor (covariance structure: Variance Components), *Sex*, *Age*, *Ethnicity*, *Caloric Density Order*, *Desirability*, *Familiarity*, and *Hunger* as covariates, and *Spatial Memory Accuracy (D)* as the dependent variable. The model selection process involved a backward stepwise approach: Fixed effects of the saturated model (above) were finalized based on Maximum Likelihood (ML) ordinary likelihood ratio tests using the $-2 \log$ likelihood ($-2LL$) test statistic between nested models. Model selection was made on the basis of parsimony and the final model (with *Caloric Density*, *Taste*, and *Desirability*) was refitted with REML estimations.

2.6.2. High-calorie spatial memory bias and food search (H_{1A})

To determine whether the high-calorie bias in spatial memory predicts a faster localization of high-calorie foods, we formulated a multiple linear regression model ($N = 1$; simultaneous entry method) with *Search time for high- versus low-calorie foods* ($\text{Time}_{\text{High-calorie}} - \text{Time}_{\text{Low-calorie}}$) as the dependent variable and demographics (i.e. Sex, Age, Ethnicity), *Hunger* ratings at encoding, *Encoding (Walking) order*, *General Sense-of-Direction*, *Familiarity with the supermarket*, *Familiarity with high- versus low-calorie foods*, *Attractiveness of high- versus low-calorie foods*, *Eye-*

catching ratings of high- versus low-calorie food aisles, and the *High-calorie spatial memory bias* ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) as predictor variables.

2.6.3. High-calorie spatial memory bias and High-calorie food choice (H_{1B})

To test whether the high-calorie bias in spatial memory predicts prospective high-calorie food purchases, we performed a multiple linear regression analysis ($N = 1$; simultaneous entry method) on *High-calorie food choice* with demographics (i.e. Sex, Age, Ethnicity), *Hunger* ratings at encoding, *Familiarity with high- versus low-calorie foods*, *Attractiveness of high- versus low-calorie foods*, *Eye-catching ratings of high- versus low-calorie product aisles*, *Healthy Eating Goals*, and the *High-calorie spatial memory bias* ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) as predictor variables.

2.6.4. Attention bias for High-calorie foods and the High-calorie spatial memory bias (H_2)

To determine whether biases in attention towards high-calorie foods covary with the expression of the high-calorie spatial memory bias, we regressed ($N = 1$; simultaneous entry method) the *High-calorie spatial memory bias* ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) on demographics (i.e. Sex, Age, Ethnicity), *Spatial memory task order*, *Hunger* ratings at encoding, *Desirability of high- versus low-calorie foods*, *Familiarity with high- versus low-calorie foods*, *Gaze direction bias*, *Initial fixation duration bias*, and *Gaze dwell time bias*.

3. Results

3.1. The high-calorie bias in human spatial memory was replicated

In the lab-based spatial memory task, the average accuracy in food spatial memory across caloric density conditions was 155.92 ($SD = 151.03$) pixels. Individuals demonstrated a more accurate memory (i.e. smaller pointing error or D) for locations of high-calorie foods compared to that of low-calorie alternatives, $F(1,1380) = 9.23$, $p = .002$, $\eta^2 = 0.007$, 90% CI $\eta^2 [0.001, 0.02]$ (Fig. 2A). In addition, a significant main effect of Taste on spatial memory accuracy was observed, with individuals better recalling locations of savoury (as opposed to sweet) tasting stimuli, $F(1,1384) = 7.90$, $p = .005$, $\eta^2 = 0.006$, 90% CI $\eta^2 [0.001, 0.01]$ (Fig. 2B), indicating the expression of high-calorie and savoury-taste biases in human spatial memory, respectively. These effects occurred regardless of demographics (e.g. Sex), hedonic evaluations, or reported familiarity with foods. Similarly, post-hoc analysis revealed that the time participants took to encode food locations did not influence spatial memory performance $F(1,1399) = 0.38$, $p = .540$, or attenuate either the high-calorie or savoury-taste bias in human spatial memory. Finally, food spatial memory accuracy improved with a higher rated desire to eat a food ($B = -0.49$, 95% CI = $[-0.75, -0.23]$), $F(1,1405) = 13.52$, $p < .001$, $\eta^2 = 0.01$, 90% CI $\eta^2 [0.003, 0.02]$.

