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Wired for harsh food environments: Human spatial memory favours the effortless location and consumption of high-calorie foods

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ABSTRACT

Human memory automatically prioritises locations of high-calorie foods, likely reflecting an adaptation for foraging in harsh ancestral food environments. We investigated whether this high-calorie bias in human spatial memory yields unhealthy obesogenic implications for individual eating behaviour in present-day food-abundant settings. In an online study, we tested the food spatial memory of a diverse sample of 405 individuals, as well as examined associations between the high-calorie spatial memory bias and the self-reported routine frequency of high-calorie snack consumption, exposure to high-calorie food environments, and BMI of a subset of 316 individuals. The high-calorie spatial memory bias was not *directly* associated with high-calorie snack consumption frequency or BMI. However, a greater expression of the bias *indirectly* predicted a higher BMI, by mediating a stronger habit of purchasing high-calorie snack foods. Although individuals from various sociodemographic groups expressed the high-calorie bias in spatial memory, our results suggest that those with a better inhibitory control to high-calorie foods were protected from bias-related tendencies to frequent high-calorie food environments (e.g. fast-food outlets).

1. Introduction

Our present-day food environment features an overabundance of palatable calorie-rich foods – promoting individuals to (over)consume these unhealthy items (Swinburn et al., 2011). However, not everyone overeats, indicating that large differences exist between individuals in their ability to successfully navigate “obesogenic” settings (Swinburn et al., 2011). A novel account for these individual differences proposes that susceptibility to the current food-rich landscape may (partially) stem from a foraging-related adaptation that evolved during our long past as hunter-gatherers. Specifically, from a cognitive adaption that enabled ancestral hunter-gatherers to efficiently locate valuable calorie-rich resources within harsh food environments: a prioritisation – or “bias” – in spatial memory for high-calorie foods (de Vries, Morquecho-Campos, et al., 2020; de Vries, de Vet, et al., 2020; New et al., 2007). Here we provide initial evidence suggesting that this “high-calorie bias” in human spatial memory favours the (routine) choosing of unhealthy high-calorie foods within our modern food context, and is expressed by individuals spanning diverse sociodemographic characteristics.

About 99 percent of human evolutionary history is characterised by extensive hunting-gathering activities within a food insecure environment, where food availability fluctuated in space and time (Chakravarthy & Booth, 2004; Eaton, 2006; Ulijaszek, 2002). In such environments, a fitness advantage was gained by individuals who evolved (cognitive) mechanisms that maximised the net energy gained during foraging (Schoener, 1971; Winterhalder, 1981). Indeed, empirical evidence for the existence of such optimised foraging-related cognitive adaptations in humans is growing. For instance, exposing individuals to environmental cues indicative of food scarcity (e.g. videos with winter or climate change content) elicits thoughts about survival and orients consumption preferences towards energy-dense foods (Folwarczny et al., 2021, 2022). Central to the present work, however, is the discovery that human spatial memory appears to show sensitivity to the caloric content of potential foods, and automatically prioritises the locations of foods higher in caloric density. This high-calorie bias in spatial memory was expressed across sensory modalities (i.e., visual versus olfactory food cues), and regardless of one’s hedonic judgements of a food, past exposure with a food, or deliberate intention (and

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corresponding time taken) to memorise food locations (cf. New et al., 2007; de Vries, de Vet et al., 2020). It is thought that this cognitive bias helped hunter-gatherers navigate harsh food landscapes, by enabling them to efficiently register and (re)locate (fitness-relevant) calorie-dense resources – without occupying attentional processes needed in other important tasks (e.g. avoiding predators, caring for offspring) (de Vries, Morquecho-Campos, et al., 2020; New et al., 2007).

What was once an adaptive cognitive mechanism for energy-efficient foraging may now be "mismatched" and counterproductive for individuals within urbanised food settings, where high-calorie foods are readily available and accessible (Cordain et al., 2005; Li et al., 2018). Evolutionary mismatch theory maintains that traits that were adaptively selected for in the ancestral environments in which we evolved still exist within vastly different surroundings today (Li et al., 2018; Lloyd et al., 2011). As a result, our selected traits may adversely interact with elements of our current (evolutionarily novel) environment – giving rise to health consequences such as obesity (Cordain et al., 2005; Eaton et al., 1988). In line with this notion, Allan and Allan (2013) found that a superior memory for high-calorie snack locations (versus that of low-calorie fruits and vegetables) was associated with a higher BMI in women – an objective marker of long-term dietary intake and strong correlate of excess body fat mass (Bouchard, 2007). Furthermore, de Vries et al. (2021) showed that a more accurate (lab-tested) memory for high- versus low-calorie food locations predicted a greater reported ease of finding high-calorie products in a real-world supermarket, which may potentiate later choice of a high-calorie food. On the other hand, null associations between the high-calorie spatial memory bias and (primarily) lab-based and single time point measures of eating behaviour have also been observed (cf. de Vries, de Vet, et al., 2020). However, the latter may have resulted from the limited spatiotemporal circumstances in which food decisions were assessed. Thus, to avoid incidental responses and gain insight into an individual's routine eating behaviour, this study investigated associations with longer-term eating-related parameters (i.e., frequency of high-calorie snack consumption in the past month, exposure to high-calorie food environments in the past month, and BMI) that covered a range of typical physical and situational food decision-making contexts.

If the high-calorie bias in human spatial memory is indeed linked to undesirable behavioural and health outcomes at present, it would be relevant to identify "at-risk" subpopulations that showcase a great expression of the cognitive bias. Studies to date have mainly utilised smaller samples of young, majority-female, highly-educated, and health-minded individuals (cf. Allan & Allan, 2013; de Vries, de Vet, et al., 2020), which questions whether an identical expression of the high-calorie spatial memory bias can be generalised to other sociodemographic groups that are subjected to systematically different environments (e.g. built food environments). That is, the evolutionary account of the spatial processing bias suggests its general presence across individuals, but the exact output of psychological adaptations is sensitive to environmental input (Lewis et al., 2017; Tooby & Cosmides, 1990). As such, the expression of the bias may be *moderated* by the quality of the food environment one is exposed to, which follows a sociodemographic gradient. Specifically, the local food environment of individuals who live or attend school in low socioeconomic status (SES) neighbourhoods typically consists of a larger presence of high-calorie food cues, due to a higher density of fast-food outlets and a greater advertisement of unhealthy high-calorie items (Larson et al., 2009; Maguire et al., 2015; Timmermans et al., 2018; Yancey et al., 2009). Concurrently, it is recognised that individuals with a lower income, education, occupation, or who live in disadvantaged areas display suboptimal diets and a higher (less healthy) BMI (Drewnowski et al., 2014; Janssen et al., 2006; Lakerveld et al., 2015; van Lenthe & Mackenbach, 2002). Those who are *perceived* to have a lower status or instrumental social value compared to others in their community (i.e., subjective SES), also exhibit less healthy dietary patterns (i.e., lower daily fruit and vegetable consumption) and body fat distributions (e.g. higher waist-hip-ratios) – independently of one's objective SES (Adler et al., 2000; Anderson et al., 2015; Ghaed & Gallo, 2007). A novel contributing factor to this discrepancy in dietary quality between sociodemographic groups could thus be a difference in the magnitude at which the high-calorie spatial memory bias is expressed (and influences routine eating behaviour) within one's local food environment.

