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Oral referral: On the mislocalization of odours to the mouth

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ABSTRACT

Oral referral is central to multisensory flavour perception. The phenomenon, first described a little over a century ago, is characterized by the mislocalization of food-related olfactory stimuli to the oral cavity. Many researchers believe that it contributes to the widespread confusion concerning which sense really provides the information that is bound together in flavour percepts. In this review, evidence supporting the role of a number of factors that have been suggested to modulate oral referral, including tactile capture of olfaction, the relative timing of olfactory and gustatory stimuli, and gustatory capture (possibly involving prior entry) is critically evaluated. The latest findings now support the view that the oral referral of orthonasal aroma (what some have chosen to call orthonasal location binding) is modulated by taste intensity, while for retronasal odours, it is the congruency between the odour-taste(s) pairing that is key. Specifically, the more congruent a particular combination of olfactory and gustatory stimuli, the more likely the component unisensory stimuli will be bound together as a flavour object (or Gestalt) and, as a result, localized together to the oral cavity. The possible roles of attention, attentional capture, and the nutritional significance of the taste in the phenomenon of oral referral are also reviewed. Ultimately, the suggestion is made that oral referral may reflect a qualitatively different kind of multisensory interaction.

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1. Introduction

Researchers have known for almost a century now that olfactory stimuli detected via the retronasal route are often mislocalized, such that they appear to originate from the oral cavity (Hollingworth & Poffenberger, 1917, pp. 11–14).[1] In turn, this perceptual illusion is commonly thought to be part of the reason why we all confuse smell with taste so frequently (Lim & Johnson, 2011, 2012). Certainly, most people typically underestimate the relative contributions of smell and taste to the perception of flavour (see Hollingworth & Poffenberger, 1917, pp. 11–14; Murphy & Cain, 1980; Murphy, Cain, & Bartoshuk, 1977; Spence, 2015b; Spence, Smith, & Auvray, 2015; see also Titchener, 1909). Another reason, or so it has been suggested, as to why the layperson may underestimate the role of olfaction in flavour perception is that they equate olfaction only with orthonasal smell (i.e., with sniffing).

1.1. Orthonasal versus retronasal olfaction

At the outset, it is going to be important to distinguish between orthonasal and retronasal olfaction (e.g., Bojanowski & Hummel, 2012; Fincks, 1886; Rozin, 1982); the term orthonasal olfaction used for when we inhale, or sniff, while retronasal olfaction occurs when volatiles are pulsed out from the back of the nose while eating and drinking. Orthonasal olfactory cues are key to setting our expectations concerning the sensory and hedonic attributes of food and drink (see Piqueras-Fiszman & Spence, 2015); by contrast, retronasal olfactory cues are central to the experience of flavour. Over the years, researchers have highlighted a number of similarities and differences between orthonasal and retronasal smell (Burdach, Kroeze, & Koster, 1984; Diaz, 2004; Voirol & Daget, 1986). Furthermore, people generally tend to be pretty good at identifying retronasally, stimuli that they may only have been exposed to previously, orthonasally (Pierce & Halpern, 1996). That said, the evidence suggests that, if anything, the retronasal identification of odours is somewhat worse than when the same odours are presented orthonasally (Sun & Halpern, 2005). Orthonasal and retronasal odorants are processed somewhat differently, with distinct neural substrates implicated (e.g., Small, Gerber, Mak, & Hummel, 2005). Oral referral might, more naturally or intuitively, be thought of as a phenomenon that applies specifically to the case of retronasal olfaction. However, as it turns out, Stevenson, Oaten, and Mahmut (2011b) have demonstrated what appears to be a very similar phenomenon following the orthonasal presentation of odours. Nevertheless, in order to maintain a clear distinction between these two situations, the latter is often referred to as orthonasal location binding (i.e., to distinguish it from the retronasal case).

