Multisensory Flavor Perception

Charles Spence[1],*
[1]Crossmodal Research Laboratory, Department of Experimental Psychology, University of Oxford, Oxford OX1 3UD, UK
*Correspondence: charles.spence@psy.ox.ac.uk

http://dx.doi.org/10.1016/j.cell.2015.03.007

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

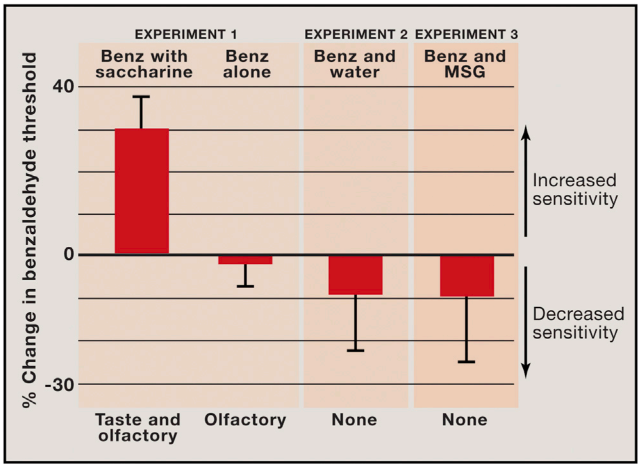

Figure 1. Multisensory Interactions between Olfaction and Gustation in Multisensory Flavor Perception

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