

Original Article

Oleogustus: The Unique Taste of Fat

Cordelia A. Running¹, Bruce A. Craig², and Richard D. Mattes³

¹Department of Food Science, Purdue University, West Lafayette, IN 47907, USA, ²Department of Statistics, Purdue University, West Lafayette, IN 47907, USA, and ³Department of Nutrition Science, Purdue University, West Lafayette, IN, USA

Correspondence to be sent to: Richard D. Mattes, Department of Nutrition Science, Purdue University, 113 Stone Hall, West Lafayette, IN 47907, USA. e-mail: mattes@purdue.edu

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Abstract

Considerable mechanistic data indicate there may be a sixth basic taste: fat. However, evidence demonstrating that the sensation of nonesterified fatty acids (NEFA, the proposed stimuli for “fat taste”) differs qualitatively from other tastes is lacking. Using perceptual mapping, we demonstrate that medium and long-chain NEFA have a taste sensation that is distinct from other basic tastes (sweet, sour, salty, and bitter). Although some overlap was observed between these NEFA and umami taste, this overlap is likely due to unfamiliarity with umami sensations rather than true similarity. Shorter chain fatty acids stimulate a sensation similar to sour, but as chain length increases this sensation changes. Fat taste oral signaling, and the different signals caused by different alkyl chain lengths, may hold implications for food product development, clinical practice, and public health policy.

Key words: basic tastes, fat taste, fatty acid structure, nonesterified fatty acid taste, oleogustus

Introduction

Despite more than 2 millennia of reflection, consensus is lacking on what constitutes a “basic taste quality,” and whether taste is limited to a discrete set of taste “primaries.” We and others have proposed criteria for “primary tastes,” including that the sensation: 1) has ecological consequence, 2) is elicited by a distinctive class of chemicals, 3) stems from activation of specialized receptors, 4) is detected through gustatory nerves and is processed in taste centers, 5) has a quality nonoverlapping with other primary qualities, and 6) evokes a behavioral and/or physiological response (Kurihara and Kashiwayanagi 1998; Mattes 2011). Considerable evidence indicates oral responses to nonesterified fatty acids (NEFA) meet criteria 1–4 and 6 (Gilbertson and Khan 2014; Tucker et al. 2014; Running and Mattes 2015). However, documentation that oral NEFA exposure elicits a perceptible and unique taste sensation, in addition to their olfactory and somatosensory sensations, is weak overall and absent in humans. Studies in rodent models indicate that taste aversions to nutritive oil and long chain fatty acids do not generalize to other taste sensations or to textural qualities (Pittman 2010), suggesting the sensation is unique in this species. In the 2 experiments that follow, a perceptual sorting task was used to show that humans experience taste from short, medium, and long chain fatty acids and that these sensations are different from

other recognized taste qualities, and from each other. The data were analyzed 3 ways for consistency: 1) hierarchical clustering showed the predominant groups at various levels of sorting; 2) multidimensional scaling (MDS) with bootstrapping generated perceptual maps and 95% contours for each sample, and 3) Bhattacharyya coefficients were used to determine the degree of overlap between pairs of samples (perfect overlap = 100%, no overlap = 0%). These findings directly address the weakest link in the proposition that fat is a basic taste quality and we suggest a new word to describe this taste: oleogustus. Fat taste signaling may hold implications for food product development (e.g., composition of fat replacers), clinical practice (e.g., management of appetite, digestion, taste disorders), and public health policy (e.g., dietary recommendations to moderate postprandial lipemia).

Materials and methods

Experiment 1

The first experiment was designed to test whether short, medium, and long chain NEFA were unique in sensation from each other as well as distinguishable from blanks and sweet, sour, salty, bitter, and umami tastes. This experiment used 15 samples, as described in Table 1. Concentrations were selected by conducting pilot tests to identify samples of similar taste intensity to 0.54 M glucose.

Table 1. Concentrations of tastants and fatty acids

	Sample	Molarity
Experiment 1	<i>trans</i> -3-Hexenoic	0.0061 M
	9-Decenoic acid	0.0059 M
	Oleic acid	0.18 M
	Linoleic acid	0.018 M
	Acetic acid	0.0083 M
	Citric acid	0.0048 M
	Sodium chloride (in duplicate)	0.094 M
	Inosine monophosphate	0.0013 M
	Monosodium glutamate	0.0069 M
	Glucose	0.54 M
	Fructose	0.31 M
	Quinine	4.5E-05 M
	Urea	0.20 M
	Blank	—
Experiment 2	Oleic acid	0.18 M
	Linoleic acid	0.018 M
	9-Decenoic acid	0.0059 M
	Urea (low)	0.20 M
	Urea (high)	0.40 M
	Quinine (low)	3.3E-05 M
	Quinine (high)	4.9E-05 M
	Caffeine	0.0046 M
	PROP	8.2E-05 M
	Sucrose octaacetate	2.2E-05 M
	Blank (in duplicate)	—

Experiment 2

Data from experiment 1 showed large perceptual overlap among bitter compounds and medium to long chain NEFA, so this relationship was further explored to determine if this similarity was attributable to hedonic (unpleasant) similarity or actual qualitative similarity. This experiment used several bitter stimuli as described in Table 1, and included 2 concentrations of urea and quinine to determine whether sorting patterns were based on intensity rather than quality of sensation (despite explicit instructions to sort on “quality or type” of sensation rather than intensity). Further, different types of bitter compounds have different transduction mechanisms, so a variety of bitter chemicals were included to ensure any perceptual similarities were not limited to specific classes of bitter stimuli (Delwiche et al. 2001; Keast and Breslin 2002; Meyerhof et al. 2010). Additionally, 2 blank solutions were included as internal controls and to identify PROP tasters and nontasters, which is a genetic trait that causes some individuals to taste this compound as bitter whereas others experience little or no sensation (Bufe et al. 2005). Participants were classified as PROP nontasters if they grouped the PROP solution with either blank solution in the first round of sorting (described later).

Samples

Oleic acid (C18:1, Spectrum Chemicals), linoleic acid (C18:2, Sigma-Aldrich), 9-decenoic acid (C10:1, Sigma-Aldrich), *trans*-3-hexenoic acid (C6:1, SAFC Sigma-Aldrich), acetic acid (C2, Sigma-Aldrich), citric acid monohydrate (Mallinckrodt Chemicals), sodium chloride (Spectrum Chemicals), L-glutamic acid monosodium salt monohydrate (MSG, Aldrich Chemistry), quinine sulfate dihydrate (Spectrum Chemicals), urea (Mallinckrodt Chemicals), caffeine (Sigma-Aldrich), 6-*n*-propylthiouracil (PROP, Sigma-Aldrich), sucrose octaacetate (SOA, Sigma-Aldrich), ethylenediaminetetraacetate (EDTA, Spectrum Chemicals), *tert*-butylhydroquinone (TBHQ, Spectrum Chemicals), glucose and fructose (www.nuts.com) were

all food grade and purchased from commercial vendors. Disodium 5' inosinate (IMP) was a gift from Ajinomoto Food Ingredients. Sodium caseinate was purchased from American Casein Company (Burlington, NJ). Xanthan gum was purchased from local grocers (Bob's Red Mill brand), and the same batch was used for all study procedures. Table 1 lists concentrations used. Concentrations were selected based on pilot work indicating the sensations were comparable in taste intensity. The blank was prepared by adding the appropriate amounts of sodium caseinate, EDTA, TBHQ, and xanthan gum to distilled water, mixing, and allowing the solution to sit overnight to fully hydrate the xanthan gum. This blank was used as the base solution for all other mixtures in experiment 1 except for acetic acid, citric acid, and hexenoic acid, as the pH of these solutions would have caused the sodium caseinate to precipitate out of solution. These solutions contained xanthan gum, EDTA, and TBHQ in addition to the acids. In experiment 2, the sodium caseinate, xanthan gum, EDTA, and TBHQ solution was again used as the base solution for all samples, but 1% ethanol was added as it aided in the dissolution of several of the less polar bitter compounds (PROP, SOA, quinine). These 3 bitter solutions were first prepared as stock solutions in ethanol, and then diluted into the blank solution of sodium caseinate, xanthan gum, and antioxidants.