Some researchers have been tempted to think of oral referral in terms of a kind of ventriloquism effect taking place in the mouth (e.g., Auvray & Spence, 2008; see also Todrank & Bartoshuk, 1991). In the ventriloquism illusion, spatially displaced sounds (that actually come from a loudspeaker, or from the ventriloquist's mouth) appear to come from the actor's lips seen moving on the screen, or from the agitated lips of the ventriloquist's dummy. While the prototypical version of the illusion is most definitely audiovisual (e.g., see Alais & Burr, 2004; Jackson, 1953), it is important to note that the terms 'ventriloquism' and 'the ventriloquist effect' have, in recent years, been used to refer to any situation in which spatially (or in some cases temporally) displaced pairs of stimuli (regardless of their modality) are mislocalized toward each other (e.g., Caclin, Soto-Faraco, Kingstone, & Spence, 2002; Keetels & Vroomen, 2008; Pavani, Spence, & Driver, 2000). It is in this latter, broader, sense that the term ventriloquism is used here. So, for example, oral-somatosensory stimuli have been shown to capture the perceived location of taste across the tongue (Todrank & Bartoshuk, 1991; see also Michel, Velasco, Salgado, & Spence, 2014), in much the same way as tactile stimuli presented to the hands have been shown to ventriloquize the perceived location of auditory stimuli through space (see Caclin et al., 2002).

At the outset, though, it is important to note that oral referral may be a qualitatively different phenomenon from the ventriloquism illusion; The reason for this being that oral referral involves not only a change in the perceived location of the olfactory stimulus (from nose to mouth), but also a change in the modality, or nature, of the ensuing perceptual experience. That is, olfactory stimuli that are referred to the mouth appear to take on the properties of tastes or flavours (see Rozin, 1982; Spence et al., 2015; see also Delwiche, 2004; Lawless, Schlake, & Smythe, 2003). As such, oral referral may constitute a relatively unique class of multisensory interaction (cf. Partan & Marler, 1999; Spence et al., 2015) – about which, more later. That said, the situation here is a little more complex than it might at first seem. In particular, what people seemingly get confused about is not the ultimate source of the chemosensory inputs that they transduce, which is obviously a food or beverage in the oral cavity – no one, I presume, gets confused about that – but rather the receptor surface (or sensory system) that has been used to detect those chemosensory signals (Shepherd, 2012). However, the latter misattribution is important because it may constitute part of the reason why we are so often confused about the senses we are using while tasting that which we are eating and drinking. So to be clear, there's the oral referral and the change of modality, or the disappearance from experience of any hint or trace that it was an experience detected partly by smell. It is the seeming disappearance of smell from the picture (of our experience) that somehow needs to be explained here.

In recent decades, researchers have investigated various factors in order to determine the extent to which they modulate olfactory referral to the oral cavity. These factors include the capture by oral-somatosensory tactile stimulation, the relative timing of olfactory and gustatory stimulus delivery, and (attentional) capture by gustatory stimuli, with stimulus intensity likely playing an important role here. In the next section, we will look at each of these putative explanations in turn.

2. Factors that have been suggested to modulate oral referral

2.1. Oral-somatosensory stimulation

The belief amongst many early commentators was that olfactory stimuli were mislocalized toward the site of tactile stimulation in the mouth (e.g., Hollingworth & Poffenberger, 1917, pp. 11–14; Murphy & Cain, 1980; Murphy et al., 1977; Rozin, 1982). As Rozin (1982, p. 400) put it in his now-classic paper: "*…the presence of a cutaneous oral stimulus (food in the mouth) might cause referral of the olfactory stimulus to the mouth locus, with a consequent blending of sensations* (Murphy & Cain, 1980)." Indeed, along just these lines, Todrank and Bartoshuk (1991) demonstrated that people's experience of the source of an in-mouth tastant tended to follow the oral-tactile stimulation felt on their tongue. This also occurs if the gustatory stimulus is static while a tasteless tactile probe (i.e., a Q-tip) is moved slowly across the tongue. Such tactile capture has even been demonstrated when the gustatory and tactile stimuli are presented from quite different positions on the tongue (cf. Jackson, 1953). In other words, given that touch can give rise to a mislocalization of taste across the tongue (see also

[1] Though as we will see later, a similar phenomenon has also been demonstrated following orthonasal odour delivery.

