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Research report

Genetic influences on dietary variety - Results from a twin study [☆]Benjamin Scheibehenne ^{a,*}, Peter M. Todd ^b, Stéphanie M. van den Berg ^c,
Peter K. Hatemi ^d, Lindon J. Eaves ^e, Christian Vogler ^f^a Department of Psychology, University of Basel, Missionsstrasse 62A, 4055 Basel, Switzerland^b Cognitive Science Program, Indiana University, 1101 E. 10th Street, Bloomington, IN 47405, USA^c Department of Research Methodology, Measurement and Data-Analysis, University of Twente, Drienerlolaan 5, 7522 NB Enschede, The Netherlands^d Department of Psychiatry, Virginia Commonwealth University, 1200 East Broad Street, Richmond, VA 23298-0710, USA^e Department of Human Genetics, Virginia Commonwealth University, 1101 East Marshall Street, Richmond, VA 23298-0033, USA^f Department of Psychology, Division of Molecular Neuroscience, University of Basel, Birmannsgasse 8, 4055 Basel, Switzerland

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ABSTRACT

The heritability of variety seeking in the food domain was estimated from a large sample ($N = 5,543$) of middle age to elderly monozygotic and dizygotic twins from the “Virginia 30,000” twin study. Different dietary variety scores were calculated based on a semi-quantitative food choice questionnaire that assessed consumption frequencies and quantities for a list of 99 common foods. Results indicate that up to 30% of the observed variance in dietary variety was explained through heritable influences. Most of the differences between twins were due to environmental influences that are not shared between twins. Additional non-genetic analyses further revealed a weak relationship between dietary variety and particular demographic variables, including socioeconomic status, age, sex, religious faith, and the number of people living in the same household.

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Introduction

Across many domains in daily life, having a variety of options to choose from is generally appealing (Bown, Read, & Summers, 2003; Catania, 1980). When choosing food, the tendency to seek variety and to avoid monotony holds for humans and other omnivores alike. Indeed, the consumption and liking of many foods decline if consumed for several days in a row (Addessi, 2008; Meiselman, deGraaf, & Leshner, 2000), and a monotonous diet of “nutriloaf” is still used as punishment in U.S. prisons (Barclay, 2014). Eating a varied diet has important health consequences as it helps to achieve an adequate intake of macro- and micronutrients, thereby reducing the risk of nutritional deficiencies (Drewnowski, Henderson, Driscoll, & Rolls, 1997; Hodgson, Hshuge, & Wahlqvist, 1994; Krebs-Smith, Smiciklas-Wright, Guthrie, & Krebs-Smith, 1987; Nicklaus, 2009). Consuming a variety of foods has also been related to a decrease in the consumption of fatty foods (Elmadfa & Freisling, 2005), increased consumption of fruits and

vegetables (Bernstein et al., 2002), and a lower risk of heart diseases among diabetics (Wahlqvist, Lo, & Myers, 1989). In line with this, according to the Food and Agriculture Organization of the United Nations, dietary guidelines around the world advise consumers to eat a variety of foods.

Increasing food variety can also lead to greater consumption in human and non-human omnivores, a phenomenon sometimes called “buffet effect” (Johnson & Vickers, 1993; Kahn & Wansink, 2004; Lyman, 1989; Rolls, Van Duijvenvoorde, & Rowe, 1983). This may help to improve nutritional status and to preserve body mass, for example, in elderly adults (Bernstein et al., 2002; Marshall, Stumbo, Warren, & Xie, 2001). However, for those individuals who do not face a risk of weight loss, a variety-driven increase in caloric intake may contribute to the growing obesity epidemic in modern societies, especially if the variety stems from high-energy foods like sweet and fatty snacks (Foote, Murphy, Wilkens, Basiotis, & Carlson, 2004). Because such unhealthy snacks increasingly outnumber healthy options like fruits and vegetables in many modern food environments (McCrary et al., 1999), chances are that any new food item added to an individual’s diet in those environments will lower the average quality of that diet. Thus, it comes as no surprise that dietary variety often correlates positively with body weight, especially if the variety stems from energy-dense foods (Foote et al., 2004; Nicklaus, 2009).

Given these wide-ranging positive and negative consequences of a varied diet, it is important to better understand the causes of food variety seeking, and how individual differences in observed

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* Corresponding author.

E-mail address: benjamin.scheibehenne@unibas.ch (B. Scheibehenne).

dietary variety can be explained. Here, we address this issue by estimating what proportion of these differences can be accounted for by heritable genetic influences. The analysis is based on data from twins who reported their eating habits. As a starting point for this empirical analysis, we distinguish different levels of dietary variety on theoretical grounds, outlined next.