That being said, earlier observations also indicate that the translation of the high-calorie spatial memory bias into eating behaviour is not always straightforward, and other individual-level psychological factors may play a role in moderating the bias' effects (see https://osf.io/nv7a9/ for a more extensive description of the corresponding literature). For instance, de Vries et al. (2021) found that the cognitive bias may potentiate high-calorie food choice by making high-calorie options seem more easy or convenient to locate in a diverse food environment. Thus, a boundary condition for the bias to materialise could be a sufficiently high (deliberated) importance of "convenience" during food choice (Furst et al., 1996). Similarly, as previous food choices create momentum for repeating the same selections at later instances of food decision making (Furst et al., 1996; Sobal et al., 2006), a stronger pre-existing habit of purchasing high-calorie snack foods might synergise obesogenic bias-induced responses in certain contexts (Allan & Allan, 2013; Verplanken & Aarts, 1999; Verplanken & Orbell, 2003). Conversely, de Vries, de Vet, et al. (2020) saw that while the high-calorie spatial memory bias was expressed in a health-minded sample of individuals, one's explicit intentions to eat healthily proved to be a better predictor of eating-related measures (e.g. high-calorie food preferences, BMI) across adjusted models. Likewise, an individual's ability to successfully inhibit "impulsive" appetitive responses to high-calorie foods – such as those supposedly elicited by the high-calorie spatial memory bias (cf. Allan & Allan, 2013) – could protect against the bias' negative effects (Batterink et al., 2010). Indeed, a greater inhibitory control towards palatable foods is shown to support healthy dietary regulation (Appelhans et al., 2011; Hofmann, Friese, & Roefs, 2009; Nederkoorn et al., 2010).

In short, the present research had three objectives. Our first objective was to investigate the effect of the high-calorie spatial memory bias on individuals' self-reported routine eating behaviour (i.e., high-calorie snack consumption frequency, exposure to high-calorie food environments, and BMI). Secondly, we examined the expression of the high-calorie bias in human spatial memory in a diverse sample of (Dutch) individuals with varying sociodemographic characteristics. Finally, we considered whether specific psychological factors moderate behavioural effects of the high-calorie spatial memory bias. We hypothesized that:

H_1: The high-calorie spatial memory bias predicts a greater routine frequency of high-calorie snack consumption, greater routine exposure to high-calorie food environments, and a higher BMI in individuals.

H_2: The magnitude of the high-calorie bias in human spatial memory varies across sociodemographic characteristics.

H_3: Psychological factors moderate effects of the high-calorie spatial memory bias on routine eating behaviour. A higher importance of convenience in food choice, as well as greater snack purchasing habit strength, will synergise behavioural effects of the high-calorie spatial memory bias. Conversely, a higher healthy eating intention and greater inhibitory control to high-calorie foods will antagonise behavioural effects of the high-calorie spatial memory bias.

2. Methodology

2.1. Design

The present study had a repeated measures design with *Caloric Density* (High versus Low) as a within-subjects factor. In an online experiment, participants had to complete a sequence of cognitive tasks (e.g. food spatial memory task) and questionnaires (e.g. high-calorie snack consumption frequency in the past month) in two online test sessions, with a washout period of approximately one week. The hypotheses, experimental design, and statistical analysis plan were preregistered, and are available with data that support the findings of this study on the Open Science Framework database (Project URL: https://osf.io/nv7a9/).

2.2. Participants

Participants were a diverse sample of healthy Dutch adults (above the age of 18) living in the Netherlands, recruited via stratified sampling (i.e., on sex, age, education level, and province) by the ISO-certified *Flycatcher* online research agency (www.flycatcher.eu). Individuals were not allowed to participate if they self-reported any dietary restrictions, a current or medical history of eating disorders, or (total or partial) colour blindness. A total of 613 individuals were initially invited, and a response rate of 66.1% was achieved. Thus, 405 individuals (56.7% Male; $M_{Age} = 47.57$ (±17.48) years, Range: 18 – 86 years; $M_{BMI} = 25.96$ (±4.71) kg/m^2; Range: 18.12 – 59.52 kg/m^2) took part in the first online session that tested food spatial memory. Of the initial sample, 321 individuals returned for the second online test session (corresponding to a drop-out rate of 20.7%), but five participants were excluded due to incomplete data. As a result, data from 316 participants (57.9% Male; $M_{Age} = 47.37$ (±17.64) years, Range 18 – 86 years; $M_{BMI} = 25.86$ (±4.59) kg/m^2; Range: 18.12 – 47.32 kg/m^2) were used for analysing behavioural outcomes. *A priori* power calculations (see https://osf.io/byuhe for details) required a minimum sample size of 312 individuals, and final participant samples (between test sessions) were well-matched on sociodemographic distributions (Table S1). After providing informed consent and completing the online experiment, participants were financially compensated. This study was approved by the Social Sciences Ethics Committee of Wageningen University.

2.3. Procedure

A general research aim was advertised to participants before testing, stating that the study was interested in "*what people think about the modern food environment and the foods typically found within it*". In the first online test session, participants filled out a preliminary questionnaire asking background characteristics (e.g. height, weight, subjective SES). Next, they provided ratings on hunger state, as well as on (randomly-presented) food stimuli (N = 24) on the aspects of *Liking*, *Desire to Eat*, and *Familiarity*. Finally, individuals performed the spatial memory task for both high- and low-calorie foods, with a five-minute rest between conditions. The first session took approximately 40 minutes.