Green, 2002; Lim & Green, 2008), it would not seem unreasonable to suggest that oral-somatosensory stimulation might do the same for olfactory stimuli too, this time resulting in their mislocalization from nose to mouth. In fact, just such a claim has been forwarded by both Murphy and Cain (1980) and Green (2002). Putting the various pieces of information together, then, one might think that, since taste can capture (or bias) the perceived location of olfactory stimuli, and since touch captures the perceived location of taste, oral-somatosensory stimulation might not indirectly capture smell as well? This, however, seems not to be the case.

Specifically, no robust empirical evidence has as yet been provided in support of the tactile capture of olfaction. Furthermore, and as we will see later, research from Stevenson et al. (2011b) and Lim and Johnson (2011, 2012) has singly failed to provide any support for a role of tactile capture in oral referral. For instance, Stevenson et al. (2011b) investigated the effect of oral viscosity, and of increasingly vigorous oral movements, on orthonasal location binding. Their results revealed that sniffed odours were not localized to the mouth as a result of enhancing oral-somatosensory stimulation in this way (though one, of course, needs to be cautious here, for the fact that orthonasal location binding is not subject to tactile capture does not necessarily mean that retronasal oral referral would not be either). Of course, given that tactile stimulation is the norm, rather than the exception, when tasting, one might be tempted, *a priori*, to suggest that a gustatory (with the attendant oral-somatosensory) input would be a better predictor of when exactly a flavour stimulus is present in the mouth, and hence when oral referral might make sense (Stevenson, 2012a). Ultimately, though, while a long-standing suggestion, the claim that the oral-somatosensory capture of olfaction underlies the phenomenon of oral referral can be ruled out, given that the weight of scientific evidence collected over the last century has failed to provide any empirical support for this particular account.

2.2. Relative stimulus timing

The next suggestion to have been put forward, historically-speaking, came from von Békésy (1964). He presented odorants orthonasally, while an equal sensation magnitude tastant was delivered in solution to the mouth. The ensuing perceptual experience was apparently localized to the nose if the olfactory stimulus was presented first, whereas the experience was more likely to be localized to the mouth for stimuli presented simultaneously, or else if the gustatory stimulus was presented first (see Fig. 1). It should, however, be noted that von Békésy provides few methodological details – such as, for example, how many participants (if any) were tested, nor even whether the observations he reports were statistically meaningful, if indeed they were suitable for statistical analysis in the first place. Pretty much all that is clear is that oral referral is reported for various combinations of smell and taste, including clove (aroma) and sour (taste). Hence, in the absence of additional data and/or replication, one should probably not place too much weight on these early results, intriguing though they may be.

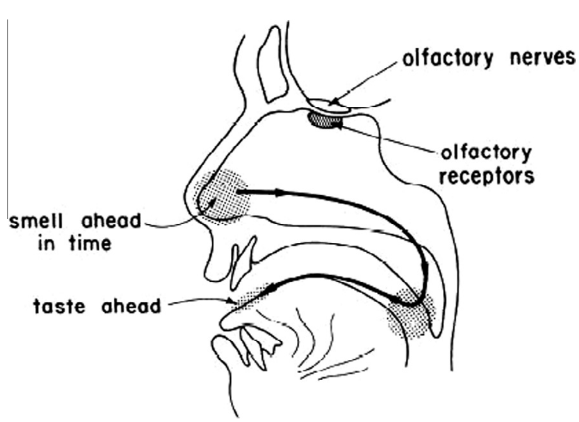

Fig. 1. Summary of the results of von Békésy's (1964) study showing the change in localization (shaded areas) as a function of the relative timing of the component olfactory (orthonasal) and gustatory stimuli. [Figures reprinted with permission.]