For experiment 1, emulsions of 0.18 M oleic acid, 0.18 M linoleic acid (10 times the final concentration), and 0.0059 M decenoic acid were prepared in 1 L batches by adding the appropriate amount of NEFA to the blank solution (sodium caseinate, EDTA, and TBHQ) and mixing with an Ultra Turrax T18 homogenizer at 14000 RPM for 10 min equipped with the S18N-19G dispersing element. Next, these mixtures were fully homogenized in 3.75 L batches using a 2-stage homogenizer (APV 15 15MR-8TBA) with the cylinder pressure set to 3500 psi. The homogenizer was set to loop the solution back through the system for a total of 5 min before collecting the final homogenate. This stabilized the emulsions against creaming over time and allowed for larger batch productions. The 10× concentrated linoleic acid emulsion was then diluted into the blank for final testing. Viscosities of fatty acid emulsions and blank were checked with a DHR-3 hybrid rheometer equipped with a 40 mm 2° cone and plate geometry, from 1 to 300 s⁻¹ at 37 °C, controlled by a Peltier plate, with 10 points per decade. Data confirmed the fatty acid emulsions matched the viscosity of the blank (Figure 1). Emulsion stability was checked using a Mastersizer 2000 equipped with a Hydro 2000 MU dispersion unit. Mean droplet diameters (both surface and volume weighted) were less than 0.5 μm (Figure 2), despite the small peak in the 1–2.5 μm range for samples made for experiment 2 using only the rotor stator mixer (Ultra Turrax T18). Hexenoic acid was soluble at the concentration used but to ensure full dissolution it was mixed into sodium caseinate-free blank using the Ultra Turrax T18 homogenizer at 14000 RPM for 10 min equipped with the S18N-19G dispersing element in 1 L batches. Other solutions were prepared by adding the compounds to the blank (sodium caseinate-free for acetic and citric acids), stirring, and allowing the solutions to sit overnight in the refrigerator to fully dissolve. All solutions were brought to room temperature for the experiment.

For experiment 2, emulsions were prepared by small batch homogenization as in previous studies (Running and Mattes 2014, 2015). Briefly, 100 mL of 0.18 M oleic, 0.18 M linoleic (10 times the final concentration), and 0.0059 M decenoic acid were homogenized with an Ultra Turrax T18 homogenizer at 14000 RPM for 10 min equipped with the S18N-19G dispersing element. The linoleic acid emulsion was then diluted to 0.018 M using the blank solution. These emulsions were checked for particle size and viscosity as detailed above. Quinine, PROP, and SOA samples were first made at 100×

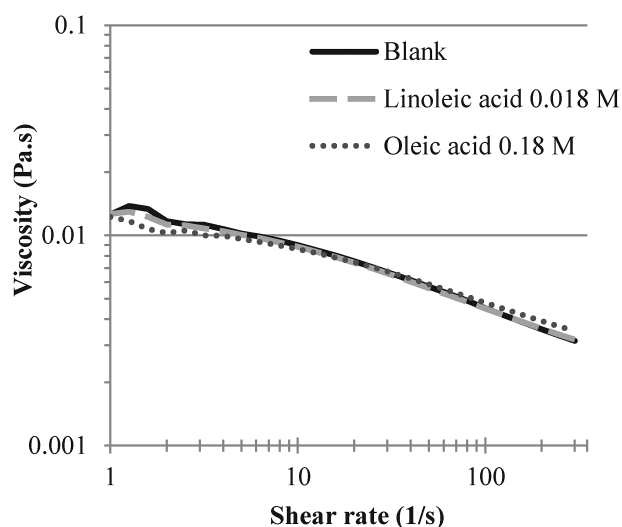


Figure 1. Viscosity of emulsions and blank.

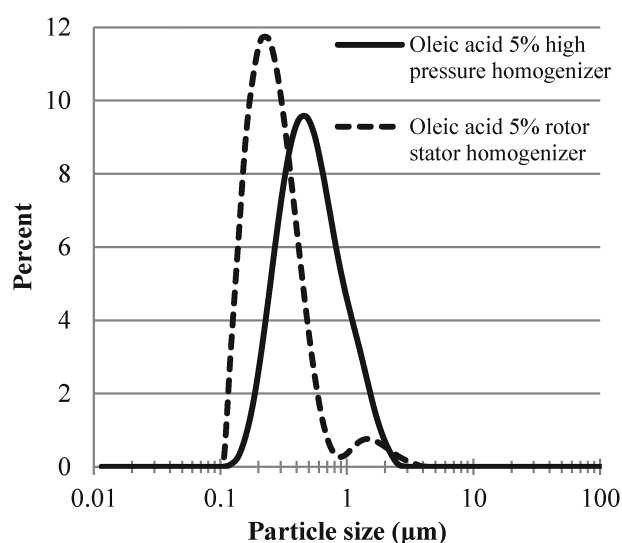


Figure 2. Particle sizes of highest concentration emulsions.

final concentration in ethanol, as these are poorly soluble in water, then diluted into the blank solution. Caffeine was dissolved into hot water at 2× final concentration then diluted into the blank. NEFA emulsions, caffeine, urea, and blank solutions all had 1% ethanol added to match the level of ethanol needed to dissolve the quinine, PROP, and SOA samples. Final solutions all contained 1% sodium caseinate, 0.05% xanthan gum, 1% ethanol, and 0.01% each EDTA and TBHQ in addition to the tastants listed in Table 1.

Participants

All protocols were approved by Purdue University's Human Subjects Institutional Review Board. Subjects were recruited through public announcements and through participant pools of the Laboratory for Sensory and Ingestive Studies and the Purdue Sensory Evaluation Laboratory. Eligibility criteria included: between the ages of 18 and 60, normal taste function, healthy (by self-report), and not allergic to dairy (because of the source of sodium caseinate). For experiment 1, panelists could not be allergic to nut products because the

glucose and fructose were purchased from a supplier who also processes nuts. Panelists were screened for their ability to discriminate 0.018 M linoleic acid emulsion from the blank using 2 sequential, tetrad tests. This required the panelists to sort 4 samples (2 each, linoleic acid emulsion and blank) into 2 groups based on similarity. The odds of correctly sorting 2 tetrad tests sequentially is 1/9. For the second experiment, we further restricted this criterion by requiring the panelists to identify the group that contained a "flavor" (i.e., linoleic acid). The odds of correctly sorting 2 sequential directed tetrad tests is 1/36.

Panelists wore nose clips during the tests and all samples were served in opaque containers with lids. Nose clips have been previously demonstrated to adequately prevent human ability to discriminate long chain fatty acids from blank solutions (Bolton and Halpern 2010). Participants were provided with water for rinsing their mouths as well as a cup to spit the samples into after tasting. The spit cup also had a lid, with a small hole that panelists were instructed to spit through. Panelists had to successfully complete both tetrads in order to qualify for the study. If panelists did not successfully complete the tetrads, they were excused from further testing. Panelists who qualified for the full studies provided written informed consent as well as data on their ethnic background, age, and their habitual fat intake using a validated food frequency questionnaire (Block et al. 2000); participants were classified as having a "high fat diet" if they scored a 23 or higher on this questionnaire (value set by questionnaire and corresponds to 35.9% fat diet for females and 33.6% fat diet for males). Heights and weights were measured. Demographic data on the participants from both studies is given in Table 2. Panelists who qualified in experiment 1 were invited back for experiment 2, so some overlap is present among these groups. Panelists who participated in the full study received financial compensation.