3.2. The high-calorie bias in spatial memory did not predict food search time, but a lower perceived search difficulty for high-calorie foods

With regard to the food search task, individuals were moderately faster at (re)locating high-calorie than low-calorie target food products within the unfamiliar supermarket (47.6 versus 54.1 s; Table S3), Mean search time difference $\text{High-Low calorie} = -6.48$ s, 95% CI = $[-12.54, -0.43]$, $t(59) = -2.14$, $p = .036$, $d = 0.35$. Upon closer inspection, follow-up (linear mixed model) analysis showed a significant Caloric Density and Taste interaction, $F(1,900) = 8.96$, $p = .003$, $\eta^2 = 0.01$, 90% CI $\eta^2 [0.002, 0.02]$. The high-calorie advantage in search time was found only for savoury products, in which high-calorie - savoury items had 9.40% lower search times compared to low-calorie - savoury counterparts (95% CI = $[3.40, 15.40]$), $p = .002$. Perceived search difficulty followed search time results closely ($r_s(954) = 0.640$, $p < .001$; Table S3), with follow-up (linear mixed model) analysis similarly yielding a significant Caloric Density and Taste interaction, $F(1,872) = 6.97$, $p = .008$, $\eta^2 = 0.01$, 90% CI $\eta^2 [0.001, 0.02]$, owing to a 9.70% lower rated difficulty

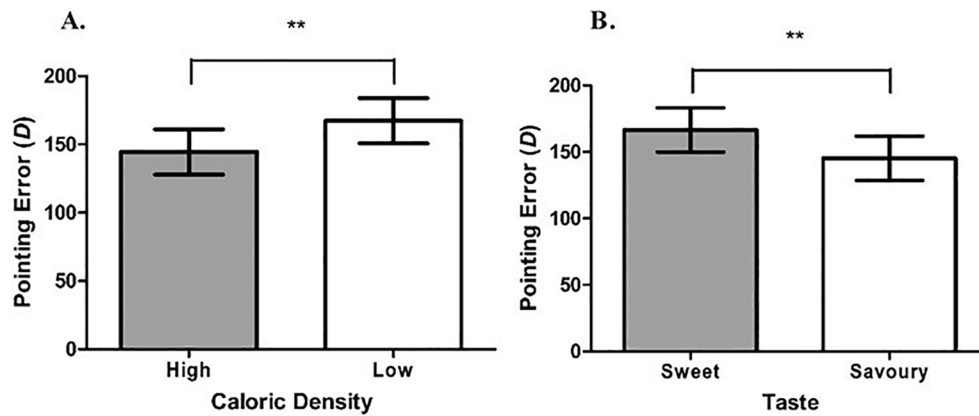


Fig. 2. Spatial memory accuracy for (A) Caloric Density and (B) Taste food groups, measured as the “pointing error” (D ; in pixels) between true and indicated food locations. Lower values indicate a lower pointing error and higher accuracy in food spatial memory. A double asterisk indicates a significant difference with $p < .01$. Error bars represent 95% confidence intervals.

of finding high-calorie - savoury (compared to low-calorie - savoury) items (95% CI = [2.40, 17.10]), $p = .010$.

However, the high-calorie spatial memory bias did not predict the faster localization of high-calorie foods in the supermarket ($B = 0.04$, 95% CI = [-0.06, 0.14]), $t(48) = 0.75$, $p = .228$. Exploratory analysis revealed the high-calorie bias in spatial memory was instead predictive of a lower perceived difficulty (i.e. greater ease) of finding high-calorie relative to low-calorie products ($B = 0.04$, 95% CI = [0.002, 0.09]), $t(56) = 2.12$, $p = .039$ (Table 1).

3.3. The high-calorie bias in spatial memory did not predict high-calorie food choice

Across participants, high-calorie food choices accounted for 47% (range: 0 – 100%) of all groceries purchased. The average caloric density of chosen foods was 230.18 ($SD = 106.87$) kcal/100 g. Contrary to expectations, the high-calorie spatial memory bias did not affect the proportion of high-calorie food products individuals purchased ($B = -6.75 \times 10^{-5}$, 95% CI = [-0.001, 0.001]), $t(50) = -0.12$, $p = .453$. As exploratory tests, we alternatively operationalized high-calorie food choice as the proportion of total costs an individual spent on high-calorie food products, as well as the average caloric density of groceries chosen. However, the high-calorie spatial memory bias was not significantly associated with either outcome (both p 's > 0.05 ; Table S4).

