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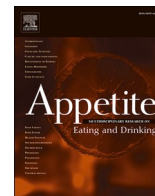
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Micronutrients and food choice: A case of ‘nutritional wisdom’ in humans?

Jeffrey M. Brunstrom^{a,*}, Mark Schatzker^b

^a Nutrition and Behaviour Unit, School of Psychological Science, University of Bristol, UK

^b Modern Diet and Physiology Research Center, Affiliated with Yale School of Medicine, Yale University, USA

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ABSTRACT

Many reports show that non-human animals have the ability to select foods based on their micronutrient composition. However, it is unclear whether humans also have this ability, and researchers have lacked appropriate methods to investigate this question. In response to this challenge, we developed an approach that derives evidence from patterns of choices across a range of food images. In two studies (Study 1, $N = 45$; Study 2, $N = 83$) adults selected one of two pairs of fruits and vegetables in a series of trials ($N = 210$). Consistent with variety seeking, they preferred ‘varied’ over ‘monotonous’ pairs (same-food pairs were less attractive). However, and even after controlling for explicit nutritional knowledge (Study 2) and food energy density (Study 1 and 2), we observed a significant tendency to select pairings that offered: i) greater total micronutrient intake and ii) greater ‘micronutrient complementarity’ (MC), i.e., a broader range of micronutrients. In a separate analysis, a similar pattern was observed in two-component meals (e.g., steak and fries) drawn from a large national nutrition survey in the UK (1086 records). Specifically, the MC of these meals was greater than would be predicted by chance ($p < .0001$) and when a meal provided an excess of micronutrients ($>100\%$ daily recommended amount) then this occurred less often than by chance ($p < .0001$), i.e., ‘micronutrient redundancy’ was avoided. Together, this work provides new evidence that micronutrient composition influences food choice (a form of ‘nutritional wisdom’) and it raises questions about whether nutritional requirements are otherwise met through dietary ‘variety seeking’. In turn, it also exposes the potential for a complexity in human dietary decision making that has not been recognised previously.

1. Introduction

In 1912 Casimir Funk published his discovery that ‘vital amines’ are essential to prevent ‘deficiency disorders’ (e.g., rickets) (Funk, 1975). Prior to this, however, scientists had already recognised the question of food choice as it relates to diet and good health. The notion that animals possess an inbuilt ability to select a diet that is optimal for health was outright dismissed by many. Jordan, for example, contrasted the modern agricultural scientist’s knowledge with that of an ‘old cow’ whose “judgement is just about as good as that of a child with a ‘sweet tooth’” (Jordan, 1906).

Speculation gave way to a number of studies using a ‘cafeteria diet,’ in which chickens (Dove, 1935), pigs (Evvard, 1915), and rats (Richter, Holt, & Barelare, 1938) were offered free access to a variety of foods, and were found to develop as well and sometimes better than those consuming formulated feed. Building on these early studies, Paul Rozin and Fred Provenza (Provenza, Meuret, & Gregorini, 2015; Richter, 1943; Rodgers & Rozin, 1966) generated a significant body of research

showing how various species adapt their dietary choices to address requirements for specific micronutrients (For a comprehensive review see Provenza (2018)). Importantly, this research has also extended to observations in primates, where food choice is found to adapt to a sudden reduction in dietary mineral abundance, caused by a change (Hurricane Iris) in natural habitat (Behie & Pavelka, 2012).

Only one scientist has attempted to extend this to humans. In 1939, Clara Davis published her most ambitious investigation, a six-year study in which 15 infants, many of them malnourished, were given free access to a cafeteria diet comprising 33 foodstuffs. Although no child ate the same combination of foods, they all achieved and maintained a state of good health, which was taken as evidence for an innate capacity to acquire ‘nutritional wisdom’ (Davis, 1939). The conclusions drawn from Davis’s ambitious study have since been critically scrutinized, and so have similar findings in non-human animals (Galef, 1991; Strauss, 2006). Nevertheless, the essential question remains—does the micronutrient composition of food influence food choice in humans?

The question is more relevant than ever today. Concerns abound around the benefits of ‘natural eating’ (e.g., paleo and gluten-free diets),

* Corresponding author. Nutrition and Behaviour Unit, School of Psychological Science, University of Bristol, 12a Priory Road, Bristol, BS8 1TU, UK.
E-mail address: Jeff.Brunstrom@Bristol.ac.uk (J.M. Brunstrom).

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Abbreviations

2AFC	Two-Alternative Forced Choice
ED	Energy Density
MC	Micronutrient Complementarity
RDA	Recommended Dietary Allowance
TM	Total Micronutrient

the importance of nutritional education (Wardle, Parmenter, & Waller, 2000), and the need to promote healthy eating behaviours in children (Wood et al., 2020). Yet in humans, no study has attempted to replicate the findings of Clara Davis, which were published over 80 years ago. Accurately monitoring food intake in a large cohort and over long periods is a major undertaking. Furthermore, Davis's work would fail to meet current ethical standards. And although nutritional wisdom can and has been shown in animals (Provenza, 2018), modern humans, by comparison, are much more 'domesticated'—they dine in an environment that bears little relation to the one to which they are adapted (Brunstrom & Cheon, 2018).

Many also believe this question was obviated by the discovery of 'sensory-specific satiety' (broadly, the observation that reward value is diminished in a recently eaten food but is otherwise preserved in other uneaten foods). Early accounts concluded that this 'variety seeking' must be an "an inbuilt mechanism which helps to ensure that a variety of foods, and thus of nutrients, is consumed" (Rolls, Rolls, Rowe, & Sweeney, 1981), and this simple proposition has become generally accepted.

In response to the urgency of the question and these longstanding experimental challenges, we have developed a novel approach that avoids the need to: a) induce a nutrient deficit; b) assess changes in dietary patterns over time; and c) monitor attendant changes in health or growth. Rather than studying single micronutrients, our approach assesses patterns of food selections across a range of foods, each containing numerous micronutrients. We reasoned that when foods are combined that are rich in *different* micronutrients, then this confers an *advantage*, because a more complete range of nutrients is made accessible to the body in a single meal. Conversely, when foods are rich in the *same* micronutrients then their combination will promote *redundancy*, especially if a single micronutrient exceeds a daily Recommended Dietary Allowance (RDA).

Here, we tested the hypothesis that human volunteers choose nutritionally advantageous food pairings more often than by chance. After comparing choices across many food pairs, we find an independent and subtle tendency to select combinations that are predicted by micronutrient content, even after accounting for a basic tendency to favour variety over monotony. Thus, in two psychological experiments and in an analysis of data drawn from a large national nutrition survey, we demonstrate evidence that micronutrient composition influences food choice.