Free sorting task

In the first experiment, demographic data and tetrad tests were administered with CompuSense 5 software. In the second experiment, Qualtrics was used. After completing the screening tests and the demographic questions, panelists received the sorting samples in opaque, 4 oz cups with lids labeled with randomized 3 digit codes. Samples were presented all at once on a tray in a randomized arrangement. Two sodium chloride samples were used in experiment 1; this allowed an internal control for whether panelists understood the task. For experiment 2, 2 blanks were included to verify the success of the task. In experiment 1, panelists who did not sort the 2 identical sodium chloride solutions together in the first round of sorting were removed from the data analysis. Fifty-three of 78 participants passed screening, 4 panelists failed to sort the 2 sodium chlorides together, and 1 panelist did not taste all the samples for sorting, leaving 48 panelists in the final analysis. In experiment 2, all qualified panelists (54) were included in the final results, and the output data were analyzed to confirm substantive overlap among the 2 identical blank samples.

The free-sorting task was modified from other published methods (Courcoux et al. 2012). After panelists had donned the nose clips, they were instructed to taste each sample, expectorate it into the waste cup, and rinse with water. Then, they sorted the samples into groups they believed were similar in "quality or type" of sensation (caution was used to avoid the use of the word "taste"). Groups could contain as many or as few samples as desired, and participants could make as many or as few groups as they desired. Panelists wrote a description for each group. After finishing this initial sorting task, if panelists had more than 2 total groups, they were instructed to

Table 2. Participant characteristics

	Experiment 1	Experiment 2		
		Nontaster	Taster	Total
Total	48	26	28	54
Low/high fat	24/24	10/16	15/13	25/29
Male/female	23/30	9/17	9/19	18/36
Mean age in years (range)	28.4 (18–51)	27.6 (18–54)	29.6 (19–52)	28.6 (18–54)
BMI in kg/m ² (range)	26.3 (18.5–46.6)	27.6 (19.7–54.4)	27.8 (19.0–48.0)	27.7 (19.0–54.4)

select the 2 groups they believed were most similar to each other and combine them. If panelists still had more than 2 total groups (the new, large group counting as a single group), they were instructed to combine the 2 most similar groups again, either by adding a third group to their new, large group or by creating another combined group of 2 previously separate groups. This continued until panelists only had 2 groups remaining.

Statistics

Data were organized into dissimilarity matrices for each participant's groupings. For the first study, the 2 identical sodium chloride samples were collapsed into one, as participants were required to sort these 2 samples together in order for their data to be included; these samples are referred to as "sodium chloride" or "salts" for the purpose of analysis. Additionally, inspection of the data revealed that all participants also put both glucose and fructose samples together in the first round of sorting. To reduce error in the analysis, these samples were also collapsed into one for the analysis, and are referred to as "sugars." The total number of rounds of combining groups was noted for each panelist, and the dissimilarity matrices were normalized by dividing all group numbers by each panelist's total number of groups. Thus, all data were on a scale of 0–1. SAS 9.4 was used for bootstrapping, MDS, and procrustean transformations. Random bootstrapping with replacement was conducted using panelist as a sampling unit. MDS was conducted on each bootstrapped replicate with settings of ordinal level data and 2 dimensions. Output from MDS was put through procrustean transformation to optimally align the sample coordinates. This generated a data set with 500 pairs of (X,Y) coordinates for each sample type. The 2D binning procedure in OriginPro 2015 b9.2.214 was used to calculate the number of points from each sample located in a 30 × 30 grid superimposed over the data map. For experiment 1, the data map stretched from X: (–3,2) and Y: (–2,2). For experiment 2, the data map stretched from X: (–2,2) and Y: (–2,2). The axes for both experiments are completely arbitrary and are determined from the first MDS output, which was used as the basis for the procrustean transformations. The bin counts from OriginPro were then entered into Excel spreadsheets, where the total number of each sample in each bin (900 bins total) were counted. Probability of a sample having a point in each bin was calculated as the bin count/500, because there were 500 points for each sample. Bhattacharyya coefficients were calculated as: $\sqrt{[\text{Prob}_{\text{bin}_i}(\text{Sample A}) \times \text{Prob}_{\text{bin}_i}(\text{Sample B})]}$ for $i = 1-900$ (sum of the probabilities for all of the bins). A Bhattacharyya coefficient of 100% indicates perfect overlap and 0% indicates no overlap. In OriginPro, 2D Kernel densities were calculated using the Bivariate Kernel Density Estimator with 50 points in X/Y. The output matrices for each sample were then mapped using 3D surface contour maps, showing horizontal lines at each 10th percentile. Additionally, 2D maps were generated of the 95th percentile density contour for each sample. Hierarchical

cluster analysis using Ward's method was conducted in OriginPro using the participants' dissimilarity matrices.

Results

Textural cues of fatty acids were adequately masked, as there were no measurable differences in viscosity and particle sizes were, on average, below 1 μm (Figures 1 and 2) (Running and Mattes 2014, 2015).

The first experiment's results show clear separation of sweet, salty, sour, and bitter stimuli, as predicted, in all 3 methods of analysis (Figure 3, Table 3). Consistently in all 3 analyses, the short chain NEFA overlapped and was grouped with the sour stimuli, which was expected as acetic acid is also a short chain fatty acid. Also in all 3 analyses, some overlap occurred among umami compounds and the medium to long chain NEFA, especially for IMP. MSG, which is the prototypical stimulus for umami, is clearly distinct from the long chain NEFA in the perceptual contour maps (Figure 4), Bhattacharyya's coefficients reveal minimal overlap with oleic acid (2.3%) or linoleic acid (4.3%), and MSG is in a separate cluster in the hierarchical data (Table 3, Figure 3).

In the second experiment, all 3 analytical approaches revealed distinctions among the NEFA, bitter, and blank compounds (Figure 5, Table 3), with clear separation between the medium and the long chain NEFA. Hierarchical clustering (Figure 5B) demonstrates that the 3 main sorting groups from this experiment are blank samples, bitter samples, and NEFA samples. This pattern can also be seen in the perceptual contour map (Figure 5A) where the bulk of the NEFA density is clustered in the upper right hand portion of the map (axes are arbitrary). Additionally in the perceptual map, there is no overlap between decenoic acid (medium chain) and any other sample. Linoleic acid and oleic acid have very similar contours (Figure 6), with limited low density overlap with the bitter compounds. Considering Bhattacharyya's coefficients (Table 3), again there is no overlap between decenoic acid and any other sample (all below 5%), and overlap is greatest between oleic acid and linoleic acid (86.2%). There were low levels of overlap between oleic acid and caffeine (14.8%), low concentration quinine (6.5%), and both concentrations of urea (low: 8.1%, high: 15.3%) as well as between linoleic acid and caffeine (16.6%), low concentration quinine (5.8%), SOA (8.7%), and both concentrations of urea (low: 5.9%, high: 20.2%). However, overlap among the bitter samples is much greater than the overlap between bitter compounds and long chain NEFA, and t -tests conducted on the percent overlap among all bitter compounds compared with percent overlap between bitter compounds and long chain NEFA indicated greater overlap among the bitter compounds (34.4% mean overlap among bitters, 8.4% mean overlap between bitter and long chain NEFA, $P = 0.0003$; excluding PROP from this analysis yields 43.2% and 9.5% overlap respectively, $P = 0.0002$; unequal variance assumed for both tests).

