



Foraging minds in modern environments: High-calorie and savory-taste biases in human food spatial memory



Rachelle de Vries^{a,b,*}, Emely de Vet^b, Kees de Graaf^a, Sanne Boesveldt^a

^a Wageningen University & Research, Sensory Science & Eating Behavior - Division of Human Nutrition & Health, P.O. Box 17, 6700, AA Wageningen, the Netherlands

^b Wageningen University & Research, Consumption & Healthy Lifestyles, Postbus 8130, 6700, EW Wageningen, the Netherlands

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ABSTRACT

Human memory may show sensitivity to content that carried fitness-relevance throughout evolutionary history. We investigated whether biases in human food spatial memory exist and influence the eating behavior of individuals within the modern food environment. In two lab studies with distinct samples of 88 participants, individuals had to re-locate foods on a map in a computer-based spatial memory task using visual (Study 1) or olfactory (Study 2) cues that signaled sweet and savory high- and low-calorie foods. Individuals consistently displayed an enhanced memory for locations of high-calorie and savory-tasting foods – regardless of hedonic evaluations, personal experiences with foods, or the time taken to encode food locations. However, we did not find any clear effects of the high-calorie or savory-taste bias in food spatial memory on eating behavior. Findings highlight that content matters deeply for the faculty of human food spatial memory and indicate an implicit cognitive system presumably attuned to ancestral priorities of optimal foraging.

1. General introduction

The prevailing view in cognitive psychology assumes that human memory consists largely of domain-general mechanisms that are insensitive to the content which is processed (Tulving & Thomson, 1973). Conversely, advocates of a more functionalist agenda of human cognition contend that much like other biological systems, memory and its operational systems did not evolve in a vacuum (Nairne & Pandeirada, 2008). Rather, memory faculties were subject to the constraints of nature's criteria and thus should be functionally designed to preferentially process fitness-relevant information and solve adaptive problems (Nairne & Pandeirada, 2010).

One such adaptive problem encountered across species is the efficient location and acquisition of nutritional resources (Schoener, 1971). This research entertains the notion that natural selection processes shaped a cognitive adaptation that enabled ancestral humans to thrive within erratic food habitats of the past – a bias in spatial memory for high-calorie foods.

During the substantial majority of human evolution, hunter-gatherers needed to forage intensively to attain sufficient nutrition (Eaton, 2006). Survival was thus contingent upon an individual's ability to efficiently identify and gather high-quality resources within a complex

and variable physical environment, as well as to retrace those resources as they became valuable over time, by using input from various sensory modalities (New et al., 2007; Winterhalder, 1981, pp. 13–35). As a result, natural selection pressures might have favored a functional 'bias' in spatial processing that enables the effortless registration and memory of locations of valuable calorie-dense foods (Krasnow et al., 2011; New et al., 2007). Such an inbuilt spatial processing bias entails a preference in location memory for high-calorie foods, irrespective of individual hedonic evaluations or personal experiences. It follows that a once adaptive spatial memory mechanism could yield adverse obesogenic effects for individuals with a greater expression of the bias in present-day food-replete settings, by enhancing the navigational ease through which unhealthy high-calorie items are obtained and subsequently consumed (Allan & Allan, 2013). However, literature on a potential high-calorie bias in spatial memory – and its implications for food choice and dietary intake within a modern food context – remains relatively nascent. Only two pieces of evidence have accumulated so far: New, Krasnow, Truxaw, and Gaulin (2007) were the first to discover that a food's caloric content positively predicted the accuracy with which (blinded) individuals pointed to previously visited vendor locations within an outdoor farmers' market. Subsequently, Allan and Allan (2013) found that an improved spatial memory for high-calorie snacks

* Corresponding author. Wageningen University & Research, Sensory Science & Eating Behavior - Division of Human Nutrition & Health, P.O. Box 17, 6700, AA Wageningen, the Netherlands.

E-mail addresses: rachelle.devries@wur.nl (R. de Vries), emely.devvet@wur.nl (E. de Vet), kees.degraaf@wur.nl (K. de Graaf), sanne.boesveldt@wur.nl (S. Boesveldt).

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(versus low-calorie fruits and vegetables) was associated with a higher BMI in women, although they did not explicitly test the existence of the high-calorie spatial memory bias itself. Therefore, the present paper represents the first to systematically investigate the expression and potential behavioral effects of food-specific biases in human spatial memory under rigorous lab conditions.

It is similarly unknown what food- or person-specific characteristics are associated with this cognitive bias. Optimal foraging models of evolutionary ecology posit taste to be one such food-related factor. Taste perception is thought to bear great relevance to the course of hominid evolution, with sweet and savory (i.e. umami) representing the two dominant 'appetitive' taste modalities across many species (Breslin, 2013; Yarmolinsky, Zuker, & Ryba, 2009). Namely, tastes are thought to have aided hunter-gatherers in productive food selection by signaling specific nutritional contents of consumed resources – sweet for the presence of (energy-rich) sugars and carbohydrates, and savory for amino-acid or protein content (Breslin, 2013; Teo et al., 2018; Yarmolinsky et al., 2009, although see van Langeveld et al., 2017 and Lease, Hendrie, Poelman, Delahunty, & Cox, 2016 for discussion on the relationship between sweet taste and energy content). As sweet- and savory-tasting foods (e.g. fruit versus meat) serve distinct functional roles and varying priorities were potentially placed on energy versus nutrient (protein) intake during foraging, differences in spatial memory adaptations may have manifested between the respective taste modalities and their associated foods (Eaton, 2006).

The magnitude of the high-calorie bias in food spatial memory may also vary meaningfully with person-specific characteristics such as (trait) eating styles or reward sensitivity. Within an evolutionary context, a high reactivity to external (rewarding) cues is assumed to have carried a survival advantage under conditions of resource constraint (Lieberman, 2006; Ulijaszek, 2002). Based on empirical observations, individual propensities for restrained eating, external eating, as well as sensitivity to rewarding stimuli, facilitate overeating through pathways such as disruptions in self-control and are positively associated with BMI (Castellanos et al., 2009; Davis et al., 2007; van Strien, Frijters, Bergers, & Defares, 1986). In a similar vein, restrained eaters, external eaters, and those high in reward sensitivity are documented to exhibit marked attentional biases towards high-calorie food stimuli (Hou et al., 2011; Meule, Vögele, & Kübler, 2012; Tapper, Pothos, & Lawrence, 2010). However, whether any of the former outcomes are systematically associated with a high-calorie bias in spatial memory has not been investigated to date and merits further exploration.

The aim of the present research was two-fold: In two lab studies, we sought to demonstrate the existence of a high-calorie bias in human food spatial memory and its consequent effects on eating behavior and objective long-term markers of dietary intake. As a secondary objective, we explored potential food (i.e. Taste) and person-specific factors (i.e. Eating Styles and Reward Sensitivity) associated with an enhanced location memory for high-calorie foods. To this end, a computerized food spatial memory paradigm was used with varying caloric density (High versus Low) and taste (Sweet versus Savory) conditions. Two classes of sensory food stimuli with evolutionary significance to the process of food navigation were used in the experimental paradigm: visual (Study 1) and olfactory (Study 2) food cues.

In line with previous findings, the following outcomes were hypothesized:

H1A. Individuals display a greater overall accuracy in spatial memory for high-calorie foods compared to low-calorie alternatives – regardless of hedonic evaluations or familiarity with foods.

H1B. The high-calorie bias in spatial memory predicts unhealthy eating behaviors (e.g. food choice) and higher anthropometric markers of dietary intake (e.g. BMI).

H2. Taste and person-specific factors interact with the caloric density of foods, such that sweet and savory high-calorie food locations are

differentially retained, and an enhanced reward sensitivity – as well as restrained and external eating tendency – confers a larger degree of bias expression.