Different levels of dietary variety

Variety seeking describes the tendency to choose different options from one occasion to the next, even if this requires switching to options that were less preferred initially (Ariely & Levav, 2000; Pessemer & Handelsman, 1984). The variety of a diet can be assessed on different levels of abstraction (Van Trijp & Steenkamp, 1990). On a broad level, variety can refer to the proportions of whole groups of foods like vegetables and fruits, a measure that provides the basis for many dietary guidelines and food pyramids. Besides this categorical level, variety can also be assessed on the level of individual food items or products. This approach typically takes into account the number of different food items that a person consumes within a given period of time and possibly also its share in total consumption (Van Trijp & Steenkamp, 1990). Here, a typical finding is that an increase in available variety increases consumption, as in the case of the buffet effect mentioned above (Rolls et al., 1983).

Variety on the item level can be further distinguished from the level of specific sensory attributes like the taste and the texture of single foods. Here, the key idea is that a set of foods consisting of distinct items that are similar in taste and texture yields less variety than a same-sized set consisting of items with disparate attributes. Monotony due to low variety at this level yields a decrease in consumption, presumably triggered by sensory-specific satiety (e.g. Inman, 2001; Rolls, Rolls, Rowe, & Sweeney, 1981). Furthermore, dietary variety can also be analyzed on the level of specific nutrients, for example, by distinguishing different carbohydrates, fats, or amino acids, which is a common approach in clinical nutrition studies (e.g. Foote et al., 2004).

Research on dietary variety has also distinguished different time frames, ranging from short term or acute periods (e.g. observing a single meal at home or at a buffet), to long-term studies that extend over the course of weeks or months (e.g. monitoring food consumption and preferences at different occasions; Schutz & Pilgrim, 1958). Here we focus on long-term dietary variety that is most likely to influence health, at the level of single food items consumed over an extended period of time.

Factors that influence dietary variety seeking

The degree of variety that different individuals include in their daily diets varies considerably, even among individuals who share the same cultural background (Van Trijp, Lähteenmäki, & Tuorila, 1992). While some people tend to live on a rather restricted range of foods, others consume considerable variety across many food categories (Rozin & Markwith, 1991).

These observable differences may be partly explained by external or situational factors, including fluctuations in what food options are available or constraints due to religious beliefs, budget constraints, knowledge about different food options, or medical conditions that demand a restricted diet (McAlister & Pessemer, 1982; Van Trijp, 1994; Van Trijp et al., 1992). Within a family, food choices may also depend on the needs and taste preferences of other family members, in particular nutritional gatekeepers who govern food purchase and preparation (Wansink, 2003).

However, past research further indicates that individual differences in variety seeking seem to be somewhat stable over time and situations, suggesting that variety seeking may resemble a person-

ality trait and thus be partly governed by internal factors. For example, one longitudinal study (Nicklaus, Boggio, Chabanet, & Issanchou, 2005) found that dietary variety at ages 2 to 3 was a good predictor for individual differences in food variety seeking in early adult life (see also Siegel & Pilgrim, 1958). Individual levels of food variety seeking also seem relatively consistent across different food categories, including soups, fruits, and sodas (Rozin & Markwith, 1991; Van Trijp & Steenkamp, 1992). To better understand these internal factors that drive food variety seeking, we briefly turn to related personality traits, outlined next.

Personality traits

Individual differences in dietary variety seeking may be driven by a range of internal factors, including the desire to seek (external) stimulation across different domains of daily life (Howard & Sheth, 1969; McAlister & Pessemer, 1982; Zuckerman, 1979). From that perspective, dietary choices may provide a means to regulate the experienced level of stimulation, for example, by increasing the degree of variety through choosing familiar but dissimilar food items (Van Trijp et al., 1992; Venkatesan, 1973).

To the degree that dietary variety seeking is driven by a desire for an optimal level of (external) stimulation, it may also be related to explorative traits like novelty seeking, the desire to consume novel or unfamiliar foods, and its opposite, food neophobia. Both tendencies have been shown to apply across different food categories and to be stable over time (Pliner & Hobden, 1992). In line with the idea that these traits share a common source, food neophobics have been shown to include less variety in their diet than those without neophobia (Falciglia, Couch, Gribble, Pabst, & Frank, 2000).