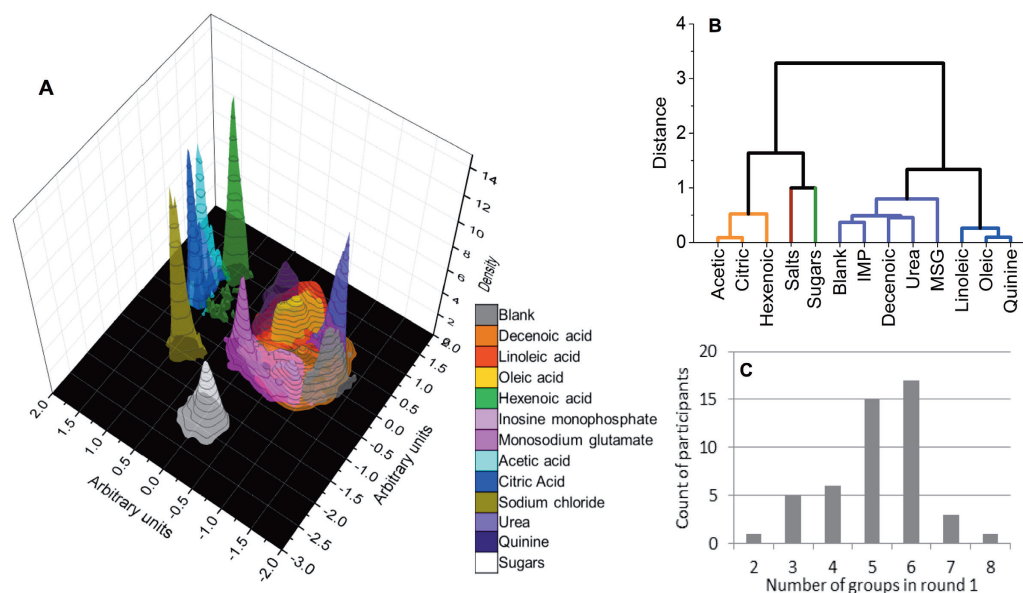


Figure 3. (A) Kernel density of experiment 1 samples in perceptual map representing 500 bootstrapped replicates of the MDS data generated with panelists' dissimilarity matrices. Horizontal lines are 10% increments of density; X and Y dimensions are arbitrary. (B) Dendrogram from hierarchical clustering of all participant ($N = 48$) dissimilarity matrices using Ward's method. (C) Histogram of number of groups created in first round of sorting.

Findings from PROP reflect the presence of tasters and nontasters in this analysis, as expected, and the MDS procedure averages over the groupings from these 2 populations. Analyzing the data separately for tasters and nontasters displayed only small changes in the perceptual maps, except for the movement of the PROP solution, which overlaps with blank for nontasters and with bitter compounds for tasters (Figure 6). The only noticeable shift for the NEFA was more overlap between the medium and both long chain NEFA for the tasters compared with nontasters, and more overlap among the long chain NEFA and PROP for tasters. Similarly, comparing participants reporting consumption of a high fat diet to those with a lower fat diet ($N = 29$ and 25 , respectively), a small shift was observed with more overlap between the medium and both long chain NEFA as well as between PROP and both long chain NEFA for participants on the low fat diet compared with those on a high fat diet (Table 3).

Discussion

The data from these studies provide substantial new evidence not only that fat, in the form of long-chain, nonesterified fatty acids, has a percept we believe is taste ($64 \pm 5\%$ of people in experiment 1 could identify the linoleic acid emulsion compared with the blank with no prior training, and olfactory and somatosensory cues are inconsistent with the findings), and there was no overlap in any of the 3 analyses between the blanks and the fatty acids in experiment 2), but also that the oral sensations of fatty acids are altered according to alkyl chain lengths. The findings for the unique qualities of short, medium, and long chain NEFA are discussed below.

Our first study shows that short chain fatty acids have a sour note. This is unsurprising as acetic acid itself is actually a short chain fatty acid (C2). At some point, extending the alkyl chain of NEFA creates a perceptual shift from the sourness of short chain NEFA to the quality experienced at a length of 10 carbons, which was clearly distinct as seen in experiment 1. Medium chain fatty acids such as decenoic acid may have their own unique sensation from both short and long chain NEFA. From the descriptions given during the

second sorting experiment and from prior work, this sensation could be irritating or pungent (Running and Mattes 2014). Considerable overlap was observed among decenoic acid, IMP, and MSG in the first study, but this is likely due to less experience by participants with pure umami sensations, rather than a true perceptual overlap. Further, IMP and MSG in combination potentiate the umami signal, so if participants did not thoroughly rinse between such samples, the intensity of the flavor from these solutions could have varied (Kurihara and Kashiwayanagi 1998). This could have led to greater discrimination of the MSG sample from the other samples, but left a wider distribution for sorting of IMP, as observed in both analyses of the MDS data from experiment 1.

In our prior studies, self-reported qualitative descriptions indicated medium chain fatty acids are more potent irritants than long chain fatty acids (Running and Mattes 2014). Considering that no other irritants were included in the sample set, the diffuse sorting of decenoic acid in the first study and overlap with less familiar umami sensations may reflect participants' confusion on how to sort sensations that did not have obvious matches among the other samples. Additionally, many participants sorted the decenoic acid with the blank solution in the first study, as demonstrated by the overlap between these samples in all 3 methods of analysis. Potentially, there could be a bimodal distribution of perception for medium chain fatty acids such as decenoic acid, where some individuals perceive an unpleasant sensation and others perceive no sensation from the stimulus.

Given the variety of samples presented in the first sorting study, participants may have initially sorted out the familiar sensations of sweet, salty, and sour, and then grouped the others together based on low palatability (descriptive terms reflect this). Data from the second study show the medium chain NEFA was clearly unique from bitter, long chain NEFA, and blank solutions. Analyzing the data separately for PROP tasters and nontasters, there is still evidence that nontasters may experience less sensation from this compound (Table 3). However, PROP tasters and consumers of a low-fat diet appear to have grouped the medium chain NEFA with the long chain