In the second online test session, approximately one week later, participants first recorded their hunger state. Individuals then had to complete the food-specific go/no-go task and five questionnaires (i.e., snack FFQ, food environment visits, importance of convenience, snack purchasing habit strength, and healthy eating intentions) in a randomised manner, to circumvent possible order effects on answering. The second session took approximately 20 minutes.

2.4. Apparatus and stimuli

2.4.1. Food stimuli in cognitive tasks

Standardised images depicting high- and low- calorie foods were sourced from the *Food Pics* database[1] (Blechert et al., 2014). Consistent with earlier investigations (e.g. de Vries, de Vet, et al., 2020), items were considered high-calorie if they contained at least 225 kcal – and low-calorie if they contained at most 60 kcal – per 100 g of food. For cognitive tasks, a set of 24 (unbranded) food pictures was used as food stimuli, with 12 images for each caloric density category (cf. de Vries et al., 2021). Importantly, an equal number of sweet and savoury items were present across caloric density groups (e.g. *High-calorie*: hamburger and chocolate bar; *Low-calorie:* tomato and watermelon), as (spatial) memory mechanisms may respond to taste modalities differently (de Vries, de Vet, et al., 2020; Meule et al., 2012). High- and low-calorie food stimuli were equivalent in macronutrient balance (i.e., protein to carbohydrate and fat ratios; Simpson & Raubenheimer, 2005), recognisability, and a wide range of image characteristics (see Table S2 in the Supplemental Material). Conversely, high-calorie food images displayed a greater caloric density (kcal/100 g) as well as total energy content (kcal), and were correctly perceived to contain more calories and to be less healthy compared to low-calorie alternatives in a separate pilot study (Table S2).

2.4.2. Spatial memory task

The computer-based spatial memory task has been validated for use in the target population in previous studies (cf. Allan & Allan, 2013; de Vries et al., 2021). For the task, participants were instructed to imagine that an international food market with 24 food stalls was taking place within an (unfamiliar) university campus setting. They were then shown 12 images of either high-calorie or low-calorie foods, followed by an image of the university campus map showcasing all 24 possible stall locations, at a fixed duration of three seconds each. Next, the location of the stall selling a food item was indicated on the campus map by a green crosshair, and this was done in a sequential manner for all food stimuli within a caloric density condition (N = 12). During viewing, participants were instructed to remember the food locations as accurately as possible (i.e., encoding was instructed). After a two-minute rest, participants performed a series of 12 spatial memory tests, in which they were randomly-presented with one of the previous food images and required to click on its correct assigned stall location on the campus map. All possible stall sites were displayed anew each recall round, and participants could select the same stall location more than once, even though locations did not overlap between foods. Following a five-minute intermission, participants repeated the spatial encoding and recall procedure for the remaining 12 foods of the other caloric density condition. Task stimuli (i.e., food-locations pairs within the campus map), as well as the stimuli presentation order, were randomised differently for each participant. The order in which participants completed the spatial memory task between caloric density categories was also counterbalanced. Prior to the actual task, participants first practiced encoding and recalling locations of non-food objects on the campus map, to familiarise themselves with the spatial memory paradigm.

2.4.3. Food-specific go/no-go task

The food-specific go/no-go task used to measure individuals' ability to inhibit responses to high-calorie foods was adapted from Chen et al., 2018. A similar paradigm was shown to directly recruit neural circuitry implicated in inhibitory control (Batterink et al., 2010). The task consisted of one practice block and six experimental blocks in total.

First, participants underwent a practice block consisting of six (randomised) trials with non-food images[1], in order to associate "go" responses (i.e., spacebar press) and "no-go" responses (i.e., no spacebar press) with specific cues (i.e., a blue or grey-coloured image border). The assignment of a (blue or grey) border colour as a "go "or "no-go" cue was counterbalanced across participants. At the onset of a trial, an image appeared immediately on the screen and a (blue or grey) coloured border was presented after 150 ms. Both image and border were then shown for 1500 ms, followed by a fixation cross. To facilitate accurate performance on the task (Wodka et al., 2009), we jittered the duration of the fixation cross between trials (i.e., from 1000 to 1500 ms, in 100 ms increments). A minimum number of practice trials (≥80%) needed to be successfully responded to before individuals could proceed on to the experimental phase, and feedback was provided during practice trials.

During experimental blocks, low-calorie food images (N = 12) were consistently paired with a "go" cue, and high-calorie food images (N =

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[1] *Food Pics* Catalogue Numbers: *High-calorie: 2, 16, 27, 44, 53, 60, 104, 116, 134, 286, 400, 517; Low-calorie: 199, 233, 250, 251, 260, 274, 389, 393, 407, 413, 442, 453; Non-food: 1086, 1094, 1129, 1143, 1155, 1210.*

12) with a “no-go” cue. Participants were instructed to respond as quickly and accurately as possible to the cues after the presentation of a food image. Each experimental block encompassed 24 trials, with each food image appearing once in a randomised order, resulting in 144 experimental trials ($N = 72$ for both high- and low-calorie stimuli) per participant. We chose a 1:1 ratio for go to no go trials, as we reasoned that the bias itself would (proportionally) provide for the prepotent behavioural response towards high-calorie foods (cf. Allan & Allan, 2013). Thus, we expected such a design to adequately parse out differences in response inhibition within the greater framework of the cognitive bias, as well as confer a more representative availability of high- versus low-calorie foods within the modern food environment. Unlike the practice block, feedback was not given during experimental trials.

2.5. *Measurements*

2.5.1. *Primary outcome variables*

Routine frequency of high-calorie snack consumption was gauged using a modified snack-specific food frequency questionnaire, that was designed and validated for use in the Dutch population (Dutch snack FFQ; Streppel et al., 2013). Individuals had to report how frequently in the past month they consumed a wide range of (sweet and savoury) high-calorie snack foods commonly eaten in the Netherlands (e.g. baked goods, chocolate bars, cheese, and potato chips). Response categories spanned from “none” to “six to seven times per week” (i.e., every day). The frequency of consumption was averaged across all snack foods for each participant.

