

Review

# The multisensory perception of flavor

Malika Auvray <sup>\*</sup>, Charles Spence

*Department of Experimental Psychology, Oxford University, South Parks Road, Oxford OX1 3UD, UK*

Received 2 February 2007

Available online 3 August 2007

---

## Abstract

Following on from ecological theories of perception, such as the one proposed by [Gibson, J. J. (1966). *The senses considered as perceptual systems*. Boston: Houghton Mifflin] this paper reviews the literature on the multisensory interactions underlying the perception of flavor in order to determine the extent to which it is really appropriate to consider flavor perception as a distinct perceptual system. We propose that the multisensory perception of flavor may be indicative of the fact that the taxonomy currently used to define our senses is simply not appropriate. According to the view outlined here, the act of eating allows the different qualities of foodstuffs to be combined into unified percepts; and flavor can be used as a term to describe the combination of tastes, smells, trigeminal, and tactile sensations as well as the visual and auditory cues, that we perceive when tasting food.

© 2007 Elsevier Inc. All rights reserved.

*Keywords:* Multisensory perception; Flavor; Taste; Smell; Trigeminal system; Ecological theory; Synesthesia

---

## 1. Introduction

One important reason for the rapid growth of research interest on the topic of flavor perception in recent years (e.g., see [Verhagen, 2007](#); [Verhagen & Engelen, 2006](#), for a recent review) stems from the light that gaining a better understanding of how the multisensory integration taking place in the context of food perception might shed on theories of multisensory integration in general (e.g., [Simons & Noble, 2003](#)). On the other hand, it is also widely believed that the study of the multisensory processes involved in flavor perception will have a number of important consequences for the food and beverage industries, such as, for example, a better understanding of the processes used by people to assess the acceptability and flavor of new products (e.g., [Blake, 2004](#); [Gilbert & Firestein, 2002](#); [Shepherd, 2006](#); [Stillman, 2002](#)).

One robust finding to have emerged from recent psychophysical research on flavor perception is that odors can elicit changes in the perceived sweetness (i.e., taste) of foodstuffs (e.g., [Stevenson, Prescott, & Boakes, 1999](#)). Such results have led [Stevenson and Boakes \(2004\)](#); see also [Stevenson and Tomiczek, 2007](#)) to suggest that odors can induce a synesthetic experience of taste that is common to all. Alternatively, however, it has

---

<sup>\*</sup> Corresponding author. Fax: +44 1865 310447.

E-mail address: [malika@malika-auvray.com](mailto:malika@malika-auvray.com) (M. Auvray).

also been argued that such ubiquitous interactions between smells and tastes may instead reflect the existence of an additional (i.e., separate) flavor sense (e.g., Abdi, 2002; McBurney, 1986; Prescott, 1999). Here, we review the published literature on multisensory interactions between taste, smell, and the trigeminal system in order to argue that flavor perception, rather than reflecting a kind of synesthetic experience between the senses of taste and smell, should be used as the term for the combinations of taste, smell, the trigeminal system, touch, and so on, that we perceive when tasting food. More precisely, following on from ecological theories of perception, such as the one proposed by Gibson (1966), flavor will hereby be defined as a perceptual modality. That is, we will argue that the unification of sensory impressions enabled by the act of eating does not occur at the level of sensation, but rather at the level of perception.

## 2. Smell–taste interactions

### 2.1. Examples of perceptual interactions between different components of flavor

One everyday example that highlights a widespread confusion between the senses of taste and smell is the fact that people commonly report losing their sense of taste when their nose is blocked. Similar effects can be experienced simply by pinching one's nose and trying to guess what someone else has given us to eat (e.g., apple or onion; e.g., see Tichener, 1909; see also Ross, 2001, pp. 501–502). Indeed, it has been reported that most of what people commonly think of as the taste of foodstuffs actually originates from the nose (i.e., from the sense of smell; e.g., Rozin, 1982). Conversely, however, the attribution of taste qualities to odors highlights the rich nature of the interactions taking place between the senses of smell and taste (e.g., Laing, Link, Jinks, & Hutchinson, 2002): When participants are asked to evaluate the perceptual qualities of a set of odors, they typically use terms that derive originally from the gustatory sensory system, such as “sweet” and “sour”, even though the olfactory system does not itself contain receptors sensitive to such tastants (e.g., Burdach, Kroeze, & Koster, 1984; Harper, Land, Griffiths, & Bate-Smith, 1968; Voirol & Daget, 1986). For example, the odor of vanilla is consistently reported (at least by western participants) as smelling sweet, although sweetness is normally associated with the stimulation of another sense, that of taste (e.g., Stevenson & Boakes, 2004).

A second example of the confusion that can occur between the different components of flavor is provided by the taste–temperature illusion. That is, for a proportion of the population, putting an ice cube (which has no taste) on the side of their tongue will give rise to a clearly perceptible salty taste sensation (see Cruz & Green, 2000). In this case, delivering a sensation via one sensory modality (touch or temperature) gives rise to an additional sensation in a different sensory modality (taste). A nice example of the confusion between taste and smell sensations comes from the elegant research conducted by Andy Taylor and his colleagues (e.g., Davidson, Linfoth, Hollowood, & Taylor, 1999). In Davidson et al.'s experiments, participants had to continuously rate the perceived intensity of flavor in their mouths while chewing a piece of mint-flavored gum. The taste of the mint-flavored gum comes from the sugar contained in it, while the menthol gives rise to the olfactory and trigeminal components. The perceived/actual intensity of the menthol odor was shown to increase very rapidly when people initially started to chew the gum. Then, while the actual intensity of the menthol odor stayed fairly constant over the course of 4–5 min of chewing, its perceived intensity declined rapidly (tracking the decline in the sugar taste in the mouth), and could only be brought back up again by the release of additional sugar (i.e., by the addition of a tastant which has no smell). Davidson et al.'s results therefore show that people's perception of the intensity of the menthol flavor was actually being driven by the release of sugar in their mouths (and detected on their tongues).

A series of experiments showing the interactions between the senses of smell and taste are based on the detection threshold of odor and taste compounds. Dalton, Doolittle, Nagata, and Breslin (2002) found that for certain combinations of stimuli, a subthreshold concentration of an odor compound is more easily detected when presented orthonasally in conjunction with a subthreshold concentration of a taste compound than when it is presented alone. It should be noted that the study controlled for any physicochemical interactions by using a benzaldehyde/saccharin system. Since saccharin is not volatile and has a high sweetness intensity, the amounts used would have had no effect on the detection of benzaldehyde (almond odor). Delwiche and Heffelfinger (2005) also reported a facilitation of the detection of taste–odor pairs at subthreshold concentrations when presented in combination than when the stimuli were presented separately. Furthermore, they

showed that taste and smell could combine in a completely additive fashion (i.e., they obtained a threshold detectability when both stimuli were presented simultaneously at 50% of the threshold levels of the same stimuli presented alone) when the taste–odor pairs were presented orally. It should be noted that contrary to the results reported by Dalton et al., Delwiche and Hefelfinger found this facilitation for both commonly paired and less commonly paired combinations of taste and odor.

## 2.2. *The phenomenon of sweetness enhancement*

Another set of experiments on sweetness enhancement has provided strong support for the ability of odors to modify taste qualities. When ‘sweet’ odors, which in themselves possess no taste (they cannot be detected by the taste receptors) are added as flavorings to solutions that participants have to taste, they tend to increase the perceived sweetness of those solutions (Cliff & Noble, 1990; Frank & Byram, 1988; Frank, Shaffer, & Smith, 1991; Schifferstein & Verlegh, 1996). For example, when caramel odor is added to a sucrose solution, the taste of the resulting mixture is perceived as being sweeter than the pure sucrose solution when presented by itself; and conversely, adding a caramel odor has also been shown to suppress the sourness of solutions containing citric acid (see Stevenson et al., 1999). The reverse phenomenon, sweetness suppression, has also been documented. For example, certain odors, such as angelica oil, have been reported to reduce the perceived sweetness of a sucrose solution to which they have been added as a flavoring (Stevenson et al., 1999).

The odors that typically induce sweet tastes appear to be related to previous instances of co-exposure with a sweet taste, such as might naturally occur during eating (e.g., Prescott, 2004; Stevenson, Prescott, & Boakes, 1995; Stevenson, Boakes, & Prescott, 1998). For example, the odors of vanilla, caramel, strawberry, and mint induce sweetness enhancement in western countries where people often experience those odors with sucrose. On the other hand, non-western participants do not describe some of these odors as sweet, probably due to a less frequent pairing of these odors with sweetness in their food culture (Nguyen, Valentin, Ly, Chrea, & Sauvageot, 2002). The modifications of the attribution of taste qualities to odors can also be obtained in laboratory settings thanks to the repeated pairing of novel odors with a particular tastant. For example, novel odors (such as lychee or water chestnut) repeatedly paired with sucrose are later reported to be sweeter than their initial ratings (Stevenson et al., 1995, 1998; Yeomans & Mobini, 2006; Yeomans, Mobini, Elliman, Walker, & Stevenson, 2006). Similarly, novel odors are subsequently reported to be sourer than their initial ratings if they are repeatedly paired with citric acid (Stevenson, Boakes, & Wilson, 2000a, 2000b), or more bitter, if paired with bitter tastes such as sucrose octa-acetate (Yeomans & Mobini, 2006).

