



Brunstrom, J. M., Drake, A. C. L., Forde, C. G., & Rogers, P. J. (2018). Undervalued and ignored: Are humans poorly adapted to energy-dense foods? *Appetite*, *120*(1), 589-595.
<https://doi.org/10.1016/j.appet.2017.10.015>

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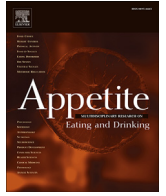
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Undervalued and ignored: Are humans poorly adapted to energy-dense foods?



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ARTICLE INFO

Article history:

Received 21 July 2017

Received in revised form

10 October 2017

Accepted 10 October 2017

Available online 14 October 2017

Keywords:

Nutrition

Obesity

Diet

Food

Food choice

Expected satiation

Energy density

ABSTRACT

In many species the capacity to accurately differentiate the energy density (kcal/g) of foods is critical because it greatly improves efficiency in foraging. In modern humans this ability remains intact and is expressed in a selective preference for types of fruit and vegetables that contain more calories. However, humans evolved consuming these low energy-dense foods (typically < 1.75 kcal/g) and it remains unclear whether they can also discriminate more energy-dense foods that now feature in modern Western diets. In two experiment participants (both $N = 40$) completed four tasks that assessed the 'value' of different sets of 22 foods that ranged in energy density (0.1 kcal/g–5.3 kcal/g and range 0.1 kcal/g to 6.2 kcal/g in Experiment 1 and 2, respectively). In Experiment 1 three measures (expected fullness, calorie estimation, and food choice), and in foods less than approximately 1.5 kcal/g (typically fruits and vegetables), the relationship between perceived value and energy density is linear. Above this, we observed clear compressive functions, indicating relative and progressive undervaluation of higher energy-dense foods. The fourth task (rated liking) failed to provide evidence for any relationship with energy density. In Experiment 2 the same pattern was replicated in measures of expected fullness, and in two different assessments of subjective calorie content. Consistent with the concept of 'evolutionary discordance', this work indicates that modern human physiology is poorly adapted to evaluate foods that have a historically unusual (high) energy density. This has implications both for our understanding of how 'modern' energy-dense foods affect choice and energy intake, and for strategies aimed at removing calories from highly energy-rich foods.

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1. Introduction

Obesity is widely regarded as a global public health crisis (Swinburn et al., 2011). Although highly heritable (Wardle, Carnell, Haworth, & Plomin, 2008), there is broad agreement that the expression of any genetic predisposition has required a change in dietary environment. In this regard, increasing attention is being paid to the expansion of global food systems and an economic transition to inexpensive and highly palatable, energy-dense (ED) foods (Drewnowski & Darmon, 2005; Popkin, 1998). Energy density is a particular concern because in controlled studies a positive relationship is observed with ad libitum energy intake (Karl & Roberts, 2014).

The pursuit of industrial efficiency has paralleled an increase in

the incidence of diet-related conditions such as type 2 diabetes, obesity, hypertension, and cardiovascular disease. One idea is that this trend reflects a form of 'evolutionary discordance' – a mismatch between intake of an energy-rich diet and a lower ED diet to which humans became adapted through natural selection (Cordain et al., 2005). Wild honey is one of the most ED 'natural' foods (~3.2 kcal/g) (Ajibola, Chamunorwa, & Erlwanger, 2012). However, it is unlikely that it comprised a large proportion of the diet, and before smoke from fire could be controlled (to pacify bees), collection of this favoured food would have been risky (Marlowe et al., 2014). Although climate and geographical location influenced human dietary patterns, pre-agricultural humans would have been limited to wild plants and animals, with minimal processing (Cordain et al., 2005). Studies of contemporary hunter-gatherers, the best surrogates for stone-age hominids, such as the !Kung, indicate a balance of approximately 33% animal to 67% plant foods (Lee, 1968). However, wide variation has been observed depending on season and food availability. Large wild ruminants

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would have provided an important source of protein but were not especially energy dense (although subcutaneous fat might have varied with season). For example, the energy densities of elk and caribou are approximately 1.1 kcal/g and 1.3 kcal/g, respectively, while tubers and fruits tend to range from roughly 0.15 kcal/g to 1.0 kcal/g. By contrast, modern foods are often much more energy dense—fries from fast-food restaurants are roughly 3.2 kcal/g and many popular snacks are even higher.

