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OBSERVATION

A Crossmodal Role for Audition in Taste Perception

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Our sense of taste can be influenced by our other senses, with several groups having explored the effects of olfactory, visual, or tactile stimulation on what we perceive as taste. Research into multisensory, or crossmodal perception has rarely linked our sense of taste with that of audition. In our study, 48 participants in a crossover experiment sampled multiple concentrations of solutions of 5 prototypic tastants, during conditions with or without broad spectrum auditory stimulation, simulating that of airline cabin noise. Airline cabins are an unusual environment, in which food is consumed routinely under extreme noise conditions, often over 85 dB, and in which the perceived quality of food is often criticized. Participants rated the intensity of solutions representing varying concentrations of the 5 basic tastes on the general Labeled Magnitude Scale. No difference in intensity ratings was evident between the control and sound condition for salty, sour, or bitter tastes. Likewise, panelists did not perform differently during sound conditions when rating tactile, visual, or auditory stimulation, or in reaction time tests. Interestingly, sweet taste intensity was rated progressively lower, whereas the perception of umami taste was augmented during the experimental sound condition, to a progressively greater degree with increasing concentration. We postulate that this effect arises from mechanostimulation of the chorda tympani nerve, which transits directly across the tympanic membrane of the middle ear.

Keywords: multisensory perception, crossmodal, taste, sound, gustation

Appreciation of flavor in foods requires the diverse interaction of all basic sensory systems. Thus, the integration of sensory information within flavor is an example of crossmodal perception. When an individual experiences food, they receive input from the visual and auditory systems, as well as more recognized input from taste, olfaction, and mechanoception (the physical perceptions of the feel of food in the mouth). The amalgamation of these sensations underpins our experience of flavor (Delwiche, 1996).

There are many varying definitions of *flavor*. Modern definitions include olfactory and trigeminal modalities, indicating recognition of the scope for multisensory interaction. From the surface of the tongue to the roof of our mouths, as well as the back of the oral cavity, taste receptors, located in collections of around 100 cells termed *taste buds*, are the major relay of sensory information to the gustatory centers of our brain. Humans show remarkable variation in both sensitivity to taste and density of taste buds (Miller & Reedy, 1990), but on average have between 5,000 and 10,000 taste buds in their mouths, with the life span of a taste bud averaging 7 to 21 days (Breslin & Huang, 2006). Bilateral branches of the facial nerve (cranial nerve VII), termed the *chorda tympani*, innervate taste buds in the anterior two thirds of the tongue and part of the soft palate and throat. This anterior region of the tongue contains dense collections of fungiform papillae. From the anterior of the tongue, the chorda tympani closely abuts the middle ear, crossing the tympanic membrane, before proceeding medially into the brain. Research performed on the chorda tympani of chimpanzees shows a composition consisting of varying bundles of neural fibers, each fiber group transmitting a specific taste quality or group of qualities (Hellekant, Ninomiya, & Danilova, 1997). The proximity of the chorda tympani nerve to the eardrum (Rahilly, 2008), the prevalence of dysgeusia in individuals prone to otitis media (inflammation of the middle ear) in early life (Seaberg et al., 2010), and the delicate nature of neural excitability collectively leads to an intriguing question: Do loud noises have an impact on the tastes we perceive?

Multisensory Perception

Beginning with Moir (1936), changing the visual aspect of “food-stuffs” has been long noted to influence the perception of the substance being consumed (reviewed by Spence, Levitan, Shankar, & Zampini, 2010). The integration of sensory inputs during the process of consumption allows for eating to become a truly crossmodal experience, and perhaps partially explains the cultural weight we place on the dining experience (see Spence & Piqueras-Fiszman, 2014). Charles Spence of the Crossmodal Research Laboratory (CRL) in Oxford, United Kingdom, and Ferran Adrià, of the elBulli restaurant in Spain, recently performed experiments concerning plate color and its influence on the perception of taste. Using the same dessert, placed on either a white plate

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or black plate, researchers found that panelists who were served the dessert on the white plate rated it as tasting sweeter than panelists served from a black plate (Piqueras-Fiszman, Alcaide, Roura, & Spence, 2012). Similarly, the shape of the plate a substance is consumed from (as well as again, its color) has a similar effect in influencing the perception of the food's sweetness (Stewart & Goss, 2013). This seems in agreement with the observation that simply looking at shapes that were more rounded was shown to increase the perceived intensity of sweetness (Liang, Roy, Chen, & Zhang, 2013), as opposed to more geometric, angular shapes, which appeared to have no effect on perceived sweetness.