It should be noted that such sweetness enhancement and suppression effects cannot be accounted for simply in terms of chemical interactions between the odors and tastes present in the solution, because the effect can be abolished simply by pinching the participants’ nose (e.g., Schifferstein & Verlegh, 1996). Furthermore, the same odors are typically reported as being tasteless when they are experienced alone in solution (see Prescott, 2004). Sweetness enhancement cannot be accounted for by the stimulation of the taste receptors by the added odor either because the effect also occurs when the odor stimuli are presented orthonasally that is, direct to the nasal cavity (e.g., Sakai, Kobayakawa, Gotow, Saito, & Imada, 2001). Furthermore, Pfeiffer, Hort, Hollo-wood, and Taylor (2006) found that while the sucrose and acid tastants presented in the solution played a critical role in the perception of the intensity of strawberry flavor, the release of the volatiles most characteristic of strawberry flavor were shown to be unaffected by the presence of sucrose and/or acid. In addition, the fact that the same unfamiliar odor can induce different taste qualities (i.e., sweet or sour) as a function of its repeated pairing with a specific tastant shows that the modification of taste qualities by odors is not due to a particular feature of the odor but is a consequence of learning instead (Stevenson & Tomiczek, 2007).

One also needs to question the extent to which the attribution of taste qualities to odors reflects a change in their hedonic valence, based on the idea that sweetness is related to those food qualities that we like (e.g., Zellner, Rozin, Aron, & Kulish, 1983). However, Stevenson et al. (1998) have attempted to rule out this potential account of the data by showing that an increase in the smelled sweetness or sourness of novel odors does not necessarily change participants’ liking ratings for those odors. Similarly, Yeomans and his colleagues (Yeomans & Mobini, 2006; Yeomans et al., 2006) have shown that changes in the perceived sweetness of odors do not reflect changes in the liking of those odors. According to Prescott (2004, see also Stevenson and Tom-

iczek, 2007), these results therefore argue against the interpretation of sweetness enhancement as simply reflecting participants' use of sweetness as a metaphor for liking.

### 2.3. *Can flavor perception be considered as a form of synesthetic experience?*

The perception of tastes induced by odors has been described by [Stevenson and Boakes \(2004\)](#) as an example of synesthetic experience that is common to all (i.e., to synesthetic and non-synesthetic individuals alike).<sup>1</sup> The question arises as to whether flavor perception in itself can also be considered as a form of synesthetic experience. We believe, however, that two main arguments question the appropriateness of considering flavor perception as a ubiquitous example of synesthetic experience between the senses of smell and taste. First, synesthesia has been explicitly defined by certain researchers as a conscious experience of systematically induced sensory attributes that are not experienced by most people under comparable conditions (e.g., [Grossenbacher & Lovelace, 2001](#)). According to such a definition, it simply cannot be the case that flavor perception represents a synesthetic experience, since it is experienced by everyone. Of course, one might argue that synesthesia does not necessarily need to be defined in this way (i.e., in terms of its limited occurrence in the populace). For example, elsewhere, synesthesia has been defined less restrictively as simply a condition in which the stimulation of one sensory modality gives rise to a perceptual experience in another sensory modality (e.g., see [Cytowic, 1989](#); [Robertson & Sagiv, 2005](#)).<sup>2</sup> It is, however, important to note that, although the phenomenon of sweetness enhancement can to some extent be seen as a form of learned synesthesia between the senses of smell and taste (we will address this phenomenon in more detail below), not all of the smell–taste interactions fulfill this criterion for qualifying as synesthetic. Indeed, in most of the situations, the stimulation of one of these two sensory modalities does not give rise to an additional (i.e., distinct) perceptual experience in the other sensory modality; rather, what is obtained instead is the replacement of one sensory experience by another. For example, participants in the experiment by [Davidson and colleagues \(1999\)](#) described above should not be considered as having a synesthetic experience because what they perceived was not the original sensory impression (that of sweetness) plus the individuated sensory impression of menthol odor, but instead one sensory impression replaced the other (i.e., the sensory impression of sweetness was replaced by the sensory impression of the menthol odor). As explained in more detail below, we do not believe that the multisensory perception of flavor necessarily represents a synesthetic experience. Rather, we think that it may simply reflect the unification of the qualities of taste and smell into a single percept unified by the act of eating.

### 2.4. *The synthetic versus analytic perception of flavor*

In order to account for the numerous interactions between the senses of taste and smell, [McBurney \(1986\)](#) proposed that a distinction ought to be drawn between two types of flavor perception, namely synthetic and analytic. Analytic perception occurs when two stimuli mixed in a solution keep their individual qualities of sensation. By contrast, synthetic perception occurs when two stimuli that have been mixed in a solution lose their individual qualities in order to form a new (third) sensation. Our perception of color provides one everyday example of synthetic perception. For example, the mix of two colored pigments: red and yellow gives rise

<sup>1</sup> This claim is of importance in the context of synesthesia research, given its low prevalence: For example, the most common form of synesthesia, the perception of words, numbers, or letters as having specific colors has been estimated to affect around 1 in every 2000 people (e.g., [Baron-Cohen, Burt, Smith-Laittan, Harrison, & Bolton, 1996](#)). As a consequence, if flavor perception really does constitute a form of synesthetic experience then it would provide an excellent model system for the study of synesthesia, as every one of us experiences flavor (and hence represents a potential participant). Furthermore, the multisensory integration taking place in the perception of flavor may provide a model for theories of multisensory integration in general. However, it should be noted that there are also some important differences in the processes of multisensory integration depending on the particular pairings of sensory modalities concerned. For example, it has been argued that spatial and temporal coincidence is central to audio–visual integration (e.g., [Spence, 2007](#); [Stein & Meredith, 1993](#)); whereas learned associations between different sensory attributes seem to be much more important for the multisensory integration that gives rise to flavor perception ([Spence, 2002](#)).

<sup>2</sup> It should be noted that the definition of synesthesia ought to be extended to include intramodal associations, such as when the visual perception of a particular number gives rise to a synesthetic experience of a specific color (e.g., [Ramachandran & Hubbard, 2001](#); [Wollen & Ruggiero, 1983](#)).

to a third color: orange (note that under such conditions of color mixing, we are no longer aware of the constituent colors). On the other hand, the auditory perception of location provides an example of analytic perception. While attending to multiple simultaneously-presented sounds, when listening to an orchestra for example, one can still determine the location of the various different instruments (cf. Kubovy & Van Valkenburg, 2001). McBurney suggested that a third category may apply to the case of flavor perception, one that he termed ‘fusion’ (see also Andersen, Tiippana, & Sams, 2004, for a discussion of the appropriateness of this term for describing the multisensory percepts obtained following the presentation of spatially and temporally coincident auditory and visual information). According to McBurney, the different smell and taste components of a flavor are not combined synthetically to form a new sensation (where the smell and taste components would lose their individual qualities of sensation), but rather they are combined in order to form a single percept. This explains why the components of a flavor are perceived as a whole but still remain analyzable when people specifically attend to each component.

### 2.5. Does sweetness enhancement depend on the analytic versus synthetic strategy adopted?

A direct implication of McBurney’s (1986) definition of flavor is that different task requirements may lead to different perceptual approaches by participants. According to Prescott (2004), a task that requires participants to treat the elements of a flavor as a synthetic whole is likely to encourage the blurring of the perceptual boundaries between smell and taste, and thereby to produce more pronounced odor–taste interactions (cf. Sinnott, Spence, & Soto-Faraco, submitted for publication, for similar claims regarding the effects of changing the task requirements on audio–visual multisensory interactions). On the other hand, tasks that encourage the adoption of an analytical perceptual strategy by participants, by emphasizing the distinctiveness of the different components of an odor–taste solution, will tend to decrease the extent of any odor–taste interactions that are observed.