In light of the prior finding that the high-calorie spatial memory bias

covaried with the reported difficulty of finding high-calorie (versus low-calorie) products, a corresponding analysis was conducted to explore the relationship between perceived search difficulty and prospective high-calorie food choice. A trend was found for a negative correlation between the perceived difficulty of finding high-calorie products and the proportion of high-calorie foods purchased ($r_s(60) = -0.25$), $p = .058$, whereas no association between prospective high-calorie food choice and objective search time for high-calorie foods was observed ($r_s(60) = -0.06$), $p = .655$.

3.4. The high-calorie spatial memory bias was not associated with a bias in visual attention for high-calorie foods

Individuals displayed an average gaze direction bias score of 0.51 ($SD = 0.06$), which did not significantly differ from chance level, $t(59) = 1.12$, $p = .269$, indicating an equal initial attention orientation towards high- and low-calorie food stimuli. Regarding early attention maintenance, participants initially fixated on high-calorie items for a duration of 250.88 ms (versus 239.16 ms on low-calorie counterparts), although the high-calorie bias in initial fixation duration did not reach statistical significance (Initial fixation duration bias = 11.72, $SD = 324.32$), $Z = -0.55$, $p = .586$. Finally, participants maintained their overall attention equally long on high- and low-calorie food images (274.71 versus 289.55 ms, Gaze dwell time bias = -14.84, $SD = 56.31$), $Z = -1.72$, $p = .086$.

Table 1

Predicting the perceived difficulty of finding high-calorie versus low-calorie food products in an unfamiliar supermarket environment from the high-calorie bias in spatial memory.

Variable	B	95% CI	Beta	t	p	R	R ²
Model 1^a							
Constant	-3.33	-6.21 to -0.47		-2.33	0.024*	0.422	0.178
Eye-Catching High - Low Calorie	-0.41	-0.64 to -0.18	-0.42	-3.54	<0.001***		
Model 2							
Constant	-2.58	-5.5 to 0.35		-1.77	0.083	0.475	0.226
Eye-Catching High - Low Calorie	-0.42	-0.65 to -0.20	-0.44	-3.76	<0.001***		
High-calorie Spatial Memory Bias ^b	0.04	-0.003 to 0.08	0.22	1.88	0.066		
Model 3							
Constant	-2.37	-5.23 to 0.50		-1.66	0.103	0.526	0.276
Eye-Catching High - Low Calorie	-0.49	-0.71 to -0.26	-0.51	-4.25	<0.001***		
High-calorie Spatial Memory Bias ^b	0.04	0.002 to 0.09	0.24	2.12	0.039*		
Attractiveness High - Low Calorie	0.24	-0.002 to 0.48	0.24	1.98	0.052		

* $p < .05$; ** $p < .01$; *** $p < .001$.

^a From a stepwise regression analysis, with sex, age, ethnicity, hunger ratings, encoding (walking) order, general sense-of-direction, familiarity with the supermarket, familiarity with high- versus low-calorie foods, attractiveness of high- versus low-calorie foods, and eye-catching ratings of high- versus low-calorie food aisles entered as covariates.

^b $D_{\text{High Calorie}} - D_{\text{Low Calorie}}$ (Lower values denote a greater bias in spatial memory for high-calorie foods).

Results do not support an association between the high-calorie spatial memory bias and high-calorie biases in visual attention (Table S5): A more accurate memory for high-calorie food locations was not predicted by a heightened attention orientation towards high-calorie foods ($B = 69.40$, 95% CI = $[-235.4, 374.2]$), $t(49) = 0.46$, $p = .325$, longer early attention maintenance on high-calorie foods ($B = -0.03$, 95% CI = $[-0.10, 0.03]$), $t(49) = -1.10$, $p = .138$, or prolonged overall attention maintenance on high-calorie foods ($B = 0.06$, 95% CI = $[-0.29, 0.42]$), $t(49) = 0.35$, $p = .364$.