Experiment 1

Experiment 1														
	Acetic acid	Blank		Citric acid	9-Decenoic	<i>trans</i> -3-hex- enoic acid	IMP	Linoleic acid	MSG	Oleic acid	Quinine	Sodium chloride	Sugars	Urea
9-9-Decenoic acid	0.0%	53.7%		0.0%	—	0.0%	72.6%	22.7%	25.3%	14.7%	8.2%	0.0%	0.0%	38.8%
	23.3%	0.0%		23.5%	0.0%	—	0.2%	0.3%	0.7%	0.0%	0.4%	0.0%	0.0%	0.0%
	0.0%	6.8%		0.0%	22.7%		20.3%	—	4.3%	87.6%	70.5%	0.0%	0.0%	40.2%
	0.0%	3.6%		0.0%	14.7%	0.0%	13.8%	87.6%	2.3%	—	57.0%	0.0%	0.0%	25.8%
Experiment 2														
	9-Decenoic acid	Linoleic acid		Oleic acid	Blank 1	Blank 2	Caffeine	PROP	Quinine low	Quinine high	Sucrose octaacetate	Urea low	Urea high	
9-9-Decenoic acid	—			1.8%	3.0%	0.6%	2.0%	4.1%	0.3%	0.2%	0.3%	4.3%	0.0%	
	1.8%			—	86.2%	0.0%	16.6%	1.5%	5.8%	4.4%	8.7%	5.9%	20.2%	
	3.0%			86.2%	—	0.2%	14.8%	1.6%	6.5%	4.4%	3.4%	8.1%	15.3%	
	0.0%			0.0%	0.0%	85.6%	0.5%	20.3%	0.0%	0.0%	0.0%	1.8%	0.0%	
	0.6%			0.0%	0.2%	—	0.2%	22.1%	0.0%	0.0%	0.0%	3.3%	0.0%	
	2.0%			16.6%	14.8%	0.2%	—	10.4%	66.8%	68.1%	49.4%	36.9%	66.7%	
	4.1%			1.5%	20.3%	22.1%	10.4%	—	9.8%	5.9%	0.0%	46.8%	2.2%	
	0.3%			5.8%	6.5%	0.0%	66.8%	9.8%	—	84.3%	13.0%	43.0%	35.4%	
	0.2%			4.4%	4.4%	0.0%	68.1%	5.9%	84.3%	—	18.3%	34.5%	40.7%	
	0.3%			8.7%	3.4%	0.0%	49.4%	0.0%	13.0%	18.3%	—	3.2%	75.2%	
4.3%			5.9%	8.1%	1.8%	3.3%	36.9%	46.8%	43.0%	34.5%	—	12.5%		
Experiment 3														
	9-Decenoic acid	Linoleic acid		Oleic acid	Blank 1	Blank 2	Caffeine	PROP	Quinine low	Quinine high	Sucrose octaacetate	Urea low	Urea high	
9-9-Decenoic acid	—			1.8%	3.0%	0.6%	2.0%	4.1%	0.3%	0.2%	0.3%	4.3%	0.0%	
	1.8%			—	86.2%	0.0%	16.6%	1.5%	5.8%	4.4%	8.7%	5.9%	20.2%	
	3.0%			86.2%	—	0.2%	14.8%	1.6%	6.5%	4.4%	3.4%	8.1%	15.3%	
	0.0%			0.0%	0.0%	85.6%	0.5%	20.3%	0.0%	0.0%	0.0%	1.8%	0.0%	
	0.6%			0.0%	0.2%	—	0.2%	22.1%	0.0%	0.0%	0.0%	3.3%	0.0%	
	2.0%			16.6%	14.8%	0.2%	—	10.4%	66.8%	68.1%	49.4%	36.9%	66.7%	
	4.1%			1.5%	20.3%	22.1%	10.4%	—	9.8%	5.9%	0.0%	46.8%	2.2%	
	0.3%			5.8%	6.5%	0.0%	66.8%	9.8%	—	84.3%	13.0%	43.0%	35.4%	
	0.2%			4.4%	4.4%	0.0%	68.1%	5.9%	84.3%	—	18.3%	34.5%	40.7%	
	0.3%			8.7%	3.4%	0.0%	49.4%	0.0%	13.0%	18.3%	—	3.2%	75.2%	
4.3%			5.9%	8.1%	1.8%	3.3%	36.9%	46.8%	43.0%	34.5%	—	12.5%		
Experiment 4														
	9-Decenoic acid	Linoleic acid		Oleic acid	Blank 1	Blank 2	Caffeine	PROP	Quinine low	Quinine high	Sucrose octaacetate	Urea low	Urea high	
9-9-Decenoic acid	—			1.8%	3.0%	0.6%	2.0%	4.1%	0.3%	0.2%	0.3%	4.3%	0.0%	
	1.8%			—	86.2%	0.0%	16.6%	1.5%	5.8%	4.4%	8.7%	5.9%	20.2%	
	3.0%			86.2%	—	0.2%	14.8%	1.6%	6.5%	4.4%	3.4%	8.1%	15.3%	
	0.0%			0.0%	0.0%	85.6%	0.5%	20.3%	0.0%	0.0%	0.0%	1.8%	0.0%	
	0.6%			0.0%	0.2%	—	0.2%	22.1%	0.0%	0.0%	0.0%	3.3%	0.0%	
	2.0%			16.6%	14.8%	0.2%	—	10.4%	66.8%	68.1%	49.4%	36.9%	66.7%	
	4.1%			1.5%	20.3%	22.1%	10.4%	—	9.8%	5.9%	0.0%	46.8%	2.2%	
	0.3%			5.8%	6.5%	0.0%	66.8%	9.8%	—	84.3%	13.0%	43.0%	35.4%	
	0.2%			4.4%	4.4%	0.0%	68.1%	5.9%	84.3%	—	18.3%	34.5%	40.7%	
	0.3%			8.7%	3.4%	0.0%	49.4%	0.0%	13.0%	18.3%	—	3.2%	75.2%	
4.3%			5.9%	8.1%	1.8%	3.3%	36.9%	46.8%	43.0%	34.5%	—	12.5%		
Experiment 5														
	9-Decenoic acid	Linoleic acid		Oleic acid	Blank 1	Blank 2	Caffeine	PROP	Quinine low	Quinine high	Sucrose octaacetate	Urea low	Urea high	
9-9-Decenoic acid	—			1.8%	3.0%	0.6%	2.0%	4.1%	0.3%	0.2%	0.3%	4.3%	0.0%	
	1.8%			—	86.2%	0.0%	16.6%	1.5%	5.8%	4.4%	8.7%	5.9%	20.2%	
	3.0%			86.2%	—	0.2%	14.8%	1.6%	6.5%	4.4%	3.4%	8.1%	15.3%	
	0.0%			0.0%	0.0%	85.6%	0.5%	20.3%	0.0%	0.0%	0.0%	1.8%	0.0%	
	0.6%			0.0%	0.2%	—	0.2%	22.1%	0.0%	0.0%	0.0%	3.3%	0.0%	
	2.0%			16.6%	14.8%	0.2%	—	10.4%	66.8%	68.1%	49.4%	36.9%	66.7%	
	4.1%			1.5%	20.3%	22.1%	10.4%	—	9.8%	5.9%	0.0%	46.8%	2.2%	
	0.3%			5.8%	6.5%	0.0%	66.8%	9.8%	—	84.3%	13.0%	43.0%	35.4%	
	0.2%			4.4%	4.4%	0.0%	68.1%	5.9%	84.3%	—	18.3%	34.5%	40.7%	
	0.3%			8.7%	3.4%	0.0%	49.4%	0.0%	13.0%	18.3%	—	3.2%	75.2%	
4.3%			5.9%	8.1%	1.8%	3.3%	36.9%	46.8%	43.0%	34.5%	—	12.5%		
Experiment 6														
	9-Decenoic acid	Linoleic acid		Oleic acid	Blank 1	Blank 2	Caffeine	PROP	Quinine low	Quinine high	Sucrose octaacetate	Urea low	Urea high	
9-9-Decenoic acid	—			1.8%	3.0%	0.6%	2.0%	4.1%	0.3%	0.2%	0.3%	4.3%	0.0%	
	1.8%			—	86.2%	0.0%	16.6%	1.5%	5.8%	4.4%	8.7%	5.9%	20.2%	
	3.0%			86.2%	—	0.2%	14.8%	1.6%	6.5%	4.4%	3.4%	8.1%	15.3%	