In order to understand the effect of the strategies adopted by participants on sweetness enhancement, two situations have to be distinguished: The effect of the strategies adopted during the conditioning phase and the effect of those strategies adopted during the rating phase. With regard to the conditioning phase, the manipulation of participants’ perceptual strategies in order to investigate the extent of any odor–taste interactions has given rise to somewhat contradictory results in the literature. For instance, Stevenson and Case (2003) reported no effect on sweetness enhancement as a function of whether the participants in their study were trained to distinguish the individual odor and taste components of flavor or not. Thus, the analytic versus synthetic strategy adopted during learning had no impact on acquiring odor–taste associations. In addition, Stevenson and colleagues’ studies have also demonstrated that sweetness enhancement is not modulated by whether or not participants are explicitly aware of the particular pairings of odors and tastes being tested during the experiment (Stevenson et al., 1998, 1995). On the other hand, Bingham, Birch, de Graaf, Behan, and Perring (1990) reported a reduced sweetness enhancement effect in their study when participants were trained to concentrate only on taste. Their participants had to taste sucrose solutions mixed with maltol. Untrained participants found the sucrose–maltol solutions sweeter than odorless solutions containing an equivalent concentration of sucrose. However, this effect disappeared when trained participants were tested.

During the rating phase, the phenomenon of sweetness enhancement seems to be crucially dependent on the particular strategies used by the participants when responding in such experiments. For example, Frank, van der Klaauw, and Schifferstein (1993) have shown that the sweetness enhancement of a sucrose solution that can be elicited by adding strawberry odor only occurs when the participants are asked to rate sweetness (and nothing else); however, when they are also asked to judge other qualities, such as sweetness, saltiness, sourness, and bitterness, the sweetness enhancement effect disappears. Similar findings have also been reported by Clark and Lawless (1994). These authors observed significantly less sweetness enhancement in their study when their participants were asked to rate, in addition to sweetness, the strength of the vanilla-flavor in a solution of sucrose and vanilla, and the strength of strawberry-flavor in a solution of sucrose and strawberry, than when they were asked to rate only the sweetness of the solutions. van der Klaauw and Frank (1996) subsequently argued that when participants are required to individually evaluate the different components of a flavor, the phenomenon of sweetness enhancement may well disappear. Prescott and his colleagues (Prescott, 2001; Prescott, Johnstone, & Francis, 2004) have also shown that the extent to which an odor will enhance

the perceived sweetness of a solution depends on the particular strategies used by participants during their exposure to the odor–taste mixtures. The participants in Prescott et al.'s study made sweetness intensity ratings of an odor–taste combination that promoted either synthesis (by requiring them to attend only to the overall flavor intensity) or analysis of the individual elements in the mixtures (by requiring the participants to rate the taste and odor components of a mixture separately). The results of their study revealed that only the adoption of a synthetic strategy resulted in a significant sweetness enhancement effect. Overall these studies seem to indicate that, participants will be more likely to respond to an odor–taste mixture synthetically if only one rating scale is provided, whereas they will be more likely to respond to the same odor–taste mixture analytically when multiple ratings scales are provided, in this latter case, the phenomenon of sweetness enhancement diminishes or simply disappears in some cases (e.g., Frank et al., 1993).

It has been proposed that the dependence of sweetness enhancement on the number and type of rating scales provided to participants may reflect a form of ‘halo-dumping’ effect (Clark & Lawless, 1994; Lawless, 1996; Lawless & Schlegel, 1984). ‘Halo-dumping’ can occur whenever the appropriate response alternative for a salient attribute is unavailable to participants. This can lead participants to ‘dump’ the values for a salient attribute that is not available in the range of alternative response scales provided (e.g., the strength of a fruity odor) onto one of the other rating attributes that have been provided (e.g., the sweetness of the fruity odor). When multiple ‘appropriate’ scales are provided, there is no longer any need to ‘dump’ the values for one salient property of the mixture onto the scale used to rate another property, since the participants are able to rate all of the qualities that they experience properly; and hence, sweetness enhancement is less likely to occur (see Clark & Lawless, 1994; Kappes, Schmidt, & Lee, 2006).

Overall, these results are indicative of the way in which flavor perception is constructed as a function of the particular strategy that is adopted by participants during their exposure to odor–taste mixtures. In other words, different rating requirements lead to different perceptual approaches which, in turn, influence the degree of perceptual interaction that subsequently occurs. Crucially, the variations in the sweetness enhancement effect seen as a function of the different strategies adopted by participants are of importance should we want to interpret how odors and tastes are integrated into a unified percept. On the one hand, the fact that Stevenson and Case (2003) did not find any effect of prior training on sweetness enhancement led them to suggest that odor–taste integration is ‘cognitively impenetrable’ (cf. Radeau, 1994). This view is similar to the suggestion made by Stevenson and Boakes (2004) of a learned synesthesia between the senses of taste and smell. On the other hand, the results of Bingham et al.'s (1990) study, as well as those obtained by Prescott et al. (2004), suggest instead that the adoption of an analytic versus synthetic approach to the perception of flavor strongly influences the extent to which odor–taste integration is observed. In particular, encouraging the participants to adopt a strategy of analyzing the individual elements in the mixtures resulted in a decrease in sweetness enhancement.

## 2.6. *The difficulty of analyzing the different components of flavor*

As was just stressed in the previous section, there are two sides to the question of whether sweetness enhancement reflects a genuine perceptual phenomenon or whether instead it simply reflects the consequences of the particular strategies adopted by the participants. On the one hand, the effect of the rating scales provided on sweetness enhancement seems to suggest that an aspect of this phenomenon is due to a response bias induced by the particular instructions given to the participants. On the other hand, the pre-post changes in the ratings of the sweetness of an odor might be taken to reflect a genuine perceptual process. The existence of such a process involved in the perception of flavor can be enlightened by the participants’ difficulties in discriminating the taste and smell components of a mixture.

Ashkenazi and Marks (2004) investigated participants’ abilities to detect the gustatory and olfactory components of a solution in a two-alternative forced-choice task procedure. Their results revealed that directing attention to a gustation-based flavorant (sucrose) improves its discriminability (both when the alternative was water and when it was vanillin). On the other hand, attention to an olfaction-based component (vanillin) does not improve the detectability of this odor (no matter whether the alternative was water, sucrose, or citric acid). Ashkenazi and Marks suggested that the greater difficulty of attending to the olfactory component than to the gustatory component of a mixture might be due to the fact that attention to flavor is spatially directed toward

the tongue where gustatory, but not olfactory, receptors are located. Marshall, Laing, Jinks, and Hutchinson (2006) also reported an impaired ability to detect the components of a flavor–taste mixture with participants exhibiting a greater difficulty in detecting the olfactory component than the gustatory component of the mixture. The participants in their study were trained to identify three odors and three tastes and were then asked to identify their occurrence in solutions containing one to six of these components. Although the participants were able to identify the odor and taste components of most binary mixtures, they encountered difficulties with more complex mixtures with only two components being identified in the four-, five-, and six-component mixtures. In general, the taste components were more easily identified than the smell components: Taste components were the only stimuli identified in the mixtures composed of five and six components.

Several factors have been proposed in order to account for the difficulty of identifying the different components of odor–taste mixtures. The first possible factor affecting identification may relate to the limited capacity of working memory. It is, according to Marshall et al. (2006), the most likely factor affecting the participants' performance in their study, given that smell and taste components were usually identified with binary mixtures but performance decreased with more complex mixtures. The dominance of taste over smell can be accounted for both by the fact that attention to flavor is directed spatially toward the tongue (Ashkenazi & Marks, 2004) and by the difficulty that is associated with the labelling of odors. Indeed, Stevenson and Tomiczek (2007) underlined that people's poor ability to label odors (e.g., Cain, 1978) affects their ability to discriminate them (e.g., Epstein, 1967; Rabin, 1988) both when they are presented in complex mixtures and during the course of conditioning in the phenomenon of modifications of taste qualities by odors through repeated pairing. In addition, the difficulty of analyzing the components of an odor–taste mixture might also be due to the automatic character of the smell–taste associations (e.g., Dalton, Doolittle, Nagata, & Breslin, 2000). Stevenson and Boakes (2004) suggested that such automatic associations account for the modifications of taste qualities by odors. According to these authors, the act of eating and drinking generates implicit learning of the associations of the paired stimuli. Subsequently, these learned implicit associations could be activated when experiencing one of the stimuli presented alone (rendering an odorant sweet or sour smelling as a function of its repeated pairing with tastants).

### 3. The specificities of the olfactory system

#### 3.1. The duality of the olfactory system

In this section, we review the specificities of the olfactory system that further support the view of flavor as a distinct perceptual system. According to their physiological definitions, taste has the status of a minor sense, as the channel of only a limited number of sensations: Sweetness, sourness, bitterness, saltiness, and umami (e.g., Chandrashekar, Hoon, Ryba, & Zuker, 2006; Smith & Margolskee, 2006, although see Schiffman, 2000, for the view that that the range of tastes is more extensive than five); whereas smell is elevated to the status of a dual sense given its role in both sniffing the air around us and in savoring food. The olfactory receptors can thus be stimulated by two distinct routes: Either via the nose, by sniffing (orthonasal olfaction), or via the mouth, during eating and drinking, as volatile chemicals rise up through the nasopharynx (retronasal olfaction). Olfaction thus appears to constitute a 'dual modality' in that it explores objects both in the external world and within the body. However, in the ordinary usage of these words, 'to smell' means to detect a substance outside of the mouth. While 'to taste' simply means to sample a substance inside the mouth and to savor it, as when we consume food and drinks. The ordinary usage of the terms taste and smell refers to what will be called here a perceptual system: A sense for perception, not simply for the having of sensations.