A food environment questionnaire was developed to assess routine exposure to high-calorie food environments. The questionnaire asked individuals to report the frequency of visits (i.e., to either eat or purchase foods) made within the past month to a range of (randomly-presented) physical food retail outlet types typically found in the Netherlands (e.g. supermarket, cafeteria; see *Food Environment Questionnaire* in the Supplemental Material; USDA Foreign Agricultural Service & Report, 2017). We intentionally excluded online food retailers and food delivery services, as we were specifically interested in the influence of the cognitive bias on how individuals spatially navigate the physical food environment. The questionnaire was piloted in a separate sample of Dutch individuals ($N = 35$; 51.4% Male; $M_{Age} = 22.03$ (± 2.79) years) to ensure that selected food retail outlet types were sufficiently recognisable. The classification of a food retail outlet as a “high-calorie food environment” was advised by guidelines on healthy food environments from the Netherlands Nutrition Centre Foundation (*Voedingscentrum*), and was centred on the availability criterion (2020). Namely, we classified high-calorie food environments as those having more than 40% of “unhealthy” high-calorie products on offer, the latter defined as (high-calorie) foods that are not included in the *Wheel of Five* Dutch dietary guidelines (Brink et al., 2019; 2020). As such, a more conservative approach was adopted during classification, as we only considered outlets that offer an overrepresentation of high-calorie foods (e.g. fast-food outlets and confectionary stores; $N = 13$ in total) as high-calorie food environments. Our final classification was cross-checked – and confirmed to be in line with – expert-derived “healthiness scores” of urban Dutch food outlet types (Timmermans et al., 2018). As with the snack FFQ, response categories spanned from “none” to “six to seven times per week” (i.e., every day), and the frequency of visits to high-calorie food locations in the past month was averaged per individual.

In addition, individuals self-reported their height (cm) and weight (kg), in order to obtain information on BMI (kg/m^2).

2.5.2. *Predictor variables*

Spatial memory accuracy for high- and low-calorie foods was determined by averaging the ‘pointing error’ or Euclidian distance (D) between correct and recalled stall locations of each food group (cf. Allan & Allan, 2013; de Vries, de Vet, et al., 2020). Therefore, *lower* D scores correspond to a *higher* accuracy in food spatial memory. The high-calorie bias in spatial memory was calculated by taking the difference in spatial memory accuracy for high- and low-calorie foods ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$). As such, *lower* (negative) values denote an *enhanced* memory for high-calorie food locations.

We adapted the food choice questionnaire (Steptoe et al., 1995) to measure the importance of convenience to the food decision making process of individuals. Participants had to rate five statements, such as “It is important to me that the food I eat on a typical day is easily available in shops and supermarkets”, on a four-point scale (from “Not Important At All” to “Very Important”). Responses were averaged, with larger values representing a higher importance attached to convenience in food choice. The questionnaire showed a good internal consistency in our sample (Cronbach’s $\alpha = 0.84$).

Snack purchasing habit strength was assessed with an adapted version of the self-reported habit index (SRHI), which focused on the core SRHI elements of frequency and automaticity (de Vet et al., 2015; Verplanken & Orbell, 2003). “Snacks” were explicitly defined as high-calorie items through the provision of examples (e.g. chips, cookies, candy, and fries) on questionnaire instructions. The questionnaire inquired about (high-calorie) snack purchasing behaviour, and comprised of six items that individuals had to rate on a five-point scale (ranging from “Strongly Disagree” to “Strongly Agree”). Sample statements include “Buying snacks is something I do frequently” and “Buying snacks is something I do without thinking”. Separate scores on scale items were averaged, with a higher overall score indicating a greater snack purchasing habit strength. The questionnaire displayed a good internal consistency (Cronbach’s $\alpha = 0.92$).

Participants’ healthy eating intentions were recorded with two items (i.e., “In my daily life, I strive to eat healthy” and “It is important to me to eat healthy foods”) rated on a seven-point scale anchored from “Strongly Disagree” to “Strongly Agree” (Raghoebar et al., 2021).

An individual’s inhibitory control to high-calorie foods was established by calculating the rate of commission errors (i.e., number of failures of inhibition divided by the total number of no-go trials) committed in the food-specific go/no-go task (Batterink et al., 2010; Chen et al., 2018). A *higher* proportion denotes a *lower* ability to inhibit responses towards high-calorie food stimuli.

Finally, we collected sociodemographic information on sex, age, ethnicity, objective SES (i.e., annual household income, highest education level, and occupation), subjective SES (10-point MacArthur Subjective Social Status Scale; Adler et al., 2000), and neighbourhood SES (Table S1). Household income was composed of five categories: (1) minimum (less than 14,100 euros per year), (2) below the national average (14,100 – 36,500 euros per year), (3) approximately the national average (36,500 – 43,500 euros per year), (4) one to two times the national average (43,500 – 73,000 euros per year), and (5) two or more times the national average ($\geq$73,000 euros per year). Highest education level followed the Dutch education classification system and was coded as 11 categories, spanning from (1) none or primary school education to (11) university master, doctoral, or postdoctoral (Table S1). Occupation was categorised into two groups: (1) employed and (2) unemployed. Due to the absence of income information on 71 participants (22.5%) of the second test session, and the lower robustness of linear regression models to missing data (Hughes et al., 2019), objective SES was operationalised as a composite measure (i.e., by standardising each available variable and taking their mean; Adler et al., 2000) in the analysis of behavioural outcomes. Neighbourhood SES was obtained from individual postal codes, which were translated into respective (z-distributed) neighbourhood SES scores using the *Statusscores* database of the Netherlands Institute for Social Research (Sociaal en Cultureel Planbureau, 2017).

2.5.3. *Control measures*

As hedonic valuations of – and previous exposure to –a food can impinge on the accuracy of recalling its location (cf. de Vries, Morquecho-Campos, et al., 2020; de Vries, de Vet, et al., 2020), we required participants to rate each food stimulus along the parameters of Liking and Desire to Eat on a 100 mm VAS (anchored from “Not At All” to “Very Much”), as well as Familiarity on a five-point scale (Tuorila et al., 2001). Furthermore, hunger states at the onset of testing were documented using a 100 mm VAS (anchored from “Not At All” to “Very Much”).

2.6. Data analysis

Data analysis was conducted with IBM SPSS Statistics 25. Statistical significance was defined as $p < .05$, with the exception of the second and third confirmatory analyses, which made use of a Bonferroni correction for multiple (N = 3) behavioural outcomes. The α_{adjusted} for the latter two tests was therefore set at 0.017. We first examined the existence and expression of the high-calorie spatial memory bias in our sample, before dissecting the bias’ behavioural implications.