Another factor that may influence dietary variety seeking is individual differences in sensory-specific satiety – the degree to which the subjective value or reward of specific (food) stimuli or tastes gradually declines over time. Sensory-specific satiety provides a lower-level mechanistic explanation of the common finding that the acceptance and consumption of many food items decreases if they are repeatedly served for several days or even months in a row (Meiselman et al., 2000; Rolls & De Waal, 1985; Schutz & Pilgrim, 1958; Siegel & Pilgrim, 1958), even if it was highly attractive initially (Addessi, 2008). Thus, people who satiate more quickly to a particular taste may be more prone to seek greater diversification in their diet across a given period of time (Addessi, Mancini, Crescimbeni, Ariely, & Visalberghi, 2010; Epstein, Temple, Roemmich, & Bouton, 2009; Pessemer, 1985; Van Trijp, 1994). However, even though sensory-specific satiety has a strong biological basis and is relatively stable over time (Rolls, 2007), it usually refers to similarities of specific food attributes, including taste, appearance, smell, and texture, that are presented within a short time frame (Hetherington, Rolls, & Burley, 1989; Rolls et al., 1981). Thus, it is not clear how far it relates to variety seeking on the level of food items that are consumed over an extended period of time, which is the focus of this paper.

Evolutionary factors

From an evolutionary perspective, seeking dietary variety has both advantages and disadvantages. As an advantage, dietary variety helps omnivores to maintain a balanced food intake, and to avoid a reliance on a limited number of food sources that might deplete or disappear in variable environments (Addessi, 2008; Raynor & Epstein, 2001). On the other hand, each additional food source also increases the chances of eating contaminated or pathogen-bearing food that can impose high fitness costs on the individual. While this risk might be less prevalent in our modern food environments, it may have been an important selection force

in past times, and today in situations where hygiene is questionable or where the source of a food is unknown (Arnesen, Fagerlund, & Granum, 2008). Such risks constrain the degree of variety seeking and necessitate making a trade-off between the motivation to eat a variety of potentially harmful foods and the tendency to stick to a limited range of foods (Rozin, 1977). As a consequence of this, no single degree of variety seeking will be universally advantageous across environments or individuals, and hence individual differences in how much variety is preferred and sought should be expected on top of a general tendency to seek dietary variety (McCrorry et al., 1999); there could even be advantages to having a mix of variety- or novelty-seeking levels, with some more risk-taking exploratory individuals who try new potential foods and others who more cautiously copy successful food discoveries (e.g. Vickery, Giraldeau, Templeton, Kramer, & Chapman, 1991).

Heritability

To help explore the extent to which dietary variety seeking is driven by external factors (whether short-term situational ones or long-term environmental ones) versus internal factors (whether personality variables or lower-level biological mechanisms), we can assess the heritability of this behavior. The heritability of a trait, commonly established through twin studies, points toward relevant genetic variation in the population that can explain observed differences in the observed behavior of interest. For food variety seeking, such a genetic influence seems plausible given its presumed biological basis and the fact that many related behaviors, including dietary choices in general (Reed, Bachmanov, Beauchamp, Tordoff, & Price, 1997), taste preferences (Keskitalo et al., 2008), preferred serving sizes, consumption frequencies (Van Den Bree, Eaves, & Dwyer, 1999), and energy intake from different food groups (Hasselbalch, Heitmann, Kyvik, & Sørensen, 2008) have been shown to have a heritable component. Likewise, related personality traits including the tendency to seek novelty and the opposite tendency to avoid novel foods have also been linked to genetic factors (Bardo, Donohew, & Harrington, 1996; Cooke, Haworth, & Wardle, 2007; Knaapila et al., 2010; Loehlin, 1982).

Twin study

To estimate the heritability of dietary variety seeking among a defined set of single food items, we compare the eating patterns of monozygotic (MZ) and dizygotic (DZ) twins from a large twin registry over a one-year period. We also use data on the twins' social background and current living conditions, including their family status, health conditions, and socioeconomic status, to explore the strength of influence of particular environmental factors on dietary variety.

Method

The heritability analyses were based on survey data from adult twins residing throughout the US, who volunteered to participate in the Mid Atlantic Twin Registry maintained by the Virginia Commonwealth University in Richmond, Virginia. Twins were recruited as part of a follow-up to the larger Virginia 30,000 Health and Life-Style (HLS) Survey for twins and family members (Maes, Neale, & Eaves, 1997). A subset of middle-aged to elderly adults who had taken part in the original HLS questionnaire were contacted again for a second survey on diet, work, and stress (DWS) that provided the basis for the present analysis. Information about zygosity was readily available in the data set as it had been assessed previously with two questions about physical similarity during childhood, which has been shown to have better than 95% agreement with blood typing (Martin & Martin, 1975).