In recent years, attention has turned toward a possible interaction between auditory and gustatory perception (reviewed by Spence, 2014). Almost 30 years previously, Ferber and Cabanac (1987) noted the negative effect of exposure to loud noise on gustatory affective ratings. More recently, Woods and colleagues (2011) noted that the perception of sweet intensity was impaired under loud noise conditions. Crisinel and Spence found an implicit association between pitch and taste, when participants matched the sound of various instruments with a selection of flavors. They confirmed the association between high-pitched notes and sweet or sour tastes, and lower pitched notes with bitter and umami, for example, a trombone producing a match with bitterness (Crisinel & Spence, 2009, 2010). Further, they were able to find associations between specific flavor solutions and accompanying musical notes (Crisinel & Spence, 2011). There seems, then, to be an inbuilt association between the experience of external sounds and our sense of taste.

Sound from the consumption of foods also exhibits an effect on our perception of flavors (Drake, 1970; Vickers & Bourne, 1976). Vickers (1991) found that panelists judged food as less crispy when the distinctive higher pitch sounds associated with crispiness were muffled by chewing with the mouth closed, while also demonstrating that there was no decrease in crunchiness in the sample. In another study, participants were asked to consume various alcoholic beverages in an environment of background music delivered with headphones, as well as during a quiet control. The study found that sweetness perception of alcohol was altered in the music condition when compared with the control condition, and other distracting conditions, confirming the results of a previous study that used music or a news story to show similar results (Stafford, Agobiani, & Fernandes 2013; Stafford, Fernandes, & Agobiani, 2012).

In 2010, airline giant Lufthansa and LSG Sky Chefs, the largest in-flight catering company in the world, simulated in-flight airline meals at the Fraunhofer Institute for Building Physics. Their preliminary results indicated that perception of sweet and salty may show some decline, whereas sour, bitter, and spicy were rated as unchanged (Michaels, 2010). This result was, however, more attributed to pressure change than to sound condition. More recently Spence, Michel, and Smith (2014) suggested that perhaps it may be the interaction of cabin noise and umami taste transduction that is responsible for the demand for umami-rich tomato juice in airline cabins.

In our present study, we investigated the effect of loud audio stimulation on the perception of the five basic tastes. To date, this is the most intensive study of the effects of loud noises on the taste perception. To best emulate a set of conditions in which preference changes are widely reported, in air travel, we delivered continuous simulated airplane noise at levels of 80 to 85 dB, replicating conditions found during flight and landing (Ozcan & Nemlioglu, 2006). Aircraft cabin noise is a significant part of the atmosphere in which we travel, especially in long-term flights, effecting passengers and crew in both comfort and psychological well-being. As cabin conditions during air transport can have such an influence on the body, some interest has focused on beverage and meal consumption during flight, in this difficult time for the airline industry. We tested the hypothesis that airplane cabin noise can affect the perceived intensity of the five basic tastes, and whether this effect is specific to taste, or disrupts the other senses, or our levels of attention.

Panelists evaluated multiple concentrations of prototypic basic taste solutions, for sweet, salty, sour, bitter, and umami, on the general Labeled Magnitude Scale (gLMS; normalized here from 0 to 15). This scale has been verified to accurately gauge the perception of a variety of stimuli both within and across individuals, and has been particularly well verified in taste research (Bartoshuk, 2000; Bartoshuk et al., 2004), despite some studies questioning whether the data produced is ratio-level (Schifferstein, 2012). These measurements were combined with ratings for tactile stimuli, various controls, and scores on an attention test, to exhaustively model the effects of such an auditory environment on our perception of taste.

Method

Participants

Panelists (*N* = 48; 11 males and 37 females) were recruited predominantly from the student and staff population at Cornell University, Ithaca, New York. All procedures were verified and approved by the Cornell Institutional Review Board for human participants (protocol ID# 1403004526). Subjects were not informed of the objective of the experiment. Participants were financially compensated $15 for each of two sessions, lasting a little over an hour each, and were tested individually in isolated sensory booths. Panelists ranged from 18 to 55 years and were screened for any taste or hearing impairments, instructed prior to testing on the use of the gLMS across modalities, and assessed prior to taste testing to confirm they understood all instructions and could scale accurately. Participants were instructed to read or to "work" during the pretest priming, and not to concentrate on the sound as they tasted with or without the experimental sound condition.