2. Study 1

2.1. Methodology

2.1.1. Participants

A total of 88 healthy university students (68% female; $M_{Age} = 24.7$ years, $SD = 2.7$, range 18–35 years) from various ethnic (65% Caucasian; 23% Asian; 9% Latino; 3% African and Arab) and educational backgrounds (76% postgraduates; 24% undergraduates) took part in the research. The sample size was determined by *a priori* power calculations: On the basis of previous work (Allan & Allan, 2013; New et al., 2007), we estimated an effect size f^2 of 0.14 and power of 0.80 for the association between the high-calorie spatial memory bias and BMI (as a proxy for long-term dietary intake). The final sample size would also allow us to systematically adjust for any order effects, by ensuring that an equal number of individuals were assigned to the different treatment orders. Participants were limited to the BMI range of 18.5–30 kg/m² ($M = 22.5$ kg/m², $SD = 2.2$), to control for differential cognitive processing of food stimuli in extreme (i.e. underweight < 18.5 kg/m² and obese > 30 kg/m²) weight classes (Castellanos et al., 2009; Giel et al., 2011). Furthermore, individuals did not take part in the study when reporting a psychological or physical intolerance to tested foods (e.g. meat), or in case of a (self-reported) medical history of eating or psychiatric disorders. Recruitment was achieved through the advertisement of study posters and flyers on campus buildings, social media platforms, and participant mailing lists. After providing written informed consent and completing two test sessions, participants were compensated with a 10 euro giftcard. This study received ethical approval from the Social Sciences Ethics Committee of Wageningen University, and was preregistered on the Open Science Framework database (Project URL: osf.io/ufrqv).

2.1.2. Design

The current study had a 2 (Caloric Density: High versus Low) by 2 (Taste: Sweet versus Savory) within-subjects crossover design. Participants were randomly assigned to complete four caloric density - taste conditions (High-Sweet [H_SW] e.g. Chocolate; High-Savory [H_SA] e.g. Chips; Low-Sweet [L_SW] e.g. Fruit; Low-Savory [L_SA] e.g. Vegetables) in two successive test sessions separated by a washout period of (at least) one week. Within a test session, each participant was required to perform a spatial memory task for two conditions. Importantly, the final randomization of orders was balanced; an equal number of individuals began in each caloric density - taste condition.

2.1.3. Apparatus and Stimuli

2.1.3.1. Spatial memory task. The original E-Prime scripts and university campus setting of Allan and Allan (2013) were used to test food spatial memory. Participants were asked to imagine that an international food market – encompassing 24 food stalls – was taking place on a (unfamiliar) university campus. Depending on the treatment condition, participants were then shown a sequence of 12 pictures of either (sweet/savory) high-calorie items or low-calorie alternatives, followed by an image of a university campus map showcasing all possible stall locations ($N = 24$), at a fixed duration of three seconds each. Next, the locations of the stalls selling each food item ($N = 12$) were sequentially indicated 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, and this was done at a self-determined pace. Following a two-minute break, participants were exposed to a series of 12 spatial memory tests in which they were randomly presented with one of the previously shown 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 ($N = 24$) was displayed for the spatial memory tests, and a stall location could be selected more than once. Assigned stall locations did not overlap for foods within a test session.

2.1.3.2. Stimulus presentation. The psychology software tool E-prime (version 2.0) was used for stimulus presentation and subsequent spatial memory tasks. Computers were standardized across the parameters of screen size (15.6 inches), resolution (1920 x 1080), and refresh rate (60 Hz). The order of stimulus presentation and the stimuli itself (i.e. food-location pairs within a campus map) were randomized differently for each participant.

2.1.3.3. Food images. Images of (sweet/savory) high- and low-calorie foods were obtained from the *Food Pics* database, where available pictures are homogenous with respect to resolution (600 x 450 pixels), color depth (96 dpi), background color (white), and camera distance (~80 cm) (Blechert, Meule, Busch, & Ohla, 2014). A set of 12 (unbranded) food pictures was selected to represent each caloric density - taste category - encompassing fruits and vegetables for the low-calorie condition, and baked and fried goods as high-calorie variants [Fig. 1]. 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, de Vries, de Graaf, Boesveldt, & Jager, 2017; World Cancer Research Fund/American Institute for Cancer Research, 2007). Chosen food stimuli ($N = 48$; see *Food Pics* Catalogue Numbers in the Supplemental Material) were matched on recognizability and subjective palatability across caloric density and taste groups using metadata from the *Food Pics* database [all p s > .05], and additionally piloted in a separate sample of students ($N = 32$, 53% female; $M_{Age} = 23.6$ years, $SD = 2.75$) to ensure consistencies in caloric content, taste, and healthiness perceptions (see Supplementary Material for the pilot questionnaire).

The final selection of high-calorie images displayed a significantly greater mean caloric density (High-calorie: $M = 368.40$ kcal/100g, $SD = 108.40$; Low-calorie: $M = 30.21$ kcal/100g, $SD = 16.61$), $t(24) = 15.11$, $p < .001$, as well as total energy content (High-calorie: $M = 638.37$ kcal/image, $SD = 731.72$; Low-calorie: $M = 135.96$ kcal/image, $SD = 234.84$), $U = 72.00$, $p < .001$, compared to the low-calorie group. High-calorie images were also perceived as higher in caloric content (High-calorie: $M = 76.44$ mm, $SD = 14.92$; Low-calorie: $M = 24.40$ mm, $SD = 17.45$), $Z = -11.63$, $p < .001$, and less healthy (High-calorie: $M = 24.24$ mm, $SD = 19.30$; Low-calorie: $M = 77.53$ mm, $SD = 15.92$), $Z = -11.36$, $p < .001$, than low-calorie images. Likewise, sweet pictures scored higher on sweet taste

expectations (Sweet: $M = 74.87$ mm, $SD = 17.29$; Savory: $M = 24.05$ mm, $SD = 20.60$), $Z = -11.45$, $p < .001$, and savory pictures were valued greater on expected savoriness (Savory: $M = 58.20$ mm, $SD = 25.00$; Sweet: $M = 34.27$ mm, $SD = 29.95$), $Z = -7.29$, $p < .001$.

2.2. Procedure

Prior to starting, participants were informed that the experiment aimed to investigate individuals' memory for specific foods. The spatial faculty of memory was intentionally not emphasized to diffuse suspicions on the true aim of the study, and post-hoc (open-ended funneling) debriefing interviews confirmed the efficacy of the cover story. Participants were also informed that good performance would earn them a prize at the end of the experiment, in an effort to disguise our (covert) food choice measure and motivate participants to complete tasks as accurately as possible. Hunger states were standardized before testing by instructing individuals to consume their habitual meals or snacks no later than two hours - and no sooner than 45 min - before test sessions, during which only water intake was permitted.

Upon arrival, participants' height and weight were recorded. After, participants were directed to and seated in isolated testing booths fitted with a laptop. Demographics (e.g. subjective SES), hunger state, restrained eating, external eating, and reward sensitivity data were first collected via a questionnaire. Individuals then had to perform a series of computer-based spatial memory tasks (adapted from Allan and Allan (2013), see detailed explanation above): A practice trial that involved the encoding and recall of (non-food) object locations was first carried out, to familiarize participants with the spatial memory task. Participants then proceeded to complete the actual spatial memory task with food images from the first caloric density- taste condition. After finishing, they evaluated their (perceived) performance on the preceding task. Following a brief (five minute) intermission, the protocol was repeated for the other assigned caloric density - taste condition. A test session lasted, on average, 40 min.

After participants completed the study procedure for the remaining two caloric density- taste conditions approximately one week later in the second test session, they answered questions about healthy eating goals. Regardless of performance, participants were then led individually to a cubicle and presented with a preselected array of foods. Individuals were instructed to choose one food as their prize for performing and were left alone to make their decision. Results of the covert food choice task were noted down by the experimenter.