Furthermore, there are also other reasons to believe that relative timing is probably not all that critical when it comes to the oral referral of olfactory stimuli to the mouth. If one thinks for a moment about what happens during the regular consumption of food and drink, the problem with the stimulus timing account should soon become apparent. In particular, retronasal olfactory signals are only periodically available during consumption (Trelea et al., 2008), given that the velopharyngeal flap often closes (e.g., during chewing & swallowing), in order to prevent the reflux of volatile odorants from reaching the posterior nares (Stevenson, 2012a). This effectively precludes retronasal olfaction (Buettner, Beer, Hannig, Settles, & Schieberle, 2002; though note that the closure is sometimes imperfect, Trelea et al., 2008). The velopharyngeal flap opens briefly following swallowing during exhalation, and can also open when an individual chews rhythmically, with the latter allowing pulses of odorized air to reach the olfactory receptors retronasally (Hodgson, Linforth, & Taylor, 2003; see also Ni et al., 2015).[2] Hence, while the relative timing of olfactory and gustatory stimulation might well be found to modulate oral referral under a small subset of highly-controlled laboratory conditions (cf. von Békésy, 1964), there seems little reason to believe that this factor really plays that much of a role in everyday acts of consumption.

2.3. Gustatory capture

According to a third account of oral referral, olfactory stimuli may be mislocalized to (and misclassified in) the oral cavity as a result of gustatory stimulation. Specifically, Stevenson et al. (2011b) demonstrated that a tastant (sucrose or citric acid) had to be present, and the more intense (i.e., concentrated) the tastant, the more likely that the orthonasal location binding of strawberry and vanilla odorants would be seen. Stevenson et al. suggested that attentional capture might underlie this form of gustatory capture. For those who are unfamiliar with the term, 'attentional capture' refers to the phenomenon, oft-studied by cognitive psychologists, whereby the presentation of a task-irrelevant stimulus in one sensory modality appears to draw attention exogenously to its location. This leads to a short-lasting facilitation of information processing for other stimuli (no matter whether they are from the same or different modality) presented from around the same (i.e., cued) location for a few hundred milliseconds after the onset of the cue (see Spence, 2001, for a review).

According to Stevenson et al. (2011b), the more intense the tastant, the more pronounced the attentional capture, and hence the greater the oral referral (see also Stevenson, Oaten, & Mahmut, 2011a). Here, though, bear in mind that neither cross-modal audiovisual attentional capture (Spence & Driver, 1999),

[2] I'll leave to one side the question of why it is, if retronasal olfactory stimulation really does occur in occasional bursts that our experience of flavour tends to be constant – that is, there are no gaps in our experience (Sela & Sobel, 2010; Stevenson, 2014). One might wonder, then, whether there is some kind of perceptual filling-in going on here (cf. Gallace & Spence, 2014; Kitagawa, Igarashi, & Kashino, 2009; Stevenson, 2009).

nor the audiovisual ventriloquism effect (Vroomen, Bertelson, & de Gelder, 2001) is necessarily enhanced by increased stimulus intensity (see also Bertelson, Vroomen, de Gelder, & Driver, 2000). Hence, perhaps Stevenson et al.'s (2011b) notion of attentional capture is not actually strictly appropriate, or even necessary, here. That said, one should also not forget that in these attentional capture/ventriloquism studies (typically using auditory, visual, and/or tactile stimuli), participants were presented with many hundreds of trials (sometimes more than 1000) within an experimental session (typically lasting less than an hour). Contrast this with the much smaller number of trials that are typically presented in studies of oral referral. The influence of such methodological differences on the pattern of results obtained (i.e., on the role of stimulus intensity on attentional capture) should probably not be underestimated (cf. Ho, Gray, & Spence, 2014, on this point).

While the reliance on taste (gustatory stimulation) to elicit the olfactory localization illusion can perhaps help to explain the everyday confusion between smelling and tasting in the mouth, it should be noted that the olfactory stimuli in Stevenson et al.'s (2011b) studies were presented orthonasally. Furthermore, the participants had to respond by choosing either "odor jar" or "mouth" (as end anchors on a 7-point scale, with "uncertain of the location" in the middle) as their response when trying to identify the source of the odour. This experimental situation is, then, rather unlike that encountered when we normally eat and drink, and where olfactory stimuli are typically experienced retronasally. As noted earlier, Stevenson and colleagues' use of purely orthonasal olfactory stimuli in their studies means that they were probably not looking at the classic oral referral phenomenon, and hence the effects they study are often referred to under the header of 'olfactory localization binding' instead, in order to distinguish it.