Stimuli

The stimuli consisted of aqueous food grade solutions from Sigma Aldrich (St. Louis, MO) listed in Table 1, delivered in distilled deionized water at three concentration levels, with and without background noise treatment. Concentrations were based on both pilot bench testing and on published psychophysical data. Cabin noise was recreated from actual airplane cabin noise recordings (broad spectrum, peak ~290 Hz), delivered to participants at 80 to 85 dB through high-definition headphones (B&O Play Form 2, Bang and Olufsen, Struer, Denmark). Decibel level was verified using a basic decibel meter (Skypaw v3.8.2). During the noise-free condition, a low level of ambient room noise was audible, and

Table 1
Solutions Evaluated by Panel, Sucrose, Sodium Chloride, Citric Acid, Monosodium Glutamate, Quinine Hydrochloride (mM/L)

	Low	Medium	High
Sucrose	27	81	243
NaCl	33	100	300
Citric acid	1	3	9
MSG	3	9	27
Quinine HCl	.056	.166	0.5

headphones did not cut off panelist-generated noises from oral consumption.

Experimental Design and Procedure

The experiment was based on a crossover design with sound condition and solution as factors, counterbalanced with one group receiving the sound condition first and the other receiving the control. The panelists were trained on the gLMS, and tested for acuity using auditory and visual stimuli. The gLMS is a scaling technique that uses verbal cues as anchors (e.g., barely detectable, strongest imaginable), and with quasi-logarithmic spacing determined at approximate perceptual magnitudes. Studies verify the acuity of this scaling system across modalities (Bartoshuk et al., 2004; Lawless & Heymann, 2010). After panelists were introduced to the gLMS, they completed a number of scaling tasks. Each rated the color saturation of a red circle at various levels to ensure that the task was understood. After this, the panelists rated a beep, delivered through the headphones, to ensure that each had sufficient hearing acuity. This auditory sensitivity was also tested as a factor in the final statistical model built for the experiment. Participants evaluated 15 samples: five basic taste solutions in three concentrations each, with enforced rest periods between each trial in which panelists cleansed their palette, rinsing and expectorating with deionized water between solutions. Sessions were scheduled as closely together as possible, usually on the next day, and at a similar time of day. Ballots were programmed into Compusense at-hand (Compusense Inc., Guelph, Canada) sensory evaluation software and administered through iPad minis (Apple Inc., Cupertino, CA). In each experimental trial, the participant was asked a series of demographic, and short-answer questions. Under all conditions, the solution samples were presented in 2-oz. sample cups, labeled with random three-digit blinding codes. The participants were instructed to sample the solution with their whole mouths and then expectorate into a cup. Panelists evaluated each sample in parallel sessions, with and without simulated airline cabin noise. Airline cabin noise was delivered for 30 min prior to the testing while the panelist read or studied. After this, solutions were presented as the audio continued to play for the rest of the experiment. During the quiet sound condition, participants also had a 30-min priming period, when the same headphones were worn with only ambient room noise. The order of the solutions was randomized in each experimental trial. At the end of the experiment, participants rated the roughness of a piece of sandpaper on the same scale. In order to ensure that the effects observed were not merely an artifact of a difficulty in concentrating when in the loud noise condition, all panelists also performed a simple reaction time (RT) test using visual cues relating to colors (Human Benchmark RT test, five trials, test global mean RT = 261 ms), while still receiving sound or near silence from the headphones. The color saturation ratings of panelists for a red circle at two saturation levels are shown in Figure 1A and B, with panelists' auditory ratings in Figure 1C. Dependent Student's *t* tests of these ratings revealed no significant difference between ratings of either color saturation ($n = 48$, $p = .097$; .566) or sound intensity ($p = .436$) in the quiet (hereafter referred to as "silence") or experimental (sound) conditions.