2.2.1. Measurements

2.2.1.1. Primary outcome variables. Spatial memory accuracy for

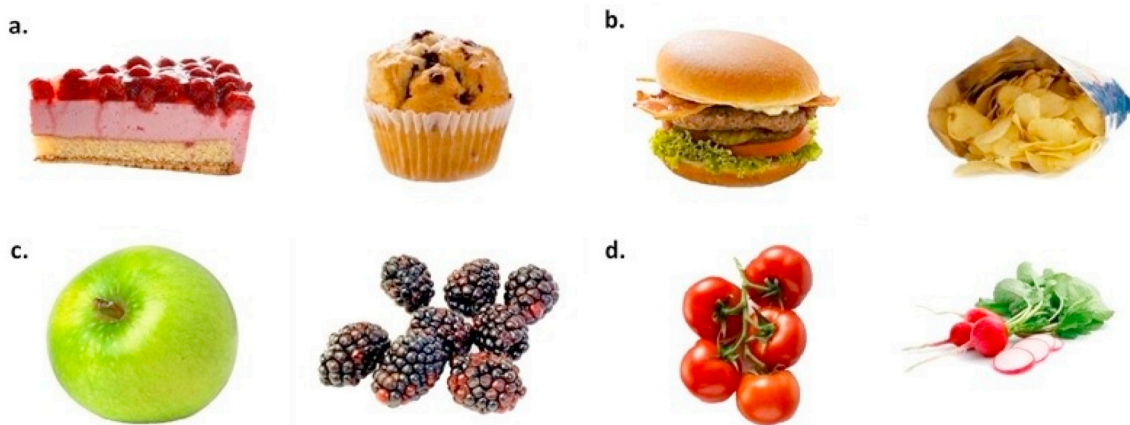


Fig. 1. Selection of food images from the *Food Pics* database (Blechert et al., 2014). Examples of (a) high-sweet, (b) high-savory, (c) low-sweet, and (d) low-savory items.

(sweet/savory) high- and low-calorie foods was tabulated as the average 'pointing error' or Euclidian distance (D) between true and indicated stall locations of each food type (cf. Allan & Allan, 2013; Nairne, VanArsdall, Pandeirada, & Blunt, 2012). Consequently, lower D scores denote a higher accuracy in food spatial memory. *Spatial memory bias* for (sweet/savory) high-calorie foods was operationalized as the discrepancy in spatial memory accuracy between high- versus low-calorie foods ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) (cf. Allan & Allan, 2013). Accordingly, negative values indicate an enhanced spatial memory for calorie dense foods.

2.2.1.2. Secondary outcome variables. Food choice was assessed through the means of a covert forced-choice task, as a first step in exploring whether effects on relevant proximal aspects of eating behavior could manifest. A selection of foods comprising the previously tested caloric density - taste groups (H_SW: Chocolate bars; H_SA: Chips; L_SW: Apples; L_SA: snack tomatoes) was placed in wooden baskets and presented to participants individually at the conclusion of testing as a reward. Foods on offer represented small 'snack' items and were deemed appropriate within a university and day setting to control for possible contextual effects on choice. Moreover, locations of food groups within the baskets were randomized in each test session to rule out accessibility or convenience issues.

In addition, height (m) and weight (kg) measures were collected with an electronic scale (SECA 704) and stadiometer (SECA 213) to obtain accurate BMI (kg/m^2) values.

2.2.1.3. Predictor variables. Individual predispositions for *Restrained* and *External Eating* were quantified through averaging associated subscales of the Dutch Eating Behavior Questionnaire (Cronbach's $\alpha = .86$ and 0.86 , respectively) (van Strien et al., 1986). Higher scores, from a possible range of 1–5, point at greater tendencies towards respective eating styles.

Furthermore, the Behavioral Activation System (BAS) scale was used to gauge individuals' degree of *Reward Sensitivity* (Carver & White, 1994). Scores range from 1 to 4 for all three BAS-related subscales (Reward Responsiveness; Drive; Fun Seeking), with lower values denoting greater behavioral activation sensitivities to rewarding stimuli. As two BAS subscales proved to have poor internal consistencies in our sample (Cronbach's $\alpha \leq 0.68$), scores of the three subscales were aggregated in order to form a more reliable total BAS measure (Cronbach's $\alpha = .79$). In doing so, the number of parameters to be estimated in statistical models was also favorably reduced relative to our sample size.

2.2.1.4. Control measures. To account for extraneous effects of 'wanting' of food types on spatial memory accuracy, we instructed participants to rate each item's *Desirability* by indicating on a 100 mm VAS (anchored from "Not At All" to "Very Much") their desire to eat the displayed food item (see Food Stimuli Ratings in the Supplemental Material). In addition, effects of individual exposure to a food type were controlled through the use of a five-item *Familiarity* scale (Tuorila, Lähteenmäki, Pohjalainen, & Lotti, 2001). Two socioeconomic indexes – postal codes and the 10-point MacArthur Subjective Social Status Scale – were also recorded owing to the respective relationships of suboptimal dietary patterns with low neighborhood and (subjective) individual SES (Goodman et al., 2001; Lakerveld et al., 2015). For the former, postal codes were transformed into z -distributed scores of neighborhood SES using information from the *Statusscores* database of the Netherlands Institute for Social Research (SCP *Statusscores*, 2017).

As dietary behaviors and BMI may likewise be contingent upon the strength of an individual's explicit nutritional intentions, 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" (Raghoobar, van Kleef, de Vet, under review). *Perceived Performance*

was additionally measured on a 100 mm VAS (anchored from "Not Good At All" to "Very Good"), as proxy of awareness of the bias. Finally, a general questionnaire documented both pertinent demographic characteristics (e.g. *Sex, Age, Ethnicity*) and *Hunger* states (100 mm VAS anchored from "Not At All" to "Very Much") at encoding.

2.2.2. Data Analysis

Data were analyzed using IBM SPSS Statistics 23 with statistical significance defined as $p < .05$. A linear mixed effects model was chosen to analyze food spatial memory data, as it represents a flexible and robust manner of modelling continuous outcomes when the assumption of independent errors is relaxed (Krueger & Tian, 2004). With regards to linear mixed effects modelling, a backward elimination approach was adopted for model selection, given that it is less prone to underfitting data and yielding biased (fixed effect) estimates (Cheng, Edwards, Maldonado-Molina, Komro, & Muller, 2010). First, the covariance structure of saturated models (see below) was determined based on Restricted Maximum Likelihood (REML) likelihood ratio tests using the -2 log likelihood ($-2LL$) test statistic; fixed effects were subsequently finalized based on Maximum Likelihood (ML) ordinary likelihood ratio tests using the $-2LL$ test statistic. In either case, a selection was made on the basis of parsimony and final models were refitted with REML estimations. Hypotheses and corresponding statistical analyses were registered prior to observing data. Slightly deviating from our pre-registration form, *perceived performance* ratings were correlated with actual spatial memory performance and compared between caloric density - taste conditions.

2.2.2.1. Caloric density, taste, person-specific factors, and food spatial memory accuracy (H_{1A} and H_2). To determine whether the accuracy of food spatial memory varies meaningfully with caloric content or taste aspects, we formulated a random intercept and slope linear mixed model with main and interaction effects of *Caloric Density* and *Taste* as fixed factors, *Participant* and *Test Session* as random factors (covariance structure: Unstructured), *Sex, Age, Ethnicity, Neighborhood SES, Subjective SES, Taste Order, Desirability, Familiarity*, and averaged *Hunger* scores as covariates, and *Spatial Memory Accuracy (D)* as the dependent variable.

To examine person-specific factors that could predict the magnitude of food spatial memory accuracy, we included main and interaction effects (with *Caloric Density*) of *Restrained Eating, External Eating*, and *Reward Sensitivity* as predictor variables.

2.2.2.2. Spatial memory bias for high-calorie foods and food choice (H_{1B}). To ascertain the effects of a high-calorie bias in spatial memory on eating behavior, we conducted a binomial logistic regression ($N = 1$; simultaneous entry method) with the log odds ratio of *High-Calorie Food Choice* as the dependent variable and *Sex, Age, Ethnicity, Neighborhood SES, Subjective SES, Restrained Eating, External Eating, Reward Sensitivity, Desirability of High- and Low-calorie foods, Familiarity with High- and Low-calorie foods, Hunger* ratings of the final test session, *Healthy Eating Goals* and *Spatial Memory Bias for High- versus Low-calorie foods ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$)* as predictor factors.