Many years ago, Gibson (1966) proposed that perceptions are not based on the having of sensations, which implies that the perceptual systems cut across the classification of the available receptor types. That is, some receptors may be anatomically similar but functionally separated and conversely, other receptors may be functionally united while being anatomically separated. Thus, smelling and tasting need not be defined by receptors and nerves; they can instead be defined by their functions in use. As a consequence, the same olfactory receptors can be incorporated into two different perceptual systems, one for sniffing (i.e., inhaling) and the other for eating (and exhaling through the nose). Smelling would be restrained to its main function, that is, the detection of stimuli at a distance by means of their odors. On the other hand, the different receptors

for the volatile and the soluble components of food can be incorporated into the same perceptual system, the ‘gustatory’ or ‘tasting’ system.

Rozin (1982) defended the idea that these two olfactory systems are not only functionally distinct but that they also give rise to different qualities of perceptual experience. The same olfactory stimulus can be perceived and evaluated in different ways depending on whether it is referred to the mouth or to the external world. First, Rozin underlined the discrepancy between the affective values associated with tastes and with odors of the same substance. For instance, people often report liking the smell but not the taste of unsweetened black coffee. However, this distinction can easily be understood, as there is an additional bitter taste added to the odor. The reverse effect is perhaps more informative: Half of the participants in Rozin’s study indicated that they disliked the smell but liked the taste of strong cheese. In this case, the odor component is supposed to be the same no matter whether the object is presented at a distance or in the mouth, with an extra taste being present in the latter case. Additional support for the duality of olfaction comes from research on the exposure to (and learning of) unfamiliar odors. The participants in Rozin’s study had to learn to identify unfamiliar odors, such as those associated with exotic fruits juice and exotic soups. However, after having learned to identify the odors externally, they reported having difficulties in identifying the same odors when presented retronasally. For Rozin, psychophysical findings such as these underline the qualitative discrepancy between retronasal and orthonasal odors. Furthermore, there are differences in the perception of the duration of retronasal and orthonasal odors. The temporal pattern of the perception of the odors of citral or vanillin was perceived as having shorter onset and extinction times, and also a higher maximum intensity when presented orthonasally than when presented retronasally (Kuo, Pangborn, & Noble, 1993). In addition, more recent neuroimaging data (e.g., Gerber, Small, Heilmann, & Hummel, 2003; Small, Gerber, Mak, & Hummel, 2005) have highlighted the fact that different neural substrates underpin these two forms of olfactory perception.

### 3.2. Object-based perception

Following on from this view, the function of the olfactory system is first and foremost to evaluate and identify the source of an odor in the environment and second, to orient and control behavior, including locomotion, to or away from that source. For this reason, Cain (1978; see also Humphrey, 2000), following on from Gibson (1966), proposed that the qualities of smell are secondary with regard to the identification of objects: The characteristics of the different odors are first and foremost a way to identify objects (that is without discriminating its component parts) and to discriminate them one from the other. In order to provide support for this view, Gibson (Chapter VIII) underlined the fact that there are few odor names that do not refer to specific objects. Furthermore, it is interesting to note that the few words that do, such as ‘acrid’ or ‘pungent’, refer not to olfactory but to trigeminal components of an odor sensation. Thus, with regard to odor perception there seem to be no primary qualities from which the others can be derived as blends or compounds, the name of odors are always the name of objects or classes of events.

Another manifestation of the object-based nature of olfactory perception is the constant error made, when eating, of attributing to taste what really belongs to the sense of smell (e.g., Tichener, 1909). The error of localizing the odors coming from food as originating in the mouth has been termed the olfactory illusion (e.g., Prescott, 1999). It has been compared to the ventriloquism effect, that is, the influence of visual cues on the identification of the location of a sound source (Bertelson & de Gelder, 2004; Marks, 1991). Green (2001) has provided a similar explanation for the fact that although flavor is perceived by receptors on the tongue, in the nose, and even in the eyes, the brain interprets the overall sensation as originating from within the mouth. According to Green, all of the sensory information is localized in the mouth in order that we associate this information with the food being consumed, in the same way that we typically use both touch and vision to localize a point on our bodies.

However, this spatial mislocalization may be critically dependent on the temporal co-occurrence of the odor and taste stimuli. For example, von Bekeesy (1964) reported that varying the time delay between the delivery of odor and taste stimuli changes the perceived spatial localization of the resulting percept. Von Bekeesy reported that the mixture was subjectively localized at the tip of nose when the odor preceded the taste; at the back of the throat when both components were presented simultaneously, and on the tip of the tongue when the taste preceded the odor. These fascinating results, if they were shown to be replicable, would suggest

that the mislocalization of an odor–taste mixture reflects the fact that the perceptual processes involved are object-oriented and not sensation-based.<sup>3</sup>

#### 4. The role of the trigeminal system, vision, and audition in flavor perception

##### 4.1. Flavor and the trigeminal system

The trigeminal system provides information concerning chemical irritation and nociception, as well as information concerning the temperature, texture, and consistency of food (e.g., [Delwiche, 2004](#)); and all of these sources of information influence the overall perception of flavor that we experience. In this review, we have outlined a number of interactions between taste and smell, and shall mention here the influence of the tactile and trigeminal systems on the perception of taste and smell. With regards to irritation, gustatory stimuli such as salt or citric acid (when presented at a sufficiently high concentration) can have irritant qualities (e.g., [Prescott, Allen, & Stephens, 1993](#); [Stevens & Lawless, 1986](#)). Similarly, olfactory compounds such as butyl acetate (which has a fruity odor) can elicit activity in the trigeminal nerve ([Cain, 1974](#)). Reciprocally, some irritants such as capsaicin have been shown to inhibit the perceived sweetness of sucrose and tomato soup ([Prescott & Stevenson, 1995](#)). Some irritants have also been shown to inhibit the perception of odors, and conversely, odor compounds can inhibit the perception of oral irritation ([Cain & Murphy, 1980](#); see also [Stevenson, Case, & Mahmut, in press](#)). In addition, certain taste–smell mixtures can contain irritants that increase the perceived intensity of the mixture without necessarily being perceived either as burning or stinging (for a review, see [Delwiche, 2004](#); [Verhagen & Engelen, 2006](#)). Temperature has also been shown to interact with orthonasal ratings of beef-type flavoring ([Voirol & Daget, 1989](#)) and with flavor ratings of beef steaks ([Caporaso, Cortavarria, & Mandigo, 1978](#); [Olson, Caporaso, & Mandigo, 1980](#)).

With regard to the influence of texture, it has been shown that somatosensory stimuli modulate both taste and flavor perception. For example, increasing the levels of sucrose, citric acid, or sodium chloride has been shown to decrease the perceived viscosities of various solutions ([Christensen, 1980b](#)). Correspondingly, increasing the viscosity of a solution can lead to a decrease in both taste and flavor intensity ratings (e.g., [Arabie & Moskowitz, 1971](#); [Christensen, 1980a](#); [Cook, Hollowood, Linforth, & Taylor, 2003](#); [Kokini, 1985](#)); this occurs despite the fact that such changes in viscosity have no measurable effect on the concentration of the odorous volatiles released in the nose ([Hollowood, Linforth, & Taylor, 2000](#)). It should be noted here that a recent study by [Bult, de Wijk, and Hummel \(2007\)](#) has also demonstrated the reverse interaction between viscosity and flavor: Namely, that the perceived flavor intensity of a liquid can be reduced by increasing its viscosity.

The numerous interactions between the signal from the receptors of taste and texture led [Green \(2001\)](#) to suggest that all the receptors in the mouth should actually be considered as constituting one integrated somatosensory system. Indeed, an fMRI study by [Cerf-Ducastel and colleagues \(2001\)](#) has provided some support for just such an integrative account. In their study, [Cerf-Ducastel et al.](#) showed that taste stimuli sensed on the tongue and somatosensory stimuli from the mouth activated common areas of the brain, including the insula, the rolandic, frontal, and temporal operculum.