Data Analyses

Data were analyzed with Graphpad Prism 5.0 (Graphpad software, La Jolla, CA), and IBM SPSS (IBM, Endicott, NY). Individual tastant responses were analyzed using simple repeated measures Student's *t* tests, and additional linear mixed models were built for both umami and sweet taste. In these models, sound condition, stimulus concentration, RT, hearing acuity, and stimu-

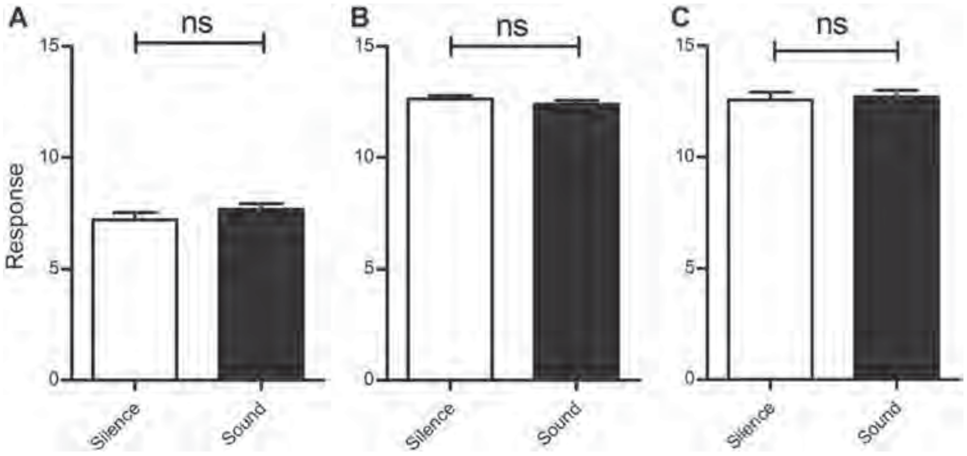

Figure 1. (A, B) Color saturation response rating on the general Labeled Magnitude scale (gLMS) in both sound and no sound (silent) condition. (C) Panelists rated a beep delivered through the same headphones on the gLMS. No significant differences were observed between sound and silent condition. Errors represent mean ± *SEM*, ns = nonsignificant.

lus order were fixed effects, as well as an interaction between noise condition and stimulus concentration level. The panelist IDs were set as a random effect in the model.

Results

Dependent Student's *t* tests assessed whether the simulated airplane sound had an effect on participants' intensity ratings of basic taste. For all three concentrations of salty ($p = .085$; .962; .921), bitter ($p = .684$; .851; .497) and sour ($p = .216$; .663; .285) taste, no effect was evident (see Figure 2A through C), despite both salty and sour tending to approach significance at low concentrations.

Interestingly, however, in sweet taste ratings, exposure to the loud noise condition resulted in a pronounced suppression of taste intensity across all concentrations measured ($p = .044$; .001; .040; see Figure 3).

To date, no reports have quantified the effects of auditory stimulation on the perception of umami taste. Spence et al. (2014) did, however, postulate that perhaps the popularity of umami-rich foods such as tomato juice onboard commercial airliners could be justified by umami taste being impervious to the inhibition observed to sweet taste perception. Surprisingly, when rating intensity of umami taste, panelists rated solutions delivered in the loud condition to in fact be more intense than the same solutions delivered in the near-silent condition, in the two higher concentrations, with escalating effect size with dosage (Figure 4; $p = .518$; .010; $< .0001$). Our results suggest that instead of merely being immune to the effects of loud noise, auditory conditions in air travel may actually serve to enhance this already appetitive and sought-after taste quality.

Attention test results after both the control and noise conditions indicated no change in attentiveness between sound conditions (Figure 5A; $p = .351$), suggesting a similar concentration level across the testing conditions.

Finally, to evaluate whether such loud and consistent stimulation affected other the senses, and not merely taste, participants were asked to evaluate and rate the roughness of a 2 × 2-in. piece of coarse sandpaper between the thumb and forefinger, in both conditions. Again, no effect was observed between conditions ($p = .194$; Figure 5B), indicating that the effects observed were specific to taste sensitivity.

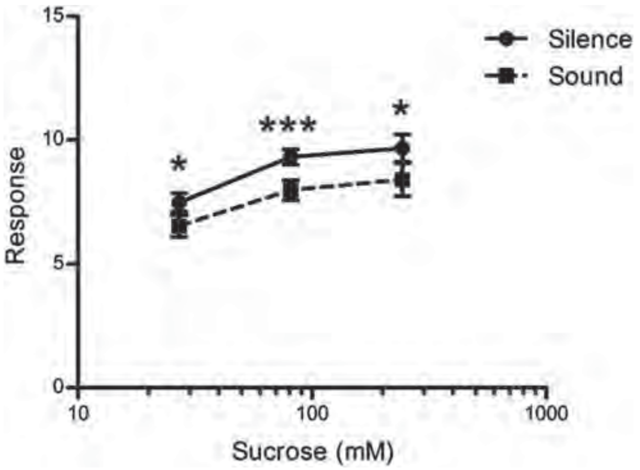

Figure 3. The response to sweet (sucrose) solution showed considerable decrement, when delivered in the simulated cabin noise condition, across all three concentration levels. Errors represent mean ± *SEM*. $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$.