2.2.2.3. Spatial memory bias for high-calorie foods and BMI (H_{1B}). A multiple linear regression ($N = 1$; simultaneous entry method) was performed on BMI, with *Sex, Age, Ethnicity, Neighborhood SES, Subjective SES, Restrained Eating, External Eating, Reward Sensitivity, Desirability of High- and Low-calorie foods, Familiarity with High- and Low-calorie foods, Healthy Eating Goals*, and *Spatial Memory Accuracy of respective food groups ($D_{\text{High Calorie}}$ and $D_{\text{Low Calorie}}$)* as predictors, to test whether food spatial memory would account for variation in long-term markers of dietary intake.

A final multiple linear regression model ($N = 1$; simultaneous entry method) was formulated to determine the relative effects of high- and low-calorie food spatial memory on BMI. Accordingly, *Sex, Age,*

Ethnicity, Neighborhood SES, Subjective SES, Restrained Eating, External Eating, Reward Sensitivity, Desirability of High- versus Low-calorie foods, Familiarity with High- versus Low-calorie foods, Healthy Eating Goals, and Spatial Memory Bias for High- versus Low-calorie foods ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) were entered as independent variables.

2.3. Results

2.3.1. Food Spatial Memory: Accuracy and Biases

The average pointing error in food spatial memory across all caloric density-taste conditions amounted to 129.71 pixels (95% CI = [124.09,135.32]). Perceived performance ratings mirrored actual spatial memory performance (i.e. pointing errors) moderately well ($r(350) = -.66; p < .001$). Perceived performance did not differ between caloric density ($\text{Mean difference}_{\text{High-Low calorie}} = 2.44$ mm, 95% CI = [-1.05,5.93]), $t(87) = 1.39, p = .169, d = 0.15$, or taste conditions ($\text{Mean difference}_{\text{Sweet-Savory}} = -2.99$ mm, 95% CI = [-7.38,1.39]), $t(87) = -1.36, p = .179, d = 0.14$.

Individuals displayed an overall enhanced memory for the location of high-calorie foods (i.e. smaller pointing error or D) relative to low-calorie counterparts, $F(1,4049) = 8.25, p = .004, \eta^2 = 0.002, 90\% \text{ CI } \eta^2 [0.0004, 0.005]$, indicating a bias in spatial memory in favor of high-calorie foods [Fig. 2]. Similarly, a main effect of Taste was shown with savory food locations more accurately recalled than sweet alternatives, $F(1,4063) = 36.35, p < .001, \eta^2 = 0.009, 90\% \text{ CI } \eta^2 [0.005, 0.01]$, suggesting the further presence of a savory-taste bias in food spatial memory. These bias effects persisted regardless of demographics (e.g. Sex), hedonic evaluations, or personal familiarity with respective foods. Controlling for the time participants spent rating foods and encoding corresponding locations only marginally attenuated Caloric Density effects on food spatial memory accuracy, $F(1,4047) = 5.46, p = .019$, and exerted no influence on Taste effects, $F(1,4064) = 29.04, p < .001$. The time participants took to recall food locations did not have an effect on spatial memory performance, $F(1,84) = 0.17, p = .679, \eta^2 = 0.002, 90\% \text{ CI } \eta^2 [0, 0.04]$.

2.3.2. Taste and Person-specific Moderators

The effect of Caloric Density on food spatial memory accuracy was not moderated by the Taste of a food, $F(1,86.14) = 0.88, p = .352, \eta^2 = 0.01, 90\% \text{ CI } \eta^2 [0, 0.07]$. Likewise, none of the included person-specific factors (i.e. Restrained Eating, External Eating, Reward Sensitivity) and associated interactions (with Caloric Density) predicted spatial memory performance (all $p > .05, \eta^2 = 0.001 [0,0.003], 3 \times 10^{-6} [0, 3 \times 10^{-4}]$, and $1 \times 10^{-4} [0,0.001]$, respectively).

2.3.3. Food Choice

Contrary to expectations, the high-calorie bias in spatial memory was not predictive of prospective high-calorie food choice (OR = 1.00, 95% CI = [0.99,1.01]), Wald statistic (1) = 0.01, $p = .925$. Rather, an individual's reported healthy eating intentions negatively predicted the odds of choosing a high-calorie food reward (OR = 0.49, 95% CI = [0.24,0.97]), Wald statistic (1) = 4.17, $p = .041$. A corresponding

analysis was conducted to explore the influence of the savory-taste bias in spatial memory on savory food choice. Similarly, the bias in spatial memory for savory-tasting foods was not associated with the odds of choosing a savory reward (OR = 1.01, 95% CI = [1.00,1.01]), Wald statistic (1) = 2.47, $p = .116$.

2.3.4. Spatial Memory Bias for High-calorie Foods in relation to BMI

BMI was not significantly associated with neither spatial memory for high- ($B = -0.004, 95\% \text{ CI} = [-0.01,0.002]$), $t(72) = -1.31, p = .194$, nor low-calorie food items ($B = .002, 95\% \text{ CI} = [-0.004,0.01]$), $t(72) = 0.64, p = .527$. Taking into account the relative difference in high- versus low-calorie food spatial memory (i.e. the high-calorie spatial memory bias), the high-calorie bias in spatial memory was likewise not predictive of BMI ($B = -0.003, 95\% \text{ CI} = [-0.01,0.002]$), $t(75) = -1.18, p = .122$. Conversely, an individual's Healthy Eating Goals, Sex, and Desirability (bias) for high-calorie foods were significant correlates across statistical models (see Table S1 in the Supplemental Material for the complete statistical output).

2.4. Interim Discussion

Using visual food cues in a controlled lab setting, results show that individuals displayed a more accurate memory for high-calorie food locations relative to low-calorie counterparts. Interestingly, a main effect of taste was found, as individuals also better remembered locations of savory- as opposed to sweet-tasting foods. These effects were not explicated by differences in hedonic evaluations of foods, personal familiarity with foods, or the (objective) time taken to encode and recall food locations. The magnitude of the high-calorie bias was not further moderated by eating style tendencies or reward sensitivity. Finally, the high-calorie spatial memory bias elicited small and non-significant changes in prospective food choice and BMI, whereas an individual's healthy eating goals was largely associated with both a lower likelihood of high-calorie food choice and BMI.

Given that olfaction is an evolutionary old (anticipatory) sense that is intrinsically linked to spatial memory and food decision making (Boesveldt & de Graaf, 2017; Dahmani et al., 2018), Study 2 investigated whether biases in food spatial memory would likewise manifest with odors signaling (sweet/savory) high- and low-calorie food items. The sense of smell is important across foraging species for navigational tasks such as locating food sources, and the ability of humans to utilize odor information as spatial cues appears to be intact (Jacobs, 2012; Schifferstein, Smeets, & Postma, 2009). Moreover, in light of the fact that the previous food choice measure encompassed a limited variety of foods and "reward" connotations may have influenced decision making, Study 2 explored potential effects of biases in food spatial memory on a wider spectrum of eating-related outcomes. We included a validated measure of food preference – an established psychological determinant of food choice – which reliably predicts individual preference for a large assortment of (sweet/savory) high- and low-calorie products (de Bruijn et al., 2017; Furst, Connors, Bisogni, Sobal, & Falk, 1996; Yeomans, 2006). Finally, in addition to BMI, we

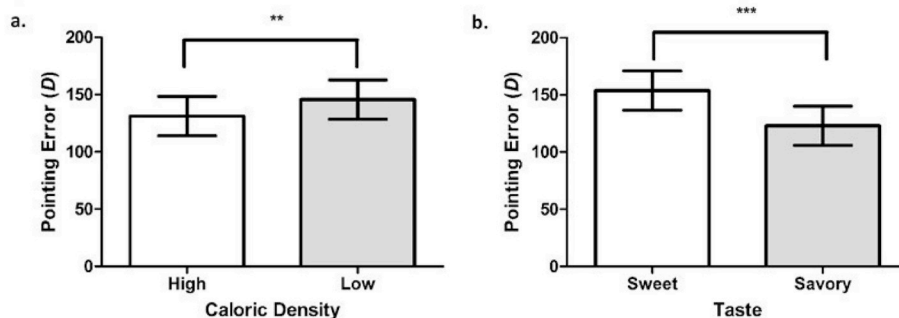


Fig. 2. Spatial memory for (a) Caloric Density and (b) Taste food groups. Spatial memory accuracy was operationalized as the "pointing error" or distance in pixels (D) between true and indicated food locations, with lower D values denoting a higher accuracy in food spatial memory. A double asterisk indicates a significant difference with a p value lower than 0.01 and a triple asterisk indicates a significant difference with a p value lower than 0.001. Error bars represent 95% confidence intervals.

