Multisensory Flavor Perception

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The perception of flavor is perhaps the most multisensory of our everyday experiences. The latest research by psychologists and cognitive neuroscientists increasingly reveals the complex multisensory interactions that give rise to the flavor experiences we all know and love, demonstrating how they rely on the integration of cues from all of the human senses. This Perspective explores the contributions of distinct senses to our perception of food and the growing realization that the same rules of multisensory integration that have been thoroughly explored in interactions between audition, vision, and touch may also explain the combination of the (admittedly harder to study) flavor senses. Academic advances are now spilling out into the real world, with chefs and food industry increasingly taking the latest scientific findings on board in their food design.

Introduction

According to many authors, foraging and feeding are among the most important of the everyday tasks that our brains have evolved to deal with. As J.Z. Young (1968, p. 21), the eminent British biologist, once put it, "No animal can live without food. Let us then pursue the corollary of this: Namely, food is about the most important influence in determining the organization of the brain and the behavior that the brain organization dictates."

Indeed, some of the most dramatic changes in brain activity are seen when a hungry participant is presented with appetizing food images while lying passively in the brain scanner (van der Laan et al., 2011). It can therefore be argued that, even if one is not interested in flavor perception per se, ultimately studying the perception of food and drink may be central to our understanding of brain function.

However, despite its obvious importance, psychologists and cognitive neuroscientists have been slow to show much interest in studying flavor perception. In part, this neglect may reflect the difficulty of controlling stimulus delivery (this kind of research can't be done with a participant sitting obediently in front of a PC). Part of the problem, I think, also links to the fact that subjects rapidly adapt and hence may become sated after a few presentations of the experimental stimuli. This often necessitates multiple testing sessions. However, neglect of this field may also link to a more deep-seated belief that taste and smell constitute "lower," or "common," senses. Such a view is captured by the following quote from William James from a little over a century ago: "Taste, smell, as well as hunger, thirst, nausea and other so-called 'common' sensations need not be touched on…as almost nothing of psychological interest is known concerning them." One sometimes finds oneself wondering just how much has changed in the intervening years!

One of the most intriguing facts about the sense of taste is that we are all, in a very real sense, born into different taste worlds. Indeed, individual differences in taste receptor density on the tongue are far higher than for any of the other senses. To give you an idea, some people (called supertasters) have 16 times more taste buds on their tongues than other individuals—the non-tasters (see Bartoshuk, 2000). That said, the latest research suggests that the profound differences in people's sensitivity to bitter-tasting foods, such as cruciferous vegetables like Brussels sprouts and lab compounds such as propylthiouracil PROP, depend far more on the status of the PROP receptor encoded by the TAS2R38 gene than on the density of taste buds (Garneau et al., 2014). Supertasters are also more sensitive to the oral-somatosensory attributes of foods, such as the fat in a salad dressing (Eldeghaidy et al., 2011). Expertise, as for instance in wine tasters, has also been shown to predict taste phenotype (Hayes and Pickering, 2012).

Flavor involves the combination of gustatory and olfactory stimuli, giving rise to descriptors such as "fruity," "meaty," "floral," "herbal," etc. Here, it is important to distinguish between orthonasal smell when we sniff (that tells us about the aroma of food, the bouquet of the wine) and the retronasal smell when air is pulsed out from the back of the nose as we swallow (e.g., Rozin, 1982). While the distinction between these two senses of smell has been recognized for more than a century (see Shepherd, 2012), only recently have researchers been able to provide empirical support for the claim that different neural substrates may actually be involved in processing these two kinds of olfactory information (see Small et al., 2005). It is the retronasal aromas that are combined with gustatory cues to give rise to flavors. On top of these two senses, trigeminal inputs also contribute to flavor perception. As for the other senses, such as vision, audition, and oral somatosensation, the jury is currently still out as to which if any of these senses should be considered as constitutive of flavor perception or, rather, as factors that merely modulate the experience of flavor (see Spence and Piqueras-Fiszman, 2014).

Olfactory-Gustatory Interactions underlying Multisensory Flavor Perception

While it is only natural to think of taste (i.e., gustation) as playing a key role in multisensory flavor perception, the majority of

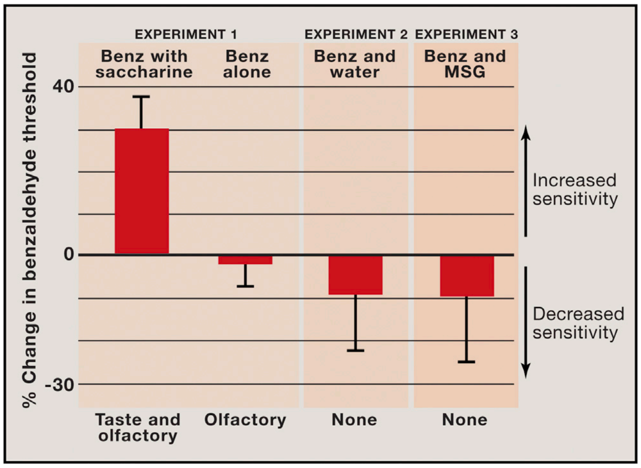

Figure 1. Multisensory Interactions between Olfaction and Gustation in Multisensory Flavor Perception

Results of a series of experiments by Dalton et al. (2000), showing the integration of orthonasal olfactory and gustatory cues. Figure reprinted with permission from Figure 6.2 of Spence and Piqueras-Fiszman (2014).

commentators agree that it is the sense of smell (or olfaction) that actually contributes the majority of the information to our experience (see Spence et al., 2015). In fact, it has been suggested that as much as 80%–90% of the taste of food comes from the nose (e.g., Chartier, 2012; Stuckey, 2012), and we have all experienced food tasting of nothing much when we have a head cold, thus providing anecdotal support for the importance of olfactory input to the enjoyment of food and drink. That olfaction contributes disproportionately more to the experience of flavor seems an easy claim to accept (Murphy et al., 1977). That said, one might question whether it is possible to put a meaningful numerical value on this, given that the relative contribution of each of the senses presumably depends on the particular foodstuff under consideration—just compare your experience of a ripe French brie cheese to that of a water biscuit!