When plotting individual data points, it was evident that some sensory segmentation of responses was occurring, whereby most panelists consistently demonstrated a robust modulation of both sweet and umami, and a smaller number were virtually unaffected when rating either. Analysis to decipher this segmentation parsed the group by sex (14 male vs. 34 female), age (19 over 25 years vs. 29 under 25 years), and ethnic origin (32 European vs. 16 non-European descent). There was no significant variation between gender (two-tailed chi-square test, $p = .27$) or age groups ($p = .22$), but segmenting ratings between European versus non-European origin implied the presence of two distinct segments ($p = .0475$) for participants displaying a modulation in intensity ratings.

More advanced mixed-model linear analysis of data for both sweet and umami tastes was carried out on the data set, controlling for additional variables, such as order effects, with a random effect inserted for panelist ID to account for correlation between ratings. With this approach, more attention could be paid to within subject effects, accounting for multiple ratings in the crossover design, with Bonferroni corrections for multiple comparisons. No significance was found for the efficacy of the panelist's hearing ($p = .839$ for umami, .795 for sweet), quantified through the sound rating, or the panelist's order of test condition ($p = .238$ for umami, .931 for sweet). The models confirmed, however, the significance of the sound treatment

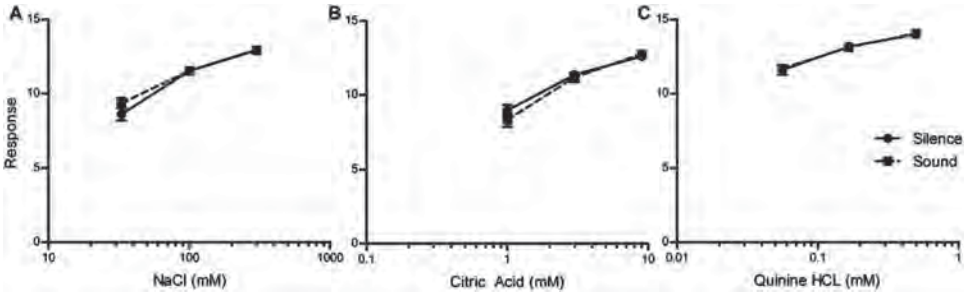

Figure 2. Salty (A: NaCl, sodium chloride), sour (B: citric acid), and bitter (C: quinine hydrochloride) stimuli were delivered to panelists at three concentrations. Panelists rated the intensity of taste on the general Labeled Magnitude scale. No significant differences were observed between sound and silent condition. Errors represent mean ± *SEM*.

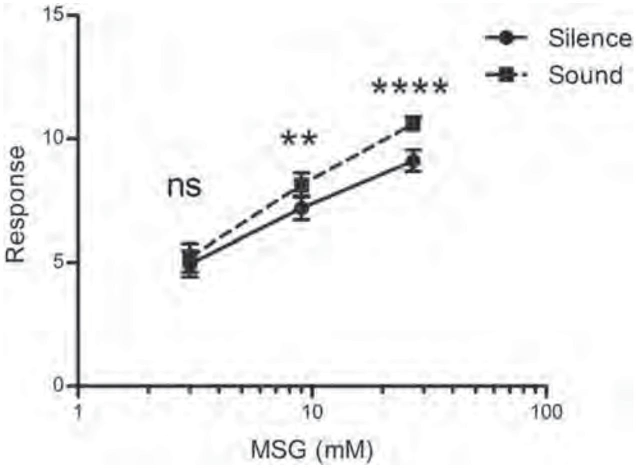

Figure 4. Umami (MSG, monosodium glutamate) taste appeared to be significantly augmented by the noise condition, particularly at higher concentrations. Errors represent mean ± *SEM*; ns = nonsignificant. * $p < .05$; ** $p < .01$; *** $p < .001$; **** $p < .0001$.

for all but the lowest concentration levels in both umami (Bonferroni-corrected *p* value < .001) and sweet (*p* = .002). As would be expected, dosage level was also highly significant in the model. Estimated marginal means for each of the fixed effects and interaction terms from both linear mixed models are displayed in summary in Figure 6.