While on the theme of attentional capture, it has been suggested that oral referral does not occur in the case of those olfactory stimuli that have a strong trigeminal component, which can, after all, be thought of a kind of tactile stimulation (Cain, 1976; Spence, Kettenmann, Kobal, & McGlone, 2001). As Stevenson (2012a) puts it: *"One would predict that odors with greater irritant properties would be less likely to be localized to the mouth."* Certainly, the experience that one has on tasting sushi with a generous dose of wasabi is localized as an oftentimes painful hit at the bridge of the nose. According to Stevenson et al. (2011a), then, it is the relative attention-capturing properties of the gustatory and olfactory stimuli, rather than necessarily the modality of stimulation, *per se*, that may be key here (see also Stevenson, 2012a). In fact, Stevenson et al. have suggested that any salient feature of olfactory stimulation that captures a person's attention (relative to the gustatory stimulus), no matter whether it be a novel odorant, or perhaps an odorant that is especially intense or pungent, should reduce the magnitude of any referral or olfactory stimuli to the oral cavity. Consistent with this view, Stevenson and his colleagues have demonstrated that the degree of oral referral (of orthonasally-presented odours) to the mouth is modulated by varying the relative attention-capturing capacity of the component olfactory and gustatory stimuli. In particular, these researchers reported less orthonasal odour binding (which was, anyway, not that pronounced in any of the three experiments that they reported) when an unpleasant trigeminal odorant (namely, glacial acetic acid) was added to a base plum odour that was relatively innocuous.

The suggestion here then is that attention is (for whatever reason) normally directed to the stimuli localized in the oral cavity (so far, as a result of exogenous attentional capture by the tastant). It is this that results in orthonasal oral referral (i.e., orthonasal location binding) and perhaps also the confusion between what one is tasting and what one is actually smelling retronasally.[3] However, returning to our earlier comparison of orthonasal and retronasal olfaction, another suggestion here might be that the somewhat impaired identification of retronasal odours (Sun & Halpern, 2005) results in people focusing their attention on the more salient sensory system (i.e., taste/gustation) when it comes to flavour perception.

2.4. On the role of olfactory/gustatory congruency on retronasal oral referral

Over the last 5 years, Juyun Lim and her colleagues have published a number of intriguing studies in which they have varied the congruency between olfactory and gustatory stimuli, demonstrating that this factor significantly modulates the magnitude of oral referral (Lim, Fujimaru, & Linscott, 2014; Lim & Johnson, 2011, 2012). For example, the participants in one study had to inhale either vanilla or soy sauce aroma by sucking on a straw (Lim & Johnson, 2011). The experimenter pipetted, air, deionized water (i.e., a putatively tasteless tactile control), a sweet taste solution, or a salty solution into the participant's mouth at the same time. The participants inhaled through the straw and exhaled through their nose (thus engaging retronasal olfaction). The taste stimulus in this particular between-participants study was deposited on to the participant's tongue from the pipette while they continued to breathe, thus ensuring simultaneous olfactory and gustatory stimulation. The participants reported where exactly they experienced the odour as originating. In order to help them do this, they were presented with a cross-section line drawing of a human head, with the following labels – throat, tongue, oral cavity, and nose – added at the appropriate locations (see Fig. 2). The participants had to respond in each trial by stating the location(s) that had been stimulated – (1) the front or back of nose; (2) the oral cavity; (3) the front and back of the tongue; and (4) the throat (though the latter option was chosen so rarely by the participants that these data were not used).