2. Study 1: evidence that micronutrients influence food choice

2.1. Method

2.1.1. Participants

Since effects of nutrient pairings on food choice have not been studied in this context previously, we were unable to conduct an informed *a priori* sample-size calculation to ensure adequate power. However, using similar methods, researchers have previously reported large effect sizes for relationships between choice and food energy-density, in samples comprising 40 participants (Brunstrom, Drake, Forde, & Rogers, 2018). To be conservative, we recruited a convenience sample of 45 participants, drawn from the population of staff and

students at the University of Bristol. Participants were excluded if they were under 18 years old and if they had a food allergy or intolerance. All confirmed that English was their first language and they received financial remuneration (£10). Approval was granted by the University of Bristol Science Faculty Ethics Committee.

2.1.2. Stimuli

Several studies show a close correspondence between behavioural responses to food images and actual dietary decisions (Cox et al., 2021; Fay, Rogers, Ferriday, Shakeshaft, & Brunstrom, 2011; Sim, Lim, Forde, & Cheon, 2018; Wilkinson et al., 2012). On this basis, we captured and used six different images of a fruit or vegetable as stimuli (Fig. 1a; for information about image acquisition see Supplemental Methods). We chose fruits and vegetables because, compared to other foods such as grains and meat, they differ greatly in their micronutrient composition and in the levels of these micronutrients (Glendinning, 2021). We selected these specific fruits and vegetables (celery, carrots, apple, blackberries, banana, and cucumber) because we expected them to be highly familiar to our participants.

Table 1 shows the extent to which each food portion provides the recommended daily intake of 22 micronutrients (US Department of Agriculture A. R. S, 2016), together with information about macronutrient composition. The six foods yielded 21 unique food pairs. Of these, six were double helpings of the same food, a 'monotonous' pair, and 15 were a 'varied' pair (Fig. 1b).

2.1.3. Food choice task

Food choice was assessed using a two-alternative forced choice (2AFC) task, in which participants selected one of two pairs of foods. Every pair was compared with every other pair, rendering 210 trials. In each trial, participants chose the pair of foods that they would prefer to include in a meal (Fig. 1c). For a more detailed account see Supplemental Methods.

2.1.4. Total micronutrient and micronutrient complementarity scores

For each food-pair combination we calculated a Total Micronutrient (TM) score. To achieve this, we computed a set of percentages reflecting the extent to which each individual food delivers recommended amounts (%) of 21 separate micronutrients (values were obtained from the USDA SR-21 database). Across the pair, we then summed the percentages for each micronutrient. On occasions when a pair exceeded 100% of a given micronutrient, we capped the total at 100%, reflecting the fact that higher values are biologically redundant (higher concentrations will be poorly absorbed and will be excreted). Finally, for each food pair, we summed the resultant 21 micronutrient values to derive a single TM score.

To capture the extent to which a food-pair combination offers a more complete range of micronutrients, we also computed Micronutrient Complementarity (MC) scores. For each pair, we calculated the absolute *difference* in the extent to which the two foods meet a daily requirement for each micronutrient (again based on USDA SR-21 database). By definition, monotonous pairs have an MC score of zero, whereas varied pairs with a high MC score will comprise foods that differ considerably in micronutrient composition, and thus produce a more balanced portfolio of nutrients when eaten together. For example, if food A is rich in vitamin C but is lacking in vitamin B6 and food B is rich in B6 but lacking in vitamin C, then this will generate a higher MC score. MC and TM scores are likely to be positively correlated. But unlike TM scores, which indicate absolute amounts of micronutrients, MC scores reflect the extent to which a food pairing better addresses the array of micronutrients necessary for optimal nutrition.

2.1.5. Procedure

Participants completed the 2AFC task and then indicated their familiarity with the test foods (see Supplemental Methods). To characterise our sample, participants indicated whether they were currently