##### 4.2. Vision, audition, and the perception of flavor

It is perhaps also worth briefly discussing the role that visual and auditory cues play in flavor perception. For instance, the identification of odors has often been shown to be impaired when they are presented without color cues or when paired with an inappropriate color (e.g., [Blackwell, 1995](#); [Zellner & Kautz, 1990](#); see also [Clydesdale, 1984, 1993](#), for reviews). More recently, it has been shown that certain white wines when colored red are described using more red wine odor terms than the same wine naturally colored ([Morrot, Brochet, & Dubourdieu, 2001](#)). Furthermore, taste and flavor intensity have been shown to increase as the color level in a

<sup>3</sup> Note that [von Bekeesy's \(1964\)](#) results would appear to reflect some compensation for any differences in transduction latencies of the inputs coming from the senses of taste and smell (cf. [Spence & Squire, 2003](#)).

solution increases (e.g., DuBose, Cardello, & Maller, 1980; Hyman, 1983; Johnson & Clydesdale, 1982; Zampini, Sanabria, Phillips, & Spence, *in press*). In addition, an fMRI study by Osterbauer et al. (2005) has shown increased activity in the olfactory parts of brain when the congruency between simultaneously-presented color and aroma is increased (e.g., when strawberry odor is paired with a simultaneously-presented red color as compared with a turquoise color). So far, the influence of audition on the perception of food has mainly been focused on the textural properties of food; showing, for example, that the perceived crispness (Sherman & Deghaidy, 1978) and crackliness (Vickers, 1984) of food varies with the auditory cues that are presented. The perception of the crispness and staleness of potato chips has also been shown to increase with an overall increase in the loudness and/or boosting of the high frequency components ( $>2$  kHz) of the auditory feedback provided during the biting action (Zampini & Spence, 2004; see also Zampini & Spence, 2005). The influence of the visual and auditory cues on flavor perception has given rise to a large body of research highlighting the numerous interactions between vision, audition, touch, taste, and smell. Unfortunately, however, reviewing this very large body of research falls beyond the scope of the present review (the interested reader should refer to Clydesdale, 1993; Spence & Zampini, 2006; Verhagen & Engelen, 2006, for reviews).

## 5. The flavor perceptual system

### 5.1. Questioning the taxonomy of our senses

It seems possible that the multisensory nature of human flavor perception reflects the fact that the taxonomy of the human senses used by science does not necessarily correspond to the categories used by ordinary people to describe the senses of taste and smell. This was the hypothesis put forward by Gibson (1966, see chapter VIII, ‘Tasting and smelling as perceptual systems’). He argued that taste should be considered in a broad sense (that we will refer to as flavor perception) as a perceptual modality and not as a sensory modality. In order to understand this distinction, it should be noted that there are two main approaches to defining our perceptions: The modal and the amodal. According to the modal approach, perceptions are based on sensations and remain linked to the particular sensory modality by which they were generated (e.g., Berkeley, 1709; Locke, 1690; Tichener, 1909). The classification of the senses in terms of the different types of sensory receptors involved is perhaps the most widespread in science. This definition was inherited from Aristotle who conceived of the senses as passive containers of external data. The external impressions are engraved in the mind in the same way as we affix one’s seal (Aristotle, *De Anima*, II, 12). On the other hand, according to the amodal (or supramodal) approach, perceptions are not based on sensations but rather result from a process of information extraction. The information is abstract and does not depend on the particular sensory modality in which it was generated. Properties of objects can thus be ‘interpreted’ by different sensory channels. As a consequence, sensations are specific to each sensory modality, but perceptions are not (e.g., Gibson, 1966, 1979; O’Regan & Noë, 2001; Varela, Thompson, & Rosch, 1991).

The ecological approach to perception developed by Gibson (1966, 1979) is based on just such a distinction between sensory stimulation and perceptual information that specifies two different ways of defining the senses. Senses can be conceived of either as channels of sensations, mainly passive, that constitute the origin of the qualities associated with experience; or as perceptual systems, mainly active, that constitute the origin of our knowledge about the world. It is the latter view that Gibson adopted. The term “direct perception” was used to reject the idea that our only immediate contact with the external world occurs by means of sensations, impressions, sense data, or the mere patterns of stimulation of the sensory receptors. Direct perception is thus not based on ‘the having of sensations’; rather, it is based on the pick-up of information. Thus, the function of perception is not the production of experience or representation, but rather the enabling of the organism to function appropriately within its environment.

Perception is an act undertaken by the whole animal, the perceptually-guided exploration of the environment. The function of perception is to keep the perceiver ‘in touch’ with the environment and to guide action, not to produce inner experiences and representations. For instance, seeing takes place *in* the environment thanks to the engagement of the whole animal with its surroundings. Vision is thus a way of acquiring information by coming into direct contact with the environment, thanks to active exploration (Gibson, 1966). Thus, Gibson does not define the different senses as producers of visual or auditory sensations, but rather

as active seeking mechanisms that allow seeing, hearing, and so on. This view is in opposition with the modal approach to perception according to which perceptions are based on the inputs available for sensation. The hypothesis put forward by Gibson (1966) that the constituents of our perception are not based on the passive having of sensations but stems from the activity of the perceiver has been developed in many theories of perception (e.g., Brooks, 1999; Noë, 2005; Piaget, 1937; Stoffregen & Bardy, 2001; von Uexküll, 1909).

### 5.2. *The multisensory perception of flavor*

The multiplicity of interactions between taste, smell, touch, and the trigeminal system (not to mention hearing and vision) has led numerous researchers to propose flavor as the term for the combinations of these systems, unified by the act of eating (e.g., Abdi, 2002; McBurney, 1986; Prescott, 1999; Small & Prescott, 2005). For example, Abdi argued that although the taste, smell, and trigeminal systems are obviously anatomically separated with separate functions, they are not cognitively independent. He developed the parallel with vision. The visual system involves two anatomically separated channels: The “what” and the “where” systems (see Milner & Goodale, 1995; Ungerleider & Mishkin, 1992). The “where” system corresponds to a dorsal cortical pathway, primarily involving the parietal lobes. It processes information related to motion, depth, contrast, and position. The “what” system corresponds to a ventral cortical pathway, involving essentially the temporal lobes, which processes information related to color, object recognition, and face recognition. However, we do not experience the different types of information coming from these different pathways as being independent properties of objects. On the contrary, we experience the position, shape, color, and movement of a perceived object as being indissociable properties of this object. That is, vision integrates different independent neuro-anatomical systems. In a similar manner as visual experiences are seen as a unitary experience of their properties of shape, colors, and so on (e.g., for face perception see Tanaka, Kiefer, & Bukach, 2004), although taste, smell, and the trigeminal systems are anatomically independent, that does not necessarily mean that they cannot be cognitively or psychologically unified. Following on from this view, the co-influence of smells and tastes does not reflect anymore of a synesthetic process than other forms of interactions between or within sensory modalities. However, it should be mentioned that the way in which the different multisensory processes differ can be seen as a function of the extent to which these processes occur consciously. For example, the modifications of taste qualities by odors seems to involve processes that are beyond consciousness (Stevenson, 2001). Similarly, the influence of vision on performance in tactile change detection tasks, for instance, occurs despite the fact that the participants in such studies are trying to focus their attention only to the tactile stimuli (e.g., Auvray, Gallace, Tan, & Spence, 2007).

The idea of a functional flavor perceptual system which includes both smell and taste was actually anticipated many years ago by Brillat-Savarin (1835, p. 41) who wrote that he was “tempted to believe that smell and taste are in fact but a single sense, whose laboratory is in the mouth and whose chimney is the nose”. This conception of flavor as a perceptual system has also been proposed by Gibson (1966) under the term “tasting system” which additionally includes the sense of touch. The different receptors for the volatile and the soluble components of food can be incorporated into the same perceptual system. Furthermore, this perceptual system should also include the haptic components associated with the act of eating. As one of the most important functions of the mouth is testing substances for their palatability, the tongue and the oral cavity are sensitive to size, shape, texture, consistency, and temperature. Indeed, although we usually think of the mouth as an entirely different organ belonging to a different sensory modality, it actually overlaps with the tactile/haptic system. Thus, when drinking or eating, we experience a multitude of sensations, including taste and smell, but also touch, temperature, and sometimes pain/irritation in the oral cavity and/or nose.