A total of 5,543 individual twins returned this questionnaire, including 1104 pairs of MZ, 524 pairs of DZ same-sex, and 290 pairs of DZ opposite-sex twins. The remaining 1,707 individuals counted as singletons because the respective co-twin was not included in the data set. The majority of twins (3,946 or 71%) were female. At the time of data collection between 1989 and 1991, participants' average age was 59 years (SD = 14 years). The mean Body Mass Index (BMI) was 24.7 kg/m² (SD = 4.3 kg/m²), which is comparable to the average BMI in the US at that time (Ogden, Fryar, Carroll, & Flegal, 2004). A detailed description of the sample and the survey design can be found in Eaves et al. (1999) and Van Den Bree et al. (1999).

Food frequency questionnaire

Dietary choices within the DWS survey were assessed through the semi-quantitative food frequency questionnaire (FFQ) using a list of 99 items, including 81 solid and 18 liquid foods (Block et al., 1986). Together, these listed foods were intended to capture the most prevalent sources of energy and nutrition in the American diet at that time. For each food item on the FFQ, respondents stated whether they had consumed the food during the last 12 months. For all consumed food items, they further indicated consumption frequency (number of times per day, week, month, or year) and usual serving size (small, medium, or large, with standard serving sizes indicated).

Dietary recall measures like the FFQ have been found to provide a reliable measure of actual food consumption and thus can be used to infer people's behavior in the past (Drewnowski et al., 1997; Molag et al., 2007; Nicklaus et al., 2005; Willett, 1994). As a proxy for the healthfulness of individual diets, we further counted how many of the 32 fruits and vegetables listed on the FFQ and how many of the 11 presumably unhealthy salty or sugary snacks each twin had consumed.

Health and demographic measures

Participants also provided health and demographic data, some of which are potentially related to dietary variety. In particular, they provided a self-reported health rating, on a scale from "very poor" (1) to "very good" (5), whether they were on a diet, the number of years spent in the education system (ranging from 0–7 years of school to 4+ years in college), family income in US dollars, the number of people currently living in the same household, age, and religious faith.

Measures of dietary variety

To quantify the degree of dietary variety that people include in their daily diets, different measures have been proposed in the literature. One common approach is to estimate a dietary variety (DV) score based on the number of different food items a person consumes during a given period of time. Here, we calculate the DV score as the proportion of foods consumed at least once during the preceding 12 months relative to the list of all 99 food items listed on the FFQ. This measure ranges from 0 (indicating no variety) to 1 (indicating maximum variety).

To also take the relative share of each food into account, we further calculated the Hirschman–Herfindahl index of concentration (HH) as suggested by Van Trijp and Steenkamp (1990). Originally developed in economics, the HH index can also be used to quantify the degree of variety in a diet. It is defined as the sum of squares across the relative shares of all foods in total consumption:

$$HH = \sum_{j=1}^{99} p_j^2 \quad (1)$$

where p is a vector that contains the proportional shares of each of the $m = 99$ foods listed on the FFQ with respect to the total con-

sumption of a person. To calculate p , we counted the reported number of consumption units for each food during the past year (up to a maximum of one unit per day) and divided it by the sum of all units. The size of a consumption unit for each food was described to participants in the questionnaire. The HH index ranges from $1/m$ to 1. Lower values that are closer to $1/m$ indicate that foods are consumed in rather equal quantities (i.e. a low concentration and hence high variety) whereas higher values that are close to 1 indicate that consumption mainly stems from a few foods (i.e. high concentration and hence low variety).

A closely related dimension of dietary variety concerns the randomness of the food consumption over time. The more random the dietary choices are, the higher the uncertainty about what a person will eat on any given day, which makes it more difficult to predict the diet. From that perspective, variety would be highest when there is a 50% probability that the person will consume any particular food on a given day, and hence food consumption will be evenly distributed across the available options. If variety decreases, the uncertainty gets lower and an individual's diet will become more predictable – for instance, if a person consumes the same foods every day while eating others very rarely. This aspect of uncertainty or randomness of a diet over a given period of time can be quantified with a measure of dietary entropy (DE):

$$DE = -\sum_{j=1}^{99} p_j \cdot \log_2(p_j)$$

Here, in contrast to the HH index outlined above, we calculated p by dividing the reported number of consumption units for each consumed food during the past year by the number of days in a year. Thus, p can be interpreted as the probability of eating a given food item on an average day. Dividing DE by the maximum possible entropy (49.5 in this case with 99 food items) yields an interpretable measure that indicates the uncertainty of a diet; this is referred to as the proportion of realized entropy, or PRE, in the literature (Pessemier & Handelsman, 1984). This score (PRE = DE/49.5) is 0.0 when there is minimum uncertainty, for example, if the same three foods are consumed every day, and is 1.0 when there is maximum uncertainty, that is, if a person consumes each food with a probability of 0.5 per day.