Although some hunter-gatherer communities have subsisted on higher ED foods (e.g., Alaskan Eskimos (Ho, Mikkelsen, Lewis, Feldman, & Taylor, 1972)), this merely indicates that humans can survive on varied diets, not that these diets are ideal. Humans evolved consuming a much lower ED diet in Africa and, although it is difficult to be precise, almost all foods would have had an energy density less than ~1.75 kcal/g and many would have been much lower (<0.8 kcal/g) (Milton, 2000), with one estimate suggesting an average energy density of 1.1 kcal/g, based on recent diets in Gambia (Prentice & Jebb, 2003). In relation to these observations it is surprising that questions are rarely asked about relative differences in the discrimination and evaluation of high and low ED foods—arguably, evidence for evolutionary discordance. In one study Gibson and Wardle assessed children's liking for a range of fruits and vegetables (all < 1.0 kcal/g). Remarkably, they report a clear linear relationship between preference and energy density (Gibson & Wardle, 2003), suggesting a conserved optimal attribution of 'value', even at a young age. However, it remains unclear whether the same linearity is observed in adults and across a broader range of foods that have an energy density both within and outside that to which humans have been exposed historically.

In this paper we report two studies that were designed to address this important question. Specifically, we sought to quantify the value that is placed on a broad range of foods with different energy densities. In so doing, we also illustrate how psychophysical methods can address a question that interests a broad constituency of researchers in fields such as biological anthropology, nutrition, and public health.

1.1. Participants

Separate groups of 40 healthy adult participants assisted with Experiment 1 (females $n = 21$) and Experiment 2 (females $n = 32$).¹ Participants were recruited from the population of staff at the University of Bristol (UK) and from the surrounding area. All had normal or corrected-to-normal vision and were reimbursed for their time (£10 sterling). Participants were excluded if they had a food allergy, a food intolerance, or were vegetarian or vegan. In Experiment 1, one participant declined to provide anthropometric measures. The BMI (kg/m^2) of both samples was mostly in the normal range (Experiment 1, $M = 24.0$, $SD = 3.93$; Experiment 2, $M = 22.1$, $SD = 2.66$). Both experiments were approved by the University of Bristol Science Faculty Ethics Committee.

2. Experiment 1

2.1. Methods

2.1.1. Overview

Participants were shown images of 22 weight-matched 100-g portions of foods that differ markedly in energy density (range 0.1 kcal/g to 5.3 kcal/g). Following Gibson and Wardle (2003) we

assumed that an optimal linear relationship between perceived value and energy density can be taken as evidence that humans are able to accurately determine and discriminate foods on this basis. The behavioural expression of value can be expressed in different ways. Therefore, we assessed four different judgments that reflect a range of possibilities; (1) 'food choice' (which would you choose when no other food is available?) (2) liking (for the taste), (3) 'expected satiation' (how filling is this food?), and (4) 'estimated calorie content' (how many calories are in this food?). The decision to use images rather than actual meals was motivated by three concerns: (a) the advantage gained by standardizing the format of the stimuli (achieving visual consistency in actual meals is technically challenging); (b) observations from several studies show a close correspondence between behavioural responses to food images and actual dietary decisions (Wilkinson et al., 2012); and (c) ecological validity—foods decisions before a meal (often based on visual characteristics) are an excellent predictor of actual consumption (Fay, Rogers, Ferriday, Shakeshaft, & Brunstrom, 2011). Raw data and stimuli from both experiments can be downloaded from the Open Science Framework (<https://osf.io/gvux5/>).

2.1.2. Stimuli

Eleven of the stimuli were low ED fruits and vegetables and seven of these were also used by Gibson and Wardle (2003). The remaining 11 foods were selected to create an even distribution of energy densities ranging from cucumber (0.1 kcal/g) to chocolate (5.3 kcal/g). Overhead images of 100-g portions were taken against a white background using a high-resolution digital camera (Nikon D50). Foods were presented on the same white plate (255-mm diameter) and lighting conditions remained constant. The name of each food was inserted as a label in the background of the images. Information about the test foods and their respective energy density and macronutrient composition is provided in Table S1.

2.1.3. Materials and procedure

In all tasks the foods were presented on a computer monitor in a randomized order. Participants were shown the test foods in turn and selected 'yes' or 'no' in response to the question 'Have you eaten this food before?' They then assessed their liking for the taste of each food using a 100-mm visual-analogue scale headed 'Do you like the taste of this food' with end anchors, 'I hate it' and 'I love it.' To evaluate food choice, pairs of foods were presented side-by-side in a two-alternative forced-choice task. In each trial they were instructed to "Imagine that you will be receiving only one of these foods tomorrow. Only these portions are available and no other foods will be offered! Pick the food that you would choose." The 22 foods were each compared against all others in a random order, yielding 231 trials.