2.6.1. Expression of the High-calorie spatial memory bias

To demonstrate the existence of a high-calorie bias in human spatial memory, we analysed food spatial memory data using a linear mixed effects model (LMM), due to its flexibility and robustness in modelling continuous correlated outcomes (Krueger & Tian, 2004). Our saturated LMM comprised of a random intercept and slope with main and interaction effects of *Caloric Density* and *Taste* as fixed factors, *Participant* and *Time* as random factors (covariance structure: Unstructured), *Sex*, *Age*, *Ethnicity*, *Household Income*, *Education*, *Occupation*, *Subjective SES*, *Neighbourhood SES*, *Liking*, *Desirability*, *Familiarity*, and *Hunger* as covariates, and $\log_{10}(y + 1)$ transformed *Spatial Memory Accuracy* (*D*) as the dependent variable. Food spatial memory data were $\log_{10}$-transformed to improve homoskedasticity of error terms, yielding percentage changes in pointing errors (*D*) between groups as the outcome variable. To test for sociodemographic moderators of the bias, we entered respective interactions between *Caloric Density* and all sociodemographic factors as additional fixed effects.

The model selection process made use of a backward stepwise approach. First, the covariance matrix of random effects in the saturated LMM was determined using Restricted Maximum Likelihood (REML) ratio tests using the -2 log likelihood (-2LL) test statistic. Then, the fixed part of the saturated LMM was simplified based on Maximum Likelihood (ML) ratio tests using the -2LL test statistic. In both cases, the most parsimonious model was selected and the final LMM was refitted with REML estimations. The finalised LMM was cross-checked with a forward stepwise modelling method.

2.6.2. High-calorie spatial memory bias and routine eating behaviour

To test whether the high-calorie bias in spatial memory predicts routine eating behaviour, we carried out a multiple linear regression analysis on each outcome variable (N = 3), with *Sex, Age, Ethnicity, Objective SES* (composite), *Subjective SES*, *Neighbourhood SES*, *Liking of high- vs low-calorie foods, Desirability of high- vs low-calorie foods, Familiarity with high- vs low-calorie foods, Importance of Convenience, Snack purchasing habit strength, Healthy Eating Intentions*, *Inhibitory Control,* and the *High-calorie spatial memory bias* ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) as predictor variables.

As models for high-calorie food environment exposure and BMI violated the assumption of homoskedasticity, we performed regression analyses using the “HC 3” heteroskedasticity-consistent standard error estimator (Hayes & Cai, 2007).

2.6.3. High-calorie spatial memory bias, psychological moderators, and routine eating behaviour

To determine whether individual psychological factors moderate potential effects of the high-calorie spatial memory bias on routine eating behaviour, we included respective interactions between the *High-calorie spatial memory bias* ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) and *Importance of Convenience, Snack purchasing habit strength, Healthy Eating Intentions,* and *Inhibitory Control* as additional predictors in previous multiple linear regression models.

Again, regression analyses for high-calorie food environment exposure and BMI employed robust (HC3-generated) standard errors.

3. Results

3.1. The high-calorie bias in human spatial memory is replicated and equally expressed across sociodemographic groups

The average accuracy in spatial memory (i.e., pointing error or *D*) observed across food stimuli was 236.35 (*SD* = 217.44; Range = 0 – 1370.43) pixels.

The caloric density of a food positively predicted how accurate its location was recalled, as individuals demonstrated 4.67% lower pointing errors on average for high-calorie food locations compared to low-calorie counterparts, F(1,308) = 5.66, $p = .018$, $\eta p2 = 0.02$, 90 %CI $\eta p2 = [0.002, 0.05]$. The high-calorie bias in spatial memory, though small in size, remained significant after controlling for demographic characteristics, hunger state, hedonic food evaluations, and familiarity with foods. In contrast, an individual’s food spatial memory performance was not affected by the Taste (i.e., sweet or savoury) of an item, F (1,6796) = 2.51, $p = .113$. Among the tested covariates, only Education, F(1,306) = 16.99, $p < .001$, $\eta p^2 = 0.05$, 90% CI ηp^2 [0.02,0.10], and Age, F(1,306) = 31.53, $p < .001$, $\eta p^2 = 0.09$, 90% CI ηp^2 [0.05,0.15], influenced *overall* food spatial memory accuracy, and to a similar degree as Caloric Density. A higher education level corresponded to having 3.50% lower pointing errors on average, whereas a unit increase in age yielded a 0.81% rise in pointing errors.

None of the interactions between Caloric Density and sociodemographic factors (e.g. Sex, Age, Education) reached significance, indicating that the magnitude of the high-calorie spatial memory bias did not differ across sociodemographic groups (all $p > .05$).

3.2. The high-calorie bias in human spatial memory does not directly predict routine snack consumption frequency, high-calorie food environment visits, or BMI

Participants consumed high-calorie snack foods an average of 3.50 (*SD* = 1.94; Range = 0.16 – 10.03) times (days) in a month, and visited high-calorie food environments to eat or purchase foods an average of 0.5 (*SD* = 0.65; Range = 0 – 7.15) times (days) in a month.

No evidence was found for a direct (main) effect of the high-calorie spatial memory bias on the frequency of high-calorie snack consumption in a month, B = 0.001, 95% CI = [0.001,0.003], t(301) = 0.92, $p = .181$ (Table S3). Furthermore, an enhanced memory for high-calorie food locations did not directly result in more frequent exposure to high-calorie food environments, B = 0.00, 95% CI = [0.00, 0.001], t(301) = 1.14, $p = .128$ (Table S4), or a higher BMI in individuals, $B = -7.29 \times 10^{-5}$, 95% CI = [-0.01, 0.01], t(301) = -0.03, $p = .489$ (Table S5).

3.3. Inhibitory control moderates the effect of the high-calorie spatial memory bias on routine high-calorie food environment visits

Participants reported a medium snack purchasing habit strength of 2.17 (*SD* = 0.89; Range = 1–5), an above-average importance of convenience when making food decisions (M = 2.71 (±0.59), Range: 1.2 – 4.0), and a high intention to eat a healthy diet in daily life (M = 5.31 (±1.07), Range: 1 – 7). Finally, the mean commission error rate observed in the food-specific go/no-go task was 0.02 (*SD* = 0.05; Range = 0 – 0.58), amounting to a mean of 1.44 failed no-go trials (*SD* = 3.6; Range = 0 – 42).