Participants who did not report the consumption of any liquids (the last category on the FFQ questionnaire) were counted as missing and were removed from further analyses, reducing the number of valid individual cases by 66 for all of the scores. A further 181 individual participants were removed for the HH and PRE analyses because they did not answer any questions about consumption units for liquid foods. For DV, this left 1,083 MZ pairs (823 female and 260 male pairs), 798 DZ pairs (410 female, 106 male, and 282 mixed pairs), and 1,716 single individuals (1,199 female and 517 male pairs) for the analysis. For HH and PRE, the numbers were 1,033 MZ pairs (784 female and 249 male pairs), 755 DZ pairs (384 female, 98 male, and 273 mixed pairs) and 1,635 single individuals (1,138 females and 497 males).

Heritability estimates

Using these three variety measures, we proceeded to calculate the heritability of dietary variety seeking by comparing their levels across different sets of twins. Specifically, by comparing the phenotypic covariance of these measures in MZ and DZ twin pairs, we estimated the percentage of the phenotypic variance explained by latent genetic versus environmental factors, separately for male and female participants (Martin, Eaves, Kearsley, & Davies, 1978). In the classical twin design, the total variance in the phenotype (Vt) is decomposed into three parts: additive genetic variance (A) that captures the combined genetic effects of all genes, common environment variance (C) that captures the environmental influ-

ences that are shared between twins such as the effects of other family members or familial socialization, and unique environmental variance (E) that captures all environmental influences that are not shared between twins, including measurement error (Neale & Cardon, 1992). This so-called ACE model focuses on the variance, not on the mean. Accordingly, the A, C, and E parameters indicate proportions of variance.

The ACE model for the data on hand data was estimated within a Bayesian modeling framework using Monte-Carlo Markov Chain techniques implemented in JAGS (Plummer, 2011) based on a method by Van Den Berg, Beem, and Boomsma (2006).¹ This method yields full posterior probability distributions for all model parameters of interest that lend themselves to an intuitive interpretation.

Results

The mean DV score across all participants was 0.752 (SD = 0.119), indicating that on average participants ate 75% of all foods listed in the FFQ at least once a year. The mean HH score was 0.044 (SD = 0.026), indicating relatively high variety. As the distribution of HH scores across participants was somewhat skewed (a few diets were highly concentrated, indicating low variety), we conducted further analyses using log-transformed HH scores (lnHH). The mean PRE score was 0.353 (SD = 0.1), indicating that the observed entropy was about a third of the maximum possible value. The three variety measures were correlated. In particular, there was a strong relationship between PRE and lnHH ($r = -0.83$),² indicating high convergent validity. The correlations between DV and both PRE ($r = 0.52$) and lnHH ($r = -0.34$) were somewhat lower, suggesting that DV measures a slightly different aspect of variety seeking.

The correlations between self-reported health and all three variety scores were rather low ($r_{DV} = 0.09$; $r_{lnHH} = 0.04$; $r_{PRE} = -0.08$); the DV and PRE scores among the extreme group of people who describe themselves as “very healthy” was about 4% higher than for people who rate their health as “poor”. While this is weakly in line with the idea that greater dietary variety goes with greater health, it is not clear what direction any causal relationship might go – it could also be that the correlations come from certain (unhealthy) medical conditions that require people to maintain a restricted (lower variety) diet. In any case, this small health improvement could not be explained through an increase in the proportion of healthier foods in the healthier twins' diets: An increase in food variety (DV) led to an increase in the total number of fruits and vegetables included in individual diets ($r = 0.81$) and also in the total number of salty and sugary snacks ($r = 0.79$), but the higher the DV score, the lower was the proportion of fruits and vegetables relative to the total number of consumed foods ($r = -0.32$) while the proportion of salty or sugary snacks slightly increased ($r = 0.08$). Comparable correlations were obtained for the other two variety scores. On average, participants eat 25 (SD = 4.5) out of the 32 fruits and vegetables and 9 (SD = 2.1) out of the 11 salty and sugary items listed on the FFQ. Participants who reported to be on some sort of diet (N = 1,765) had comparable variety scores to the rest of the sample. There was a small correlation between BMI and all three variety scores though ($r_{DV} = 0.07$, $r_{lnHH} = -0.05$, $r_{PRE} = 0.07$). Expressed differently, the BMI of participants within the lowest quartile of the DV score was 24.3 as compared with 25.1 for the highest quartile.