In the west, we describe the aromas of strawberry, caramel, and vanilla as smelling “sweet” (Stevenson and Boakes, 2004). (Those who have tried eating a raw vanilla pod know only too well how bitter it actually tastes.) It turns out that this is more than merely a synaesthetic or metaphorical use of language (Stevenson and Tomiczek, 2007). Olfactory stimuli that have regularly been paired with sweet, bitter, salty, or even sour-tasting foods can, in fact, come to enhance the associated taste quality, even when they are presented at a sub-threshold level. There can be no doubt that such crossmodal interactions make it all the more difficult to try and draw a clear line between experiences of taste and of flavor (see Spence et al., 2015). No wonder then that philosophers, too, are starting to take an interest in some of the thornier problems raised by the study of flavor perception. Stevenson (2009, pp. 3–4) succinctly captures one of the central issues for the philosopher when he notes that, “It is possible to conceive of flavor in several ways; as a multimodal object, a sensory system, a unique sense in and of itself, and a set of discrete senses bound together by centrally mediated processes…Flavor is clearly multimodal, but where does one draw the boundary? After all, visual and auditory stimuli influence flavor perception, so are they part of a flavor sense? One way of navigating around these issues is to regard all of the senses that contribute to flavor, as part of a flavor system (as so far done…), but to retain the term ‘flavor’ for the stimulus experienced in the mouth.”

Some of the most convincing evidence concerning the multisensory integration of orthonasal olfactory and gustatory cues comes from seminal research conducted by Pam Dalton and her colleagues at the Monell Chemical Senses Center in Philadelphia (Dalton et al., 2000). Participants in their studies were given two pairs of bottles to sniff, each containing a clear odorless liquid. An almond-cherry-like scent (i.e., benzaldehyde) had been added to one of the bottles. On each trial, the participants had to try and determine which bottle contained the benzaldehyde. The concentration of the olfactant was varied on a trial-by-trial basis in order to home in on each participant’s detection threshold. Surprisingly, when the participants performed this task while holding a sub-threshold solution of saccharin in their mouths (i.e., a solution that had no discernible taste or smell), the cherry-almond smell was perceived as being significantly more intense relative to a baseline condition in which a tasteless water solution was held in the mouth instead (see Figure 1). By contrast, holding a sub-threshold solution of monosodium glutamate (MSG) on the tongue did not give rise to any such change in the ability of Dalton et al.’s participants to smell the aroma in the bottle. Taken together, such a pattern of results highlights the stimulus-specific integration of tastants and olfactory stimuli (a specificity that turns out to be characteristic of a number of the studies that have been published in this area; see Spence, 2012 for a review).

Similar results have now been reported in several subsequent studies. For instance, Pfeiffer et al. (2005) demonstrated a 50% lowering of the olfactory threshold—that is, complete additivity in the majority of their participants when the relevant gustatory and olfactory stimuli were presented simultaneously. Intriguingly, similar results were observed regardless of whether the odor was delivered orthonasally or retronasally. And moving the experimental situation even closer to everyday life, similar effects have now been reported with participants tasting actual flavored solutions (see Delwiche and Heffelfinger, 2005).

There is also an intriguing cross-cultural angle to this research. Japanese participants tend to show perceptual enhancement in the MSG condition, but not in the saccharin condition (i.e., the opposite pattern to that shown by western participants in Dalton et al., 2000; see Breslin et al. 2001). It turns out that pickled condiments containing the savory almond combination are common in Japanese cuisine, whereas sweet almond desserts (just think of Bakewell Tart) are more commonly experienced in the west. These results therefore suggest that our brains learn to combine tastes and smells that regularly co-occur in our home cuisine. The underlying idea here then is that, while everyone’s brain may use the same rules to combine the inputs from their senses, the particular combinations of tastants and olfactory stimuli (and possibly also visual stimuli) that lead to multisensory enhancement (or suppression, when the taste and smell don’t match; see, e.g., de Araujo et al., 2003) depends on the combination of ingredients and, hence, of sensory cues that tend to co-occur in the cuisine of the region where people have grown up. Such learning apparently starts in utero (see Schaal et al., 2000; see Bremner et al., 2012 for a review). French researchers have, for example, demonstrated that neonates whose mothers consumed anise-flavored food during pregnancy are more likely to orient toward the smell of anise after birth, while elsewhere it has been shown that young children are more likely to eat carrots if their mothers happened to drink carrot-flavored milk during pregnancy.

Visual Contributions to Multisensory Flavor Perception

Moir (1936), a chemist by training, was perhaps the first to report that simply changing the color of food could affect people's perception of taste/flavor. In the years since, more than 150 further studies examining vision's influence over taste and flavor have been published. The majority, but by no means all, of this research has demonstrated that changing the hue and/or intensity of the color added to a food or, more frequently, a beverage can influence the perceived identity and/or intensity of the flavor. While varying the color intensity impacts the rated taste and flavor intensity in some studies, such a crossmodal effect is not always found (see Spence et al., 2010 for a review). The reasons behind such mixed results may well be explained by the different taste/flavor expectations that can sometimes be associated by different people with one and the same food color (see below).

One of the most common observations has been that changing the hue of a drink changes the perceived flavor. Many people will, for example, say that a cherry-flavored drink tastes of lime if colored green while perceiving it to taste of orange if colored orange (see Zampini et al., 2007, 2008). One intriguing but as yet unconfirmed observation in this area comes from Zampini et al. (2008). These researchers found that supertasters were significantly less influenced by inappropriate coloring of a beverage than were medium tasters who, themselves, were less influenced than were the non-tasters (see Figure 2).