Taking psychological constructs into account as possible moderators of behavioural effects, we observed a significant interaction between the high-calorie spatial memory bias and inhibitory control, B = -0.02, 95 % CI = [-0.03, -0.003], t(297) = -2.38, $p = .009$, as well as a trend for a moderating role of snack purchasing habit strength, B = 0.001, 95 %CI = [1.98×10^{-5}, 0.002], t(297) = 2.02, p = .023, on the frequency of visits to high-calorie food environments in a month. Interaction terms between the high-calorie spatial memory bias and all possible moderators, in either high-calorie snack consumption frequency or BMI models, were otherwise not significant (all p > .017; Tables S3 and S5).

Follow-up simple slopes analysis on the significant interaction revealed that individuals with low commission error rates (i.e., high inhibitory control towards high-calorie foods) visit high-calorie food environments *less regularly* as expression of the high-calorie spatial memory bias *increases*, B = 0.001, p = .001. Furthermore, exploratory (simple slopes) analysis into the trending moderation by snack purchasing habit strength showed opposing effects to the high-calorie spatial memory bias: individuals with a greater habit strength visit high-calorie food environments *less regularly* as expression of the high-calorie bias in spatial memory *increases* (and visit high-calorie food environments *more regularly* as expression of the high-calorie spatial memory bias *decreases),* B = 0.001, p = .017 .

3.4. The high-calorie spatial memory bias indirectly predicts a higher BMI, by promoting a greater snack purchasing habit strength

Guided by the counterintuitive observation that snack purchasing habits seemingly minimise effects of the high-calorie spatial memory bias on high-calorie food environment visits, we further explored the relationship between the two predictors.

A Spearman's correlation revealed, albeit weakly, that as expression of the high-calorie bias in spatial memory increases, so does snack purchasing habit strength, $r_s(316) = -0.11$, $p = .049$ (Table S6). As snack purchasing habit strength was shown to predict BMI in prior confirmatory analysis (Table S5), we reasoned that it could act as an intermediary component within the behavioural pathway. Therefore, we tested for an *indirect* association between the high-calorie spatial memory bias and BMI, via an individual's snack purchasing habit strength. Mediation analysis was carried out using the bias corrected bootstrapping method – producing 95% bias corrected confidence intervals for the total indirect association, derived from 5.000 bootstrap resamples (Hayes, 2017). Results yielded a significant indirect effect of the high-calorie spatial memory bias on BMI that was mediated by snack purchasing habit strength, B = -0.001, 95% CI [-0.003, −0.0002]. An enhanced memory (i.e., lower pointing errors) for high-calorie food locations predicted a greater snack purchasing habit strength (B = -0.001, p = .037), and consequently a higher individual BMI (B = 1.07, p < .001).

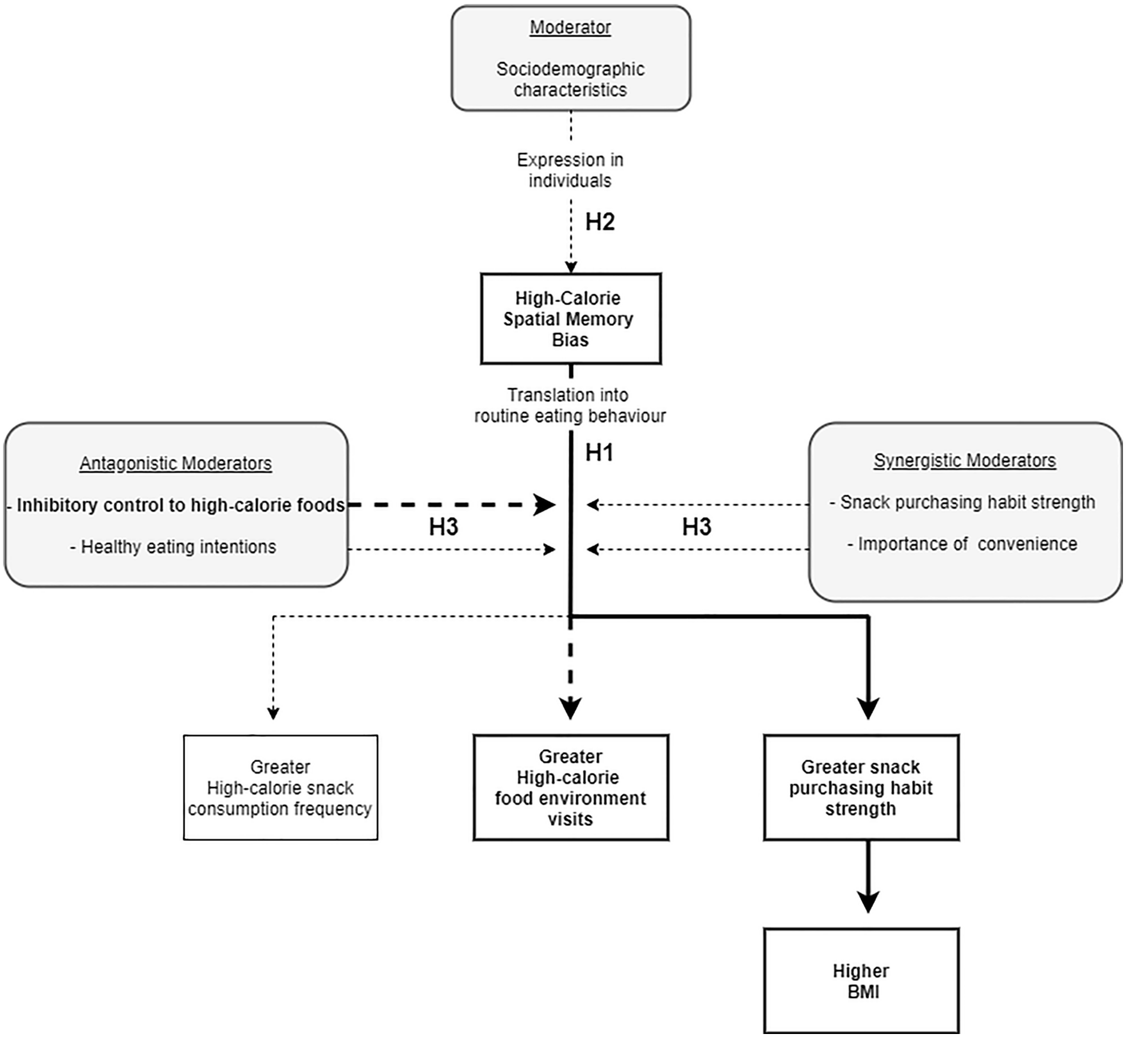

Fig. 1. Synthesis of main findings. Relationships shown by bolded lines were significant. The high-calorie bias in human spatial memory was replicated and expressed to a similar degree across sociodemographic groups. In turn, the high-calorie spatial memory bias indirectly predicted a higher BMI, by mediating a stronger habit of purchasing high-calorie snack foods (*bolded unbroken line*). Furthermore, the cognitive bias (directly) predicted greater routine visits to high-calorie food environments, but this effect was antagonised by an individual's inhibitory control to high-calorie foods (*bolded broken line*).