Discussion

Our study confirmed that in an environment of loud noise, our sense of taste is compromised. Interestingly, this was specific to sweet and umami tastes, with sweet taste inhibited, as others have shown largely through affective testing, and umami taste significantly enhanced. This perturbation in the balance of our perception of taste would undoubtedly lead to altered hedonic properties of foods. Thus, the multisensory properties of the environment we consume our food within can alter our perception of the foods we eat.

Multisensory perception stems from the integration of sensory neuronal inputs, with many containing overlapping receptive fields. These interactions seem independent of one another and yet become merged into a single perception (Small, 2012; Stein, 1998). In studies of alcohol perception and consumption, researchers were able to confirm a role for audition in taste perception (Guéguen, Jacob, Le Guellec, Morineau, & Lourel, 2008; Stafford et al., 2012, 2013). Although some have pondered on the perception of umami, or even hypothesized that it may be impervious to input from audition (Pettit, 1958; Spence et al., 2014), our results indicate significant augmenting of umami taste, at least by the sound pattern provided in our own test. This may not be true, however, of alternative frequency audio stimulation. Dissatisfaction with the sensory quality of airline food is so common that it intimates a more complex underlying problem, such as the interaction we report. The study is of course bounded by a number of limitations. Our auditory stimulus simplifies the air travel experience, and, likewise, our experimental design does not include complex foods, but their underlying tastants in isolation. Our study does however, highlight an intriguing cognitive effect, one which could guide reformulations of airline food products specifically for the sensory atmosphere in which they are served. Our results are somewhat reminiscent of the experimental outcomes of Woods et al. (2011), whereby a more complex food stimulus, sweet in nature, was rated as significantly less sweet when accompanied by auditory stimuli at levels similar to our own. These results are likely the underlying reason that the hedonic qualities of airline food are consistently rated lower than would be expected, and could offer actionable and directional guidance toward improved acceptance.

Fungiform taste-bud distortion after chorda tympani nerve trauma has been well characterized in rats, hamsters, and gerbils

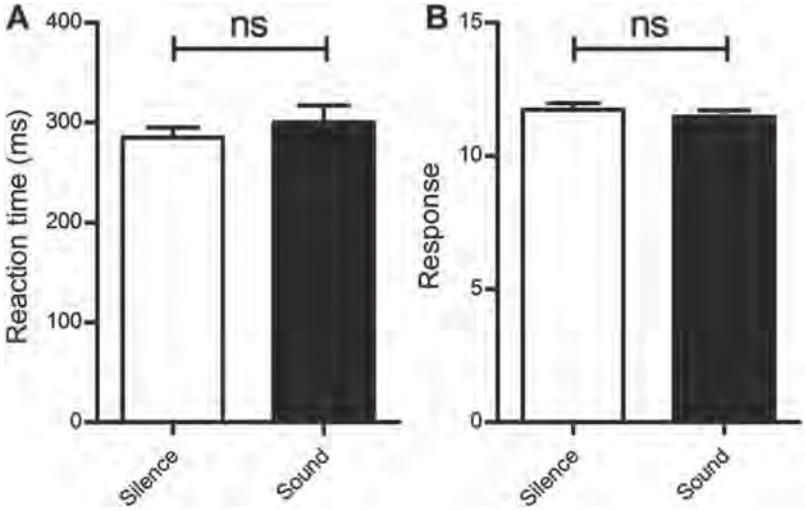

Figure 5. (A) Reaction time was not affected by sound condition. (B) Panelists rating the tactile sensation of a coarse piece of sandpaper were also not affected by sound treatment. Errors represent mean ± *SEM*; ns = nonsignificant.