In one of the classic studies, Morrot et al. (2001) investigated the effects of color on people's perception of wine aroma. These researchers were able to fool more than 50 students enrolled in a university wine degree course in Bordeaux, France into believing that they were holding a glass of red wine, simply by coloring a white Bordeaux wine artificially red with an odorless food dye! The participants were initially given a glass of white wine and instructed to describe its aroma. Next, they were given a glass of red wine and had to do the same. As one might have expected, the students used completely different terms in order to describe the aromas of the two wines—terms like citrus, lychee, straw, and lemon for the white wine and chocolate, berry, and tobacco to describe the red wine. Finally, the students were given a third glass of wine and had to decide which of the aroma terms that they had chosen previously constituted the best match for the wine. The third glass again looked like red wine but was, in fact, the white wine that the students had been originally given, colored so as to be visually indistinguishable from the red wine. Surprisingly, they mostly choose the red wine odor descriptors, apparently no longer perceiving the aromas that they had previously reported when drinking the untainted white wine. This result therefore powerfully demonstrates vision's dominance over orthonasal olfaction. Further, it is also consistent with other studies showing that "experts" are no less susceptible to such crossmodal effects than are regular consumers.

Similar results have subsequently been reported in New Zealand wine experts (including professional wine tasters and wine makers) who were actually allowed to taste the wine that they had to evaluate (Parr et al., 2003). In particular, the experts' descriptions of the aroma of a barrique-fermented young Chardonnay that had been artificially colored red were more accurate when the wine was served in an opaque glass than when it was served in a glass that was clear. Indeed, wine may well be the single most extensively studied drink when it comes to looking at the impact of color (and expertise) on the crossmodal influence of visual cues on multisensory flavor perception (see Spence, 2010, for a review).

Intriguingly, the crossmodal effects of color on both wine and fruit-flavored soft drinks occur even when participants are explicitly told to try and ignore what they see (Parr et al., 2003; Zampini et al., 2007, 2008). Such results hint at the automaticity of the crossmodal effects of vision (color) on flavor. It would appear that both the hue and intensity of the coloration automatically set expectations in the mind of the observer about the likely identity and intensity of the taste/flavor of food and drink. Remember that we nearly always see what we are going to eat or drink in advance (one of the few exceptions being the dine-in-the-dark restaurant, where, according to most published accounts, the food tastes disappointing; see Spence and Piqueras-Fiszman, 2014), and those expectations will either be confirmed or disconfirmed when a person comes to taste/evaluate the food or drink. Now, if the expected taste/flavor happens not to be too dissimilar from the actual taste/flavor, people will likely report that their experience matches their expectation. By contrast, should the discrepancy between what we expect and what we actually taste be too great, then a disconfirmation of expectation response is likely. One critical question here is how much of a discrepancy between the expectation and the experience is needed in order to trigger a disconfirmation of expectation response (see Shankar et al., 2010 on this topic).

It is important to remember that disconfirmed expectations can occur in both the sensory-discriminative and hedonic domains (Zellner et al., 2004; see Piqueras-Fiszman and Spence, 2015 for a review). In everyday life, such disconfirmation of expectation tends to be negatively evaluated, hence perhaps helping to explain the failure of clear cola drinks in the marketplace a few years back (e.g., see Triplett, 1994). That said, the influence of context cannot be ignored here. Indeed, it is intriguing to note how many people seem to positively relish the opportunity of having their expectations disconfirmed, providing that it occurs within the confines of the modernist restaurant (see Spence and Piqueras-Fiszman, 2014). It probably helps if they are neophilic rather than neophobic when it comes to experimenting with new foods. This pleasure in surprise is something that is difficult to capture (and hence study) in the setting of the laboratory. In fact, it may rely on our believing that we are in capable hands (e.g., of the star modernist chef), so interpreting the disconfirmation as a carefully crafted multisensory flavor experience rather than merely reflecting poor design.