4. Discussion

We demonstrate once again that human memory gives priority to locations of foods with higher caloric payoffs (cf. New et al., 2007; de Vries, de Vet, et al., 2020). More importantly, our findings indicate that this high-calorie bias in human spatial memory may operate counterproductively within a modern foraging context, as a greater expression of the bias predicted a stronger habit of purchasing high-calorie snack foods and a higher subsequent BMI (H_1) – although no direct associations with high-calorie snack consumption frequency were observed. The expression of the high-calorie spatial memory bias was similar across sociodemographic characteristics (H_2), and we found variation in the circumstances under which the bias translates into routine eating behaviour (H_3). Specifically, individuals with an improved ability to inhibit impulsive responses to high-calorie foods were seemingly shielded from bias-related tendencies to frequent high-calorie food outlets (Fig. 1).

Our findings, though correlational, provide preliminary evidence that snack purchasing habit strength may be a mediating (as opposed to moderating) factor in the association between the high-calorie spatial memory bias and a higher (less healthy) BMI in individuals. Habit theory states that a defining feature in the development and strengthening of a habit is when a behavioural response is sufficiently and satisfactorily repeated within a specific context, until the point of "automaticity" in which solely environmental cues can elicit the corresponding behaviour (Verplanken & Aarts, 1999; Verplanken & Orbell, 2003). Therefore, our results suggest that it is not merely the frequency of high-calorie food choice that is targeted by the bias. Rather, it is a high frequency *coupled* with a high automaticity of choosing to consume high-calorie foods within a specific context, that is essential for the bias' behavioural effects. In other words, the high-calorie spatial memory bias is likely able to automatise certain patterns of undesirable responses in particular situations; the bias may strengthen the mental association between a specific environmental cue (i.e., sight or smell of a high-calorie snack food) and unhealthy behaviour (i.e., purchasing the snack food), when a "goal" such as satisfying (physiological or hedonic) hunger is activated. Moreover, the observation that individuals with a greater expression of the cognitive bias (and a lower inhibitory control) tend to visit high-calorie food locations more frequently implies another pathway through which the bias could indirectly stimulate routine high-calorie food consumption (Fig. 1). That is, the high-calorie bias in spatial memory may favour placing individuals in physical contexts that increase the likelihood of choosing a high-calorie item (Cardello, 1994; Meiselman, 2006).

One conceptual implication of these insights is that the high-calorie spatial memory bias and its immediate downstream psychological targets are expected to fall under the category of automated "impulsive" precursors of eating behaviour (Evans & Stanovich, 2013; Hofmann, Friese, & Strack, 2009; Strack & Deutsch, 2004; cf. Allan & Allan, 2013). In the health psychology literature, a distinction is made between estimates of variance in health-related behaviour that can be attributed to automated "ïmpulsive" versus controlled "reflective" processes (Armitage & Conner, 2001; Hardeman et al., 2002; Sheeran et al., 2001). While estimates vary, it is generally agreed upon that both types of processes compete with one another to gain control over resulting behaviour when in conflict (Evans & Stanovich, 2013; Hofmann, Friese, & Strack, 2009; Nederkoorn et al., 2010; Strack & Deutsch, 2004). Indeed, our finding that bias-related impulses to visit calorie-rich food environments appear to be antagonised by an individual's controlled response inhibition to high-calorie foods, points towards such a dual-systems perspective. Another more practical outgrowth of our results could be that, in order to interrupt the behavioural translation of the cognitive bias, two classes of intervention strategies merit consideration and further investigation. Firstly, a strategy using implementation intentions (i.e., specific if-then plans for acting in line with one's healthy eating goals) in tandem with cue monitoring (i.e., identifying personally relevant appetitive cues), may reduce habitual purchases of snack foods and later BMI (Adriaanse et al., 2011; Verhoeven et al., 2014). The latter combination has also proven successful at reinforcing healthy dietary habits (e.g. increasing fruit and vegetable consumption) (Adriaanse et al., 2011). Secondly, one's inhibitory control towards calorie-rich foods – and resistance to visiting high-calorie food outlets – could be trained using food-specific Go/No Go paradigms (Jones et al., 2016; Veling et al., 2017). Notably, this strategy may be particularly beneficial in situations when "reflective" self-control processes typically fail (e.g. during energy-depleted states; Hofmann, Friese, & Strack, 2009), as food Go/No Go training is thought to strengthen a more automatised form of response inhibition with time (Littman & Takács, 2017; Veling et al., 2017).

Relatedly, although behavioural changes associated with the spatial processing bias appear small (e.g. a 0.001 increase in BMI), these outcomes are for a one-unit (pixel) increase in the *overall* expression of the bias, which is not representative of the actual scale of differences between individuals. Individuals differed in their overall expression of the high-calorie spatial memory bias (i.e., aggregated across all effects) at a magnitude of 102 pixels on average, resembling estimates from previous investigations (de Vries, de Vet, et al., 2020; de Vries et al., 2021). Thus, a bigger impact on eating-related parameters is forecasted in practice. For instance, assuming a between-subjects deviation of 102 pixels in the bias' overall expression (and an approximately normal distribution of the foraging adaptation within a population; Pyke et al., 1977), one could expect an increase of at least 0.1 in snack purchasing habit strength, as well as a 0.11 rise in BMI, in 15.8% of individuals – which would amount to meaningful cumulative changes in the average weight of a population (Heaney, 2011; Hill et al., 2013). Furthermore, drawing from earlier research, the former could result in a 4% increase in the reported ease of locating high-calorie (versus low-calorie) products within a supermarket, which would potentiate high-calorie food choice to a similar degree as other (structural) predictors of perceived food search performance, such as how eye-catching a product aisle is rated to be (de Vries et al., 2021). Taken together, there are good empirical indications that the cognitive bias can materialise in the real-world foraging behaviour of individuals in small – yet relevant – ways.