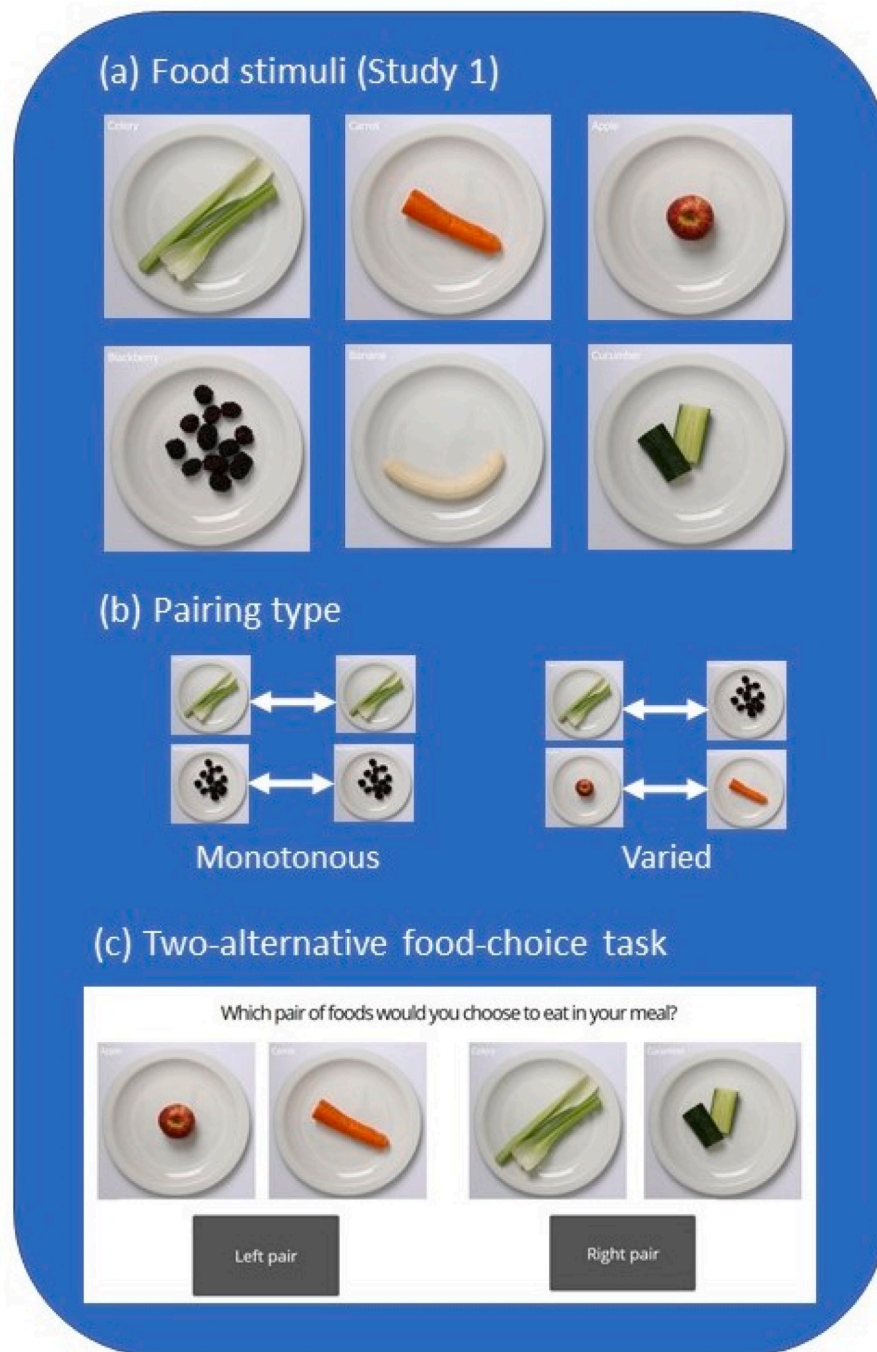


Fig. 1. Paradigm illustration for Study 1. Participants were shown 6 different foods (a), which were paired with other foods to generate six types of monotonous pair and 15 types of varied pair (b). In a two-alternative forced-choice task, each pair ($N = 21$) was presented next to every other pair in a series of 210 trials (c). Participants responded by selecting ‘left pair’ or ‘right pair’ using a computer mouse.

dieting to lose weight and then completed the Three-Factor Eating Questionnaire (TFEQ). The TFEQ is used to quantify three eating behaviour traits: cognitive restraint, uncontrolled eating, and emotional eating (Karlsson, Persson, Sjostrom, & Sullivan, 2000). Participants then provided basic demographic information (age, ethnicity, and gender identity). Finally, a measure of height and weight was obtained, and participants were debriefed.

2.1.6. Analysis strategy

In 90 trials, participants were asked to choose between a monotonous and a varied pair. To assess variety seeking, for each participant,

we computed the proportion of times that a varied pair was selected, and then assessed whether it deviated from 0.5.

We then explored evidence that choice is predicted by micronutrient composition. Foods are complex, each providing a unique blend of micro- and macronutrients. Because these dimensions covary, isolating a subtle tendency to select foods based on micronutrient content is non-trivial. Our solution relies on the fact that food pairs can have a synergistic and *advantageous* effect on the delivered range of nutrients. We reasoned that if this nutrient advantage predicts food choice, then we can reasonably claim that food choice can be predicted by micronutrient content. To quantify this advantage, we used the TM and MC scores for

Table 1
Macro and micronutrient composition^a of test foods in Study 1 and Study 2.

	Study 1						Study 2					
	Apple	Banana	Blackberry	Carrot	Celery	Cucumber	Blueberry	Strawberry	Broccoli	Boiled potato	Corn	Grape
Vitamin A	0.01	0.01	0.04	2.76	0.09	0.02	0.01	0	0.12	0	0.04	0.01
Vitamin C	0.08	0.15	0.35	0.04	0.05	0.05	0.16	0.98	1.49	0.09	0.11	0.18
Vitamin D	0	0	0	0	0	0	0	0	0	0	0	0
Vitamin E	0.01	0.01	0.06	0	0.01	0	0.03	0.01	0.04	0	0	0.01
Vitamin K	0.03	0.01	0.25	0.12	0.37	0.21	0.24	0.03	1.27	0	0	0.18
Thiamine	0.01	0.02	0.01	0.02	0.01	0.02	0.02	0.02	0.05	0.02	0.13	0.05
Riboflavin	0.02	0.04	0.02	0.02	0.03	0.02	0.02	0.01	0.07	0.02	0.04	0.04
Niacin	0	0.03	0.03	0.03	0.02	0	0.02	0.02	0.03	0.06	0.09	0.01
Vitamin B6	0.02	0.18	0.01	0.05	0.04	0.02	0.03	0.02	0.09	0.12	0.03	0.04
Folate	0.01	0.05	0.06	0.07	0.09	0.02	0.01	0.06	0.16	0.02	0.11	0
Vitamin B12	0	0	0	0	0	0	0	0	0	0	0	0
Pantothenic acid	0.01	0.03	0.03	0.04	0.02	0.03	0.01	0.01	0.06	0.04	0.08	0.01
Calcium	0.01	0.01	0.03	0.03	0.04	0.02	0.01	0.02	0.05	0.04	0	0.01
Iron	0.01	0.01	0.03	0.05	0.01	0.02	0.02	0.02	0.04	0.34	0.03	0.02
Magnesium	0.01	0.07	0.05	0.02	0.03	0.03	0.01	0.03	0.05	0.08	0.09	0.02
Phosphorus	0.01	0.02	0.02	0.03	0.02	0.02	0.01	0.02	0.07	0.05	0.09	0.02
Potassium	0.03	0.1	0.05	0.07	0.07	0.04	0.02	0.04	0.09	0.12	0.08	0.05
Zinc	0	0.01	0.04	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0
Copper	0.01	0.04	0.08	0.05	0.02	0.02	0.03	0.02	0.02	0.44	0.03	0.06
Manganese	0.02	0.13	0.32	0.08	0.05	0.04	0.17	0.19	0.1	0.67	0.08	0.04
Selenium	0	0.01	0.01	0.01	0.01	0	0	0.01	0.04	0	0.01	0
Sodium	0	0	0	0.03	0.03	0	0	0	0.01	0.01	0.01	0
Fat	0	0.01	0.01	0	0	0	0.01	0	0.01	0	0.02	0
Protein	0.01	0.02	0.03	0.01	0.01	0.01	0.01	0.01	0.06	0.06	0.06	0.01
Carbohydrate	0.05	0.08	0.03	0.03	0.01	0.01	0.05	0.03	0.02	0.06	0.06	0.06
Kcal/g	0.52	0.89	0.43	0.35	0.16	0.15	0.57	0.32	0.35	0.78	1.08	0.69

^a Proportion of daily value (DV) for adults, based on 100-g portions and a 2000-calorie reference diet.

each pair. Remember, TM captures absolute amounts of micronutrients and MC captures the extent to which nutrient levels in each pair complement one another.

To determine whether TM and MC scores predict food choice, we followed a procedure introduced by Buckley et al. (2019). In every participant and every trial (individual food-choice decision), we computed the difference between the TM score of the pair on the left and the TM score of the pair on the right (Δ TM). Similarly, we computed difference scores for MC and ED (Δ MC and Δ ED, respectively). Then, for each participant, we computed two binary regression models, one assessing Δ TM scores and the other assessing Δ MC scores. With 45 participants, this rendered 90 models of choice. Because ED is a good predictor of food choice in similar foods (Brunstrom et al., 2018), in every case Δ ED was entered competitively (alongside Δ MC or Δ ED). We reasoned that if choice is predicted by 'nutritional advantage,' then the resultant beta weights for TM and MC will tend to be greater than zero. All regressions were conducted in the R environment (Team, 2013). Predictors were standardised and sets of betas were inspected using Q-Q plots and histograms (Fig. S1) (all were approximately normal). A pre-registered analysis strategy, study materials, and raw data (Study 1 & 2), can be accessed here: <https://osf.io/qanft/>.