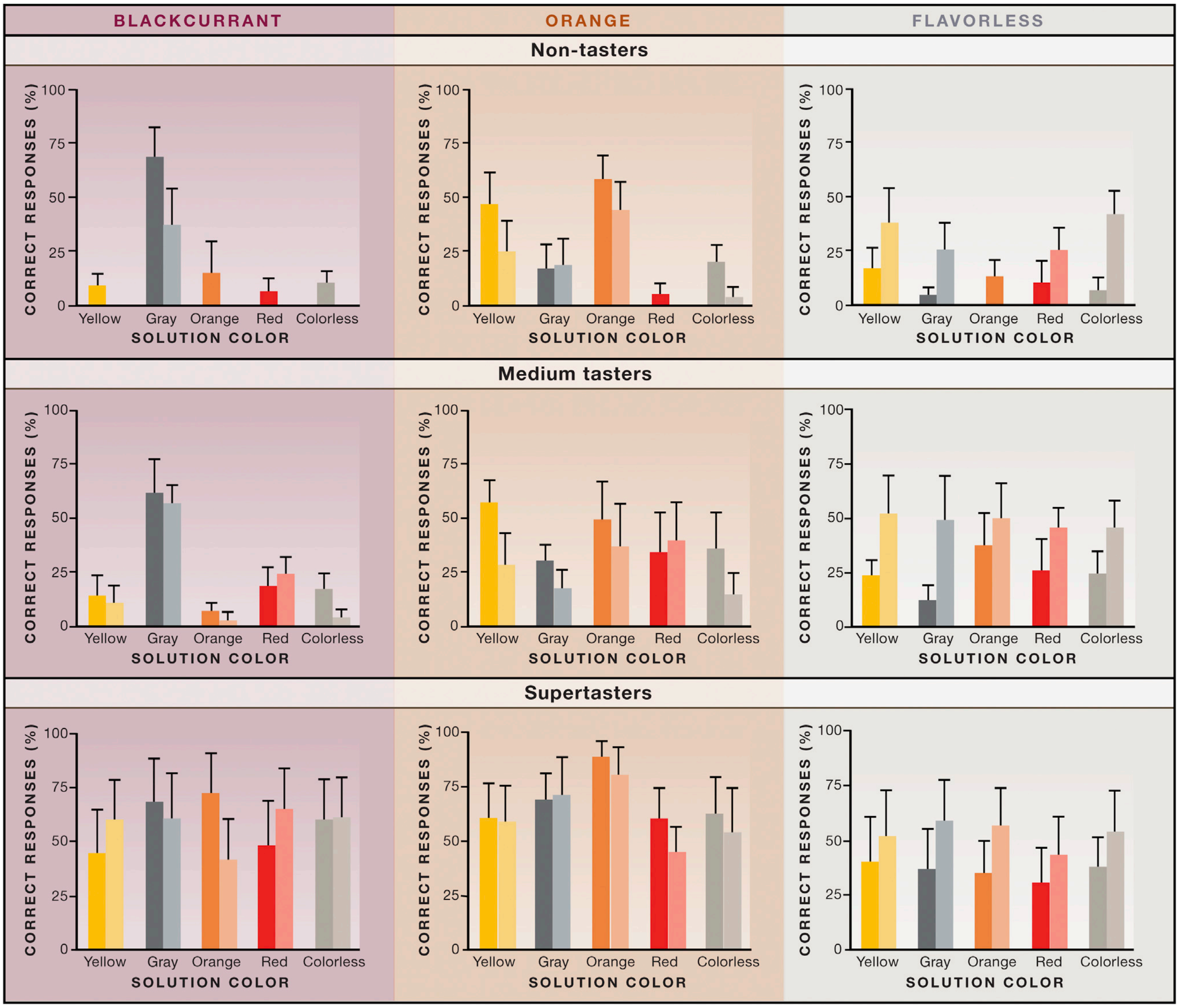

Figure 2. The Influence of Color on Flavor Identification as a Function of Taster Status

Mean percentages of correct flavor identification responses for the three groups of participants (non-tasters, medium tasters, and supertasters) for the blackcurrant, orange, and flavorless solutions presented in Zampini et al.'s study (2008) of the effects of color cues on multisensory flavor perception in humans. The darker columns represent solutions where fruit acids had been added, and the lighter columns represent solutions without fruit acids. The error bars represent the between-participants standard errors of the means. Figure reprinted with permission from Figure 1 of Zampini et al. (2007).

Children seem to enjoy artificially (i.e., brightly) colored and miscolored foods more than their parents (see Bremner et al., 2012). One example is the green-colored ketchup that was successfully launched into the marketplace a little over a decade ago or the miscolored candies, where the challenge for children is to try to ignore the evidence before their eyes and discern the product's actual flavor. At the opposite end of the age spectrum, it has been suggested that the intelligent use of food coloring might help to deliver better-tasting foods for those whose sense of taste and smell has started its inevitable decline. This impairment becomes especially noticeable when people reach their sixth or seventh decade (see Bremner et al., 2012), leading to unhealthy eating behaviors. For example, old people have to add as much as two to three times more salt to a bowl of tomato soup in order to achieve the same taste/flavor as young people (see Stevens et al., 1991). Worryingly, medications that are commonly used in these populations have been shown to increase the need for salt by as much as twelve times. Here one is reminded of the old line from Brillat-Savarin's 19th century classic text, *The Philosopher in the Kitchen*: "The pleasures of the table, belong to all times and all ages, to every country and to every day; they go hand in hand with all our other pleasures, outlast them, and remain to console us for their loss."

One aspect of the influence of color and other visual cues that has not received as much attention from researchers to date concerns the powerful aversive responses that off-colors in

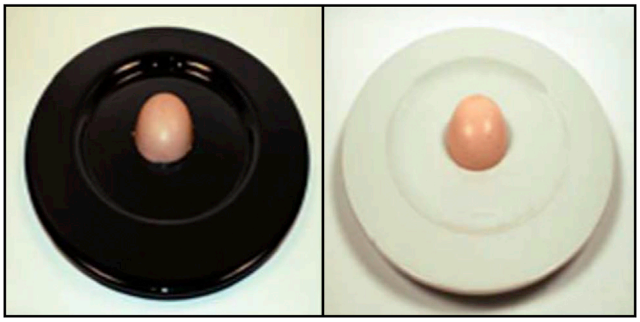

Figure 3. Can You Taste the Plate?
Black and white plates with red frozen strawberry dessert. Participants rated the dessert tasted from the white plate as tasting significantly sweeter and more flavorful than exactly the same food when served from the black plate instead. Figure reprinted with permission from Figure 2 of Piqueras-Fiszman et al. (2012).

foods can induce (see Spence and Piqueras-Fiszman, 2014 for a number of anecdotal examples). Early on, for example, Moir (1936) reported that a number of participants felt ill after his early experimentation on his work colleagues. As one commentator notes, "Moir prepared a buffet of foods for a dinner with scientific colleagues of the Flavor Group of the Society of Chemistry and Industry in London. Many of the foods were inappropriately colored, and during the dinner several individuals complained about the off-flavor of many of the foods served. Several of the individuals reported feeling ill after eating some of the foods, despite the fact that only the color was varied. The rest of the food was perfectly wholesome, with the requisite taste, smell and texture." There may, of course, have been a historical shift in the acceptability of unusual food coloring over the decades. Indeed, the indomitable Fanny Cradock, one of the UK's first celebrity chefs, may have a lot to answer for here as she was particularly fond of presenting foods such as mashed potatoes in a variety of psychedelic colors (though fortunately not all at once) in her television shows back in the 1960s and 70s.

Similarly, back in the 1970s, one mischievous marketer invited a group of friends over to dine on a meal of steak, chips, and peas (it was the 1970s, after all; Wheatley, 1973). The only thing that may have struck any of the guests as strange or unusual was how dim the lighting was. When the lighting was turned back up, imagine the guests' horror as they saw that they were actually eating a blue steak, green chips, and red peas. A number of them apparently started to feel decidedly ill, some heading for the bathroom. In a similar vein, Alfred Hitchcock used to enjoy discomforting his guests by serving entirely blue meals while entertaining at a private dining room at the Trocadero in London (see Spence and Piqueras-Fiszman, 2014, p. 224). The potential commercial relevance of such findings was highlighted by the negative response of people to a batch of brown but otherwise normal-tasting grapefruit juice donated to a food bank in 1981. As yet, it is unclear whether such aversive responses to such putatively off-colors in foods involve the same neural substrates as the other examples of visual dominance that have been described so far in this Perspective.