Participants then completed a measure of expected satiation. Following Brunstrom and Rogers (2009), each food was presented on the left-hand side of the screen. On the right-hand side the participants were shown a portion of potato fries. Participants were asked to use the arrow keys on the keyboard to manipulate the quantity of fries in response to the instruction "Change the size of the portion on the right so that both foods will leave you feeling equally full." Participants were able to select a portion in the range 20 kcal–1000 kcal and images were loaded with sufficient speed that the change in portion appeared animated. When a large portion of fries is selected then this indicates that the adjacent test food has high expected satiation.

Finally, we obtained a measure of the estimated calorie content of the test foods. Participants were shown each food in turn and they entered a numerical value in response to the question "How many calories are in this food?" At the end of the session the height and weight of each participant was measured and they were

¹ Taking the smallest effect size in Experiment 1 ($d = 0.59$) we determined that with a two-tailed one-sample t -test and an α of 0.05, a sample of 25 was needed to replicate our results with 80% power.

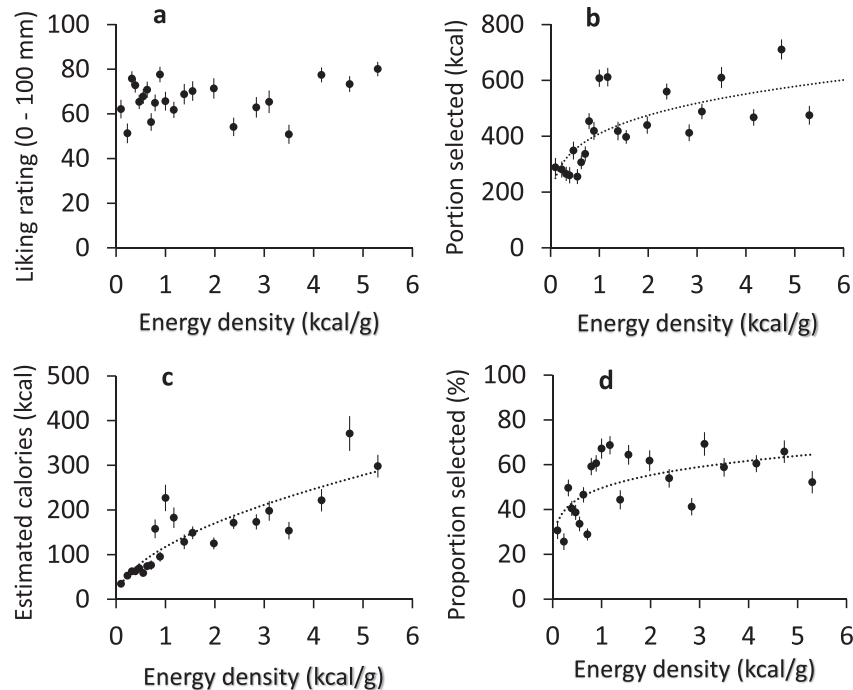


Fig. 1. Results from Experiment 1. Mean responses to test foods as a function of their energy density. Error bars in a-d represent ± 1 SEM. (a) liking, (b) expected satiation, (c) calorie estimation, and (d) food choice. Dotted lines in b-d are power functions illustrating non-linearity.

debriefed and thanked for their assistance. All participants were tested alone and an experimenter was available throughout to address questions about the procedure.

2.2. Results

The foods were mostly familiar. Sixteen participants were unfamiliar with one or more foods and only one was unfamiliar with four foods. The percentage of participants who were familiar with each food is provided in [Table S1](#). In both experiments responses to an unfamiliar food were treated as missing data.² Mean liking ratings were in the range 50 mm (Ryvita crackers) to 80 mm (chocolate), suggesting generally positive responses to the test foods.