¹ See supplementary material for details about the Bayesian model.

² Given the large sample size, almost any statistic will be significant (i.e. $p < .05$). Therefore we refrain from reporting conventional null-hypothesis significance tests.

Heritability estimates

As shown in Fig. 1 (upper panel) and in Table 1, the Bayesian analysis indicated that additive genetic influences (*A*) explained about a third of the variation in the DV score, with negligible differences between males (30%) and females (27%). The results further indicated that the influence of common environmental influences was rather small (14% and 15% for women and men, respectively). This is in line with past research showing that shared environments often do not have a strong influence on phenotypic differences in personality traits (Bouchard, 1998; Bouchard & McGue, 2003). For both men and women, the bulk of the variance was due to unshared environmental factors (*E*) unique to each individual twin.

Figure 1 (middle and lower panel) and Table 1 further show that about one-fifth of the variance of the lnHH and PRE scores was explained by additive genetic influences (*A*) which is slightly lower than the estimates obtained for DV. The results indicate that the genetic influence was slightly higher for females (20% and 23% for lnHH and PRE, respectively) than for males (12% and 16%). However, the error bars in Fig. 1 for the females (indicating 95% highest posterior density intervals, HPD₉₅) overlap the mean estimate for males and vice versa, suggesting that these estimates were not credibly different from one another. As for DV, the bulk of the variance was explained by *E* and only a small proportion was due to the *C* component.

Comparable heritability estimates were obtained if the Bayesian ACE analysis was conducted based on the residuals of all three variety scores after partialing out the influence of family income, education, and religion.

Table 1 further shows Pearson's correlation coefficients between DZ and MZ twins. Heritability estimates obtained from comparing these coefficients (following Plomin, DeFries, Knopik, & Neiderhiser, 2013) corroborated the main results from the Bayesian ACE model showing a heritable influence for all three variety scores.

The genetic correlations for opposite-sex twins in the Bayesian ACE model were estimated at 29% (HPD₉₅ 5% to 50%) for DV, 20% (HPD₉₅ 0% to 44%) for lnHH and 17% (HPD₉₅ 0% to 42%) for PRE. For lnHH and PRE, the HPD ranges were reasonably far from 50%, suggesting that there are some qualitative sex differences. However, presumably due to the relatively small number of twins in our sample, the obtained HPD₉₅ ranges were rather wide, which makes it difficult to draw definite conclusions about sex differences based on this correlation measure.

Demographic influences

Further exploring the influence of available demographic measures indicated that food variety seeking (DV) increased with education and family income. People with a family income of more than \$35,000 on average consumed about 5% more different foods than those with a family income of \$10,000 or less. (This sample was assessed in 1990–1992, when the median household income in the US was about \$29,000. Adjusting for inflation, an income of \$10,000 in 1991 would be equivalent to about \$17,000 in 2012, according to the Consumer Price Index provided by the U.S. Department of Labor). A similar difference was found between those who finished college and those who did not finish high school. Food variety seeking slightly decreased with age, at a level indicating that people on average ate one food item less for 15 more years of age. There were also differences between religious faiths, with Jewish participants consuming the least variety (about 6% fewer foods than the average). Comparable results were found for the lnHH and PRE scores as well. Finally, there was a small positive correlation between food variety seeking and the number of people living in the same household ($r = 0.07$ for DV; $r = -0.12$ for lnHH; $r = 0.16$ for PRE).