While the majority of research on visual contributions to flavor perception has focused on studying the impact of uniformly changing the color of a food or beverage item (see Spence et al., 2010 for a review), a growing body of research over the last 5 years has started to investigate how the background color of the plateware, glassware, and/or even the cutlery may influence taste and flavor perception. For example, in research conducted together with the Alicia-ElBulli Foundation in Spain, Piqueras-Fiszman et al. (2012) were able to demonstrate that exactly the same dessert, a frozen strawberry mousse, was rated as tasting 10% sweeter, 15% more flavorful, and significantly better liked when eaten from a white plate rather than a black plate (see Figure 3). Remarkably, follow-up research by Stewart and Goss (2013) has demonstrated even more striking effects of plateware on people's taste perception by varying both the color and shape of the plate on which a food was served. (It turns out that round plates are "sweeter" than more angular plates!)

Similarly, the perceived flavor of a hot chocolate drink has been shown to be influenced by the color of the cup in which it is served (Piqueras-Fiszman and Spence, 2012a). In particular, the chocolate flavor was rated as significantly more intense when the drink was served from an orange plastic cup than when served from a white cup. Indeed, there have been a number of anecdotal reports of customers complaining about the change in the taste of their favorite branded soft drinks, when the color of the beverage can was itself changed (e.g., see http://online.wsj.com/article/SB10001424052970204012004577070521211375302.html for one recent example).

Even the color of the cutlery can exert a small but significant influence on people's perception (or at least their rating) of the taste of yogurt (Harrar and Spence, 2013). While the explanation for results such as these has not yet been fully worked out, part of the answer may relate to color contrast. That is, the apparent color of the food may change subtly as a function of the background color against which it is seen (see Lyman, 1989). Part of the explanation may also relate to the prior associations that we have built up over the years between particular plateware/glassware and the taste and flavor experiences that have normally been associated with them (see also Wan et al., 2014a).

Beyond the color and shape of the plateware, an emerging body of research has started to look at the influence of the more complex arrangement of food on the plate (see Deroy et al., 2014; Spence et al., 2014a, 2014b for reviews). In one recent study, the young Franco-Colombian chef Charles Michel demonstrated that customers rated the same set of ingredients as tasting significantly better (and, what is more, they were willing to pay significantly more for the dish) when served in an arrangement inspired by one of Kandinsky's paintings than when served as a regular tossed salad or with the elements arranged carefully in a side-by-side manner instead (see Figure 4). While the original study was conducted in the laboratory setting, subsequent research has replicated the same finding in a restaurant setting (see Michel et al., 2015; Spence and Piqueras-Fiszman, 2014; see also Zellner et al., 2014).

I believe that, in the years to come, we are going to see a lot more research into how the more complex aspects of visual aesthetics, such as balance, harmony, and orientation, influence our

Figure 4. Salad Three Ways

(A) Three different presentations of exactly the same ingredients served to participants in Michel et al.'s Kandinsky on a plate study (2014a). Plating inspired by Kandinsky's "Painting number 201," hanging (the other way up) in the MoMA in New York (see http://www.moma.org/collection/browse_results.php?object_id=79452).

(B) Same ingredients now served as a regular tossed salad.

(C) The ingredients laid out side by side—an effortful presentation, but not an especially aesthetically pleasing one. No surprises for guessing that those participants served the artistic version of the salad liked it more and were willing to pay significantly more for the food. Figure adapted and reprinted with permission from Figure 1 of Michel et al. (2014a).

judgments of food on the plate (Michel et al., 2015; Zellner et al., 2014). Indeed, as Apicius, the Roman gourmand, is once purported to have said, "The first taste is always with the eyes." Certainly, a growing number of modernist chefs are starting to become interested in scientifically assessing the impact of plating on the appreciation of the food they serve. Conducting research over the Internet is also increasingly starting to allow both chefs and sensory scientists/psychologists to assess the impact of (sometimes subtle) changes in a dish's visual design on people's expectations, which as we have already seen, can play a surprisingly large part in determining responses of the diner to the actual dish (e.g., Michel et al., 2015; see also Wan et al., 2014a).

Indeed, the fact that visual presentation of food turns out to be especially important to our multisensory flavor experiences is consistent with the results of neuroimaging studies that have demonstrated increased activation in diverse brain regions when participants, especially hungry ones, view images of food (see van der Laan et al., 2011 for a review and meta-analysis). There is also an emerging literature looking at the attention-capturing potential of visual food images (e.g., see Harrar et al., 2011; Toepel et al., 2009). Once again, however, while food images turn out to be especially good at capturing our attention visually (we seem, in particular, to be drawn to those foods that have a high fat content), they have not, at least until very recently, been incorporated into the mainstream literature on spatial attention, for example.

Auditory Contributions to Multisensory Flavor Perception

It is almost 60 years since researchers first started thinking about the putative role of audition in the experience of food and drink (see Spence, 2015, for a review). Hearing always comes at the bottom of the list when people—whether they be professional sensory scientists or regular consumers—are asked to rank the relative importance of each of the senses to flavor perception (see Spence, 2015 on this point). Indeed, it was such neglect that led the famous British chef Heston Blumenthal (Blumenthal, 2008) to say of sound that it was "the forgotten flavor sense."

In the intervening years, a large body of sensory science research has been published, demonstrating that auditory cues do indeed play an important role in the multisensory perception of food attributes such as crispy, crackly, crunchy, carbonated, and even creamy (see Spence, 2015). And while a number of these might initially seem to be oral-somatosensory in nature, it turns out that our in-mouth experience can be radically changed by modifying the sounds of mastication. So, for example, in one of the classic studies (which was awarded the 2008 IG Nobel prize for nutrition), Zampini and Spence (2004) demonstrated that people's perception of the crispness and freshness of potato chips (crisps to the readers in the UK) could be systematically modified (by around 15%) by changing the self-generated crisp biting sounds that participants heard when biting into a selection of this not altogether healthy dry snack food (see Figure 5).

Recently, the very same approach has been extended to demonstrate the role of auditory cues in the perception of the crispness of a moist crisp food, namely apples (see Demattè et al., 2014). What is perhaps worth noting here is that the "sonic chip" paradigm came not from the sensory science labs but was, in fact, adapted from a psychophysical test that had been developed originally to measure the parchment skin illusion. In this crossmodal illusion, participants are encouraged to rub their hands together while listening to the rubbing sounds picked up by a microphone and played back in real time over headphones. Simply by changing the sound that people hear, either boosting or cutting certain components of the frequency spectrum, the person's hands switch from feeling dry and patched one moment to moist and clammy the next (Guest et al., 2002; Jousmäki and Hari, 1998). This is an example of how insights from the study of audition, touch, and vision can provide insights and approaches that are useful when it comes to trying to understand the multisensory nature of human flavor perception.