4. General discussion

The present research is grounded on the premise that during the course of our evolutionary history as hunter-gatherers, human memory systems evolved mechanisms conducive to energy-efficient foraging. In line with previous observations that support such an adaptive perspective on human memory (Nairne & Pandeirada, 2008; New et al., 2007; de Vries et al., 2020a; de Vries et al., 2020b), our results further substantiate the notion that human spatial memory shows sensitivity to content and prioritizes the locations of high-calorie (and savoury-tasting) nutritional resources. Although individuals were faster at (re) locating high-calorie relative to low-calorie foods in the unfamiliar supermarket, the high-calorie bias in human spatial memory did not directly predict a lower search time for high-calorie foods, or a higher proportion of high-calorie food choice. Rather, a greater expression of the bias was predictive of a lower perceived difficulty of finding high-calorie relative to low-calorie foods in a real-world setting. Furthermore, the magnitude of the high-calorie spatial memory bias did not correlate with a bias in either attention orientation or attention maintenance for high-calorie foods.

The high-calorie bias in human spatial memory was first reported by New et al. (2007), who found that the accuracy of recalling food locations improved linearly with the caloric density of a group of “traditionally” gatherable resources (i.e. fruits, vegetables, nuts). The present study replicates the mnemonic effect of caloric content, and demonstrates that it extends to foods more characteristic of the modern environment and of a wider range of energy densities (see also de Vries et al., 2020a; de Vries et al., 2020b). Importantly, this suggests that the spatial processing bias is not designed to respond to a fixed repertoire of foods. Rather, it is likely that the mechanism shows sensitivity to the (relative) caloric quality of a food, which we learn to associate with its other sensory characteristics (i.e. sight or smell) through eating experiences (Myers, 2018; Yeomans, 2006). Indeed, there would be little adaptive value in a foraging mechanism that attaches itself to a fixed array of nutritional resources, as (high-priority) foods do not occur in precisely the same form under varying spatiotemporal circumstances.

The savoury-taste bias in human spatial memory represents a more recent finding that is speculated to reflect a foraging adaptation for protein-rich resources (de Vries et al., 2020b). Namely, taste modality plays a functional role in the food selection and food intake of many animal species, by signalling the nutritional profile of a specific food: *Sweet* for a sugar- and carbohydrate-rich food, and *savoury* for a high amino-acid or protein content (Breslin, 2013; Yarmolinsky et al., 2009). Given that major protein resources in ancestral food environments (e.g. mobile animal prey) had more variable return rates than carbohydrate-rich resources (e.g. immobile fruits), this suggests that it was a bigger adaptive problem for foragers to secure sufficient protein intake to fulfil their relatively high nutritional protein demands (Bird et al., 2009; Cordain et al., 2000; Eaton, 2006; Stiner & Kuhn, 2009). However, as locations of protein-rich foods – including animal prey – can follow a predictable spatial and temporal distribution due to seasonal variations in environmental conditions (e.g. habitual ranging and migration animal patterns; Bracis & Mueller, 2017), we speculate that the savoury-taste spatial memory bias could have been adaptive in increasing the chances of successful protein capture (de Vries et al., 2020b).

We expected that if individuals continue to house cognitive

adaptations that are mismatched to existing evolutionary novel food-replete conditions, obesogenic consequences on foraging-related behaviour could ensue (Eaton et al., 1988; Lieberman, 2006). We found that both objective and perceived search performance were moderately better for (savoury-tasting) high-calorie products than low-calorie alternatives that were matched on spatial distributions within the supermarket. However, a greater expression of the (lab-tested) high-calorie spatial memory bias was only systematically associated with a lower reported difficulty of finding high-calorie items in the supermarket. The fact that the cognitive bias did not account for the faster localization of high-calorie foods in the field setting may be due to a number of considerations, which are outlined below.