	0.0%			0.0%	0.0%	85.6%	0.5%	20.3%	0.0%	0.0%	0.0%	1.8%	0.0%	
	0.6%			0.0%	0.2%	—	0.2%	22.1%	0.0%	0.0%	0.0%	3.3%	0.0%	
	2.0%			16.6%	14.8%	0.2%	—	10.4%	66.8%	68.1%	49.4%	36.9%	66.7%	
	4.1%			1.5%	20.3%	22.1%	10.4%	—	9.8%	5.9%	0.0%	46.8%	2.2%	
	0.3%			5.8%	6.5%	0.0%	66.8%	9.8%	—	84.3%	13.0%	43.0%	35.4%	
	0.2%			4.4%	4.4%	0.0%	68.1%	5.9%	84.3%	—	18.3%	34.5%	40.7%	
	0.3%			8.7%	3.4%	0.0%	49.4%	0.0%	13.0%	18.3%	—	3.2%	75.2%	
4.3%			5.9%	8.1%	1.8%	3.3%	36.9%	46.8%	43.0%	34.5%	—	12.5%		
Experiment 7														
	9-Decenoic acid	Linoleic acid		Oleic acid	Blank 1	Blank 2	Caffeine	PROP	Quinine low	Quinine high	Sucrose octaacetate	Urea low	Urea high	
9-9-Decenoic acid	—			1.8%	3.0%	0.6%	2.0%	4.1%	0.3%	0.2%	0.3%	4.3%	0.0%	
	1.8%			—	86.2%	0.0%	16.6%	1.5%	5.8%	4.4%	8.7%	5.9%	20.2%	
	3.0%			86.2%	—	0.2%	14.8%	1.6%	6.5%	4.4%	3.4%	8.1%	15.3%	
	0.0%			0.0%	0.0%	85.6%	0.5%	20.3%	0.0%	0.0%	0.0%	1.8%	0.0%	
	0.6%			0.0%	0.2%	—	0.2%	22.1%	0.0%	0.0%	0.0%	3.3%	0.0%	
	2.0%			16.6%	14.8%	0.2%	—	10.4%	66.8%	68.1%	49.4%	36.9%	66.7%	
	4.1%			1.5%	20.3%	22.1%	10.4%	—	9.8%	5.9%	0.0%	46.8%	2.2%	
	0.3%			5.8%	6.5%	0.0%	66.8%	9.8%	—	84.3%	13.0%	43.0%	35.4%	
	0.2%			4.4%	4.4%	0.0%	68.1%	5.9%	84.3%	—	18.3%	34.5%	40.7%	
	0.3%			8.7%	3.4%	0.0%	49.4%	0.0%	13.0%	18.3%	—	3.2%	75.2%	
4.3%			5.9%	8.1%	1.8%	3.3%	36.9%	46.8%	43.0%	34.5%	—	12.5%		
Experiment 8														
	9-Decenoic acid	Linoleic acid		Oleic acid	Blank 1	Blank 2	Caffeine	PROP	Quinine low	Quinine high	Sucrose octaacetate	Urea low	Urea high	
9-9-Decenoic acid	—			1.8%	3.0%	0.6%	2.0%	4.1%	0.3%	0.2%	0.3%	4.3%	0.0%	
	1.8%			—	86.2%	0.0%	16.6%	1.5%	5.8%	4.4%	8.7%	5.9%	20.2%	
	3.0%			86.2%	—	0.2%	14.8%	1.6%	6.5%	4.4%	3.4%	8.1%	15.3%	
	0.0%			0.0%	0.0%	85.6%	0.5%	20.3%	0.0%	0.0%	0.0%	1.8%	0.0%	
	0.6%			0.0%	0.2%	—	0.2%	22.1%	0.0%	0.0%	0.0%	3.3%	0.0%	
	2.0%			16.6%	14.8%	0.2%	—	10.4%	66.8%	68.1%	49.4%	36.9%	66.7%	
	4.1%			1.5%	20.3%	22.1%	10.4%	—	9.8%	5.9%	0.0%	46.8%	2.2%	
	0.3%			5.8%	6.5%	0.0%	66.8%	9.8%	—	84.3%	13.0%	43.0%	35.4%	
	0.2%			4.4%	4.4%	0.0%	68.1%	5.9%	84.3%	—	18.3%	34.5%	40.7%	
	0.3%			8.7%	3.4%	0.0%	49.4%	0.0%	13.0%	18.3%	—	3.2%	75.2%	
4.3%			5.9%	8.1%	1.8%	3.3%	36.9%	46.8%	43.0%	34.5%	—	12.5%		
Experiment 9														
	9-Decenoic acid	Linoleic acid		Oleic acid	Blank 1	Blank 2	Caffeine	PROP	Quinine low	Quinine high	Sucrose octaacetate	Urea low	Urea high	
9-9-Decenoic acid	—			1.8%	3.0%	0.6%	2.0%	4.1%	0.3%	0.2%	0.3%	4.3%	0.0%	
	1.8%			—	86.2%	0.0%	16.6%	1.5%	5.8%	4.4%	8.7%	5.9%	20.2%	
	3.0%			86.2%	—	0.2%	14.8%	1.6%	6.5%	4.4%	3.4%	8.1%	15.3%	
	0.0%			0.0%	0.0%	85.6%	0.5%	20.3%	0.0%	0.0%	0.0%	1.8%	0.0%	
	0.6%			0.0%	0.2%	—	0.2%	22.1%	0.0%	0.0%	0.0%	3.3%	0.0%	
	2.0%			16.6%	14.8%	0.2%	—	10.4%	66.8%	68.1%	49.4%	36.9%	66.7%	
	4.1%			1.5%	20.3%	22.1%	10.4%	—	9.8%	5.9%	0.0%	46.8%	2.2%	
	0.3%			5.8%	6.5%	0.0%	66.8%	9.8%	—	84.3%	13.0%	43.0%	35.4%	
	0.2%			4.4%	4.4%	0.0%	68.1%	5.9%	84.3%	—	18.3%	34.5%	40.7%	
	0.3%			8.7%	3.4%	0.0%	49.4%	0.0%	13.0%	18.3%	—	3.2%	75.2%	
4.3%			5.9%	8.1%	1.8%	3.3%	36.9%	46.8%	43.0%	34.5%	—	12.5%		
Experiment 10														
	9-Decenoic acid	Linoleic acid		Oleic acid	Blank 1	Blank 2	Caffeine	PROP	Quinine low	Quinine high	Sucrose octaacetate	Urea low	Urea high	
9-9-Decenoic acid	—			1.8%	3.0%	0.6%	2.0%	4.1%	0.3%	0.2%	0.3%	4.3%	0.0%	
	1.8%			—	86.2%	0.0%	16.6%	1.5%	5.8%	4.4%	8.7%	5.9%	20.2%	
	3.0%			86.2%	—	0.2%	14.8%	1.6%	6.5%	4.4%	3.4%	8.1%	15.3%	
	0.0%			0.0%	0.0%	85.6%	0.5%	20.3%	0.0%	0.0%	0.0%	1.8%	0.0%	
	0.6%			0.0%	0.2%	—	0.2%	22.1%	0.0%	0.0%	0.0%	3.3%	0.0%	
	2.0%			16.6%	14.8%	0.2%	—	10.4%	66.8%	68.1%	49.4%	36.9%	66.7%	
	4.1%			1.5%	20.3%	22.1%	10.4%	—	9.8%	5.9%	0.0%	46.8%	2.2%	
	0.3%			5.8%	6.5%	0.0%	66.8%	9.8%	—	84.3%	13.0%	43.0%	35.4%	
	0.2%			4.4%	4.4%	0.0%	68.1%	5.9%	84.3%	—	18.3%	34.5%	40.7%	
	0.3%			8.7%	3.4%	0.0%	49.4%	0.0%	13.0%	18.3%	—	3.2%	75.2%	
4.3%			5.9%	8.1%	1.8%	3.3%	36.9%	46.8%	43.0%	34.5%	—	12.5%		
Experiment 11														
	9-Decenoic acid	Linoleic acid		Oleic acid	Blank 1	Blank 2	Caffeine	PROP	Quinine low	Quinine high	Sucrose octaacetate	Urea low	Urea high	
9-9-Decenoic acid	—			1.8%	3.0%	0.6%	2.0%	4.1%	0.3%	0.2%	0.3%	4.3%	0.0%	
	1.8%			—	86.2%	0.0%	16.6%	1.5%	5.8%	4.4%	8.7%	5.9%	20.2%	
	3.0%			86.2%	—	0.2%	14.8%	1						