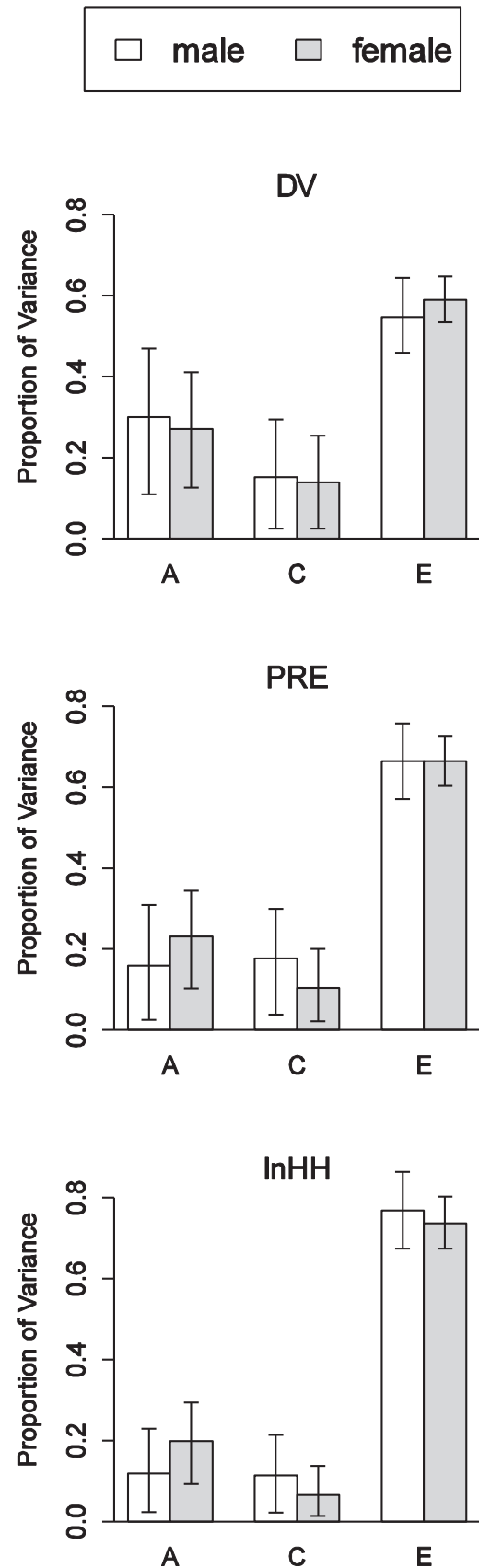


Fig. 1. Estimate of the proportion of variance due to additive genetic (*A*), common or shared environment (*C*), and unshared environment (*E*) factors for the dietary variety score DV (upper plot) the proportion of residual entropy PRE (middle plot) and the log-transformed Hirschman–Herfindahl index of concentration lnHH (lower plot). Error bars indicate the 95% highest posterior density region.

Table 1
Estimated variance proportions (posterior means) for the ACE model and Pearson's correlations between siblings.

Phenotype	ACE model						Correlations between siblings							
	A		C		E		MZ		DZ		os		h ² total	
	Male	Female	Male	Female	Male	Female	Male	Female	Total	Male	Female	os	Total	
DV	0.30	0.27	0.15	0.14	0.55	0.59	0.43	0.40	0.41	0.37	0.26	0.24	0.27	0.28
PRE	0.16	0.23	0.18	0.10	0.66	0.66	0.37	0.34	0.36	0.31	0.28	0.14	0.25	0.23
lnHH	0.12	0.20	0.11	0.07	0.77	0.74	0.27	0.27	0.27	0.12	0.19	0.01	0.14	0.27

A multiple regression that includes the combined influence of sex, age, the quadratic effect of age, family income, education, and religion as predictors explained 3.6% of the variance in DV, 3.9% in lnHH, and 7.7% in PRE. Thus, even though these predictor variables exert a reliable influence on dietary variety, in absolute terms, they only explain a rather small proportion of the observed variance.³ Thus, even though the bulk of the variance seems to be non-shared in twins, results show that this cannot be fully attributed to the assessed demographic measures or to self-reported health.

Discussion

In many countries across the world, people enjoy an ever-increasing variety of different foods readily available in grocery stores and restaurants (Scheibehenne, Greifeneder, & Todd, 2010). While such large assortments provide the necessary prerequisites for a diverse diet, they also bring the risk of overconsumption, particularly if the variety stems from energy-dense foods (Foote et al., 2004). In our data, a higher dietary variety score went along with a decreasing proportion of fruits and vegetables in individual diets. Presumably this is because in modern food environments, these healthy items are increasingly outnumbered by rather less healthy options (McCroory et al., 1999). We found small but noticeable correlations between dietary variety and both self-reported health and BMI, reflecting the double-edged effect of food variety. These impacts of dietary variety on health highlight the importance of our main objective of determining the influence of different internal and external factors on dietary variety-seeking behavior.

Genetic influences

While most of the observed variance in dietary variety was due to (unshared) environmental influences, the results show that about a third of the variance in dietary variety measured as the range of foods eaten over a year (DV score) can be accounted for by heritable factors. For the lnHH and PRE measures, the heritability estimates were lower but still noteworthy. Thus, even though humans as omnivores may not have strong biological predispositions for predictably choosing specific individual foods (as opposed to food components like fat or salt; Rozin & Millman, 1987), the degree of variety in food choices is partly due to genetic influences.