The tasting system was conceived of by Gibson (1966) basically as a system for the control of ingestion. The pick-up of all the available information about a substance in the mouth cuts across the ordinary classification of different receptors types. It includes two types of chemo-receptors. The soluble (i.e., sapid) component of the substance stimulates the receptors of the tongue and nearby tissue lining the mouth (the usual sense of taste). The volatile (odorous) component of the substance stimulates the receptors in the olfactory cavity above the mouth (via retronasal olfaction). This perceptual system also includes the receptors for oral haptic information, which are located in the skin and tissue of the tongue, in the lips, in the lining of the mouth, in the muscles of the tongue, in the muscle and in the joints of the jaw. The surface texture of the substance is reg-

istered by a sort of mouth palpation, which detects such properties as slipperiness, smoothness, and roughness. The consistency of the substance is registered by chewing, which detects such properties as viscosity, elasticity, and other tactile qualities such as softness, hardness or brittleness. In addition, the shape, size, and the condition of wholeness or granularity of a substance are also probably registered by the haptic action of the mouth. The information obtained by tasting is evidently multiple; however, the anatomical separation of the receptors involved does not prevent them from constituting parts of one and the same perceptual system, in the present usage of that term. Furthermore, all of the information that is obtained is specific to the same substance and the inputs are all concomitants, since the activity of the receptors will co-vary as a result of the activity of the mouth. We would argue that this perceptual system should not really be called a chemical sense (e.g., Small, 2004; see also Dodd & Castellucci, 1991) inasmuch as only the first two types of information listed above depend on the action of chemo-receptors.

It should be noted that the flavor system can be conceived of either as being posited on the basis of sensations, or on the basis of the extraction of information. For instance, nearly a century ago, Tichener (1909) also emphasized the curiously unitary character of the combined sensations of taste, smell, touch, and temperature when eating a peach or when drinking a cup of coffee. The taste of the peach seemed to him to be simple and unique. However, as a defender of the view that perception is based on sensations, he argued that the blend had to be analyzed and that each constituent part belonged properly to a different sense. For him, the unitary character of ‘peach perception’ was due to a fusion of the different sensory qualities within a context of associated memories of everything that had ever happened along with peach eating. On the other hand, for Gibson (1966), observers detect objects instead of sensations, and object specification is facilitated by the joint extraction of stimulus information. In a similar way, the layout of a physical surface is perceived by means of the disposition of our body-parts when touch and posture covary. It is not that the sensations emanating from the skin and joints are blended or fused when they occur together but rather that the receptors combine in one system to register one kind of invariant stimulus information. Nevertheless, while smelling, one can attend to the subjective experience itself, instead of attending to a source. In such cases, the perceiver is able in some cases to have what can be justly called a sensation, that is an access to qualities associated to her/his experience taken separately.

## 6. Conclusions

In this article, we have reviewed the literature on the multisensory interactions that take place between taste, smell, and the trigeminal system in order to determine the extent to which flavor can be defined as a perceptual system. Updating the early work of Gibson (1966) in the light of current cognitive neuroscientific findings, we propose that flavor perception should be used as a term to describe the combinations of taste, smell, the trigeminal system, and touch, to which we add visual and auditory cues, that also influence our perception when tasting food. According to this view, the act of eating allows the different qualities of an object to be combined into a whole percept. According to this view, flavor is not defined as a separate sensory modality but as a perceptual modality that is unified by the act of eating.

## References

- Abdi, H. (2002). What can cognitive psychology and sensory evaluation learn from each other? *Food Quality and Preference*, *13*, 445–451.
- Andersen, T. S., Tiippana, K., & Sams, M. (2004). Factors influencing audiovisual fission and fusion illusions. *Cognitive Brain Research*, *21*, 301–308.
- Arabie, P., & Moskowitz, H. R. (1971). The effects of viscosity upon perceived sweetness. *Perception & Psychophysics*, *9*, 410–412.
- Ashkenazi, A., & Marks, L. E. (2004). Effect of endogenous attention on detection of weak gustatory and olfactory flavors. *Perception & Psychophysics*, *66*, 596–608.
- Auvray, M., Gallace, A., Tan, H. Z., & Spence, C. (2007). Crossmodal change blindness between vision and touch. *Acta Psychologica* (in press).
- Baron-Cohen, S., Burt, L., Smith-Laittan, F., Harrison, J., & Bolton, P. (1996). Synaesthesia: Prevalence and familiarity. *Perception*, *25*, 1073–1079.
- Berkeley, G. (1709). Essay towards a new theory of vision. Reedited in A. A. Luce & T. E. Jessop (1949-1957), *The works of George Berkeley*. London: Thomas Nelson and Sons.

- Bertelson, P., & de Gelder, B. (2004). The psychology of multimodal perception. In C. Spence & J. Driver (Eds.), *Crossmodal space and crossmodal attention* (pp. 141–177). Oxford: Oxford University Press.
- Bingham, A. F., Birch, G. G., de Graaf, C., Behan, J. M., & Perring, K. D. (1990). Sensory studies with sucrose–maltol mixtures. *Chemical Senses*, *15*, 447–456.
- Blackwell, L. (1995). Visual cues and their effects on odour assessment. *Nutrition & Food Science*, *95*, 24–28.
- Blake, A. A. (2004). Flavor perception and the learning of food preferences. In A. J. Taylor & D. D. Roberts (Eds.), *Flavor perception* (pp. 172–202). Oxford: Blackwell.
- Brillat-Savarin, J. A. (1835). *Physiologie du goût (The philosopher in the kitchen/The physiology of taste)*. J. P. Meline: Bruxelles (A. Lalauze, Trans.) (1884), A handbook of gastronomy. London: Nimmo & Bain.
- Brooks, R. (1999). *Cambrian intelligence. The early history of the new AI*. Cambridge, MA: MIT Press.
- Bult, J. H. F., de Wijk, R. A., & Hummel, T. (2007). Investigations on multimodal sensory integration: Texture, taste, and ortho- and retronasal olfactory stimuli in concert. *Neuroscience Letters*, *411*, 6–10.
- Burdach, K. J., Kroeze, J. H. A., & Koster, E. P. (1984). Nasal, retronasal, and gustatory perception: An experimental comparison. *Perception & Psychophysics*, *36*, 205–208.
- Cain, W. S. (1974). Contribution of the trigeminal nerve to perceived odor magnitude. *Annals of the New York Academy of Sciences*, *237*, 28–34.
- Cain, W. S. (1978). History of research on smell. In E. C. Carterette & M. P. Friedman (Eds.), *Handbook of perception. Tasting and smelling* (Vol. 6A, pp. 197–243). New York: Academic Press.
- Cain, W. S., & Murphy, C. L. (1980). Interaction between chemoreceptive modalities of odour and irritation. *Nature*, *284*, 255–257.
- Caporaso, F., Cortavarría, A. L., & Mandigo, R. W. (1978). Effects of post-cooking sample temperature on sensory and shear analysis of beef steaks. *Journal of Food Science*, *43*, 839–841.
- Cerf-Ducastel, B., Van de Moortele, P. F., MacLeod, P., Le Bihan, D., & Faurion, A. (2001). Interaction of gustatory and lingual somatosensory perceptions at the cortical level in the human: A functional magnetic resonance imaging study. *Chemical Senses*, *26*, 371–383.
- Chandrasekar, J., Hoon, M. A., Ryba, N. J., & Zuker, C. S. (2006). The receptors and cells for mammalian taste. *Nature*, *444*, 288–294.
- Christensen, C. M. (1980a). Effects of solution viscosity on perceived saltiness and sweetness. *Perception & Psychophysics*, *28*, 347–353.
- Christensen, C. M. (1980b). Effects of taste quality and intensity on oral perception of viscosity. *Perception & Psychophysics*, *28*, 315–320.
- Clark, C. C., & Lawless, H. T. (1994). Limiting response alternatives in time-intensity scaling: An examination of the halo-dumping effect. *Chemical Senses*, *19*, 538–594.
- Cliff, M., & Noble, A. C. (1990). Time–intensity evaluation of sweetness and fruitiness and their interaction in a model solution. *Journal of Food Science*, *55*, 450–454.
- Clydesdale, F. M. (1984). The influence of colour on sensory perception and food choices. In J. Walford (Ed.), *Developments in food colours* (pp. 75–112). London: Elsevier Applied Science.
- Clydesdale, F. M. (1993). Color as a factor in food choice. *Critical Reviews in Food Science and Nutrition*, *33*, 83–101.
- Cook, D. J., Hollowood, T. A., Linforth, R. S. T., & Taylor, A. J. (2003). Oral shear stress predicts flavour perception in viscous solutions. *Chemical Senses*, *28*, 11–23.
- Cruz, A., & Green, B. G. (2000). Thermal stimulation of taste. *Nature*, *403*, 889–892.
- Cytowic, R. E. (1989). *Synesthesia: A unity of the senses*. New York: Springer-Verlag.
- Dalton, P., Doolittle, N., Nagata, H., & Breslin, P. A. S. (2000). The merging of the senses: Integration of subthreshold taste and smell. *Nature Neuroscience*, *3*, 431–432.
- Davidson, J. M., Linforth, R. S. T., Hollowood, T. A., & Taylor, A. J. (1999). Effect of sucrose on the perceived flavor intensity of chewing gum. *Journal of Agriculture and Food Chemistry*, *47*, 4336–4340.
- Delwiche, J. F. (2004). The impact of perceptual interactions on perceived flavor. *Food Quality and Preference*, *15*, 137–146.
- Delwiche, J., & Heffelfinger, A. (2005). Crossmodal additivity of taste and smell. *Journal of Sensory Studies*, *20*, 512–525.
- Dodd, J., & Castellucci, V. F. (1991). Smell and taste: The chemical senses. In E. R. Kandell, J. H. Schwartz, & T. M. Jessell (Eds.), *Principles of neural science* (3rd ed., pp. 512–529). Englewood Cliffs, NJ: Prentice Hall.
- DuBose, C. N., Cardello, A. V., & Maller, O. (1980). Effects of colorants and flavorants on identification, perceived flavor intensity, and hedonic quality of fruit-flavored beverages and cake. *Journal of Food Science*, *45*, 1393–1399.
- Epstein, W. (1967). *Varieties of perceptual learning*. New York: McGraw Hill.
- Frank, R. A., & Byram, J. (1988). Taste–smell interactions are tastant and odorant dependent. *Chemical Senses*, *13*, 445–455.
- Frank, R. A., Shaffer, G., & Smith, D. V. (1991). Taste–odor similarities predict taste enhancement and suppression in taste–odor mixtures. *Chemical Senses*, *16*, 523.
- Frank, R. A., van der Klaauw, N. J., & Schifferstein, H. N. J. (1993). Both perceptual and conceptual factors influence taste–odor and taste–taste interactions. *Perception & Psychophysics*, *54*, 343–354.
- Gerber, J., Small, D. M., Heilmann, S., & Hummel, T. (2003). Comparison of orthonasal and retronasal perception of non-food odors: A functional MR imaging study. *Chemical Senses*, *28*, 554.
- Gibson, J. J. (1966). *The senses considered as perceptual systems*. Boston: Houghton Mifflin.
- Gibson, J. J. (1979). *The ecological approach to visual perception*. Boston: Houghton Mifflin.
- Gilbert, A. N., & Firestein, S. (2002). Dollars and scents: Commercial opportunities in olfaction and taste. *Nature Neuroscience*, *5*, 1043–1045.
- Green, B. G. (2001). Psychophysical measurement of oral chemesthesis. In S. A. Simon & M. A. I. Nicolelis (Eds.), *Methods in chemosensory research* (pp. 3–20). Boca Raton, FL: CRC Press.