2.2. Results

2.2.1. Participant characteristics

All participants completed the protocol. Table 2 shows their demographic profile. All were familiar with the test foods, with the exception that three were unfamiliar with celery and one was unfamiliar with blackberries.

2.2.2. Variety seeking

When offered a choice between a monotonous or a varied pair, the latter was selected more often (Mean (M) = 57.4%, SD = 0.16, Fig. 2a) than chance, $t(44) = 3.03$, $p = .004$. From this, we conclude that variety seeking played a minor yet reliable role in food choice.

Table 2

Participant characteristics in Study 1 and Study 2.

Category	Characteristic	Study 1	Study 2
Sample size [N]		45	83
Gender identity [n]	Female	31	72
	Male	13	11
	Other	1	0
Age [mean (SD) years]		28.5 (9.6)	19.7 (2.4) ^a
Ethnicity [n]	Asian or Asian British	6	7
	Black or Black British	2	1
	Mixed	1	5
	White	36	69
Currently dieting [n]	Yes	5	8
	No	41	75
TFEQ [mean (SD)]	Cognitive restraint	52.5 (9.8)	52.7 (9.2)
	Uncontrolled eating	40.6 (11.4)	55.2 (13.0)
	Emotional eating	49.2 (28.3)	56.4 (24.5)

^a Two participants did not provide this information.

2.2.3. TM and MC scores predicting food choice

When Δ TM and Δ ED scores were considered simultaneously the mean beta for ED ($\beta_{ED} M = 0.56$, $SD = 1.26$) was roughly twice the mean for TM ($\beta_{TM} M = 0.26$, $SD = 0.62$, Fig. 3a). Nevertheless, both sets are positive and both deviate significantly from zero (ED, $t = 3.00$, $p = .004$, $d = 0.44$; TM, $t = 2.81$, $p = .007$, $d = 0.42$). (A positive beta weight indicates that a food pair with that characteristic was more likely to be selected and a negative beta weight indicates the converse.)

When MC and ED are entered competitively, again, both sets deviate significantly from zero (Fig. 3b), ED, $M = 0.61$, $SD = 1.29$, $t = 3.19$, $p = .003$, $d = 0.47$; MC, $M = 0.42$, $SD = 0.68$, $t = 4.19$, $p = .001$, $d = 0.68$. Together, these findings for TM and MC indicate that participants favoured pairs that promoted nutritional advantage and synergy.

Finally, to demonstrate that this is not explained by simple variety seeking, we repeated our analysis after removing 105 trials that included a monotonous pair. Our observations remained unchanged - values for β_{ED} were greater than zero ($M = 0.76$, $SD = 1.74$, $t = 2.95$, $p = .005$, $d = 0.44$), as were β_{TM} values ($M = 0.39$, $SD = 0.90$, $t = 2.92$, $p = .006$, $d = 0.43$) (Fig. 4a). Similarly, when Δ TMC and Δ ED were specified, both sets

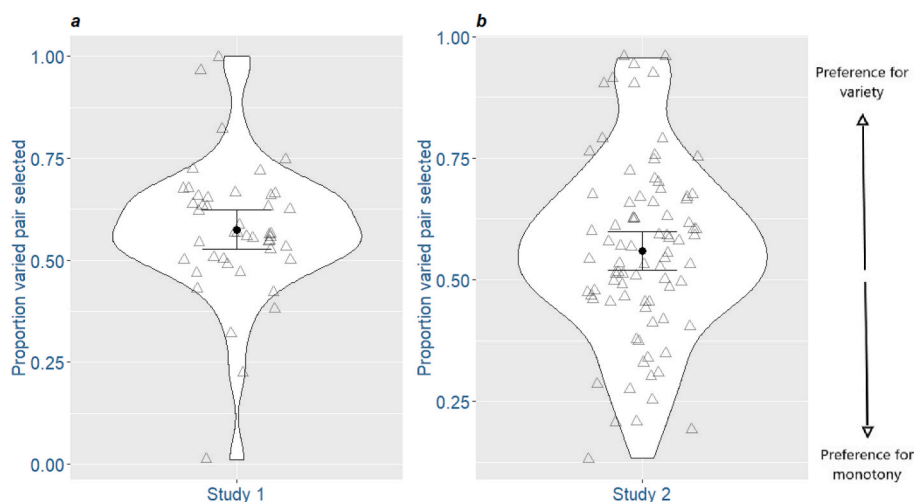


Fig. 2. Violin plots showing preference for varied pairs of foods in (a) Study 1 and (b) Study 2. Mean proportion of trials that a varied pair of foods was selected over a monotonous pair. White patch shows smoothed probability density (error bars show $\pm 95\%$ CI). Ratios for individual participants are shown as triangles and random offset has been added to avoid overlap. Values greater than 0.5 indicate a relative preference for varied pairings.

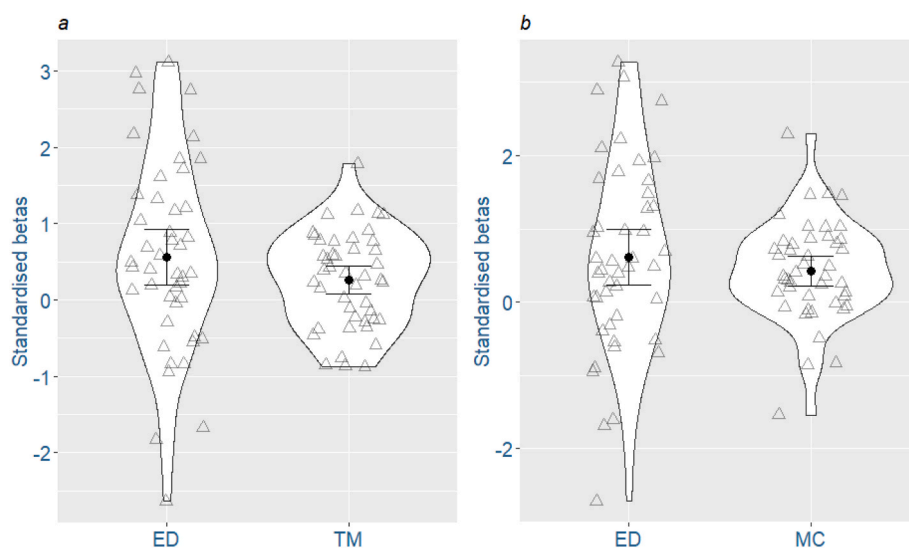


Fig. 3. Study 1: violin plots showing beta weights for variables predicting choice in all trials. Mean ($\pm 95\%$ CI) β for (a) ED and TM, and mean β for (b) ED and MC. Both panels show beta weights for individual participants and random offset has been added to avoid overlap. White patch shows smoothed probability density (error bars show $\pm 95\%$ CI). In all cases, data were modelled using 210 trials, incorporating both varied and monotonous food pairings.

deviated from zero (Fig. 4b), $\beta_{ED} M = 0.88, SD = 1.99, t = 2.96, p = .005, d = 0.44$; $\beta_{MC} M = 0.50, SD = 1.09, t = 3.1, p = .003, d = 0.46$.