Both the lnHH and PRE variety measures also take the frequency of consumption into account, whereas DV focuses on whether a particular food item is consumed at all. Thus, one possible reason for the lower heritability of lnHH and PRE could be that the assessment of consumption frequencies in the questionnaire was less accurate than the simple designation of having eaten an item and thus increased measurement error. Another possibility is that consumption frequencies could be more dependent on environmental influences such as seasonal availability or the preferences of other family members, whereas the basic decision to eat a

given food or not might be more a matter of individual preferences or traits. In line with this, the slightly higher heritability estimates for females than for males in our data could have been caused by females having more personal control over their food environment, in particular the frequency with which certain foods are consumed in the family setting. Finally, the higher heritability of DV, reflecting the range of foods eaten, than lnHH and PRE, reflecting the frequency (and amount) of foods eaten, also suggests that interventions or changes in the environment that aim to alter how much is eaten of different foods could be more successful than those aiming to change preferences for trying and eating different or new foods.

Demographic and environmental influences

In addition to genetic factors that influence variety-seeking behavior through internal paths, we also assessed the influence of external predictors that are independent of one's intrinsic motivation to seek variety (McAlister & Pessemier, 1982; Van Trijp & Steenkamp, 1992). In our data, dietary variety was correlated with socioeconomic status (family income and education) and religious faith, presumably because wealthier and more educated people may be more able and more motivated to vary their food intake, and religions differ in how much they restrict food consumption of their members (Van Trijp, 1994; Van Trijp et al., 1992). Within our sample of mostly elderly adults, food variety slightly decreased with age, which is in line with previous findings showing that elderly people often consume a smaller range of foods (Fanelli & Steinhagen, 1985; Van Trijp, 1994; but see Drewnowski et al., 1997, for an increase of variety seeking with age) and that sensory-specific satiety diminishes over the life span (Boyce & Shone, 2006; Rolls & McDermott, 1991).

The finding that food variety increased with household size fits the idea that food choices are being co-determined by other family members, for example, if one's partner is primarily responsible for food purchase and preparation (McAlister & Pessemier, 1982). In our data, food variety seeking did not differ much between people who were on a diet and those who were not, suggesting that dieters may have exchanged unhealthy items with healthy ones or altered the amounts of unhealthy items relative to healthy ones, both of which would have kept food variety constant.

Limitations and future research

While our analysis indicates that a significant proportion of the individual differences in food variety seeking are due to heritable factors, little is known about the underlying internal genetic, metabolic, and psychological pathways that moderate this relationship and that drive these differences. Hence, further molecular genetic, neural, and behavioral research is needed to better understand the mechanisms underlying food variety seeking, along with extending the largely correlational approach used in this study with tightly controlled experimental designs.

Establishing heritability also serves as a starting point to identify genes that can link observed behavior to its underlying biolog-

³ See supplementary material for a detailed Table with the regression results.

ical and neuronal processes. Towards this goal, past research has proposed candidate genes that govern differences in taste, eating inhibition, hunger, lactose intolerance, eating disorders, diabetes, and obesity (see Grimm & Steinle, 2011, and Rankinen & Bouchard, 2006 for reviews of gene candidates). In an exploratory genome-wide association study based on an independent data set from the Framingham Heart Study (N = 8,681; Dawber, Meadors, & Moore, 1951), we could not identify a strong link between any single polymorphism with known biochemical function and food variety seeking though.⁴

To the degree that food variety seeking is a specific aspect of a more general trait comprising the need for external stimulation or sensory-specific satiety, one might expect similarities between the degree of variety that people seek across different domains beyond food (Inman, 2001). Thus, a promising route for further exploration would be to test for relationships between food variety seeking, variety seeking in other domains, differences in satiety levels, the general desires to explore and seek novelty, and other related phenotypes, including “supertaster” ability (Bezdjian, Baker, & Tuvblad, 2011; Duffy & Bartoshuk, 2000; Helm & Landschulze, 2009; Pessemier & Handelsman, 1984). Along the same lines, the current analysis should be extended by using more refined measures of food variety seeking that not only go beyond the item level but also take relevant attributes, including nutrient content or texture, into account.

Given the potential health consequences of seeking and consuming a varied diet, a better understanding of how people choose food and how much variety they include in their diets can have important applied implications as well. This should only strengthen the call for a combined effort to tackle these questions with methodological and theoretical approaches from different disciplines, including behavioral, biological, and genetic research, as the current study has made initial steps toward.

Appendix: Supplementary material

Supplementary data to this article can be found online at [10.1016/j.appet.2014.03.001](http://dx.doi.org/10.1016/j.appet.2014.03.001).

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⁴ A list of the highest ranked candidate genes is available from the authors upon request.

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