The fact that the high-calorie spatial memory bias was replicated in a large sample of individuals with diverse sociodemographic characteristics adds substantial internal and external validity to previous demonstrations of the bias (e.g. de Vries, Morquecho-Campos, et al., 2020; de Vries, de Vet, et al., 2020). Indeed, the effect of caloric density on food spatial memory accuracy was comparable in size to that of earlier studies with smaller and more homogeneous participant samples (cf. (de Vries, de Vet, et al., 2020; de Vries et al., 2021). While the cross-sectional nature of the present study renders it difficult to establish a definite direction of effects, our data enable us to effectively minimise the possibility of a reversed order of events (i.e., higher exposure to high-calorie foods instead causing an enhanced memory for high-calorie food locations). In our analysis of food spatial memory data, we controlled for multiple factors that would have favoured such an "experientially-based" account of the high-calorie bias in spatial memory (i.e., higher liking, desirability, and familiarity with high-calorie foods; Craik & Lockhart, 1972). Notably, the expression of the bias has remained robust to effects of general learning mechanisms (e.g. food encoding times, food familiarity), as well as one's healthy eating intentions, in all studies to date (de Vries et al., 2020, 2021; New et al., 2007). The spatial prioritisation of high-calorie foods was further found to occur independently of the amount of visual attention individuals allocated to high- versus low-calorie items (cf. de Vries et al., 2021), which can serve as a more objective proxy of (unconscious) appetitive motivations towards high-calorie foods (2014). Collectively, our findings lend support to functional (or adaptive) conceptualisations of human memory (Nairne & Pandeirada, 2008; Nairne, 2010).

More pragmatically, because our results show that the mnemonic effect of caloric content was not moderated by sociodemographic factors, this implies that differences in the *overall* (i.e., summed) expression of the bias between groups most likely originates from general learning processes (e.g. food liking, wanting, and familiarity). Besides caloric density, hedonic evaluations and past exposures to a food also respectively determine the overall accuracy of recalling its location in space, and with comparable effect sizes (cf. de Vries, Morquecho-Campos, et al., 2020; de Vries, de Vet, et al., 2020). These aspects can vary across individuals, depending on one's accumulated experiences with a food (Sobal et al., 2006), and can equally vary along a sociodemographic gradient. For instance, (implicit) liking and frequency of consuming (low-calorie) fruits tend to correlate negatively with income and education levels (Pechey et al., 2015). Therefore, individuals (and subpopulations) with more positive learned associations and greater exposure to low-calorie alternatives would presumably be able to "mask" the inherent spatial recall advantage of high-calorie foods and fall on the lower end of the bias spectrum. This suggests that health promotion efforts can also focus on decreasing the *overall* expression of the high-calorie spatial memory bias, through fostering greater hedonic valuations of – and familiarity with – healthy low-calorie items. Possible interventions for this could include repeated taste exposures and reward-based conditioning techniques (e.g. flavour-consequence learning with fruits and vegetables; Appleton et al., 2018; Yeomans, 2006). An advantage of this approach is that (changes in) food preferences and food exposure can mutually reinforce one another over time (Birch, 1999; Corsini et al., 2013). Yet, another more parsimonious strategy policy makers could opt for – to curb *both* the expression and translation of the high-calorie bias in spatial memory – involves structural adjustments to the current obesogenic food environment. Strategically limiting the range and salience of calorie-rich items in contexts where food decisions are regularly made (e.g. supermarkets), may reduce the frequency with which the spatial processing mechanism is activated for these unhealthy options, as well as lessen opportunities for the bias to materialise in undesired eating behaviour.

Still, to strengthen an evolutionary account of the high-calorie spatial memory bias, future research could compare its expression in cultures that vary on spatial cognition (e.g. spatial relational language; Majid et al., 2004), as well as perceptions and attitudes towards food. The observation of consistent findings in spite of these culture-specific differences would empirically bolster the idea that the spatial processing bias represents a (universally expressed) cognitive adaptation (Lewis et al., 2017; Nairne, 2010). Cross-cultural replications, particularly in countries with wider socioeconomic discrepancies in built food environments and dietary quality (e.g. the USA), would similarly yield more robust insights on related (sociodemographic) differences in the magnitude of the bias (Beaulac et al., 2009; Drewnowski et al., 2014). Likewise, we underscore the need for refined investigations into the causal association between the high-calorie spatial memory bias and exposure to high-calorie foods, which would also serve to verify and optimise proposed intervention strategies on the bias. While our self-reported outcomes demonstrated sufficient content validity (Streppel et al., 2013; de Vet et al., 2015; see inter-measure correlations in Table S6), more conclusive and ecologically-valid causal inferences can be derived from prospective study designs that longitudinally track individuals' actual eating behaviour (e.g. food choices; navigation within and between food retail locations), in real-time (Elliston et al., 2017). Ecological Momentary Assessment (EMA) studies present a promising development in this regard, as tools such as GPS-based smartphone applications can deliver high-resolution (spatiotemporally-rich) data on an individual's moment-to-moment food decisions (Shiffman et al., 2008).

In closing, foraging adaptations that evolved during our extended history as hunter-gatherers seemingly persist and exert an influence on how we navigate evolutionary-novel calorie-rich food landscapes today. Our results suggest that embedded within our cognitive architecture is a calorie-sensitive spatial prioritisation mechanism that once formed part of a successful foraging strategy, but could now be adversely related to habitual high-calorie snack food purchases, visits to high-calorie food outlets, and a higher body weight. However, an improved ability to appropriately modify responses to high-calorie foods appears to mitigate the bias' unhealthy dietary associations.

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Author Contributions

R. de Vries, S. Boesveldt, and E. de Vet jointly developed the conceptual framework and study design. R. de Vries, A.S. Sainz, and J. Copier developed study materials, as well as coded and analysed the data that was collected by the Flycatcher research agency. R. de Vries drafted the manuscript under the supervision of S. Boesveldt and E. de Vet. 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.2021.104478.

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