2.3. Interim discussion

Study 1 confirmed that people prefer variety; however, after controlling for energy density, and beyond this variety seeking, participants also showed a preference for pairs that had higher TM and MC scores, which indicates a capacity to ‘recognise’ variation in the distribution and density of micronutrients in fruits and vegetables.

Although we used 21 different pair combinations, a concern is that they were formed from only six foods. A further concern is that our findings might otherwise be explained by the fact that children and adults are encouraged to ‘like’ foods that are ‘good for them.’ To demonstrate generalisability and to exclude accounts based on ‘nutritional information’ we ran a second study. Using different stimuli, participants rated liking and whether the foods contained vitamins and minerals, and we accounted for these variables in our analyses.

3. Study 2: replication after accounting for nutritional education

3.1. Methods

3.1.1. Participants

Using the smallest relevant effect size from Study 1 ($d = 0.42$), we determined (using G*Power 3.1.9.4) that 50 participants would be needed for 90% power. To exceed this conservative target, we recruited 83 participants (female, $n = 72$). Inclusion and exclusion criteria remained the same as in Study 1 and the sample was drawn from the same population. Approval was granted by the University of Bristol Science Faculty Ethics Committee.

3.1.2. Stimuli, tasks, and procedure

Table 1 shows nutritional information about the new food stimuli (all 100-g portions). The 2AFC task and the assessment of familiarity remained the same as in Study 1. Nutritional information was assessed

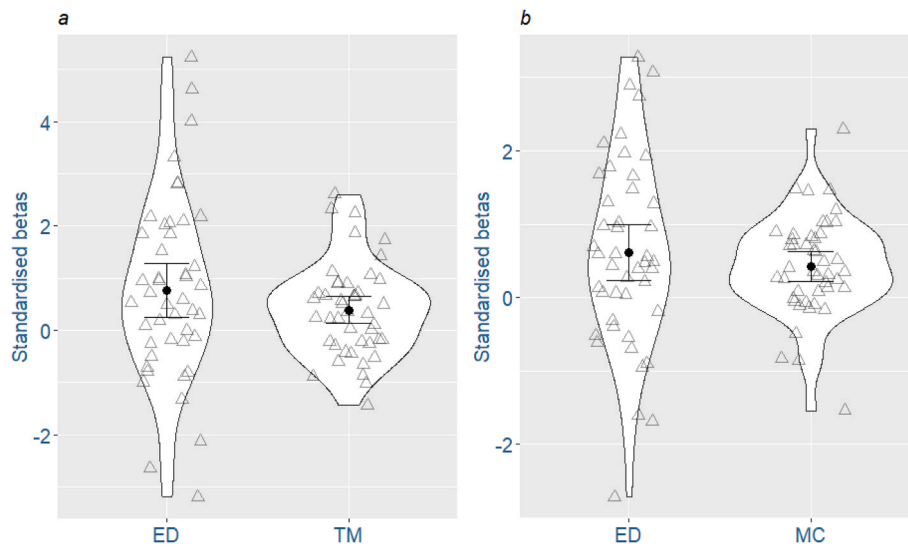


Fig. 4. Study 1: violin plots showing beta weights for variables predicting choice in trials comprising only varied pairings (105 trials). Mean ($\pm 95\%$ CI) β for (a) ED and TM, and mean β for (b) MC and ED. Both panels show beta weights for individual participants and random offset has been added to avoid overlap. White patch shows smoothed probability density (error bars show $\pm 95\%$ CI).

using two visual-analogue scales, one headed “Is this food rich in vitamins and minerals?” (NUT) and a second headed “How much do you like the taste of this food?” (LIKE).

3.1.3. Data analysis

We applied the same analysis strategy as in Study 1. Again, for each participant, we generated two pairs of regression models (4 in total), one pair assessing TM scores and the other assessing MC scores. Within each pair, one model was derived from all trials and the other was generated using only trials that comprised varied pairs. To explore a role for nutritional information, ΔNUT and $\Delta LIKE$ were included in each model. Respectively, these variables were derived from the difference between average NUT and LIKE across food pairs. Q-Q plots for corresponding beta weights are shown in Fig. S1.

3.2. Results

3.2.1. Participant characteristics

All participants completed the protocol. Table 2 shows their demographic breakdown. One participant reported being unfamiliar with broccoli and another was unfamiliar with corn.

3.2.2. Evidence for variety seeking

As in Study 1, most participants (63%) showed variety seeking (Fig. 2b), expressed as a tendency ($t = 2.93, p = .004$) to prefer varied over monotonous pairs ($M = 56\%$ of trials, $SD = 18.3$).

3.2.3. MC and TM scores predicting food choice

Respectively, Fig. 5a and b shows standardised beta weights for TM and MC. Both also include beta weights for ED, LIKE, and NUT.

For models incorporating TM (Fig. 5a), the second-stage analysis revealed that beta weights for LIKE deviated significantly from zero,

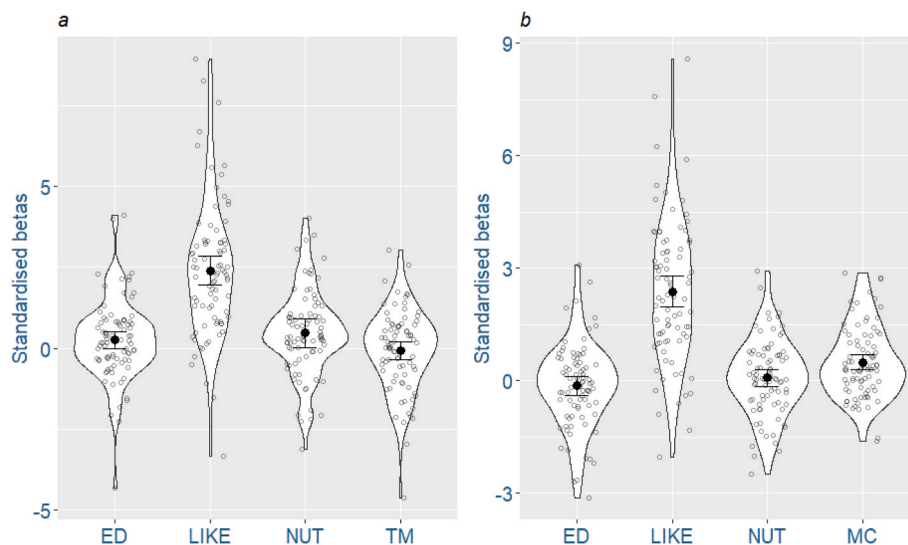


Fig. 5. Study 2: violin plots showing beta weights for variables predicting choice in all trials. Mean ($\pm 95\%$ CI) β for (a) ED, LIKE, NUT, and TM, and mean β for (b) ED, LIKE, NUT, and MC. Both panels show standardised beta weights for individual participants and random offset has been added to avoid overlap. White patch shows smoothed probability density (error bars show $\pm 95\%$ CI). In all cases, data were modelled using 210 trials, incorporating both varied and monotonous food pairings.