When presented in isolation, the participants chose the oral cavity (including the tongue) as the location where the odours were perceived as originating from on 40% to 45% of the trials where they made a localization response (see Fig. 3). Interestingly, Lim and Johnson (2011) found that having a relatively tasteless sample of water in their mouth[4] had no effect on the proportion of oral referral responses that were made (compare the "Air" and "Water" conditions in Fig. 3). This result would therefore appear to suggest that in-and-of-itself oral-somatosensory stimulation doesn't modulate oral referral. Once again, such a result obviously argues against previous suggestions (e.g., from Rozin, 1982; see also Murphy & Cain, 1980) that cutaneous oral stimulation is responsible

[3] One suggestion that might theoretically have been thought relevant here relates to the phenomenon of 'prior entry' (taken from the attention literature; Titchener, 1908; see Spence & Parise, 2010, for a review). In brief, the idea is that stimuli are perceived relatively earlier in time when attended, as compared to when they are relatively less attended (or unattended). Given that physically presenting one of two stimuli earlier in time leads to an increased weighting of that stimulus to the ensuing ventriloquism effect (Slutsky & Recanzone, 2001), part of the explanation for oral referral might be in terms of prior entry. To be absolutely clear, the presence of food in the mouth might lead to attention being focused there, which, in turn, gives rise to the prior entry (temporally-speaking) of gustatory over retronasal olfactory stimuli. However, this account, while superficially plausible, likely fails for just the same reasons as were outlined earlier when discussing von Békésy's (1964) relative stimulus timing account: Namely, precise stimulus timing does not seem to be pertinent to the case of everyday flavour perception. Furthermore, given that gustatory stimuli are likely already perceived earlier in time that the related retronasal stimuli (Spence & Squire, 2003), any additional attentional prior entry effect would seem redundant anyway.

[4] Though note that deionized water, as used in Lim and Johnson's (2011), Lim and Johnson's (2012) studies, is not, strictly-speaking, completely tasteless (de Araujo, Kringelbach, Rolls, & McGlone, 2003; see also Zald & Pardo, 2000).

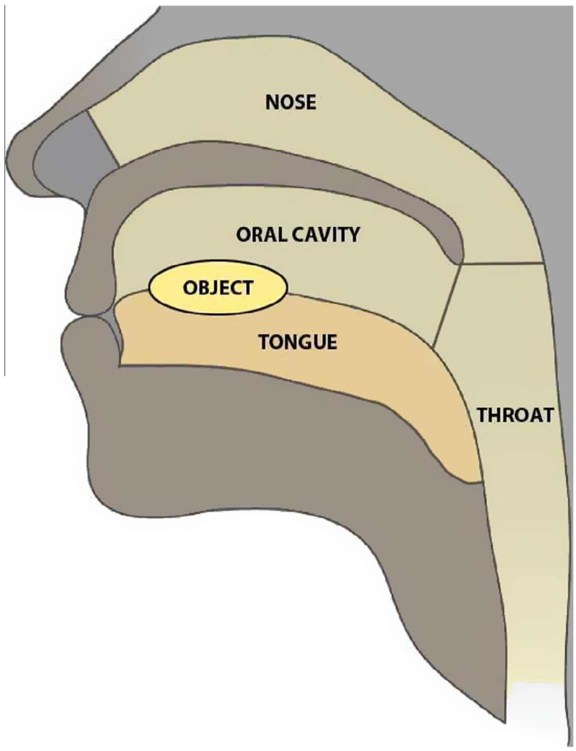

Fig. 2. The oral and nasal cavity map. The participants in Lim and Johnson's (2011, 2012) studies consulted this diagram while they performed the localization tasks. [Figures reprinted with permission.]

for oral referral. Furthermore, comparison of the results from those conditions involving the delivery of a tastant revealed that congruent odour-taste combinations (e.g., vanilla/sweet and soy sauce/salt) gave rise to significantly more oral referral (mostly to the tongue) than did those trials in which tasteless water was pipetted into the participant's mouth instead, or when the odour-taste combination was incongruent (e.g., vanilla/salt or soy sauce/sweet). So, for example, the percentage of trials on which oral referral of the vanilla odour occurred increased from 19% to 50% when a sweet taste was present, while oral referral of the soy sauce aroma went up from 22% to 49% when a salty taste was present in the mouth.

At this point, it is interesting to consider the neural correlates associated with such oral referral in the absence of any tastant or oral-somatosensory stimulation. Relevant here, Small et al. (2005) conducted a functional magnetic resonance imaging (fMRI) study in which vaporized olfactory stimuli were either presented orthonasally or retronasally. The retronasal oral referral that occurred in this study (in the absence of any specific taste or oral-somatosensory stimulation), was associated with enhanced neural activity at the base of the central sulcus, a part of the brain that is typically responsive to oral-somatosensory stimulation (e.g., Pardo, Wood, Costello, Pardo, & Lee, 1997).