Oral-Somatosensory Contributions to Multisensory Flavor Perception

Assessing the contribution of oral-somatosensory cues to multisensory flavor perception is undeniably hard. As such, we have not as yet learned as much about the undoubtedly important role of this sense in delivering the creamy, oily, velvety crispy, crunchy, etc. attributes of food and drink as we might like

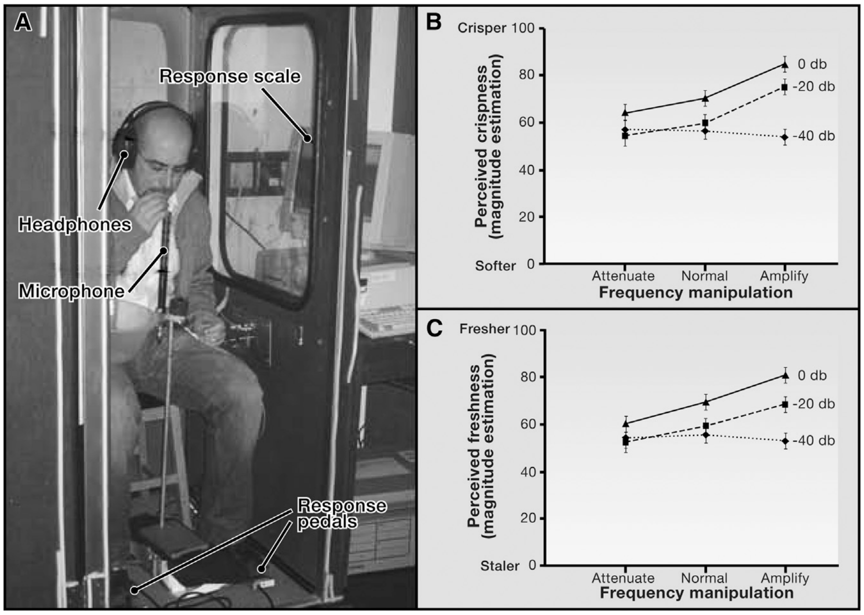

Figure 5. The "Sonic Chip" Experiment
(A) Schematic view of the apparatus and participant in Zampini and Spence (2004) study demonstrating the influence of biting sounds on crispness and freshness perception. The door of the experimental booth was closed during the experiment, and the response scale was viewed through the window in the left-side wall of the booth. Mean responses for the soft-crisp (B), and fresh-stale (C) response scales for the three overall attenuation levels (0 dB, −20 dB, or −40 dB) against the three frequency manipulations (high frequencies attenuated, veridical auditory feedback, or high frequencies amplified) are reported. Error bars represent the between-participants standard errors of the means. Figure reprinted with permission from Figure 1 of Zampini and Spence (2004).

(though see Bult et al., 2007; De Araujo and Rolls, 2004; Eldeghaidy et al., 2011 for some of the best evidence published to date). In one intriguing study, Bult and his colleagues delivered a creamy odor either orthonasally or retronasally (via an olfactometer). At the same time, milk-like substances with different viscosities were delivered to the participant's mouth. The latter was instructed to rate the intensity of the flavor, as well as the creaminess and thickness of the resulting in-mouth experience. Ratings of flavor intensity decreased as the viscosity of the liquid increased. This was true regardless of whether the olfactory stimulus was delivered via the orthonasal or retronasal route. These results highlight the important and complex role that texture (including mouthfeel) can play in the multisensory perception of flavor. Intriguingly, it turns out that retronasally delivered odors can also influence the perceived thickness of substances in the mouth (see also Roudnitzky et al., 2011).

Oral-somatosensory cues may also play an important role in localizing the flavor of food and drink to our mouths (Todrank and Bartoshuk, 1991; though see also Stevenson, 2014). Note that, while little studied to date, attention may play a role here too (see Stevenson, 2012 for a review). Researchers have speculated on the apparent similarities between "oral referral" and the ventriloquism effect that we all experience whenever we mislocalize the sounds of the actors' voices to the lips we see moving on the big screen at the cinema. Once again, given the challenges associated with studying oral referral directly, the hope is that our extensive understanding of the mechanisms of sensory dominance underlying the ventriloquism effect can be helpful to further our understanding of why what we smell retronasally gets mislocalized into the oral cavity, hence giving rise to what we commonly call the taste of food and drink.

One intriguing area of this research relates to the question of whether out-of-the-body illusions (such as "the rubber hand illusion," a kind of visual dominance over touch and proprioception; see the relevant chapters in Bremner et al., 2012; Stein, 2012 for reviews) can be extended to the tongue. Last year, Michel et al. (2014b) elicited the illusion, named the "butcher's tongue," by situating a rubber tongue in a plausible position just in front of the participant's own mouth and stroking one of the two tongues with cotton swabs, leading the participants to feel the touch on their own tongue by seeing the rubber tongue being stroked. The butcher's tongue illusion potentially offers one route to taking flavors out of the mouth in the future. Beyond the feel of the food, even the weight of the cutlery or bowl in the hand have been shown to influence taste perception and expected satiety were the food to be consumed (e.g., Piqueras-Fiszman and Spence, 2012b; Spence and Piqueras-Fiszman, 2014). The feeling of food in the hand has also been shown to modulate the oral perception of texture (see Barnett-Cowan, 2010). It turns out that the tactile feel of a pretzel while held in hand influences the oral perception of the pretzel. The softer the pretzel in the hand, the staler it was perceived in the mouth, thus suggesting something of a contrast effect. Here, one is reminded of the Italian Futurists, such as most famously Filippo Tommaso Marinetti (1876–1944), and their tactile dinner parties. In order to maximally stimulate the sense of touch, diners were encouraged to wear pajamas made of differently textured materials such as cork, sponge, sandpaper, and/or felt and to eat without the aid of knives and forks (see Spence and Piqueras-Fiszman, 2014, p. 291). In summary, touch, no matter whether in the mouth or on the hand, has a far greater influence on perception of taste, quality, and satiety than any of us realize.