indicating that food liking influenced choice ($\beta M = 2.30, SD = 2.09, t = 10.5, p < .001, d = 1.10$). Beta weights for NUT also deviated from zero ($\beta M = 0.47, SD = 1.33, t = 3.21, p = .002, d = 0.35$), but were much smaller. Beta weights for ED narrowly missed significance ($M = 0.25, SD = 1.24, t = 1.82, p = .072, d = 0.21$) and we failed to replicate the same effect of TM on choice that was observed in Study 1 ($M = -0.075, SD = 1.26, t = 0.54, p = .59, d = 0.06$). For models incorporating MC, we replicated the observation in Study 1 (Fig. 5b), but this time demonstrated that MC beta weights deviate from zero ($M = 0.49, SD = 0.95, t = 4.70, p < .001, d = 0.52$) after accounting for variance explained by nutritional information (LIKE and NUT).

We then considered trials in which only varied pairs were presented. The betas for one participant were obviously spurious (orders of magnitude greater than other participants) and were removed on this basis. As in Study 1, beta weights for TM and MC (Fig. 6a and Fig. 6b, respectively) deviated significantly from zero (TM, $M = 0.71, SD = 2.09, t = 3.06, p = .003, d = 0.34$; MC, $M = 0.42, SD = 1.69, t = 2.27, p = .026, d = 0.25$), indicating a tendency to select food pairs based on micronutrient composition. For a comprehensive set of all descriptive and inferential statistics see [Supplementary Table S1](#).

3.3. Interim discussion

Although we failed to show that TM predicts choice in the full complement of trials (Fig. 4a), all other analyses yielded anticipated results. Replication of Study 1 is an important first step, but replication can be worthless if a confound or bias is overlooked. Indeed, replication might even lead to false hope, and some researchers advocate for the added benefits of scientific ‘triangulation’ (Munafò & Davey Smith, 2018). Other objections might be that participants engaged in tasks that were unnatural and involved food images. In response, we adapted our methods to assess diet diary reports drawn from a large national nutritional survey.

4. Study 3: micronutrients and food choice in a national diet and nutrition survey

4.1. MC predicting food choice

The UK National Diet and Nutrition Survey (NDNS) includes weighed diet diaries from a large representative sample of adults. Specific details of the design can be found elsewhere (Henderson, Gregory, & Swan,

2003). Respondents ($N = 2252$) reported all meal and beverage intakes (143,383 items) over a seven-day period. On eating occasions when more than one food was consumed (e.g., burger and fries), separate items were recorded. Because all entries ($N = 312,631$) in the NDNS are coded to reveal individual micronutrient intakes, we can also compute MC scores here. Many entries provided trivial nutrition, because they were very small snacks or they were beverages (e.g., tea with milk). Removing beverages and entries less than 100 kcal left 4297 two-component meals to code and analyse. We reasoned that if a person combines two foods in a way that increases MC (evidence that food choice is influenced by micronutrients), then we would expect MC scores to be greater than chance.

To calculate chance MC scores, for each person’s entries, we took their two-component meals and then randomly swapped meal components. To ensure absolute randomness, we computed 100 sets of random pairings. Then for every individual, we compared their mean MC score (observed MC) with 100 mean MC scores after randomisation (random MC). For additional information about data cleaning see [Supplemental Methods](#).

Across participants, the mean observed MC score was 401.31. In every simulation, randomly swapping the food pairings generated lower MC scores (Fig. 7). The change is modest, $M = -3.16\%$ ($SD = 0.27$), yet highly significant, $t(99) = 177.2, p < .0001$.

4.2. ‘Micronutrient excess’ predicting food choice

As with MC, TM scores can also be calculated. Earlier, we showed that pairs with a higher TM score are preferentially selected. However, in this case the same comparison is impossible because ‘rejected’ (non-selected) food pairs were not recorded. Previously, when calculating TM, we capped the contribution of a single micronutrient to 100% in cases when the sum of both foods exceeded 100% of RDA. The underlying logic was that TM should not be influenced by amounts beyond which no additional biological advantage is gained. In everyday dietary decisions the same logic might apply - food combinations that generate a ‘nutrient excess’ are redundant and might be actively avoided.

To test this, we computed the frequency of micronutrient excess in the same two-component meals in the NDNS (observed) and compared this with 100 simulations of random two-component pairings (chance). For our purposes we categorised a meal as providing nutrient excess if it contained over 160% of RNI in one of more nutrients and, where at least 50% of this threshold was met by each meal component. Because

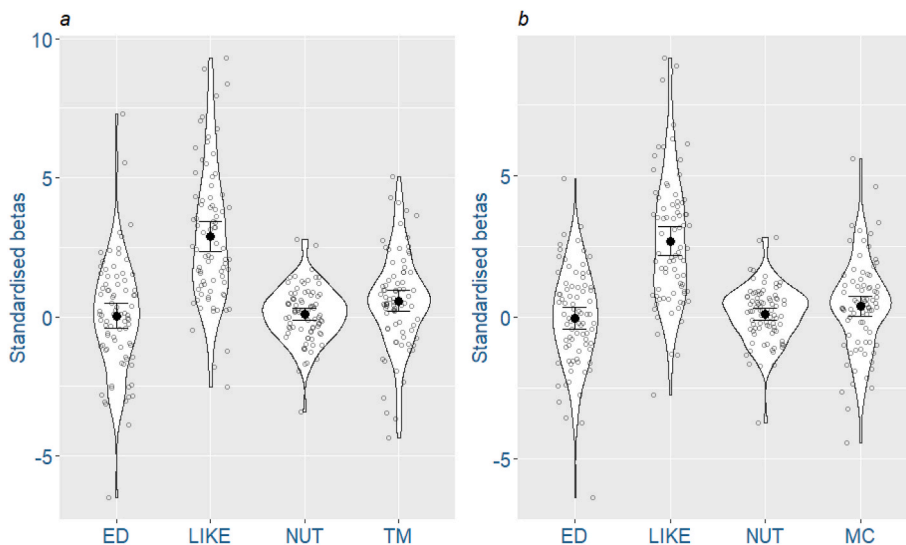


Fig. 6. Study 2: violin plots showing beta weights for variables predicting choice in trials comprising only varied pairings (105 trials). Mean ($\pm 95\%$ CI) β for (a) ED, LIKE, NUT, and TM, and mean β for (b) ED, LIKE, NUT, and MC. Both panels show standardised beta weights for individual participants and random offset has been added to avoid overlap. White patch shows smoothed probability density (error bars show $\pm 95\%$ CI).