Liking ratings were positively associated with the energy density of the foods. However, this relationship was weak and unreliable, Pearson's correlation, $r(20) = 0.23$, $p = 0.30$ ([Fig. 1a](#)). Analysis of expected-satiation judgments revealed a strong positive association with energy density, Pearson's $r(20) = 0.64$, $p = 0.001$. However, visual inspection of this relationship shows clear evidence for non-linearity ([Fig. 1b](#)). In foods with low energy density (primarily fruits and vegetables below roughly 1.5 kcal/g) linearity was observed. Above this value, expected satiation increases, but progressively less so, and to the extent that foods with an energy density above 3 kcal/g are barely distinguished with this measure. In related research estimates of the energy content of small and large portions generate a very similar function ([Chandon & Wansink, 2007](#)). In other words, a departure from linearity—when a large portion is made even larger the increase in its perceived size or perceived calorie content is smaller than when a small portion is increased by the same amount ([Chandon &](#)

[Wansink, 2007](#)). Relationships of this kind are often characterized by a simple power function that takes the form $\varphi(I) = kI^\beta$. Where, I represents the physical property of a stimulus (in this case, energy density), $\varphi(I)$ is the subjective magnitude that it evokes (in this case, expected satiation), and k is a scaling factor. For the exponent, β , values smaller than 1 indicate non linearity and relative insensitivity to an absolute increase in the magnitude of an already high intensity stimulus (for a comprehensive discussion see [Ordabayeva and Chandon \(2016\)](#)). Accordingly, we used a similar approach to calculate a power function to fit the data in [Fig. 1b](#). As anticipated, the β parameter was 0.215, which is well below 1. The associated function, expected satiation = $409.2 \times \text{energy density}^{0.215}$, is shown graphically as a dotted line ([Fig. 1b](#)). To determine whether individuals show broadly the same pattern we estimated a power function for each participant separately. All participants had an exponent less than 1 and their mean ($M = 0.22$) deviated significantly from 1, 95% CI [0.19, 0.26], $t(39) = 48.0$, $p < 0.001$, $d = 7.5$.

As with expected satiation, mean calorie estimates significantly correlated with energy density, Pearson's $r(20) = 0.85$, $p < 0.001$ ([Fig. 1c](#)). For low ED foods, judgments tend to be reasonably accurate. However, with higher ED foods they fall well below an accuracy line. For example, foods with an energy density of 5 kcal/g ($5 \times 100\text{g} = 500$ kcal) were judged to contain less than 300 kcal. Again, we fitted a power function to these mean values (shown as a dotted line in [Fig. 1c](#)) and the resulting exponent (0.535) was below 1 (calorie estimate = $117.4 \times \text{energy density}^{0.535}$). We also calculated exponents for each participant separately. Of the 40 participants tested 37 had an exponent less than 1 and their combined mean ($M = 0.66$) deviated significantly from 1, 95% CI [0.49, 0.82], $t(39) = 4.18$, $p < 0.001$, $d = 0.59$.

For each participant, we calculated the proportion of times each food was selected when compared with other familiar foods (maximum 21 occasions when all foods were familiar) in the food-choice task ([Fig. 1d](#)). The trend parallels observations of expected satiation and calorie estimation. Again, although the linear

² We repeated all analyses on complete data sets and the results remained virtually identical.

association between choice and energy density was statistically significant, $r(20) = 0.48$, $p = 0.024$, the underlying relationship shows the same compressive power function, food choice = $49.6 \times \text{energy density}^{0.158}$ with an exponent well below 1. All participants had individual exponents less than 1, ($M = 0.16$), and these deviated significantly from 1, 95% CI [0.12, 0.21], $t(39) = 35.3$, $p < 0.001$, $d = 5.58$. As with other measures, the relationship between food choice and energy density is reasonably linear, but only in foods with an energy density up to around 1.5 kcal/g.

3. Experiment 2

In Experiment 1 our observations were limited to a modest range of foods presented in small portions (100 g). In a second experiment we addressed these issues by choosing 22 different foods served in larger portions. A further concern is that responses in the calorie-estimation task might be compromised by the requirement to provide judgements in the form of a numeric calorific value. Therefore, we incorporated an additional 'implicit calorie estimation task' in which participants selected one of two foods based on their energy content. Finally, matching the test foods by weight restricts their presentation in familiar portion sizes. Although this probably applies to both low and high ED foods, in Experiment 2 we addressed this issue by presenting typical recommended portions (information obtained from product packaging) in the expected-satiation task and the explicit calorie-estimation task.

3.1. Methods

Information about the test foods is provided in [Table S2](#). Following the same procedures as in Experiment 1, participants completed computer-based assessments of the test foods in the following order; food choice, implicit calorie estimation, familiarity, liking, expected satiation, and explicit calorie estimation. The implicit calorie-estimation task was identical to the food-choice task in Experiment 1 with the exception that participants were asked to respond to the question "Which one contains the most calories?" In both the food-choice task and the implicit calorie-estimation task the participants were shown 300 g portions of the test foods. In other measures they were shown typical portions.