Ambient/Atmospheric Cues and Their Influence on Multisensory Flavor Perception

Beyond intrinsic cues of the food and their influence on the multisensory perception of flavor, it is important to note that ambient lighting, background music, and background noise have all been shown to influence taste and flavor perception (e.g., see Oberfeld et al., 2009; Spence, 2014; Spence et al., 2014a, 2014b; Velasco et al., 2013). For instance, in one experiment, almost 3,000 people were given a red wine to taste from a black tasting glass (so that they could not discern the drink's actual color). The wine was liked significantly more, and it was rated as tasting significantly fruitier when the participants found themselves in an environment with red ambient lighting and putatively sweet background music than when the lighting was turned to green and sour music was played instead (see Knöferle et al., 2015 on the development of music to match each of the four basic tastes). A growing body of research now shows that, when asked to match tastes and flavors with a particular pitch of sound or with a specific class of musical instrument, their responses are non-random (see Knöferle & Spence, 2012 for a review). The majority of people will, for example, match sweet-tasting foods with sounds having a higher pitch and the sound of the piano while matching bitter-tasting foods with lower pitched sounds and the sound of a brass instrument.

There is also much research showing that the atmosphere in the restaurant can influence taste/flavor perception, as well as the perceived ethnicity of a dish (see Spence and Piqueras-Fiszman, 2014 for a review). It is an open question though as to whether such crossmodal effects are best conceptualized in terms of sensation transference or some kind of perceptual/semantic priming effect. Nevertheless, whatever the correct explanation, it is no surprise to see that such results are of growing interest to the restaurateurs and food marketers.

Cognitive Influences on Multisensory Flavor Perception

While the majority of this Perspective has focused on the role of multisensory interactions in flavor perception (that has most typically been studied in the laboratory), in the real world, cognitive factors such as branding, labeling, packaging, and pricing also play an important role in determining our sensory-discriminative and hedonic expectations (see Piqueras-Fiszman and Spence, 2015 for a review). Certainly, there is good evidence to suggest that our cognitive expectations regarding taste or flavor can have a profound influence on some of the earliest neural sites where olfactory and gustatory information are first processed (see Grabenhorst et al., 2008; McClure et al., 2004; Plassmann et al., 2008). Even reading the word salt, for example, has been shown to activate many of the same areas as when a salty taste is actually experienced in mouth (see Barrós-Loscertales et al., 2012).

The description of a food plays a particularly important role when the expectations upon seeing a dish (what is sometimes referred to as the "visual flavor") are either ambiguous or different from the actual taste or flavor of the dish. This idea was beautifully demonstrated in a now-classic study by Martin Yeomans and his colleagues (including Heston Blumenthal) at the University of Sussex (Yeomans et al., 2008). In this collaboration, three groups of participants were given a pinkish-red ice-cream to taste. One group was given no information about the dish. A second group was informed that they would be tasting a savory ice-cream. Meanwhile, a third group of participants was told that they would be tasting a novel food called "Food 398." Those participants who hadn't been given any information about the smoked-salmon-flavored food (and who presumably would have been expecting to taste a sweet berry-flavored ice-cream based on the information before their eyes) rated the dish as tasting much saltier than either of the other two groups. What is more, these participants reported liking the dish far less, presumably due to the occurrence of a strong disconfirmation of expectation response.

Results such as these nicely illustrate how the meaning of what consumers see (or, in other words, their expectation concerning a food or drink's likely flavor and how much they would enjoy it) can be radically changed as a function of additional information that they may have been given about the food. Note that such higher-order effects of labeling tend to be especially pronounced when the stimulus itself is in some sense ambiguous. Indeed, several studies have now shown that ambiguous odors such as, for example, isovaleric acid, will light up different parts of the brain (specifically the orbitofrontal cortex) as a function of whether the smell has been described to the participant as a ripe cheese or as the distinctive smell of sweaty socks.

Perhaps understandably, given such results, some of those working a little closer to the marketing end of food research have criticized much of the laboratory research that has been published to date for focusing so much on the purely perceptual interactions taking place in flavor perception. The suggestion is that such research is in danger of underplaying the role of all the other higher-level cognitive factors that typically influence (or constrain) our expectations and hence our experience of food consumption.

Crossmodal Correspondences and Flavor Perception

One growing area of interest in the study of multisensory flavor perception comes from work on crossmodal correspondences. The latest research shows that people tend to associate tastes, food aromas, and flavors with other unrelated sensory cues in ways that are surprisingly consistent. For example, as we saw earlier, people tend to match sweet tastes with high-pitched sounds and the sound of the piano, while matching bitter tastes with low-pitched brassy sounds instead (see Knöferle and Spence, 2012 for a review). However, people also reliably match sweetness with roundness and redness. The other tastes (bitter, salty, sour, and umami) are also typically matched with particular colors and, if anything, with shapes that are more angular (see Velasco et al., 2015). A growing body of research is now coming to document the range of crossmodal correspondences in the world of taste, aroma, and flavor. While the origin of many of these correspondences is still being debated, it is exciting to see a growing number of young chefs who are starting to incorporate these findings in the design of their dishes (e.g., see Figure 6).

Neural Circuits underlying Multisensory Flavor Perception

The last few years have seen a rapid growth in our understanding of the neural networks that underlie multisensory flavor perception (see Shepherd 2012; Small, 2012 for reviews). Gustatory stimuli project from the tongue to the primary taste cortex (more specifically, the anterior insula and the frontal or parietal operculum), whereas olfactory stimuli project directly to the primary olfactory (i.e., piriform) cortex. From there, the inputs from both senses project to the orbitofrontal cortex (OFC). Gustatory stimuli are thought to project to caudolateral OFC, whereas