- Grossenbacher, P. G., & Lovelace, C. T. (2001). Mechanisms of synesthesia: Cognitive and physiological constraints. *Trends in Cognitive Sciences*, 5, 36–41.
- Harper, R., Land, D. G., Griffiths, N. M., & Bate-Smith, E. C. (1968). Odour qualities: A glossary of usage. *British Journal of Psychology*, 59, 231–252.
- Hollowood, T. A., Linforth, R. S. T., & Taylor, A. J. (2000). The relationship between volatile release and perception. In D. D. Roberts & A. J. Taylor (Eds.), *Flavor release: Linking experiments, theory and reality* (pp. 370–380). Washington: American Chemical Society.
- Humphrey, N. (2000). The privatization of sensation. In S. R. Hameroff, A. W. Kaszniak, & D. J. Chalmers (Eds.), *Toward a science of consciousness III: The third Tucson discussions and debates* (pp. 247–257). Cambridge, MA: MIT Press.
- Hyman, A. (1983). The influence of color on the taste perception of carbonated water preparations. *Bulletin of the Psychonomic Society*, 21, 145–148.
- Johnson, J. L., & Clydesdale, F. M. (1982). Perceived sweetness and redness in colored sucrose solutions. *Journal of Food Science*, 47, 747–752.
- Kappes, S. M., Schmidt, S. J., & Lee, S. Y. (2006). Color halo/horns and halo-attribute dumping effects within descriptive analysis of carbonated beverages. *Journal of Food Science*, 71, S590–S595.
- Kokini, J. L. (1985). Fluid and semi-solid food texture and texture taste interactions. *Food Technology*, 39, 86–92.
- Kubovy, M., & Van Valkenburg, D. (2001). Auditory and visual objects. *Cognition*, 80, 97–126.
- Kuo, Y.-L., Pangborn, R. M., & Noble, A. C. (1993). Temporal patterns of nasal, oral, and retronasal perception of citral and vanillin and interaction of these odourants with selected tastants. *International Journal of Food Science and Technology*, 28, 127–137.
- Laing, D. G., Link, C., Jinks, A. L., & Hutchinson, I. (2002). The limited capacity of humans to identify the components of taste mixtures and taste-odour mixtures. *Perception*, 31, 617–635.
- Lawless, H. T. (1996). Flavor. In M. P. Friedman & E. C. Carterette (Eds.), *Handbook of perception, Vol. 16 – Cognitive ecology* (pp. 325–380). San Diego, California: Academic Press.
- Lawless, H., & Schlegel, M. P. (1984). Direct and indirect scaling of sensory differences in simple taste and odor mixtures. *Journal of Food Science*, 49, 44–46.
- Locke, J. (1690). *An essay concerning human understanding*. Oxford: Oxford University Press.
- Marks, L. E. (1991). Metaphor and the unity of the senses. In H. T. Lawless & B. P. Klein (Eds.), *Sensory science theory and applications in foods* (pp. 185–205). New York: Marcel Dekker.
- Marshall, K., Laing, D. G., Jinks, A. L., & Hutchinson, I. (2006). The capacity of humans to identify components in complex odor–taste mixtures. *Chemical Senses*, 31, 539–545.
- McBurney, D. H. (1986). Taste, smell, and flavor terminology: Taking the confusion out of fusion. In H. L. Meiselman & R. S. Rivkin (Eds.), *Clinical measurement of taste and smell* (pp. 117–125). New York: Macmillan.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.
- Morrot, G., Brochet, F., & Dubourdieu, D. (2001). The color of odors. *Brain & Language*, 79, 309–320.
- Nguyen, D. H., Valentin, D., Ly, M. H., Chrea, C., & Sauvageot, F. (2002). *When does smell enhance taste? Effect of culture and odorant/tastant relationship*. Paper presented at the European Chemoreception Research Organisation conference, Erlangen, Germany.
- Noë, A. (2005). *Action in perception*. Cambridge, MA: MIT Press.
- Olson, D. G., Caporaso, F., & Mandigo, R. W. (1980). Effects of serving temperature on sensory evaluation of beef steaks from different muscles and carcass maturities. *Journal of Food Science*, 45, 627–628.
- O’Regan, J. K., & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, 24, 939–973.
- Osterbauer, R. A., Matthews, P. M., Jenkinson, M., Beckmann, C. F., Hansen, P. C., & Calvert, G. A. (2005). Color of scents: Chromatic stimuli modulate odor responses in the human brain. *Journal of Neurophysiology*, 93, 3434–3441.
- Pfeiffer, J. C., Hort, J., Hollowood, T. A., & Taylor, A. J. (2006). Taste–aroma interactions in a ternary system: A model of fruitiness perception in sucrose/acid solutions. *Perception & Psychophysics*, 6, 216–227.
- Piaget, J. (1937). *La construction du réel chez l’enfant (The construction of reality in the child)*. Neuchatel: Delachaux .
- Prescott, J. (1999). Flavour as a psychological construct: Implications for perceiving and measuring the sensory qualities of food. *Food Quality and Preference*, 10, 349–356.
- Prescott, J. (2001). Cognitive influences on odor/taste interactions in mixtures. *Chemical Senses*, 26, 1035.
- Prescott, J. (2004). Psychological processes in flavour perception. In A. J. Taylor & D. D. Roberts (Eds.), *Flavor perception* (pp. 257–277). Oxford: Blackwell.
- Prescott, J., Allen, S., & Stephens, L. (1993). Interactions between oral chemical irritation taste and temperature. *Chemical Senses*, 18, 389–404.
- Prescott, J., Johnstone, V., & Francis, J. (2004). Odor–taste interactions: Effects of attentional strategies during exposure. *Chemical Senses*, 29, 331–340.
- Prescott, J., & Stevenson, R. J. (1995). Effects of oral chemical irritation on tastes and flavors in frequent and infrequent users of chili. *Physiology & Behavior*, 58, 1117–1127.
- Rabin, M. D. (1988). Experience facilitates olfactory quality discrimination. *Perception & Psychophysics*, 44, 532–540.
- Radeau, M. (1994). Auditory–visual spatial interaction and modularity. *Current Psychology of Cognition*, 13, 3–51.
- Ramachandran, V. S., & Hubbard, E. M. (2001). Synaesthesia: A window into perception, thought and language. *Journal of Consciousness Studies*, 8, 3–34.
- Robertson, L., & Sagiv, N. (Eds.). (2005). *Synaesthesia: Perspectives from cognitive neuroscience*. New York: Oxford University Press.
- Ross, P. W. (2001). Qualia and the senses. *The Philosophical Quarterly*, 51, 495–511.
- Rozin, P. (1982). “Taste–smell confusions” and the duality of the olfactory sense. *Perception & Psychophysics*, 31, 397–401.