3.2. Results

Most (77%) participants were unfamiliar with no more than two foods. One reported unfamiliarity with 10 of the foods and two reported never consuming six. The percentage of participants who were familiar with each individual food is shown in [Table S2](#). Mean liking ratings were in the range 48 mm (celery) to 81 mm (Maltesers), suggesting that the test foods were generally acceptable to the participants.

As in Experiment 1 the relationship between liking and energy density was weak and unreliable, Pearson's $r(20) = 0.29$, $p = 0.19$. Again, we tallied responses from the food-choice task. Mean percentages are shown in [Fig. 2a](#). Unlike in Experiment 1, the linear relationship between choice and energy density failed to achieve statistical significance, Pearson's $r(20) = 0.027$, $p = 0.90$. [Fig. 2a](#) shows that this is probably because the relationship deviates from linearity even more so than in Experiment 1. Previously, we found an energy density 'cut off' at roughly 1.5 kcal/g, above which linearity was no longer observed. [Fig. 2a](#) shows the same break point in responses. Therefore, *post hoc*, we calculated a separate correlation for foods below this value. As anticipated, we observed a strong relationship between choice frequency and energy density in these

lower ED foods, Pearson's $r(7) = 0.76$, $p = 0.019$.

To compare expected satiation across foods we standardized responses by dividing the portion selected (kcal) by the weight of each food shown. Mean values are presented in [Fig. 2b](#). Across foods, expected satiation correlated significantly with ED, $r(20) = 0.72$, $p < 0.001$. However, again, the association appears to be much stronger for low than for high ED foods. Furthermore, the underlying relationship (see dotted line in [Fig. 2b](#)) shows the same compressive power function that had been observed previously, with an exponent well below 1, expected satiation = $4.3 \times \text{ED}^{0.373}$. Individually, all participants had an exponent less than 1, and their mean ($M = 0.37$) deviated significantly from 1, 95% CI [0.32, 0.29], $t(39) = 21.5$, $p < 0.001$, $d = 3.4$.

As in the expected-satiation task, typical portion sizes were presented in the explicit calorie-estimation task and so responses were also standardized. The implicit calorie-estimation task was otherwise identical to the food-choice task and so responses were tallied in the same way. Respectively, mean explicit and implicit responses are shown in [Fig. 2c](#) and [d](#). The explicit task produced a pattern that is similar to expected satiation. The linear relationship between explicit calorie estimation and energy density is highly significant, $r(20) = 0.83$, $p < 0.001$. However, it is clearer across lower than higher ED foods and, again, non-linear regression analysis indicated that the underlying pattern is in fact compressive, estimate = $1.60 \times \text{ED}^{0.667}$ (see dotted line in [Fig. 2c](#)). Individual exponents revealed that 85% of the participants had an exponent less than 1, and their mean ($M = 0.73$) deviated significantly from 1, 95% CI [0.64, 0.81], $t(39) = 6.12$, $p < 0.001$, $d = 0.97$.

The pattern of responses in the implicit calorie-estimation task also shows clear evidence for a non-linear function. Again, although the linear association between the proportion of times each food was selected and energy density was significant, $r(20) = 0.87$, $p < 0.001$, the dotted line in [Fig. 2d](#) shows compression in responses to higher ED foods, and the associated exponent is well below 1, calorie estimation = $37.6 \times \text{ED}^{0.416}$. All participants had an exponent below 1 and their mean ($M = 0.42$) deviated significantly from 1, 95% CI [0.39, 0.46], $t(39) = 31.9$, $p < 0.001$, $d = 5.0$.

4. General discussion

4.1. Evidence for undervaluation

As noted earlier, Gibson and Wardle demonstrated that the value that young children ascribe to fruits and vegetables is strongly predicted by their respective energy density (Gibson & Wardle, 2003). Building on this we incorporated a broader range of measures and explored evidence for the same relationship in adults and across foods with a wider range of energy density. Across two studies, we replicate the observation of Gibson and Wardle. However, by extending the range of foods we also exposed evidence for non-linearity. Higher ED foods (roughly > 1.5 kcal/g) are undervalued—a progressively greater change in energy density is required to produce the same change in value.