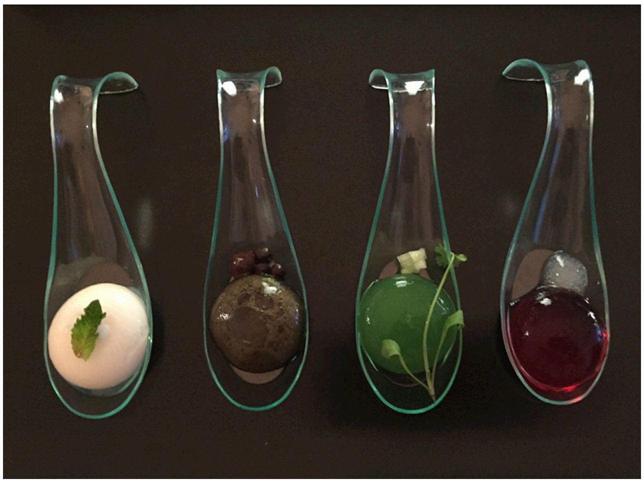

Figure 6. Salty, Bitter, Sour, and Sweet

The four amuse bouche served at Synaesthesia by *Kitchen Theory* (see https://kitchen-theory.com/). The spoons are brought to the table in a random arrangement, and it is the diner's job to sort the tastes by color. The spoons in the figure are shown in the intended order. This dish was inspired by the latest cross-cultural research demonstrating the robust crossmodal correspondences that exist between color and taste (see Wan et al., 2014b). Picture adapted and reprinted with permission from Eva-Luise Schwarz/FOUR magazine.

olfactory stimuli project to caudomedial OFC. The OFC plays a central role in representing the pleasantness (and reward value) of a food or drink (Small, 2012). The participants in one influential neuroimaging study of multisensory flavor perception had to lie still in a scanner while rating the pleasantness and congruency of various different pairings of orthonasal olfactory and gustatory stimuli (de Araujo et al., 2003). The olfactory stimuli consisted of methianol (which smells like chicken broth) and strawberry odor. The tastants were delivered in a solution and consisted of sucrose and MSG. The participants received both congruent (e.g., strawberry odor and sucrose) and incongruent (e.g., chicken broth odor and sucrose) combinations of orthonasal olfactory and gustatory stimuli. Increased OFC activity was correlated with increased ratings of the pleasantness and congruency of the olfactory-gustatory stimulus pairing that the participants were evaluating. Thus, it would appear as though the presentation of familiar (or congruent) combinations of olfactory (both orthonasal and retronasal) and gustatory stimuli can lead to enhanced neural responses in parts of the brain that code for the hedonic (i.e., pleasantness) and reward value of food. Similar results have also been reported following the presentation of congruent combinations of visual and olfactory stimuli as well—think only of the smell of strawberries and the color red (Österbauer et al., 2005).

Dana Small and her colleagues presented familiar/unfamiliar combinations of retronasal olfactory and gustatory stimuli to participants (Small et al. 2004). Superadditive neural interactions (see Stein, 2012) were observed in the OFC for familiar (or congruent, sweet-vanilla), but not for unfamiliar (or incongruent) combinations of stimuli (such as for the salty-vanilla stimulus combination). Several other areas—including the dorsal insula, the frontal operculum, and the anterior cingulate cortex—also lit up, thus constituting what could perhaps be thought of as a "flavor network" (e.g., Shepherd 2012; Small 2012).

Conclusions

As this Perspective has hopefully made clear, there has been a rapid and long overdue growth of interest in the study of multisensory flavor perception in recent years. While those researchers interested in the topic have long recognized the key role played by gustatory, olfactory, and to a lesser extent trigeminal inputs, the last decade or so has seen an explosion of new research demonstrating the impact of visual, auditory, and oral-somatosensory cues in modulating our experience of food and drink. Part of the excitement undoubtedly stems from the growing realization that many of the same neural principles known to constrain the integration of the spatial senses of vision, audition, and touch (see Bremner et al., 2012; Calvert et al., 2004; Stein, 2012 for reviews) might also help to explain the integration of sensory cues giving rise to the multisensory flavor perception.

When thinking about multisensory flavor perception, it is important to distinguish between flavor expectations and flavor experiences (Stevenson, 2009). Under the majority of everyday conditions, the former have a profound influence on the latter. However, one of the questions without a clear answer is whether the same processes of multisensory integration are involved in both cases (acknowledging, of course, the differing combination of senses involved; Stevenson, 2009). Indeed, there is intriguing preliminary evidence, at both the behavioral and neural levels, to suggest that there may be some important differences (e.g., Koza et al., 2005; Small et al., 2005, 2008; Zampini and Spence, 2005).

It would seem likely that in the years to come there will be growing interest in the developmental study of multisensory flavor perception (across the whole lifespan; see Bremner et al., 2012) in the role of culture and prior experience in determining which combinations of flavor cues (e.g., gustatory, olfactory, and visual stimuli) give rise to multisensory integration (Blumenthal, 2008; Breslin et al., 2001; Wan et al., 2014b). Studying the role of individual and genetic differences (e.g., in taster status) and their role in modulating multisensory flavor perception will likely also become increasingly popular (Bartoshuk, 2000; Eldeghaidy et al., 2011; Zampini et al., 2008). Our growing understanding in this area will likely also be aided by a better understanding of the neural circuits involved in flavor perception (see Shepherd, 2012; Small, 2012 for reviews) and the as-yet understudied role of attention in processing and, more importantly, binding of flavor cues (see Stevenson, 2012).

Let me end by highlighting the growing optimism that some of the latest insights (e.g., increasing perceived sweetness by changing the color of food or by changing the color of the plateware on which it is served) can be utilized to help nudge consumers toward healthier food behaviors (Spence and Piqueras-Fiszman, 2014; see also Marteau et al., 2012). Given the commercial opportunities associated with a better cognitive neuroscience understanding of the multisensory nature of flavor perception and the crucial individual, developmental, and cultural differences therein, it should come as little surprise that many of the world's largest food/flavor companies (think Nestlé, Unilever, and P&G on the one hand and Givaudan, Firmenich, and IFF on the other) have been investing heavily (not to mention publishing more than occasionally) in this area. That said, longer-term follow-up studies are still needed to really know how long-lasting some of these crossmodal effects are likely to be (cf., De Graaf et al., 1997), keeping in mind the fact that any multisensory interactions in flavor perception need to be considered within the wider context of branding, labeling, packaging, pricing, and other more cognitive factors that both constrain and influence our everyday experience of food and drink.

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