- Sakai, N., Kobayakawa, T., Gotow, N., Saito, S., & Imada, S. (2001). Enhancement of sweetness ratings of aspartame by a vanilla odor presented either by orthonasal or retronasal routes. *Perceptual and Motor Skills*, *92*, 1002–1008.
- Schiffstein, H. N. J., & Verlegh, P. W. J. (1996). The role of congruency and pleasantness in odor-induced taste enhancement. *Acta Psychologica*, *94*, 87–105.
- Schiffman, S. S. (2000). Taste quality and neural coding—Implications from psychophysics and neurophysiology. *Physiology & Behavior*, *69*, 147–159.
- Shepherd, G. M. (2006). Smells images and the flavour system in the human brain. *Nature*, *444*, 316–321.
- Sherman, P., & Deghaidy, F. S. (1978). Force-deformation conditions associated with the evaluation of brittleness and crispness in selected foods. *Journal of Texture Studies*, *9*, 437–459.
- Simons, C. T., & Noble, A. C. (2003). Challenges for the sensory sciences from the food and wine industries. *Nature Reviews Neuroscience*, *4*, 599–605.
- Sinnett, S., Spence, C., & Soto-Faraco, S. (submitted for publication). Assessing the automaticity of audiovisual multisensory integration. *Neuroscience Letters*.
- Small, D. M. (2004). Crossmodal integration—Insights from the chemical senses. *Trends in Neurosciences*, *27*, 120–123.
- Small, D. M., Gerber, J. C., Mak, Y. E., & Hummel, T. (2005). Differential neural responses evoked by orthonasal versus retronasal odorant perception in humans. *Neuron*, *47*, 593–605.
- Small, D. M., & Prescott, J. (2005). Odor/taste integration and the perception of flavor. *Experimental Brain Research*, *166*, 345–357.
- Smith, D. V., & Margolskee, R. F. (2006). Making sense of taste. *Scientific American*, *284*(3), 85–92.
- Spence, C. (2002). *The ICI report on the secret of the senses*. London: The Communication Group.
- Spence, C. (2007). Audiovisual multisensory integration. *Acoustical Science & Technology*, *28*, 61–70.
- Spence, C., & Squire, S. B. (2003). Multisensory integration: Maintaining the perception of synchrony. *Current Biology*, *13*, R519–R521.
- Spence, C., & Zampini, M. (2006). Auditory contributions to multisensory product perception. *Acta Acustica united with Acustica*, *92*, 1009–1025.
- Stein, B. E., & Meredith, M. A. (1993). *The merging of the senses*. Cambridge, MA: MIT Press.
- Stevens, D. A., & Lawless, H. T. (1986). Putting out the fire: Effects of tastants on oral chemical irritation. *Perception & Psychophysics*, *39*, 346–350.
- Stevenson, R. J. (2001). Is sweetness taste enhancement cognitively impenetrable? Effect of exposure, training and knowledge. *Appetite*, *36*, 241–242.
- Stevenson, R. J., & Boakes, R. A. (2004). Sweet and sour smells: Learned synaesthesia between the senses of taste and smell. In G. A. Calvert, C. Spence, & B. E. Stein (Eds.), *The handbook of multisensory processing* (pp. 69–83). Cambridge, MA: MIT Press.
- Stevenson, R. J., Boakes, R. A., & Prescott, J. (1998). Changes in odor sweetness resulting from implicit learning of a simultaneous odor-sweetness association: An example of learned synaesthesia. *Learning and Motivation*, *29*, 113–132.
- Stevenson, R. J., Boakes, R. A., & Wilson, J. P. (2000a). Counterconditioning following human odor–taste and color-taste learning. *Learning and Motivation*, *31*, 114–127.
- Stevenson, R. J., Boakes, R. A., & Wilson, J. P. (2000b). The persistence of conditioned odor perceptions: Evaluative conditioning is not unique. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *26*, 423–440.
- Stevenson, R. J., & Case, T. I. (2003). Pre-exposure to the stimulus elements, but not training to detect them, retards human odour–taste learning. *Behavioural Processes*, *61*, 13–25.
- Stevenson, R. J., Case, T. I., & Mahmut, M. (in press). Cross-modal perceptual learning between odors and trigeminal irritants. *Perception & Psychophysics*.
- Stevenson, R. J., Prescott, J., & Boakes, R. A. (1995). The acquisition of taste properties by odors. *Learning and Motivation*, *26*, 1–23.
- Stevenson, R. J., Prescott, J., & Boakes, R. A. (1999). Confusing tastes and smell: How odours can influence the perception of sweet and sour tastes. *Chemical Senses*, *24*, 627–635.
- Stevenson, R. J., & Tomiczek, C. (2007). Olfactory-induced synesthesias: A review and model. *Psychological Bulletin*, *133*, 294–309.
- Stillman, J. A. (2002). Gustation: Intersensory experience par excellence. *Perception*, *31*, 1491–1500.
- Stoffregen, T. A., & Bardy, B. G. (2001). On specification and the senses. *Behavioral and Brain Sciences*, *24*, 195–213.
- Tanaka, J. W., Kiefer, M., & Bukach, C. M. (2004). A holistic account of the own-race effect in face recognition: Evidence from a cross-cultural study. *Cognition*, *93*, 1–9.
- Titchener, E. B. (1909). *A textbook of psychology*. New York: Macmillan.
- Ungerleider, L. G., & Mishkin, M. (1992). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.
- van der Klaauw, N. J., & Frank, R. A. (1996). Scaling component intensities of complex stimuli: The influence of response alternatives. *Environmental International*, *22*, 21–31.
- Varela, F. J., Thompson, E., & Rosch, E. (1991). *The embodied mind: Cognitive science and human experience*. Cambridge, MA: MIT Press.
- Verhagen, J. V. (2007). The neurocognitive bases of human multimodal food perception: Consciousness. *Brain Research Reviews*, *3*, 271–286.
- Verhagen, J. V., & Engelen, L. (2006). The neurocognitive bases of human multimodal food perception: Sensory integration. *Neuroscience and Biobehavioral Reviews*, *30*, 613–650.
- Vickers, Z. M. (1984). Crispness and crunchiness—A difference in pitch? *Journal of Texture Studies*, *15*, 157–163.
- Voirol, E., & Daget, N. (1986). Comparative study of nasal and retronasal olfactory perception. *Lebensmittel—Wissenschaft & Technologie*, *19*, 316–319.

- Voirol, E., & Daget, N. (1989). Direct nasal and oronasal profiling of a meat flavouring: Influence of temperature, concentration and additives. *Lebensmittel—Wissenschaft Technologie*, 22, 399–405.
- von Bekesy, G. (1964). Olfactory analogue to directional hearing. *Journal of Applied Physiology*, 19, 369–373.
- von Uexküll, J. (1909). *Umwelt und Innenwelt der Tiere (The external and internal world of animals)*. Berlin: Julius Springer-Verlag.
- Wollen, K. A., & Ruggiero, F. T. (1983). Colored-letter synaesthesia. *Journal of Mental Imagery*, 7, 83–86.
- Yeomans, M. R., & Mobini, S. (2006). Hunger alters the expression of acquired hedonic but not sensory qualities of food-paired odors in humans. *Journal of Experimental Psychology: Animal Behavior Processes*, 32, 460–466.
- Yeomans, M. R., Mobini, S., Elliman, T. D., Walker, H. C., & Stevenson, R. J. (2006). Hedonic and sensory characteristics of odors conditioned by pairing with tastants in humans. *Journal of Experimental Psychology: Animal Behavior Processes*, 32, 215–228.
- Zampini, M., Sanabria, D., Phillips, N., & Spence, C. (in press). The multisensory perception of flavor: Assessing the influence of color cues on flavor discrimination responses. *Food Quality and Preference*.
- Zampini, M., & Spence, C. (2004). The role of auditory cues in modulating the perceived crispness and staleness of potato chips. *Journal of Sensory Studies*, 19, 347–363.
- Zampini, M., & Spence, C. (2005). Modifying the multisensory perception of a carbonated beverage using auditory cues. *Food Quality & Preference*, 16, 632–641.
- Zellner, D. A., & Kautz, M. A. (1990). Color affects perceived odor intensity. *Journal of Experimental Psychology: Human Perception & Performance*, 16, 391–397.
- Zellner, D. A., Rozin, P., Aron, M., & Kulish, C. (1983). Conditioned enhancement of human's liking for flavor by pairing with sweetness. *Learning and Motivation*, 14, 338–350.