Of course, we cannot rule out the possibility that linearity might otherwise be observed in a different measure (absence of evidence is not evidence of absence). One suggestion is that the brain evaluates foods outside conscious introspection (Cohen, 2008). Using functional magnetic resonance imaging (fMRI) high- and low-calorie foods have been compared in a food choice task (Charbonnier, van der Laan, Viergever, & Smeets, 2015). After controlling for liking, differential activation has been observed in the posterior region of the right superior temporal sulcus, suggesting that this area encodes for the 'biological relevance' of food. However, in this and related studies (English et al., 2016; Frank et al., 2010; Toepel, Knebel, Hudry, le Coutre, & Murray, 2009),

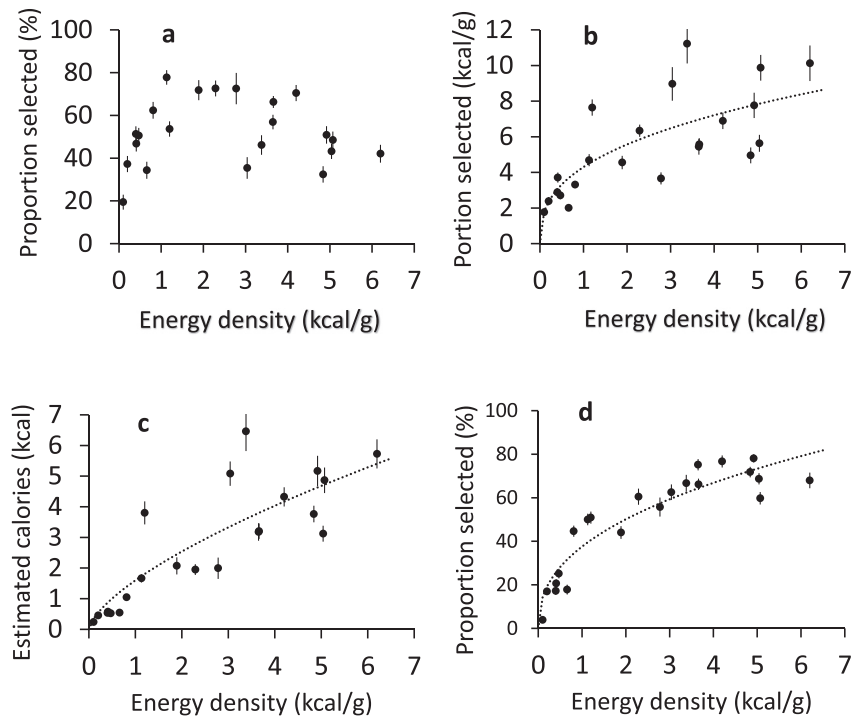


Fig. 2. Results from Experiment 2. Mean responses to test foods as a function of their energy density. Error bars in a–d represent ± 1 SEM. (a) food choice, (b) expected satiation, (c) explicit calorie estimation (after standardizing for different portion sizes), and (d) implicit calorie estimation. Dotted lines in b–d are power functions illustrating non-linearity.

foods were only categorized as high and low calorie, making it difficult to draw conclusions about progressive and subtle undervaluation. Only one imaging study has suggested a linear relationship between biological relevance and corresponding localized brain activation in predicted neural-value signals (Tang, Fellows, & Dagher, 2014). However, a concern here is that the food stimuli were not matched for their weight, which makes it difficult to determine whether differential responses reflect sensitivity to energy density or to the total energy content of food, and again, clusters of low (0.1 kcal/g–1.75 kcal/g) and very high ED foods (3.2 kcal/g–6.2 kcal/g) were assessed, using only a linear model.

4.2. Explanations

When making food choices participants were instructed to imagine that no other foods would be available for 24 h. Thus, it would seem unlikely that evaluation of the high ED options was biased by long-term concerns about health. We also note that non-linearity was also observed in other measures (e.g., expected satiation and calorie estimation) where perceived healthiness is probably irrelevant. An alternative proposition is that the foods differ in digestibility, causing a mismatch between the gross energy of foods (as derived from procedures such as bomb calorimetry) and the energy that is liberated via metabolic processes. Although this might account for the undervaluation of some foods, the human digestive tract is generally extremely efficient and there is little evidence that higher ED foods have lower digestibility. Most have a digestibility coefficient of 90% or above (Merrill & Watt, 1973) which is insufficient to explain the undervaluation that was observed. Alternatively, undervaluation might be attributed to an interaction with foods found in a modern Western diet. Several studies have shown that the expected satiation and expected satiety (anticipated fullness and suppression of hunger, respectively) of foods increases as they become familiar (Brunstrom, Shakeshaft, & Alexander, 2010; Hardman, McCrickerd, &