Firstly, whether (smaller-scale) lab-administered tests of spatial ability accurately reflect behavioural indices of navigation in larger real-world settings is unclear. Though moderately strong correlations between psychometric and field-based measures of spatial performance have been reported (Hegarty et al., 2006; Moffat et al., 1998; Murakoshi & Kawai, 2000), spatial information is learned from different visual perspectives (i.e. aerial or map-like perspective in psychometric spatial tasks versus viewer-centred perspective during actual navigation), and distinct spatial memory sub-systems are thought to function at different scales of space (Maguire et al., 1999; Piccardi et al., 2010). Secondly, variation between individuals in their preferred mode of representing spatial information (Bocchi et al., 2019; Pazzaglia & Taylor, 2007), or fluency of using heuristics (e.g. pursuing aisle locations of similar products) to aid incomplete cognitive maps (Murakoshi & Kawai, 2000; Conlin, 2009), could have enabled those with a lower expression of the high-calorie spatial memory bias to compensate for an otherwise higher search time. For instance, goals of the food search task could have been better suited for individuals with a greater affinity for constructing cognitive maps using a certain spatial representation (i.e. landmark, route, or survey “spatial cognitive style”), which would have minimized effects of the high-calorie bias in spatial memory on navigation in those individuals (Pazzaglia & Taylor, 2007). Finally, the larger variation in search times – compared to that of perceived search difficulty ratings (Table S3) – of our study sample may have compromised the power to reveal a statistically significant effect on the former parameter, and results may likewise have been restricted by using search time as the only proxy for search efficiency. A more robust test could have supplemented time readings with those of a higher specificity for activity-induced energy expenditure (e.g. pedometer; Tudor-Locke et al., 2002), or made use of technology that is able to track real-time indoor movements. As such, it would be fruitful for future investigations to document both quantitative (e.g. spatial orientation ability; Kozlowski & Bryant, 1977) and qualitative (e.g. spatial cognitive style; Pazzaglia et al., 2000) individual differences in navigation-related abilities – as well as include a broader range of performance markers – to finer decompose food searching implications of the spatial processing bias.

In a similar vein, limitations in our operationalization of food choice could have diluted a potential (direct) influence of the high-calorie bias in spatial memory. Despite the covert nature and ecologically valid context of the food choice task, it may have still elicited strategic choice behaviour, owing to the “reward” connotation attached to grocery purchases. That is, although the physical surroundings for selecting foods was appropriate, the situational framing of grocery purchases as an extra gift for participation may have activated “reward” schemas and prompted individuals to deviate away from making habitual food choices (Meiselman, 1996). In light of previous null relationships with single-point measures of food choice (de Vries et al., 2020b), and the significant association of the high-calorie spatial memory bias with a marker of habitual diet quality (i.e. BMI) (Allan & Allan, 2013), it would be worthwhile to probe associations with longer-term eating behaviour, as these measures would be less susceptible to instances of opportunistic behaviour as well.

Having said that, results reveal a potential novel pathway through which a superior location memory for high-calorie foods could indirectly

bias future choice preferences towards calorie-rich options. By lowering the perceived difficulty of finding high-calorie items, the high-calorie spatial memory bias could make these options seem relatively more convenient to obtain within a diverse food environment. Convenience, in turn, is an established value that individuals negotiate, and often prioritize, during the food decision-making process (Furst et al., 1996; Sobal et al., 2006). Indeed, our data showed a trend for a negative correlation between the reported difficulty of finding high-calorie items, and the proportion of high-calorie foods individuals later purchased. Thus, the present study yields new mechanistic insights on how the cognitive bias can translate into suboptimal (long-term) dietary outcomes within a modern foraging context (cf. Allan & Allan, 2013). Going forward, it would be interesting to explore possible bias implications on a larger scale of space, by extending investigations beyond a single resource “patch” and towards multiple food locations. For instance, the high-calorie spatial memory bias might also increase the frequency of visits made to unhealthy calorie-laden food locations (e.g. fast-food outlets).

Finally, the high-calorie bias in spatial memory was found to be expressed independently of the amount of attention individuals allocated to high-calorie (versus low-calorie) foods. This finding illustrates another functional design feature of the bias, aside from calorie-sensitivity. Namely, our results align with the operating characteristics of an autonomous or “automatic” spatial mechanism, given that its execution was also not dependent upon “higher level” processes (e.g. consciously articulated dietary preferences or motivations) in the present study (Evans & Stanovich, 2013; New et al., 2007; de Vries et al., 2020a; de Vries et al., 2020b). Collectively, these observations imply that the high-calorie bias in spatial memory may have been adaptive for sustaining a high habitual foraging efficiency, as it does not compete for valuable limited attentional resources that would have been required in other fitness-relevant activities, such as avoiding predators (Evans & Stanovich, 2013; Krasnow et al., 2011). Furthermore, the dissociation of the bias’ expression from volitional cognitive processes posits that interventional strategies targeting its downstream translation into eating behaviour may be more effective to pursue for healthy dietary regulation.