Table 1
Food odors used in the present study.

Caloric Density-Taste Condition	Odor Quality	Kcal/100g food counterpart	Company	IPC	Concentration (%) in solvent
<i>H_SW</i>	Chocolate	531 ^a	IFF ^c	10810180	5% in PG ^d
<i>H_SW</i>	Caramel (Dulce de Leche)	382 ^b	IFF	15062070	4% in PG
<i>H_SW</i>	Vanilla	288 ^b	IFF	10860896	4% in PG
<i>H_SW</i>	Apple bake	237 ^b	IFF	10927267	3.4% in PG
<i>H_SA</i>	Butter Popcorn	535 ^b	IFF	10922603	2% in PG
<i>H_SA</i>	Roast Beef	236 ^b	IFF	10924987	0.04% in demi water
<i>H_SA</i>	Roasted Peanuts	577 ^a	IFF	10809896	1% in PG
<i>H_SA</i>	Bacon	505 ^a	IFF	SC753578	0.20% In demi water
<i>L_SW</i>	Melon	30 ^a	IFF	15025874	2% in PG
<i>L_SW</i>	Pineapple	57 ^a	IFF	10866148	1% in PG
<i>L_SW</i>	Pear	55 ^a	IFF	10809904	1% in PG
<i>L_SW</i>	Blackcurrant	53 ^a	IFF	10810572	0.80% in PG
<i>L_SA</i>	Asparagus	19 ^a	IFF	SC753579	0.04% in demi water
<i>L_SA</i>	Cucumber	13 ^a	IFF	15311331	100%
<i>L_SA</i>	Tomato	20 ^a	IFF	10939812	0.03% in PG
<i>L_SA</i>	Mushroom	18 ^a	Givaudan	P-136293	0.04% in demi water

^a From The Dutch Food Consumption Table (RIVM, 2011).

^b From the USDA Food Composition Databases (USDA Food Composition Databases, 2018).

^c International Flavors and Fragrances.

^d Propylene Glycol.

collected data on waist circumference, as it has been shown to be a more sensitive anthropometric marker of (abdominal) adiposity that is less susceptible to confounding by muscle mass (Stevens, McClain, & Truesdale, 2008).

3. Study 2

3.1. Methodology

3.1.1. Participants

A total of 88 healthy Dutch university students (78% female; $M_{Age} = 21.9$ years, $SD = 2.0$, range 18–35 years; $M_{BMI} = 20.6$ kg/m², $SD = 0.8$) from various educational backgrounds (48% postgraduates; 52% undergraduates) took part in the research. The sample size was chosen to remain consistent with that of Study 1, as spatial memory performance for vision and olfaction were expected to be similar (Schifferstein et al., 2009). Participants were limited to Dutch individuals given the use of culture-specific task stimuli. All other inclusion and exclusion criteria as stipulated for Study 1 were applied. Furthermore, participants were screened for a normal olfactory sense (scoring $\geq 75\%$ correct on the 16-item Sniffin' Sticks identification test) and the absence of habitual smoking (Katotomichelakis et al., 2007; Kobal et al., 1996). Individuals that participated in the former study, reported a history of neurological or olfactory disorders, or were pregnant and/or lactating were not included (Ochsenbein-Kölblle, Mering, Zimmermann, & Hummel, 2007). Recruitment was achieved through the advertisement of study posters and flyers on campus buildings, social media platforms, and participant mailing lists. After providing written informed consent and completing a screening session in addition to two test sessions, participants were compensated with a 25 euro giftcard. This study received ethical approval from the Social Sciences Ethics Committee of Wageningen University, and was pre-registered on the Open Science Framework database (Project URL: osf.io/8u2xa).

3.1.2. Design

Paralleling Study 1, the current study had a 2 (Caloric Density: High versus Low) by 2 (Taste: Sweet versus Savory) within-subjects crossover design with a washout period of (at least) one week.

3.1.3. Apparatus and Stimuli

3.1.3.1. Spatial memory task. The original E-Prime scripts and university campus setting of Allan and Allan (2013) were used to test

food spatial memory. Participants were asked to imagine that an international food market – encompassing 12 food stalls – was taking place on a (unfamiliar) university campus. Depending on the treatment condition, participants were then asked to smell four (sequential) odor solutions that signaled either (sweet/savory) high-calorie foods or low-calorie alternatives at a fixed duration of five seconds each (Brünner, Kofeet, Benedict, & Freiherr, 2015). During the smelling of a food odor, the location of the stall selling the corresponding food item was displayed on the university campus map through the means of a green crosshair. Between presentations of odor-location pairs, individuals rested for an interval of 20 s and smelled the inner portion of their wrist in order to avoid olfactory fatigue and odor carry-over effects (Brünner et al., 2015). Following a two-minute break after the presentation of the last odor-location pair, participants were exposed to a series of four spatial memory tests in which they were randomly presented with one of the previous food odors and required to specify (via mouse-click) its correct corresponding stall location on the campus map. Similarly, individuals rested for an interval of five seconds and smelled their inner wrist between odor-location recalls. The total number of possible stall sites ($N = 12$) was displayed for the spatial memory tests, and a stall location could be selected more than once. Assigned stall locations did not overlap for food odors within a test session.

The spatial memory task was piloted beforehand to match difficulty levels as closely as possible with that of Study 1. Although the odor-based spatial memory task encompassed a lower number of food locations to encode and recall, it was not inherently easier to perform (Mean pointing error Study 2 = 196.11 pixels, $SD = 206.05$; Mean pointing error Study 1 = 129.71 pixels, $SD = 186.11$), $U = 116147.00$, $p = .003$, $d = 0.34$.

3.1.3.2. Stimulus presentation. The psychology software tool E-prime (version 2.0) was used for spatial memory tasks. Computers were standardized across the parameters of screen size (19.3 inches), resolution (1280 x 1024), and refresh rate (60 Hz). The order of stimulus presentation and the stimuli itself (i.e. odor-location pairs within a campus map) were randomized and counterbalanced across participants.

3.1.3.3. Food odors. A set of four odor solutions was selected to represent each caloric density – taste condition [Table 1]. High- and low-calorie items were defined according to the same energy density cut-offs as in Study 1, using information from The Dutch Food

Consumption table and/or USDA Food Composition Databases (RIVM, 2011; USDA Food Composition Databases, 2018). Odor solutions were diluted to medium-high perceived intensity (55–75 mm on a 100 mm VAS) and presented to participants in (unlabeled) individual brown bottles (50 ml) at a volume of 15 ml each. In addition, odor stimuli were piloted in a separate sample of individuals ($N = 30$, 89% female; Age range = 18–35 years) to ensure consistent matching between an odor and its food product, and correct perceptions of caloric density and taste parameters (see pilot questionnaire in the Supplementary Material).

Results revealed the final selection of high-calorie odors was rated higher on caloric content ($M = 73.03$ mm, $SD = 17.27$) compared to the low-calorie group ($M = 32.80$ mm, $SD = 24.24$), $t(129) = 16.65$, $p < .001$. Likewise, taste perceptions were congruent with expectations as sweet odors were rated higher on sweetness (Sweet: $M = 79.32$ mm, $SD = 16.93$; Savory: $M = 26.80$ mm, $SD = 25.94$), $Z = -9.77$, $p < .001$, while savory odors scored greater on savoriness ratings (Savory: $M = 66.90$ mm, $SD = 28.25$; Sweet: $M = 14.06$ mm, $SD = 15.96$), $Z = -9.72$, $p < .001$.