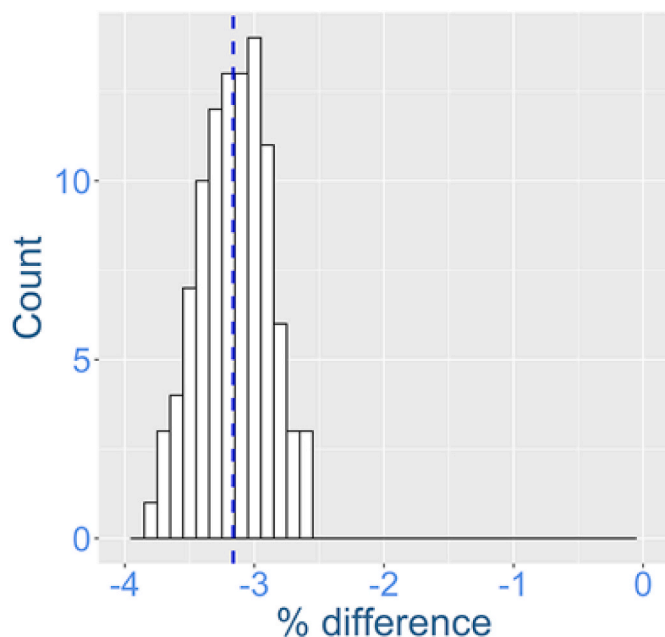


Fig. 7. Study 3: Percentage change in MC score after randomly re-pairing meal components. Data taken from 1086 individuals who reported consuming two or more two-component meals in the National Diet and Nutrition Survey. The distribution shows the outcome of 100 simulations (mean % deviation from observed MC score shown as a dotted line).

micronutrients are consumed across several meals throughout a day, we expected to categorise relatively few meals using this extreme criterion. Therefore, we also computed frequencies with lower thresholds of 140%, 120%, 100%, 80%, and 60% of RNI. If people actively avoid meals with nutrient excess, then we would expect randomisation to increase the frequency of meals that are categorised in this way, and especially when a higher threshold is applied.

Table 3 shows the number of two-component meals that were classified as having nutrient excess and the mean number classified after randomly swapping food pairs. As anticipated, at every threshold a greater proportion were classified after randomisation (all $p < .0001$), and this effect was larger with higher thresholds. In turn, this indicates that nutrient excess is avoided, which provides further evidence that micronutrients impact everyday dietary decisions.

Table 3

Meals (n) in NDNS with excess nutrients: observed frequency and frequency after randomisation.

Total RNI ^a (%)	Observed frequency of meals with excess nutrients (n)	Mean (SD) frequency of meals categorised after randomisation	Change after randomisation (%)	t (99)
60	1575	1592 (13.4)	1.2	12.7
80	957	1050 (12.5)	9.7	48.0
100	565	698 (13.6)	23.5	69.8
120	317	465 (11.1)	46.7	80.1
140	190	327 (10.4)	72.1	79.7
160	105	236 (8.3)	124.8	84.5

Note. For 4236 two-component meals drawn from the NDNS, the table shows the number that contained one or more micronutrients that exceeded each % RNI threshold and where at least 50% of this threshold was met by each meal component. Observed frequencies are shown alongside mean (+/- SD) frequencies derived from 100 randomisation simulations. In every case, randomisation increases the frequency of meals that meet each criterion level (difference between observed and mean, all $p < .0001$).

^a Reference Nutrient Intake.

5. General discussion

Given the importance of nutrition to evolutionary fitness, it is surprising how little is known about the relationship between food composition and food preference in humans. Energy-rich foods are generally preferred (Brunstrom et al., 2018), and a few studies have considered a role for protein (Buckley et al., 2019) or for combinations of fat and carbohydrate (DiFeliceantonio et al., 2018). However, this is the first research to show a selective preference for micronutrients, as measured by total amounts (TM) and by their complementarity (MC). The latter is particularly striking because it suggests a strategy that optimises micronutrient diversity. Indeed, this subtlety even appears to incorporate an active avoidance of nutrient excess (based on our analysis of NDNS), a form of foraging efficiency.

Our findings also challenge widely held beliefs about how humans maintain a balanced diet. Variety seeking has long been regarded as the key process by which micronutrient richness is achieved. However, as shown in the frequency of monotonous pair selection, and even in early long-term exposure studies (Schutz & Pilgrim, 1958), monotony is sometimes preferred. Moreover, our findings also raise the possibility that what has in the past been interpreted as instances of variety seeking may have in fact been micronutrient seeking. A further possibility is that both processes co-exist as complementary strategies for promoting nutritional diversity. In Study 2 we also provided initial evidence that micronutrient selection does not depend on nutritional education, which challenges the prevailing view that nutritional science is needed to make healthy dietary decisions (Wardle et al., 2000).

Animals are known to improve their nutritional status by consuming ‘meals’ that combine different foods (Villalba, Provenza, & Han, 2004), and humans are no different. For this reason, our food-choice task may have been especially sensitive because ‘food mixing’ is highly ingrained and it serves a key role, yet it is rarely studied.

Nevertheless, our methods have limitations. Some micronutrients may have a greater impact on food choice than others. Currently, our approach does not capture these nuances. With a stimulus as sensorially rich as food, it is also reasonable to postulate that micronutrient density correlates with some other food attribute, such as a basic taste, which itself determines preference. In such a case, the association between micronutrient density and preference would be merely incidental. A plausible candidate is sweetness, which has been mooted as a signal for the amount of carbohydrate in food (Breslin, 2013). Although we cannot presently rule out this possibility with certainty, we note that in Study 1 and Study 2, vegetables had higher (not lower) TM scores than their sweet-tasting fruit counterparts. Moreover, and especially relevant to the outcome of Study 3, a recent review of a broader range of foods (encompassing foods such as tubers, meat, and grains) found no evidence for an association between food sweetness and food micronutrient density (Glendinning, 2021). Indeed, often bland-tasting foods (endosperm and animal tissues) were found to have higher micronutrient densities than sweet-tasting fruits.