Subsequently, Lim and Johnson (2012) went on to investigate what would happen under more naturalistic tasting conditions. In particular, they wanted to know whether more pronounced oral referral might be observed when the participants actually experienced a food stimulus in their mouth (rather than just having a liquid tastant pipetted in by the experimenter). The participants performed the same odour localization task as in Lim and Johnson's (2011) earlier study, but this time they were given a gelatin disk to taste. This food matrix could either contain just an odorant or else a congruent/incongruent odorant-tastant combination. Once again, the results suggested that, by itself, oral-somatosensory stimulation wasn't especially relevant when it comes to eliciting the oral referral of retronasal odours to the

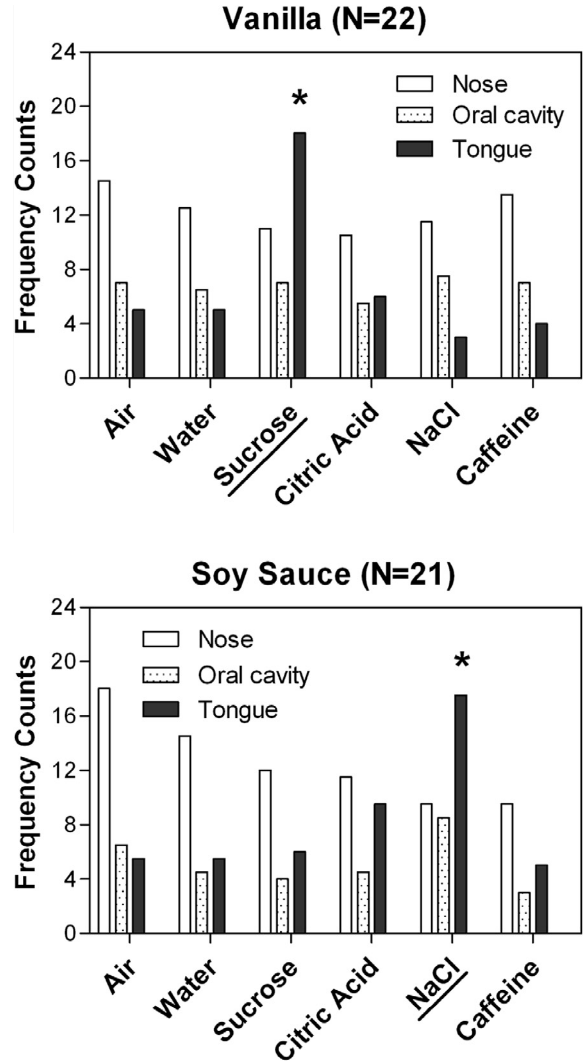

Fig. 3. Averaged frequency of participants' responses in the odour localization task in Lim and Johnson's (2011) between-participants study, separated by condition. The asterisks indicate significant differences ($p < .0001$) from the relevant odour-water pair. Notice how only the congruent tastant (sucrose in the case of the vanilla aroma, and sodium chloride, NaCl, in the case of the soy aroma) led to a significant increase in the rate of oral referral over that seen in the baseline tasteless condition. [Figures reprinted with permission from Lim and Johnson (2011).]

mouth (see Fig. 4). Specifically, retronasal odours were localized in the nose at a similar rate (about 50% of all localization responses in this condition), regardless of whether they were presented in aqueous form or as a tasteless gelatin disk.[5] However, as soon as a congruent tastant was added to the gelatin disk, odour referral to the mouth increased significantly.