3.1.4. Procedure

Prior to testing, participants were informed that the experiment aimed to investigate individuals' memory for specific odors. As in Study 1, this cover story did not explicitly mention the spatial faculty of memory and was successful in diffusing suspicions on the true study aims as revealed in post-hoc (open-ended funneling) debriefing interviews. Participants were likewise informed that good performance would earn them the chance to win an additional reward at the end of the experiment. Hunger states were standardized before test sessions in the same manner as in Study 1. Furthermore, individuals were asked to refrain from using scented products (e.g. perfume) on test days, and consuming scented items (e.g. chewing gum) starting an hour before their test sessions.

The experimental paradigm was identical to that of Study 1, except waist circumference was additionally collected at the onset of testing. Participants were also required to perform an odor recognition memory task following completion of the spatial memory task in each caloric density - taste condition. Furthermore, participants completed the *Macronutrient and Taste Preference Ranking Task* (de Bruijn et al., 2017) prior to answering questions on healthy eating goals in the second test session.

3.1.5. Measurements

3.1.5.1. Primary outcome variables. *Spatial memory accuracy* for (sweet/savory) high- and low-calorie foods, as well as *spatial memory bias for high-calorie foods*, was operationalized using Euclidian distances (D) in the same manner as in Study 1 (cf. Allan & Allan, 2013; Nairne et al., 2012). Based on findings of the previous experiment, *spatial memory bias for savory-tasting foods* was additionally calculated as the average discrepancy in spatial memory accuracy between savory-versus sweet-tasting items ($D_{\text{Savory}} - D_{\text{Sweet}}$). Accordingly, negative values indicate an enhanced spatial memory for savory-tasting foods.

3.1.5.2. Secondary outcome variables. Individual preferences for respective caloric density and taste food categories were determined using an adapted version of the *Macronutrient and Taste Preference Ranking Task* [MTPRT], ran on E-prime version 2.0 (de Bruijn et al., 2017). The MTPRT consists of three parts: practicing, liking, and ranking. For the "liking" portion, individuals are introduced to all 32 food images available and required to provide liking ratings on them (100 mm VAS anchored from "Do Not Like At All" to "Like Extremely"). The subsequent "ranking" portion of the original task encompasses two sections, one focused on macronutrients and the other on taste. In both sections, individuals are presented with four food images in a number of trials and asked to rank products on each trial in order of "what they most desire to eat at this moment", beginning with the most desired product. Utilizing

the same principles, a subset of 16 products (eight high- and eight low-caloric density) from the original selection of food images was used to construct a (new) caloric density section of the ranking task. In each of eight trials, the four presented food images came from both caloric density categories – with a sweet and savory counterpart for each category. The order in which categories were displayed on the screen was randomized and counterbalanced; both caloric density categories appeared four times in each of the available four image positions. All images were presented twice, on two different positions. Preference scores for respective macronutrient and taste categories were computed using ranking frequencies and formulas from the original authors (see de Bruijn et al., 2017), in which a higher rank corresponded to a higher preference score. Accordingly, the preference for high- (or low-) caloric foods in the newly added caloric density section was tabulated as: $(4^*(\#rank1) + 3^*(\#rank2) + 2^*(\#rank3) + 1^*(\#rank4))/16$.

Waist circumference (mm) was collected with a measuring tape at the midpoint between the lowest rib and the iliac crest, in line with World Health Organization guidelines. Similarly, height (m) and weight (kg) measures were collected with an electronic scale (SECA 704) and stadiometer (SECA 213) to obtain accurate BMI (kg/m^2) values.

3.1.5.3. Predictor variables.

Individual predispositions for *Restrained* and *External Eating* were measured as in Study 1 (Cronbach's $\alpha = .84$ and 0.75 , respectively) (van Strien et al., 1986). Furthermore to remain consistent with Study 1, we aggregated scores of the three BAS subscales to form a more reliable total BAS measure (Cronbach's $\alpha = .78$) for *Reward Sensitivity* (Carver & White, 1994). In doing so, the number of parameters to be estimated in statistical models was also favorably reduced relative to our sample size.

3.1.5.3. Control measures. To control for effects of (odor) recognition memory on spatial memory performance, we required individuals to discriminate between four "known" (target) and four "novel" (distractor) food odors in an *odor recognition memory* task following spatial memory tasks (Brünner et al., 2015; Krasnow et al., 2011). A fixed presentation order of target and distractor food odors was (randomly) generated for each caloric density - taste condition. Odor recognition memory scores were calculated as the proportion of odors correctly classified within a condition: correctly recognized target odors (0-4) plus correctly recognized distractor odors (0-4), divided by the total number of targets and distractors (8). To account for extraneous effects of 'liking' or 'wanting' of food types on spatial memory accuracy, we instructed participants to additionally rate how much they liked each odor – as well as their desire to eat the food item associated with an odor – on a 100 mm VAS (anchored from "Not At All" to "Very Much"; see Food Stimuli Ratings in the Supplemental Material) during the odor recognition memory task (Brünner et al., 2015).

Analogous to Study 1, *Neighborhood SES*, *Subjective SES*, *Healthy Eating Goals*, and *Perceived Performance* were recorded. Finally, a general questionnaire documented both pertinent demographic characteristics (e.g. Sex, Age) and *Hunger* states (100 mm VAS anchored from "Not At All" to "Very Much") at encoding.

3.1.6. Data Analysis

Data were analyzed using IBM SPSS Statistics 23 with statistical significance defined as $p < .05$. With regards to linear mixed effects modelling, the model selection procedure as described for Study 1 was applied. Due to an unforeseen error during testing, estimates for spatial memory biases were unable to be computed for one participant. Consequently, only data from 87 participants were used in the second statistical analysis onwards. As in Study 1, hypotheses and statistical analyses were formulated prior to accessing data.

3.1.6.1. Caloric density, taste, person-specific factors, and odor-cued food spatial memory accuracy (H_{1A} and H_2). To determine whether the accuracy of odor-cued food spatial memory varies with caloric content

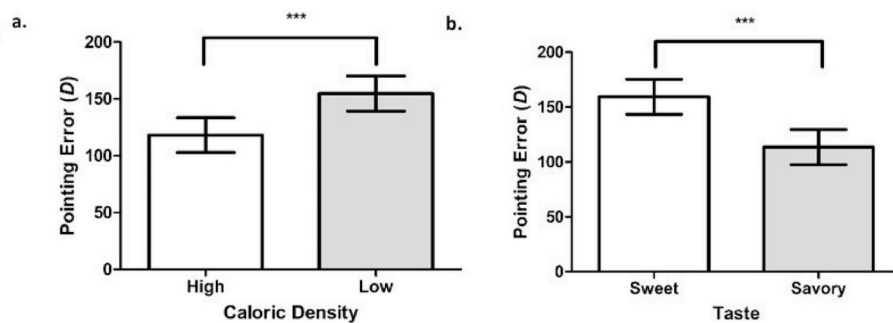


Fig. 3. Odor-cued spatial memory for (a) Caloric Density and (b) Taste food groups. Spatial memory accuracy was operationalized as the “pointing error” or distance in pixels (D) between true and indicated food locations, with lower D values denoting a higher accuracy in (odor-cued) food spatial memory. A triple asterisk indicates a significant difference with a p value lower than 0.001. Error bars represent 95% confidence intervals.

or taste aspects, we formulated a random intercept and slope linear mixed model with main and interaction effects of *Caloric Density* and *Taste* as fixed factors, *Participant* and *Test Session* as random factors (covariance structure: Unstructured), *Sex*, *Age*, *Neighborhood SES*, *Subjective SES*, *Taste Order*, *Liking*, *Desirability*, *Odor recognition memory* scores and *Hunger* scores as covariates, and *Spatial Memory Accuracy* (D) as the dependent variable.

To examine person-specific factors that could predict the magnitude of (odor-cued) food spatial memory accuracy, we included main and interaction effects (with *Caloric Density*) of *Restrained Eating*, *External Eating*, and *Reward Sensitivity* as predictor variables.