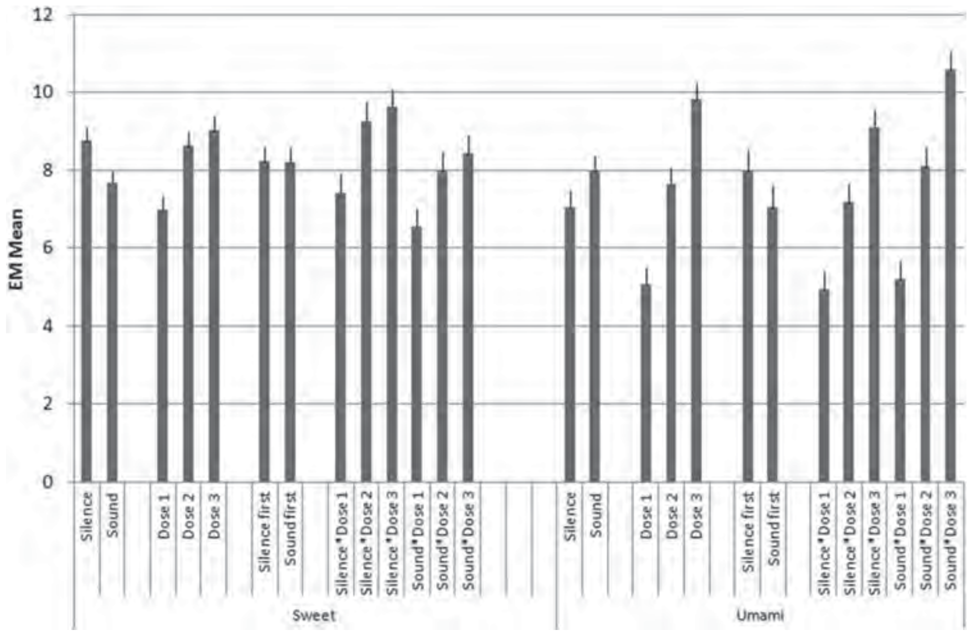

Figure 6. Estimated marginal (EM) means built by the mixed model for each factor in the analysis of both sweet and umami. Error bars represent mean ± *SEM*.

(Guagliardo & Hill, 2007). Damage to the middle ear through surgery or infection has been demonstrated to give rise to broad taste distortion, as have surgeries to the nose and throat or extraction of the molars (Nin et al., 2006). For many years, the effect of direct mechanical stimulation of nerve fibers on the electrical properties of both mechanosensitive and nonmechanosensitive nerves has been actively studied by neuroscientists (Julian & Goldman, 1962). The chorda tympani directly crosses the tympanic membrane, between the malleus and incus, making physical contact with structures actively vibrating with audio stimulation. In a situation such as that encountered on an aircraft, it is entirely possible that direct mechanical stimulation of the chorda tympani nerve has a measureable effect on the electrical properties of this important taste nerve. Yasumatsu et al. (2012) categorized the electrical properties of both sweet and umami taste nerves from the chorda tympani, and found them to show discrete and distinct patterns of excitation, indicating that such bidirectional activity as we observed would be feasible; however, we acknowledge that this is merely one of many possible explanations.

Ethnic origin of the panelists appeared to exhibit some influence over the observed effect, specifically between those of European origin and those of an alternative background. This interestingly mirrors the prevalence of genetic mutations in the sweet–umami shared receptor subunit T1R3 demonstrated by Fushan, Simons, Slack, Manichaikul, and Drayna (2009). A variation rooted in ethnic origin would imply the possibility of a genetic basis to this effect. The receptors for both umami and sweet consist of a heterodimeric arrangement of T1R proteins. Umami requires both functional T1R1 and T1R3 receptors. Interestingly, although sweet relies on the T1R2 receptor, it must be paired with the same T1R3 receptor as in umami taste detection. Thus, unlike the other basic tastes, sweet and umami share a common genetic linkage (Li, 2009). That modulation was observed in both sweet and umami tastes, but not in others, highlights T1R3 as a possible genetic locus for this observation. A common single nucleotide polymorphism (SNP) exists within the promoter region for T1R3. Intriguingly, this SNP is notably more prevalent in those of non-European origin (Kim, Wooding, Riaz, Jorde, & Drayna, 2006), mirroring what we observed in our data. We would speculate that the modulation of taste observed with prominent audio stimulation may be linked to such a polymorphism, though genetic testing would be necessary to determine this. As this mutation is within the promoter region, however, the nature of the interaction would likely be complex. Future study to assess the possible genetic basis of this observation may shed light on the segmentation in effect size observed in our study.

It is clear that taste perception depends not only on the multisensory integration of sensory inputs associated with the food or drink itself but also on the multisensory attributes of the environment in which the sample is consumed. The multisensory nature of what we consider "flavor" is undoubtedly underpinned by complex central and peripheral interactions between ascending neural inputs. Our results characterize a novel sensory interaction, with intriguing implications for the effect of the environment in which we consume food.

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