Table 3. Continued

	9-Decenoic acid		Linoleic acid		Oleic acid		Blank 1		Blank 2	
	H	L	H	L	H	L	H	L	H	L
9-Decenoic acid	—	—	—	—	—	—	—	—	—	—
Linoleic acid	2.9%	15.6%	2.9%	15.6%	5.5%	31.2%	3.6%	4.6%	3.5%	2.8%
Oleic acid	5.5%	31.2%	—	—	82.9%	65.0%	0.0%	2.3%	0.0%	0.7%
Blank 1	3.6%	4.6%	0.0%	2.3%	—	—	0.0%	4.6%	0.5%	1.9%
Blank 2	3.5%	2.8%	0.0%	0.7%	0.0%	4.6%	—	—	84.9%	73.9%
PROP	8.2%	45.5%	0.0%	35.5%	0.5%	60.8%	42.2%	13.5%	50.2%	8.7%

NEFA more frequently than nontasters and consumers of high fat diets, respectively. As noted in Table 2, tasters and nontasters were fairly evenly split among the high and low fat diet categories, so these similarities in groups are not due to confounding of these 2 factors. The mechanism for such a similarity is unclear, as the medium chain NEFA have very low affinity for proposed fatty acid taste receptors (Hajri and Abumrad 2002; Briscoe et al. 2003; Hirasawa et al. 2005; Galindo et al. 2012), and medium chain fatty acid receptors such as GPR40 have not been identified in human taste cells (Galindo et al. 2012).

The present data suggest that long chain fatty acids stimulate their own unique taste, which is unpalatable but very similar between oleic and linoleic acid when matched for intensity. This observation is in agreement with the mechanistic literature on fatty acid taste indicating the putative fat taste receptors interact predominantly with long chain fatty acids (Hajri and Abumrad 2002; Briscoe et al. 2003; Hirasawa et al. 2005; Galindo et al. 2012), though a diffusion mechanism could also still be possible (Tucker et al. 2014). Although these compounds also activate trigeminal neurons (Yu et al. 2012), the distinction between these 2 NEFA and the medium chain NEFA, which should be a more potent irritant (Stillman et al. 1975), would indicate another quality is dominant with the long chain NEFA. Although some overlap was observed among the long chain NEFA and various bitter compounds, overlap was much greater within just the bitter compounds or between the 2 long chain NEFA. In both studies, the overlap between linoleic and oleic acid was consistently high in all analyses, and the only percentage of overlap that was greater based on Bhattacharyya's coefficients was overlap of acetic and citric acids in the first experiment (90.8%, data not shown). This indicates that the sensations from oleic and linoleic acids are very comparable and also gives additional evidence that the sensation from the NEFA is unlikely to be predominantly textural in nature. Although the tests in this study did not show any textural difference among the emulsions, there are many textural properties not fully evaluated by these methods [such as tribology or salivary induced flocculation (Vingerhoeds et al. 2005, 2008, 2009; Silletti et al. 2008; van Aken et al. 2011)]. However, any textural sensation from the oleic acid emulsion should have been very different from the linoleic acid emulsion, as the concentration of oleic acid was 10-fold higher (5% compared with 0.5% w/w). As these 2 compounds mapped almost completely together in all 3 assessments, texture would not explain the similarity in sensation. Qualitative descriptions from panelists did not indicate the similarity would be explained by irritant sensations. Further if irritancy were the dominant quality, greater overlap among the medium chain NEFA and long chain NEFA would be expected, as previous work would indicate the medium chain NEFA would be the most irritating of the stimuli. Additionally, if the NEFA were irritating due to their nature as acids, the NEFA should have been grouped with the sour compounds in the first experiment, which was clearly not the case. Still, further work should be conducted to clarify whether the 2 long chain NEFA may be perceived primarily as irritating by some participants and at what concentrations the fatty acid taste becomes dominated by an irritant quality.

Conclusions

Overall, these experiments provide definitive evidence that long chain fatty acids elicit a unique, perceptible sensation at concentrations relevant to our food supply (Chang and Chow 2008; Kulkarni and Mattes 2013). The concentrations of fatty acids tested are relatively high compared with those customarily encountered in the food

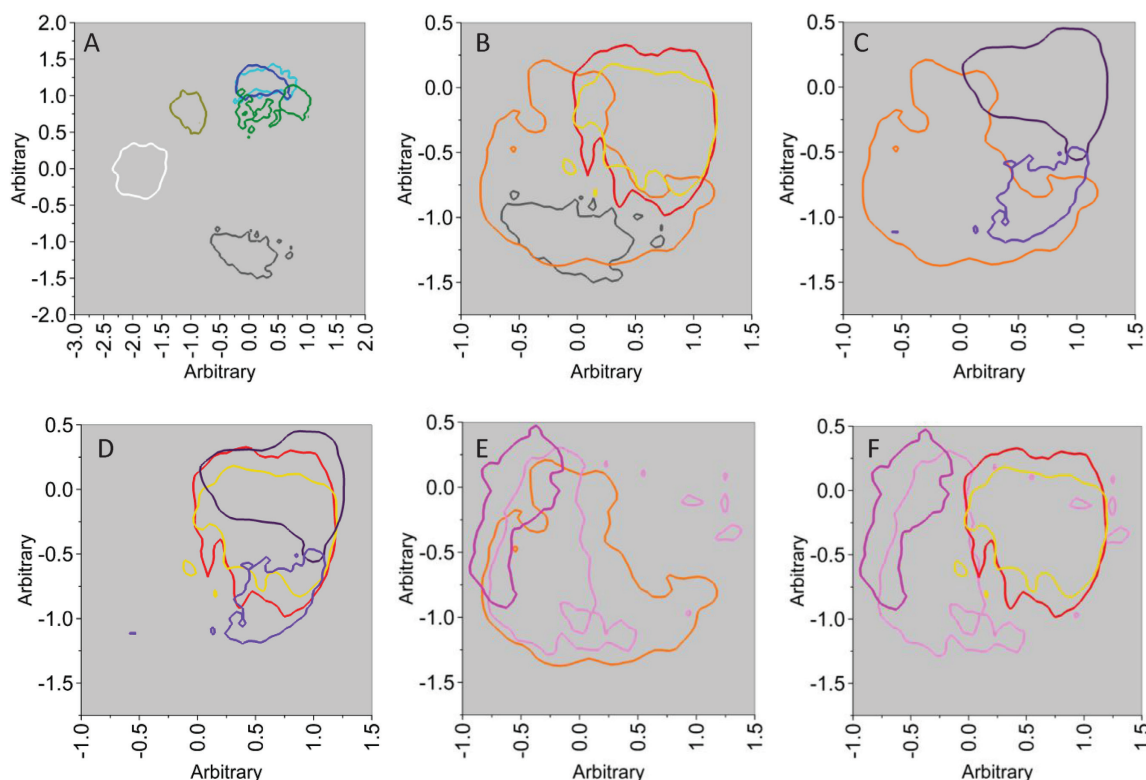


Figure 4. 95% contours experiment 1. (A) Sugars (white), sodium chloride (dark yellow), blank (gray), acetic acid (light blue), citric acid (dark blue), and hexenoic acid (green). (B) Blank (gray), decenoic acid (orange), oleic acid (yellow), and linoleic acid (red). (C) Decenoic acid (orange), quinine (dark purple), urea (light purple). (D) Oleic acid (yellow), linoleic acid (red), quinine (dark purple), and urea (light purple). (E) Decenoic acid (orange), inosine monophosphate (light pink), and monosodium glutamate (bright pink). (F) Oleic acid (yellow), linoleic acid (red), inosine monophosphate (light pink), and monosodium glutamate (bright pink).