Taken together, our findings join an increasing literature base that position a food’s energy payoffs as an important factor in the operations of human spatial memory, and make a compelling case for an evolved (food) spatial processing system with calorie-sensitivity and automaticity built-in as functional design features. Such a spatial mechanism that was adaptive in our evolutionary past for energy-efficient foraging may now maladaptively potentiate high-calorie food choice, through altering perceptions of food search convenience.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author Contributions

R. de Vries, S. Boesveldt, and E. de Vet jointly conceptualized the theoretical framework and study design. R. de Vries developed study materials, collected and analyzed data, and wrote/edited the manuscript

under the supervision of S. Boesveldt and E. de Vet. S. Boesveldt and E. de Vet acquired funding for the research. All authors approved the final article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foodqual.2021.104338>.

References

- Allan, K., & Allan, J. L. (2013). An obesogenic bias in women’s spatial memory for high calorie snack food. *Appetite*, 67, 99–104.
- Allan, K., Jones, B. C., DeBruine, L. M., & Smith, D. S. (2012). Evidence of adaptation for mate choice within women’s memory. *Evolution and Human Behavior*, 33(3), 193–199.
- Adler, D. S., Bar-Oz, G., Belfer-Cohen, A., & Bar-Yosef, O. (2006). Ahead of the game: Middle and Upper Palaeolithic hunting behaviors in the southern Caucasus. *Current Anthropology*, 47(1), 89–118.
- Arrington, C. M., Carr, T. H., Mayer, A. R., & Rao, S. M. (2000). Neural mechanisms of visual attention: Object-based selection of a region in space. *Journal of Cognitive Neuroscience*, 12(Supplement 2), 106–117.
- Becker, D. V., Kenrick, D. T., Guerin, S., & Maner, J. K. (2005). Concentrating on beauty: Sexual selection and sociospatial memory. *Personality and Social Psychology Bulletin*, 31(12), 1643–1652.
- Bird, D. W., Bird, R. B., & Coddling, B. F. (2009). In pursuit of mobile prey: Martu hunting strategies and archaeofaunal interpretation. *American Antiquity*, 74(1), 3–29.
- Blechert, J., Meule, A., Busch, N. A., & Ohla, K. (2014). Food-pics: An Image Database for Experimental Research on Eating and Appetite (p. 5). *Frontiers in Psychology*.
- Bocchi, A., Palmiero, M., Nori, R., Verde, P., & Piccardi, L. (2019). Does spatial cognitive style affect how navigational strategy is planned? *Experimental Brain Research*, 237(10), 2523–2533.
- Bracis, C., & Mueller, T. (2017). Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proceedings of the Royal Society B: Biological Sciences*, 284(1855), 20170449.
- Breslin, P. A. (2013). An Evolutionary Perspective on Food and Human Taste. *Current Biology*, 23(9), R409–R418.
- de Bruijn, S. E., de Vries, Y. C., de Graaf, C., Boesveldt, S., & Jager, G. (2017). The reliability and validity of the macronutrient and taste preference ranking task: A new method to measure food preferences. *Food Quality and Preference*, 57, 32–40.