Brunstrom, 2011; Irvine, Brunstrom, Gee, & Rogers, 2013). One suggestion is that this process is arrested by the recent expansion of numerous manufactured brands and varieties, which limits exposure to any single food item (Hardman, Ferriday, Kyle, Rogers, & Brunstrom, 2015). However, here, undervaluation was observed in several measures that are unrelated to satiety and satiation, and also in unbranded foods (especially Experiment 1) that are not available in a wide variety of formats (e.g., feta cheese). Nevertheless, it might be instructive to consider evidence for undervaluation in other human populations, including those that have not been exposed to a modern Western diet (Brunstrom, Rogers, Myers, & Holtzman, 2015).

Prima facie our findings are paradoxical. In most measures we see very little differentiation between foods that have, for example, an energy density of 2 kcal/g and foods around 4 kcal/g. Yet the return on choosing the energy dense option is considerable. By contrast, very clear discrimination is observed with lower ED foods (<1.5 kcal/g) and yet the absolute difference in energy yielded by this ability is much smaller. One interpretation is that differentiating high ED foods is irrelevant, largely because they all deliver an adequate source of energy to match requirements. However, two lines of argument challenge this simple proposition. First, as large mammals, humans do not regulate energy intake over short periods. This is because energy expenditure from one meal to the next is trivial compared to total body energy reserves (utilizable stores in a lean adult equate to the equivalent of 60 days of energy intake). Instead, fluctuations in appetite and meal size are largely governed by gut capacity and the time that is needed to for a meal to be digested and assimilated (Rogers & Brunstrom, 2016). Therefore, explanations based on responses to a potential momentary surfeit of available energy are inconsistent with the biological reality of energy balance. Second, hunter gatherers spend long periods procuring food (Milton, 2000) and also show evidence for optimal foraging (Belovsky, 1988). The ability to reduce periods of foraging confers a significant benefit, both in reducing accidental injury and

predation. Thus, there is good reason for a strong selection pressure to recognize foods that reduce these risks. We also note that most wild foods work through the human digestive tract at a relatively slow pace. Therefore, slow transit times and the consumption of low ED food probably acted as a natural check on overconsumption, making obesity a difficult state to attain and maintain (Milton, 2000). Several studies show that low ED foods are expected to be more satiating calorie-for-calorie (Brunstrom, Collingwood, & Rogers, 2010; Brunstrom, Shakeshaft, & Scott-Samuel, 2008). Therefore, it follows that higher ED foods should be especially valued (even more than predicted), because they confer both nutrients and lower satiety (greater opportunity to consume even more food should it become available). Thus, rather than reflecting the irrelevance of higher ED foods, the evidence would seem more consistent with an account based on a failure to recognize their energy content. In other words, differentiating the energy density of available food is highly adaptive, however the capacity to do so does not extend to 'historically unusual' high ED foods.

In relation to this idea, the blunted response to high ED foods might reflect a failure to adapt behavioural responses to concentrations of a specific macronutrient. Fat is an obvious candidate because in combination with water it accounts for over 95% of variation in energy density (Drewnowski & Almiron-Roig, 2010). Many flavour preferences are modified by post-ingestive reinforcement and in rodents the effect of fat on appetite (desire) is likely to be mediated by specific fatty acid sensors (Sclafani, Zukerman, & Ackroff, 2013). Although intragastric infusion of concentrated fat generates a clear dose-dependent response in preference learning (Ackroff & Sclafani, 2014), it may not be as potent as equicaloric carbohydrate (Revelle & Warwick, 2009).

Basic taste characteristics can also provide information about nutrient density. For example, across a broad range of foods moderate correlations have been observed between sweetness and mono- and disaccharides, and between savoury and protein. Interestingly, these relationships are more pronounced in raw and partially processed foods (van Dongen, van den Berg, Vink, Kok, & de Graaf, 2012), suggesting that the inclusion of additional flavourings might play a role. Why this generates systematic undervaluation is unclear. However, it may be relevant that in many other domains evolutionary biologists regard 'cautious underestimation' as an optimal response to conditions of uncertainty (Nesse, 2001). The 'smoke detector principle' captures this idea and is often presented as an example where the cost of responding to a false alarm is insignificant relative to the cost of ignoring an alarm, even though, over time, there are likely to be many more false alarms than true alarms. Similarly, when evaluating ambiguous high ED foods it may be prudent to assume a lower-than-actual value, because the relative cost of repeated mistakes (overvaluation) outweighs the cost of overconsumption.