Our findings also reveal nothing about an underlying mechanism. One possibility is that micronutrient composition is learned based on acute physiological changes associated with their consumption (a form of flavour-nutrient learning). For example, in the case of body iron homeostasis, elaborate mechanisms have evolved to sense iron levels and to adjust iron absorption and recycling (Wallace, 2016), and it is possible that preferences are modified based on changes that take place after eating iron-rich foods.

Seeing others enjoying a food can also have a powerful effect on acceptance (Holley, Farrow, & Haycraft, 2017) and the same is true in animals (Posadas-Andrews & Roper, 1983). Such ‘observational conditioning’ could play an important role in transmitting beneficial food choices across generations (Brunstrom, Rogers, Myers, & Holtzman, 2015)), and this might explain why certain food combinations are seen as ‘natural’ whereas others are widely regarded as bizarre (e.g., pairing meat with ice-cream). Of course, observational conditioning cannot

account for the tendency to form advantageous pairings in the first place, but it might be an important ‘carrier’ that is ultimately nudged and moulded by flavour-micronutrient learning to form a local cuisine that runs over generations (Brunstrom et al., 2015). If such a form of social learning occurs, then an important corollary is that it might be possible for an individual to select advantageous foods and food combinations, even though they have never previously experienced a micronutrient deficiency or had the opportunity to develop specific flavour-micronutrient associations. Individuals would draw, rather, on a collective intergenerational wisdom (a cuisine) that is derived from others who have experienced a specific deficiency and/or were exposed to conditions that promoted associative learning in the past. Extending this to our methods and the selection of food pairs, one possibility is that certain pairs feature more often in particular dishes (combinations in a dessert or salad, for example). Likewise, in entries recorded in the NDNS, nutritional wisdom might be especially evident in meals that are particularly good exemplars of a longstanding cuisine. More generally, the possibility that flavour-nutrient learning takes place over long periods might explain why short-term controlled studies produce weak or inconsistent evidence for learning (Yeomans, 2012).

Alternatively, cultural dietary norms might form as an emergent property of collective ‘trial and error’, without the need for a biological signal based on immediate nutritive feedback. It has been suggested that individuals who happen to select advantageous food combinations might be more likely to have offspring, which then provides greater opportunity to witness and carry forward their food choices. Similarly, those who select ‘unlucky’ combinations would have fewer progeny and so these combinations are less likely to be transmitted to subsequent generations (for a related argument see Galef (1999)). Nevertheless, the extent to which this can explain preferences for uncommon food pairings in Studies 1 and 2 seems tenuous.

A further concern is that the variance in food choice that is explained by TM and MC is small (especially relative to liking). It is possible that a preference for micronutrients, however powerful it may be in animals, is a vanishing capability in humans. Similarly, the recent transition to a diet rich in processed confections may overwhelm a capacity for dietary learning that evolved in a milieu where food choice was limited, creating a form of ‘evolutionary mismatch’ in foraging (Brunstrom & Cheon, 2018). Although this remains to be tested, a similar conclusion was reached in a study of the effects of dietary complexity on controls of energy intake (Hardman, Ferriday, Kyle, Rogers, & Brunstrom, 2015). However, we would caution against drawing strong conclusions regarding mechanism. Our objective was merely to show evidence for micronutrient selection (i.e., departure from choices predicted by chance) rather than to quantify or explain this capacity. One interpretation is that small acute effects add up. Over thousands of meals, minor adjustments in food choice may have a significant impact on nutrition and health. Although animals have been observed going to extreme lengths to balance their diets when faced with deficiency, it is perhaps unreasonable to expect large effects in nutritionally replete humans. From a fitness point of view, it would make more sense to make continual minor meal adjustments to avoid a deficiency rather than be faced with the morbid implications of correcting one (Early & Provenza, 1998; Villalba, Provenza, Hall, & Peterson, 2006).

The evolutionary advantage of micronutrient selection is perhaps best illustrated by the fact that when deficiencies manifest, the consequences are severe. Recent estimates suggest that anaemia affects 33% of women of reproductive age (613 million), and this plays an important role in maternal deaths (WHO, 2017). Perhaps due to the epidemic of obesity, research and public policy in the developed world is nevertheless centred around the negative role of excess macronutrients in the diet. However, if we overlook the role of micronutrients on preference, we may be blind to unseen negative consequences. For example, a substantial body of literature suggests that a function of volatile aromatic compounds is to signal the presence of micronutrients, and that animals use these aromas to correct nutritional deficiencies (Amanoe

et al., 2016; Provenza, 2018; Villalba et al., 2006). The same is likely to be the case in foods that humans consume. For example, the aromatic compounds that drive liking in tomatoes are synthesized from essential nutrients and can therefore be thought of as cues to a tomato’s nutritional value (Goff & Klee, 2006). If this reflects a general principle, then adding manufactured flavourings to processed food - a processing technology that is generally considered benign - may be covertly incentivizing the consumption of energy rich foods that would otherwise be less palatable (Schatzker, 2015).

This research presents a new tool for studying ingestive behaviour. As such, the tantalizing evidence it offers is outweighed by the flood of new questions it poses. What is the extent of nutritional wisdom in humans? Why do we individuals differ in our analysis and how is nutritional wisdom expressed in the modern food environment? How can we reconcile nutritional wisdom with the long history of vitamin deficiencies in human populations, and can this be attributed solely to a lack of access to specific foods and/or poor nutritional guidance? Did British sailors develop scurvy because they lacked nutritional wisdom, or because they lacked access to fruits and vegetables on long ocean voyages (Vilter, 1987)? Did poor farmers in the American South suffering from pellagra lack the intuitive inclination to eat foods containing niacin, or did their precarious social station preclude them from obtaining such foods (DeKleine, 1937; Marks, 2003; Otto, 1999)? Can nutritional wisdom be observed in other ways? Do culinary practices optimise palatability, or, as Solomon Katz proposed (Katz, 1990), do they represent technological adaptations that enhance nutrition?

We believe we have developed a technique that can help address these important questions. In the age-old debate between scientist and old cow, the old cow does not yet have the final word. But for now, at least, she does have the last word.

Preregistration and raw data

For Study 1 and Study 2, a pre-registered analysis strategy, study materials, and raw data can be accessed here: <https://osf.io/qanft/>.

Author contributions

Brunstrom and Schatzker contributed to all aspects of the study design and interpretation. Both authors contributed to and approved the final manuscript.

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Ethics statement

The research was performed in accordance with the Declaration of Helsinki. For Study 1 and Study 2, approval was granted by the University of Bristol Science Faculty Ethics Committee. Participants gave informed consent before taking part.

Declaration of competing interest

The authors have no conflicts to declare.

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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.2022.106055>.

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