3.1.6.2. Spatial memory biases and food preferences (H_{1B}). To determine whether the high-calorie bias in (odor-cued) spatial memory predicted an increased preference for high-calorie foods, we formulated a multiple linear regression model ($N = 1$; simultaneous entry method) with *Sex*, *Age*, *Neighborhood SES*, *Subjective SES*, *Restrained Eating*, *External Eating*, *Reward Sensitivity*, *Liking* of High- versus Low-calorie food odors, *Desirability* of High- versus Low-calorie food odors, *Hunger* ratings of the final test session, *Healthy Eating Goals*, and *Spatial Memory Bias* for High- versus Low-calorie food odors ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) as predictor variables, and the relative preference of High- versus Low-calorie foods ($\text{Preference}_{\text{High Calorie}} - \text{Preference}_{\text{Low Calorie}}$) as the dependent variable.

To determine whether the savory-taste bias in (odor-cued) spatial memory predicted an increased preference for savory-tasting foods, we formulated a multiple linear regression model ($N = 1$; simultaneous entry method) with *Sex*, *Age*, *Neighborhood SES*, *Subjective SES*, *Liking* of Savory- versus Sweet-tasting food odors, *Desirability* of Savory- versus Sweet-tasting food odors, *Healthy Eating Goals*, and *Spatial Memory Bias* for Savory- versus Sweet-tasting food odors ($D_{\text{Savory}} - D_{\text{Sweet}}$) as predictor variables, and the relative preference of Savory- versus Sweet-tasting foods ($\text{Preference}_{\text{Savory}} - \text{Preference}_{\text{Sweet}}$) as the dependent variable.

3.1.6.3. Spatial memory bias for high-calorie foods and long-term dietary intake (H_{1B}). Multiple linear regressions ($N = 2$; simultaneous entry method) were performed on *BMI* and *Waist Circumference*, with *Sex*, *Age*, *Neighborhood SES*, *Subjective SES*, *Restrained Eating*, *External Eating*, *Reward Sensitivity*, *Liking* of High- and Low-calorie food odors, *Desirability* of High- and Low-calorie food odors, *Healthy Eating Goals*, and *Spatial Memory Accuracy* (High- and Low-calorie food odors) as predictor variables.

Similarly, final multiple linear regression models ($N = 2$; simultaneous entry method) were formulated to take into account the relative effects of high- and low-calorie (odor-cued) food spatial memory on *BMI* and *Waist Circumference*. Accordingly, *Sex*, *Age*, *Neighborhood SES*, *Subjective SES*, *Restrained Eating*, *External Eating*, *Reward Sensitivity*, *Liking* of High- versus Low-calorie food odors, *Desirability* of High- versus Low-calorie food odors, *Healthy Eating Goals*, and *Spatial Memory Bias* for High- versus Low-calorie food odors ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) were entered as independent variables.

3.2. Results

3.2.1. Odor-cued Food Spatial Memory: Accuracy and Biases

The average pointing error in odor-cued food spatial memory across all caloric density- taste conditions was 135.49 pixels (95% CI = [126.74,144.25]). Correcting for differences in resolution, exploratory analysis revealed this represented a significant, but minor, increase from that observed in Study 1 with visual food cues, $F(1,184) = 7.87$, $p = .006$, $\eta^2 = 0.04$, 90% CI η^2 [0.007, 0.10]. Perceived performance ratings had a medium negative correlation with actual pointing errors ($r_s(346) = -.31$; $p < .001$). Perceived performance did not differ between caloric density conditions ($\text{Mean difference}_{\text{High-Low Calorie}} = 3.28$ mm, 95% CI = [-2.11,8.68]), $t(86) = 1.21$, $p = .230$, $d = 0.13$, but did vary significantly between taste conditions ($\text{Mean difference}_{\text{Sweet-Savory}} = -6.39$ mm, 95% CI = [-10.98,-1.81]), $t(86) = -2.77$, $p = .007$, $d = 0.30$.

Overall, individuals displayed a greater accuracy in odor-cued food spatial memory for high-calorie food odors (i.e. smaller pointing error or D) relative to low-calorie odor counterparts, $F(1,1240) = 18.43$, $p < .001$, $\eta^2 = 0.01$, 90% CI η^2 [0.006, 0.03] [Fig. 3]. Similarly, savory food odor locations were more accurately recalled than sweet alternatives, $F(1,1309) = 23.00$, $p < .001$, $\eta^2 = 0.02$, 90% CI η^2 [0.007, 0.03]. These effects persisted regardless of demographics (e.g. *Sex*), hedonic evaluations of odors, or odor recognition memory scores. Furthermore, exploratory analysis revealed that the amount of time participants spent on spatial recall tests significantly (negatively) predicted spatial memory performance ($B = 0.002$, 95% CI = [0.001,0.003]), $F(1,789) = 7.64$, $p = .006$, $\eta^2 = 0.01$, 90% CI η^2 [0.002, 0.02], but did not account for the observed bias effects.

3.2.2. Taste and Person-specific Moderators

The interaction of *Caloric Density* and *Taste* on (odor-cued) spatial memory performance was not significant, $F(1,90.26) = 0.32$, $p = .573$, $\eta^2 = 0.004$, 90% CI η^2 [0, 0.05]. *Restrained Eating*, *External Eating*, *Reward Sensitivity* and corresponding interactions (with *Caloric Density*) were similarly not associated with (odor-cued) food spatial memory accuracy (all $p > .05$; $\eta^2 = 1 \times 10^{-4}$ [0, 0.003], 0.003 [0, 0.01], and 1×10^{-4} [0, 0.003], respectively).

3.2.3. Spatial Memory Biases and Food Preferences

From the tested set of predictors, the high-calorie bias in (odor-cued) food spatial memory was not significantly associated with an increased preference for high-calorie foods ($B = -0.001$, 95% CI = [-0.003,0.001]), $t(74) = -1.44$, $p = .08$. On the other hand, an individual's *Healthy Eating Goals* correlated negatively with high-calorie food preferences ($B = -0.29$, 95% CI = [-0.54, -0.04]), $t(74) = -2.32$, $p = .023$.

With respect to preference biases towards savory-tasting foods, none of the entered predictors captured meaningful variation in measured responses (all $p > .05$) – including the savory-taste bias in (odor-cued) food spatial memory ($B = -0.001$, 95% CI = [-0.002,0.001]), $t(78) = -0.66$, $p = .257$.

3.2.4. Spatial Memory Bias for High-calorie Foods in relation to BMI and Waist Circumference

Spatial memory for high-calorie food odors was not associated with BMI ($B = 0.002$, 95% CI = $[-0.01, 0.01]$), $t(72) = 0.53$, $p = .601$, or waist circumference ($B = 0.02$, 95% CI = $[-0.14, 0.18]$), $t(72) = 0.25$, $p = .801$. Likewise, spatial memory for low-calorie food odors was not predictive of BMI ($B = 0.001$, 95% CI = $[-0.01, 0.01]$), $t(72) = 0.29$, $p = .775$, or waist circumference ($B = 0.03$, 95% CI = $[-0.10, 0.17]$), $t(72) = 0.49$, $p = .623$. The high-calorie bias in (odor-cued) spatial memory also did not systematically covary with BMI ($B = 0.001$, 95% CI = $[-0.004, 0.01]$), $t(75) = 0.29$, $p = .388$, or waist circumference ($B = 0.001$, 95% CI = $[-0.12, 0.12]$), $t(75) = 0.01$, $p = .496$. On the contrary, an individual's Healthy Eating Goals, Restrained Eating tendencies, and Liking (bias) for high-calorie food odors proved to be robust correlates of both measures across all statistical models (see Tables S2 and S3 in the Supplemental Material).