- Castellanos, E. H., Charboneau, E., Dietrich, M. S., Park, S., Bradley, B. P., Mogg, K., & Cowan, R. L. (2009). Obese adults have visual attention bias for food cue images: Evidence for altered reward system function. *International Journal of Obesity*, 33(9), 1063–1073.
- Conlin, J. A. (2009). Getting around: Making fast and frugal navigation decisions. *Progress in Brain Research*, 174, 109–117.
- Cordain, L., Miller, J. B., Eaton, S. B., Mann, N., Holt, S. H., & Speth, J. D. (2000). Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. *The American Journal of Clinical Nutrition*, 71(3), 682–692.
- Cosmides, L., & Tooby, J. (1997). *Evolutionary psychology: A primer*. Retrieved July 5, 2021, from the University of California, Santa Barbara, Center for Evolutionary Psychology Website: <http://www.psych.ucsb.edu/research/cep/primer.html>.
- Cunningham, E., & Janson, C. (2007). Integrating information about location and value of resources by white-faced saki monkeys (*Pithecia pithecia*). *Animal cognition*, 10(3), 293–304.
- Eaton, S. B. (2006). The ancestral human diet: What was it and should it be a paradigm for contemporary nutrition? *Proceedings of the Nutrition Society*, 65(1), 1–6.
- Eaton, S. B., Konner, M., & Shostak, M. (1988). Stone agers in the fast lane: Chronic degenerative diseases in evolutionary perspective. *The American Journal of Medicine*, 84(4), 739–749.
- Evans, J. S. B., & Stanovich, K. E. (2013). Dual-process theories of higher cognition: Advancing the debate. *Perspectives on Psychological Science*, 8(3), 223–241.
- Furst, T., Connors, M., Bisogni, C. A., Sobal, J., & Falk, L. W. (1996). Food choice: A conceptual model of the process. *Appetite*, 26(3), 247–266.
- Giel, K. E., Friederich, H. C., Teufel, M., Hautzinger, M., Enck, P., & Zipfel, S. (2011). Attentional processing of food pictures in individuals with anorexia nervosa—An eye-tracking study. *Biological Psychiatry*, 69(7), 661–667.
- Graham, R., Hoover, A., Ceballos, N. A., & Komogortsev, O. (2011). Body mass index moderates gaze orienting biases and pupil diameter to high and low calorie food images. *Appetite*, 56(3), 577–586.
- Hegarty, M., Montello, D. R., Richardson, A. E., Ishikawa, T., & Lovelace, K. (2006). Spatial abilities at different scales: Individual differences in aptitude-test performance and spatial-layout learning. *Intelligence*, 34(2), 151–176.
- Hendrikse, J. J., Cachia, R. L., Kothe, E. J., McPhie, S., Skouteris, H., & Hayden, M. J. (2015). Attentional biases for food cues in overweight and individuals with obesity: A systematic review of the literature. *Obesity Reviews*, 16(5), 424–432.
- Janson, C. H. (1998). Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. *Animal Behaviour*, 55(5), 1229–1243.
- Janmaat, K. R., Polansky, L., Ban, S. D., & Boesch, C. (2014). Wild chimpanzees plan their breakfast time, type, and location. *Proceedings of the National Academy of Sciences*, 111(46), 16343–16348.