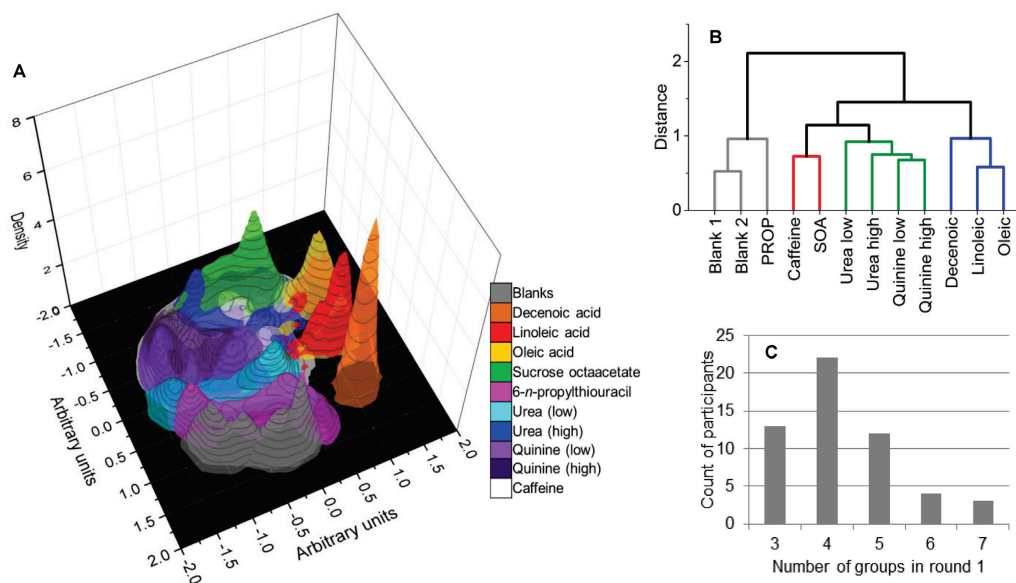


Figure 5. (A) Kernel density of experiment 2 samples in perceptual map representing 500 bootstrapped replicates of the MDS data generated with panelists' dissimilarity matrices. Horizontal lines are 10% increments of density; X and Y dimensions are arbitrary. (B) Dendrogram from hierarchical clustering of all participant ($N = 48$) dissimilarity matrices using Ward's method. (C) Histogram of number of groups created in first round of sorting.

supply, but levels of nonesterified fatty acids can reach concentrations in the low percentiles (5% = 0.18 M for oleic acid) in many fermented or rancid products, as well as in cooking oils (Chang and Chow 2008). Medium and short chain fatty acids stimulate different sensations from long chain fatty acids, with short chain species

producing a sour sensation and medium chain fatty acids characterized potentially by irritancy, yet both may have an uncertain fat quality. Further analyses should determine at what specific chain length the perceptual differences among short, medium, and long chain NEFA occur. These data added to the totality of evidence on "fat

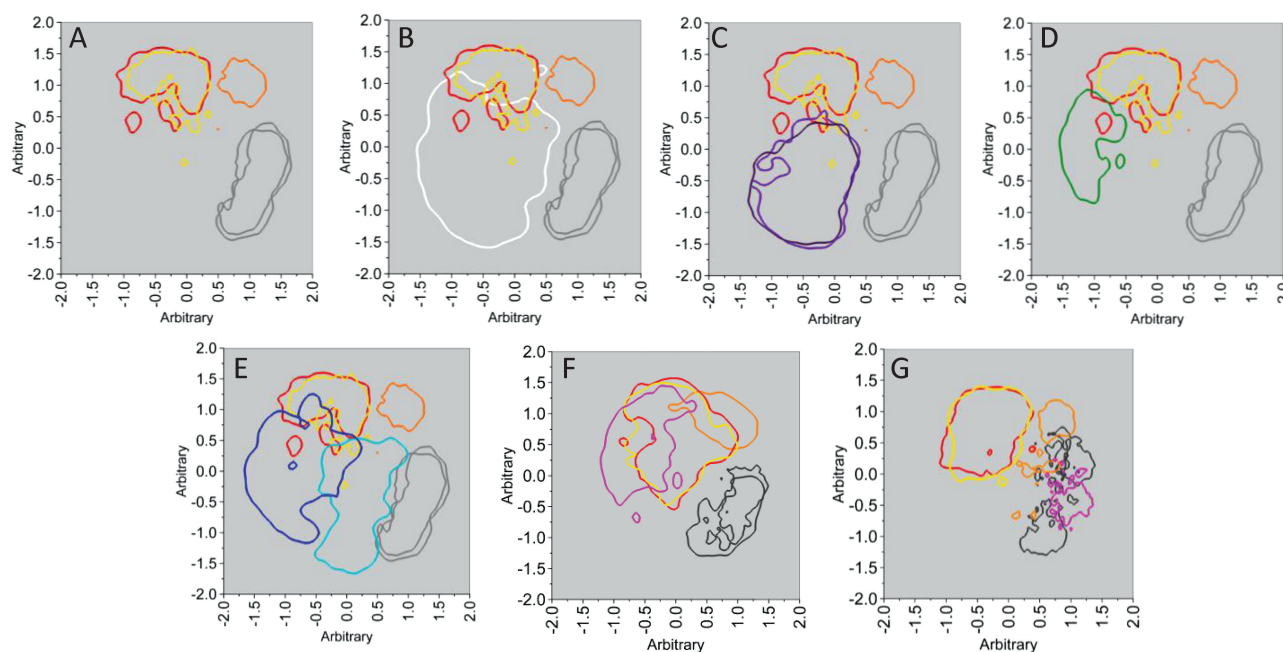


Figure 6. 95% contours experiment 2. (A) Oleic acid (yellow), linoleic acid (red), decenoic acid (orange), and blanks (gray). (B) Oleic acid (yellow), linoleic acid (red), decenoic acid (orange), blanks (gray), and caffeine (white). (C) Oleic acid (yellow), linoleic acid (red), decenoic acid (orange), blanks (gray), quinine low concentration (light purple), and quinine high concentration (dark purple). (D) Oleic acid (yellow), linoleic acid (red), decenoic acid (orange), blanks (gray), and sucrose octaacetate (green). (E) Oleic acid (yellow), linoleic acid (red), decenoic acid (orange), blanks (gray), urea low concentration (light blue), and urea high concentration (dark blue). (F) Tasters ($N = 28$), oleic acid (yellow), linoleic acid (red), decenoic acid (orange), 6-*n*-propylthiouracil (pink), blanks (gray); greater overlap overall was observed because of smaller sample size. (G) Nontasters ($N = 26$), oleic acid (yellow), linoleic acid (red), decenoic acid (orange), 6-*n*-propylthiouracil (pink), blanks (gray); greater overlap overall was observed because of smaller sample size.

taste” now provide a comprehensive body of evidence supporting the existence of another basic or primary taste quality for selected fatty acids (fat taste), whose oral activity should thus be considered when examining the health consequences of fatty acid signaling.

Notably, the taste sensation elicited by long chain fatty acids is not wholly consistent with the expectations of “fattiness.” Given the clear unpleasantness of the sensation in isolation, and the incongruity with the term “fatty,” which has strong textural context, we propose a new term to describe the taste of long chain NEFA. The term “pinguis” was used to describe fattiness as early as the 16th century (Fernel 1581; Reed and Knaapila 2010), but this term refers more to a fatty or dense characteristic without specificity to taste. Following the precedent set for umami which was derived from Japanese to mean delicious taste (umai: delicious/savory, mi: taste), we propose the term “oleogustus.” The latin term, “oleo” is a root for oily or fatty and “gustus” refers to taste. The term oleogustus would provide a word easily recognized as pertaining to taste by those in the field, but not easily confused with other sensations of fat perception.

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