4. General discussion

Across two lab studies that engaged distinct sensory modalities, while controlling for consciously mediated valuations or personal experiences with foods, individuals more accurately recalled the locations of high-calorie and savory-tasting foods (H_{1A}). These findings support an adaptive account of human memory and are compatible with the notion that spatial processing tendencies optimized for fluctuating ancestral food habitats may be preserved. However, the more accurate localization of high-calorie foods did not differ for sweet or savory foods, or across an individual's trait eating style or degree of reward sensitivity (H_2). Furthermore, effects of biases in food spatial memory were not present on eating-related parameters of food preference, food choice, BMI, and waist circumference (H_{1B}).

In line with New, Cosmides, et al. (2007) and New, Krasnow, et al. (2007), we found that individuals showcased a more accurate memory for the locations of high-calorie foods, irrespective of factors that may have accounted for a general learning mechanism (e.g. encoding time, personal affinities with foods). It is equally unlikely that this difference arose from a higher attractiveness or visual salience of high-calorie food stimuli, as paralleling results were obtained with olfactory food cues at similar perceived intensities. Notably, vision and olfaction are distant senses important for detecting food sources in the environment and directing eating behavior towards signaled products (McCrickerd & Forde, 2016; Ramaekers, Boesveldt, Lakemond, Van Boekel, & Luning, 2014). Complementing these roles, our findings corroborate the efficacy of both sensory modalities in signaling important nutritional characteristics of food sources and serving as associative cues in support of spatial navigation (Dahmani et al., 2018; McCrickerd & Forde, 2016; Schifferstein et al., 2009). The slight advantage of vision over olfaction observed in spatial memory performance may be attributed to a greater tendency and fluency of sighted-individuals to internally represent spatial information in visual terms, or an overall greater difficulty of assigning verbal labels to (and identifying) odors (Cain, 1979; Schifferstein et al., 2009). Interestingly, further reinforcing the results of New, Cosmides, et al. (2007) and New, Krasnow, et al. (2007), the high-calorie bias in spatial memory was not influenced by sex. Although sex differences in spatial abilities are widely documented in literature (Silverman, Choi, & Peters, 2007; Silverman & Eals, 1992), this finding makes sense from an evolutionary perspective, as the adaptive ancestral problem of efficiently (re)locating and exploiting high quality nutritional resources would have impinged similarly on both sexes – resulting in a sexually monomorphic but domain-specific spatial processing mechanism (Cosmides & Tooby, 2013; Krasnow et al., 2011).

A novel main effect of taste on spatial memory accuracy was additionally elucidated as individuals better remembered locations of savory- (versus sweet-) tasting foods – regardless of caloric content. Within the framework of adaptive memory (Nairne & Pandeirada, 2008, 2010), our results suggest that the attainment of sufficient

protein (relative to carbohydrates) may have posed a bigger adaptive problem faced by our hunter-gatherer ancestors. In support of this notion, ancestral protein consumption is estimated to have encompassed a substantial 30% of a 3000 kcal/day diet (Cordain et al., 2000; Eaton, 2006). This high demand coupled with a high variance in return rates of major protein sources (i.e. mobile animal prey), would have garnered a greater difficulty with meeting protein intake requirements relative to carbohydrates – the latter mainly sourced from (immobile) fruits and vegetables (Bird, Bird, & Coddling, 2009; Eaton, 2006). Therefore, we speculate that a bias in location memory for savory-tasting foods may be the expression of a fitness advantage that facilitated a more lucrative pursuit of protein-rich resources. Relatedly, studies have shown that human visual attention and episodic memory are especially adept at processing information on self-propelling animate (e.g. animals) versus inanimate objects, potentially reflecting a survival mechanism to readily detect prey or predators in the environment (Nairne, VanArsdall, & Cogdill, 2017; New, Cosmides, & Tooby, 2007). Moreover, protein intake has been demonstrated to be tightly regulated in humans across time and geographical conditions, and even ‘leveraged’ or prioritized over the consumption of other macronutrients when nutritional intake targets are not met (Cordain et al., 2000; Simpson & Raubenheimer, 2005). A compensatory pathway for restoring protein balance involves the activation of (implicit) cognitive processes that orient food preferences and choice behavior towards savory high-protein foods (Griffioen-Roose et al., 2012; Griffioen-Roose et al., 2014). Taken together, these observations add empirical weight to the idea that a savory-taste bias in human spatial memory may have been functionally selected for maintaining adequate protein status.

In light of the difficulties associated with establishing a definitive evolutionary account of our findings, our data enable us to rule out a couple alternative explanations for the observed biases in human food spatial memory. The possibility that the high-calorie bias arose from a conscious effort of (health-minded) individuals to strategically avoid high-calorie food locations can be countered with exploratory analyses that revealed healthy eating goals was not a significant predictor of food spatial memory accuracy in both studies. Indeed, such an ‘adaptive avoidance’ hypothesis, in which (dieting) individuals with the high-calorie bias would adaptively avoid high-calorie food locations and have a lower BMI, is not supported by the existing literature (Allan & Allan, 2013). It is also conceivable to suspect that within-experimental differences in name-ability or depth of processing accounted for discrepancies in spatial memory performance – congruent with the (domain-general) levels of processing framework. By this account, high-calorie and savory-tasting food locations were better recalled because they were inherently easier to assign meaning to (Craik & Lockhart, 1972). However, this prospect is unlikely as we controlled for individual experience with a food through familiarity ratings (Study 1) and odor recognition memory scores (Study 2), the latter of which is known to positively covary with odor knowledge and odor naming abilities (Frank, Rybalsky, Brearton, & Mannea, 2010).

Although biases in human food spatial memory are clearly expressed, their translation into actual eating behavior was not detected in the present work. In light of observed effect sizes, potential relationships with long-term dietary intake are also likely to be small in magnitude. This gap may be attributed to a variety of reasons. As the measurement of anthropometrics temporally preceded the selection of foods, individuals may have been primed with a dieting or health goal, thus potentially diluting effects on subsequent (high-calorie) food preference and choice (van der Laan, Papiés, Hooge, & Smeets, 2017). However, the one-week washout period and other implemented controls (e.g. anonymity/honesty reminders; covert nature of the food choice task) would have helped in mitigating any substantial confounding effects. In addition, as the current techniques used to assess food choice lacked external validity, and food spatial memory biases are thought to exert their influence by affording a greater navigational convenience, (pronounced) effects may only be present in more

naturalistic food settings that allow for navigation within a bigger scale of space. Theoretical considerations are also merited, as contrary to Allan and Allan (2013), an individual's reported healthy eating intentions – rather than the high-calorie spatial memory bias – was a robust predictor of both short- and long-term parameters of eating behavior. This suggests that obesogenic effects of the high-calorie bias may be effectively countered by an individual's explicit health attitudes and self-regulation capacity – in a manner resonant with dual-processing theories of cognition (Evans, 2003). The potential link between the high-calorie spatial memory bias and obesogenic behaviors may therefore be a more nuanced process that recruits higher-order cognitive constructs.

Finally, it would be worthwhile to explore the cognitive processes underlying food spatial memory biases. The majority of our results concerning encoding times and perceived performance ratings propose a link with more implicit mechanisms. It would therefore be interesting to see whether food-related attention biases, specifically in the orientation phase of attention, covary with the expression of these cognitive biases. These results could yield important insights to supplement existing interventional strategies aimed at decreasing cognitive reactivities to high-calorie food stimuli, in an effort to promote dietary regulation.

In closing, our work highlights that content matters deeply for the faculty of human food spatial memory. Findings are reminiscent of a cognitive system presumably attuned to ancestral priorities of optimal foraging: one capable of assessing the profitability of encountered food resources and preferentially processing the locations of those higher in nutritional quality – in an implicit manner that does not compete for volitional attention. Knowledge of these biases in human food spatial memory and their associated (proximal) mechanisms could inform new strategies to promote healthier eating behavior within the evolutionary novel “obesogenic” food landscape.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.appet.2020.104718>.

Author Contributions

R. de Vries, E. de Vet, and S. Boesveldt jointly developed the conceptual framework and study design. R. de Vries collected and analyzed the data, and drafted the manuscript under the supervision of E. de Vet and S. Boesveldt. K. de Graaf reviewed a later version of the manuscript. All authors approved the final article.

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