- Kozlowski, L. T., & Bryant, K. J. (1977). Sense of direction, spatial orientation, and cognitive maps. *Journal of Experimental Psychology: human perception and performance*, 3(4), 590.
- Krasnow, M. M., Truxaw, D., Gaulin, S. J., New, J., Ozono, H., Uono, S., ... Minemoto, K. (2011). Cognitive adaptations for gathering-related navigation in humans. *Evolution and Human Behaviour*, 32(1), 1–12.
- Lieberman, L. S. (2006). Evolutionary and anthropological perspectives on optimal foraging in obesogenic environments. *Appetite*, 47(1), 3–9.
- MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, 100(916), 603–609.
- Maguire, E. A., Burgess, N., & O'Keefe, J. (1999). Human spatial navigation: Cognitive maps, sexual dimorphism, and neural substrates. *Current opinion in Neurobiology*, 9(2), 171–177.
- McCormack, H. M., David, J. D. L., & Sheather, S. (1988). Clinical applications of visual analogue scales: A critical review. *Psychological Medicine*, 18(4), 1007–1019.
- Meiselman, H. L. (1996). The contextual basis for food acceptance, food choice and food intake: the food, the situation and the individual. In *Food Choice, Acceptance and Consumption* (pp. 239–263). Springer, Boston, MA.
- Meule, A., Skirde, A. K., Freund, R., Vögele, C., & Kübler, A. (2012). High-calorie food-cues impair working memory performance in high and low food cravers. *Appetite*, 59(2), 264–269.
- Moffat, S. D., Hampson, E., & Hatzipantelis, M. (1998). Navigation in a “virtual” maze: Sex differences and correlation with psychometric measures of spatial ability in humans. *Evolution and Human Behavior*, 19(2), 73–87.
- Murakoshi, S., & Kawai, M. (2000). Use of knowledge and heuristics for wayfinding in an artificial environment. *Environment and Behavior*, 32(6), 756–774.
- Myers, K. P. (2018). The convergence of psychology and neurobiology in flavor-nutrient learning. *Appetite*, 122, 36–43.
- Nairne, J. S., & Pandeirada, J. N. (2008). Adaptive memory: Remembering with a stone-age brain. *Current Directions in Psychological Science*, 17(4), 239–243.
- New, J., Krasnow, M. M., Truxaw, D., & Gaulin, S. J. (2007). Spatial Adaptations for Plant Foraging: Women Excel and Calories Count. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1626), 2679–2684.
- O'Neill, M. J. (1992). Effects of familiarity and plan complexity on wayfinding in simulated buildings. *Journal of Environmental Psychology*, 12(4), 319–327.
- Pazzaglia, F., Cornoldi, C., & De Beni, R. (2000). Differenze individuali nella rappresentazione dello spazio: Presentazione di un questionario autovalutativo [Individual differences in spatial representation and in orientation ability: Presentation of a self-report questionnaire]. *Giornale Italiano di Psicologia*, 3, 627–650.
- Pazzaglia, F., & Taylor, H. A. (2007). Perspective, instruction, and cognitive style in spatial representation of a virtual environment. *Spatial Cognition and Computation*, 7(4), 349–364.
- Piccardi, L., Berthoz, A., Baulac, M., Denos, M., Dupont, S., Samson, S., & Guariglia, C. (2010). Different spatial memory systems are involved in small-and large-scale environments: Evidence from patients with temporal lobe epilepsy. *Experimental Brain Research*, 206(2), 171–177.
- Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2(1), 369–404.
- Simpson, S. J., Batley, R., & Raubenheimer, D. (2003). Geometric analysis of macronutrient intake in humans: The power of protein? *Appetite*, 41(2), 123–140.
- Sobal, J., Bisogni, C. A., Devine, C. M., & Jastran, M. (2006). A conceptual model of the food choice process over the life course. *Frontiers in Nutritional Science*, 3, 1.
- Stiner, M. C., & Bar-Yosef, O. (2005). *The faunas of Hayonim Cave, Israel: A 200,000-year record of Paleolithic diet, demography, and society*, No. 48. Harvard University Press.
- Stiner, M. C., & Kuhn, S. L. (2009). Paleolithic diet and the division of labor in Mediterranean Eurasia. In *The Evolution of Hominin Diets* (pp. 157–169). Dordrecht: Springer.
- Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York: Oxford University Press.
- Tooby, J., & Cosmides, L. (2005). Conceptual foundations of evolutionary psychology. In D. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 5–67). Hoboken, NJ: Wiley.
- Tudor-Locke, C., Williams, J. E., Reis, J. P., & Pluto, D. (2002). Utility of pedometers for assessing physical activity. *Sports Medicine*, 32(12), 795–808.
- Tuorila, H., Lähteenmäki, L., Pohjalainen, L., & Lotti, L. (2001). Food Neophobia Among the Finns and Related Responses to Familiar and Unfamiliar foods. *Food Quality and Preference*, 12(1), 29–37.
- de Vries, R., Morquecho-Campos, P., de Vet, E., de Rijk, M., Postma, E., de Graaf, K., Engel, B., & Boesveldt, S. (2020a). Human spatial memory implicitly prioritizes high-calorie foods. *Scientific Reports*, 10, 15174.
- de Vries, R., de Vet, E., de Graaf, K., & Boesveldt, S. (2020b). Foraging minds in modern environments: High-calorie and savoury-taste biases in human food spatial memory. *Appetite*, 104718.
- Werthmann, J., Roefs, A., Nederkoorn, C., Mogg, K., Bradley, B. P., & Jansen, A. (2011). Can (not) take my eyes off it: Attention bias for food in overweight participants. *Health Psychology*, 30(5), 561.
- World Cancer Research Fund/American Institute for Cancer Research. (2007). *Food, Nutrition, Physical Activity, and the Prevention of Cancer: A Global Perspective*. Washington DC: AICR.
- Yarmolinsky, D. A., Zuker, C. S., & Ryba, N. J. (2009). Common Sense About Taste: From Mammals to Insects. *Cell*, 139(2), 234–244.
- Yeomans, M. R. (2006). The role of learning in development of food preferences. *Frontiers in Nutritional Science*, 3, 93.