A final explanation for our findings is that foods differ in their 'procurement cost.' It is widely recognised that the decision to seek out and consume a food is governed by both its nutrient value and the cost (e.g., effort and/or time) associated with its procurement (Collier, Johnson, & Mathis, 2002). In other words, animals optimise their behaviour to maximize their return on investment. Historically, humans almost certainly applied the same principle in their foraging efforts. But consider the following hypothetical scenario. A nominal human forager requires 2500 kcal/day to maintain energy balance. At a foraging rate of 500g of food per hour he/she would spend 10 h foraging for foods that have an ED of 0.5 kcal/g (5 kg) or 5 h for foods that are 1.0 kcal/g. The ability to differentiate these foods saves 5 h every day. By contrast the ability to differentiate 2.0 kcal/g and 2.5 kcal/g saves only 30 min (2.0 kcal/g = 1.25 kg = 2.5 h vs 2.5 kcal/g = 1.0 kg = 2.0 h). Since the cost of making a 'dietary mistake' becomes greater when lower energy-

dense foods are available it is conceivable that selective pressures favoured a refined discrimination of these foods. Whether this bias existed or is even conserved in modern humans remains to be established. Either way, over millions of years the ability to respond to procurement cost probably played a fundamental role in shaping human dietary behaviours, and it is plausible that implicit modern-equivalent calculations of 'cost' still guide dietary decisions in humans that no longer hunt and gather.

4.3. Implications and opportunities

Because the added value that can be achieved by increasing the energy density of a food diminishes, a design pressure may exist whereby new products become extremely energy dense in order to compete with other established offerings (e.g., adding cheese to pizza crust to create 'stuffed crust pizza'). Thus, the recent trend for highly energy-rich foods (e.g., fast foods) may represent an example of how food production becomes adapted to fundamental principles that govern the economics of food choice (Drewnowski & Almiron-Roig, 2010). Of course, the converse also applies. Reducing the energy density of a very energy-rich food could have a negligible impact on its perceived value. Acknowledging this opportunity might help to guide targets for product reformulation and provide benefits for healthy weight maintenance. In future, it might also be interesting to consider the valuation of meals that comprise more than one type of food (e.g., meat and vegetables). It is unclear how information is integrated and whether combinations of low and high ED foods might decrease or increase the devaluation that we observed.

Another feature of our data is the failure to observe any relationship between liking and energy density. This coincides with previous observations that palatability is often a poor predictor of food choice (Mela, 2001). We also note that flavour-nutrient learning is largely mediated by dopamine signalling, whereas liking or pleasure is governed by the opioid system. If the relationship between value and energy density results from nutrient reinforcement (as we suspect) then responses based on 'pleasure' might well deviate from the pattern that was observed using other measures. In this regard, we also note that flavour-nutrient learning is rarely observed in humans (Brunstrom, 2007) and that in most of these studies evidence for learning has relied on responses to the same liking ratings that were used here.

Finally, our experiments were neither powered nor conceived to consider individual differences in the devaluation of ED foods. An important and obvious extension would be to explore whether the degree to which these foods are devalued impacts chronic energy intake and fat mass.

5. Concluding remarks

Based on what is known about the diet of pre-agricultural humans, we predicted evidence for evolutionary mismatch, expressed as relative insensitivity to foods with an energy density greater than 1.75 kcal/g. Evolutionary mismatch accounts for a range of aberrant behaviours—the lack of fear response in the now-extinct dodo and the tendency for newly hatched turtles to turn up a beach towards artificial light (rather than to the moon), are two such examples. Many regard human obesity in much the same way—our 'thrifty' genes offered protection from famine, but now this genotype predisposes overconsumption in preparation for a food shortage that never arrives (Neel, 1962). Our data suggest another mismatch. We are evolved to seek out foods that are energy dense, and in response, technology has advanced the development of 'hyper ED foods' that we are now poorly adapted to discriminate.

Author contributions

J.M. Brunstrom was responsible for the rationale for the experiments. All authors developed the experimental designs. J.M. Brunstrom performed the data analyses and drafted the manuscript, and all other authors provided critical revisions. All authors approved the final version of the manuscript for submission.

Declaration of conflicting interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Funding

This work was supported by the EU Seventh Framework Programme [grant number 607310].

Acknowledgements

We thank Maddy Dyer and Zoë Plant for their assistance with photography and data collection.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.appet.2017.10.015>.

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