A further intriguing finding to emerge from Lim and Johnson's (2012) study was that the localization of odors in the oral cavity

[5] Potentially relevant here, the suggestion has been made that we mislocalize flavours into the texturally appropriate food substrates (see Spence & Piqueras-Fiszman, 2014). This idea, for example, crops up in descriptions of the bacon and egg ice cream dish formerly served at Heston Blumenthal's *The Fat Duck* restaurant in Bray (see http://www.thefatduck.co.uk/). According to informal reports, people would localize the bacon flavour in the texturally appropriate (but relatively tasteless) crispy brioche, whereas the eggy flavour tended to stay behind in the more texturally appropriate ice-cream instead (cf. Delwiche, Lera, & Breslin, 2000). While the appropriate research has yet to be conducted, such suggestions, if validated empirically, might hint that Lim and Johnson's (2012) use of a gelatin matrix, while a step in the right direction, might simply not have been texturally rich or meaningful enough.

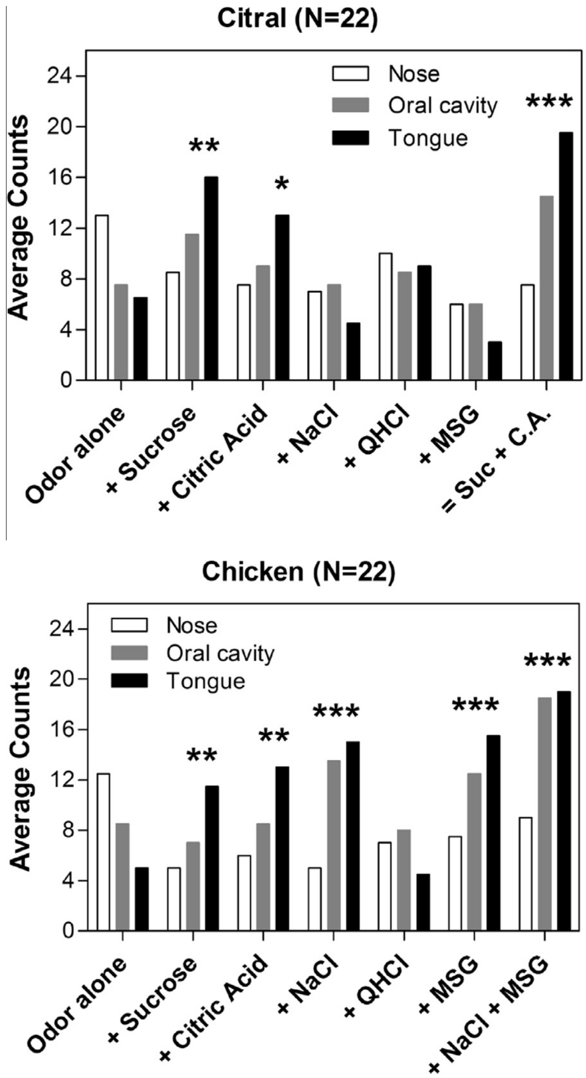

Fig. 4. Participants' averaged frequency responses in the odour localization tasks for each odour-blank or odour-taste pair. (NaCl = sodium chloride; MSG = monosodium glutamate; QHCl = quinine hydrochloride). Asterisks indicate that the comparison with the odour alone condition revealed a significant difference ($^{*}p < .05$, $^{**}p < .01$, $^{***}p < .0001$). [Results reprinted with permission from Lim and Johnson (2012).]

was more pronounced when the binary taste mixtures closely mimicked a familiar food source (i.e., citral aroma – which has a citrusy smell, sucrose, and citric acid, think here only of a lemony gelatin dessert; or chicken aroma, salt, and monosodium glutamate, MSG, as one might expect to find in a piece of chicken). As Lim and Johnson (2012, p. 519) note: *"When sampled with citric acid, sucrose, or the mixture of sucrose and citric acid, citrus odor was localized to the tongue 2, 2.5, and 3 times more often than when it was sampled alone in a gelatin matrix."* Taken together, then, Lim and Johnson's (2011, 2012) results provide convincing empirical support for the suggestion that the oral referral of retronasal odours to the mouth is primarily modulated by the presence of a congruent tastant (or tastants) in the oral cavity. Their results also support the suggestion that the degree of congruency (or consistency) between the olfactory and gustatory inputs modulates the extent (or magnitude) of oral referral.

Further evidence in support of this hypothesis comes from another study in which the participants were orally presented with

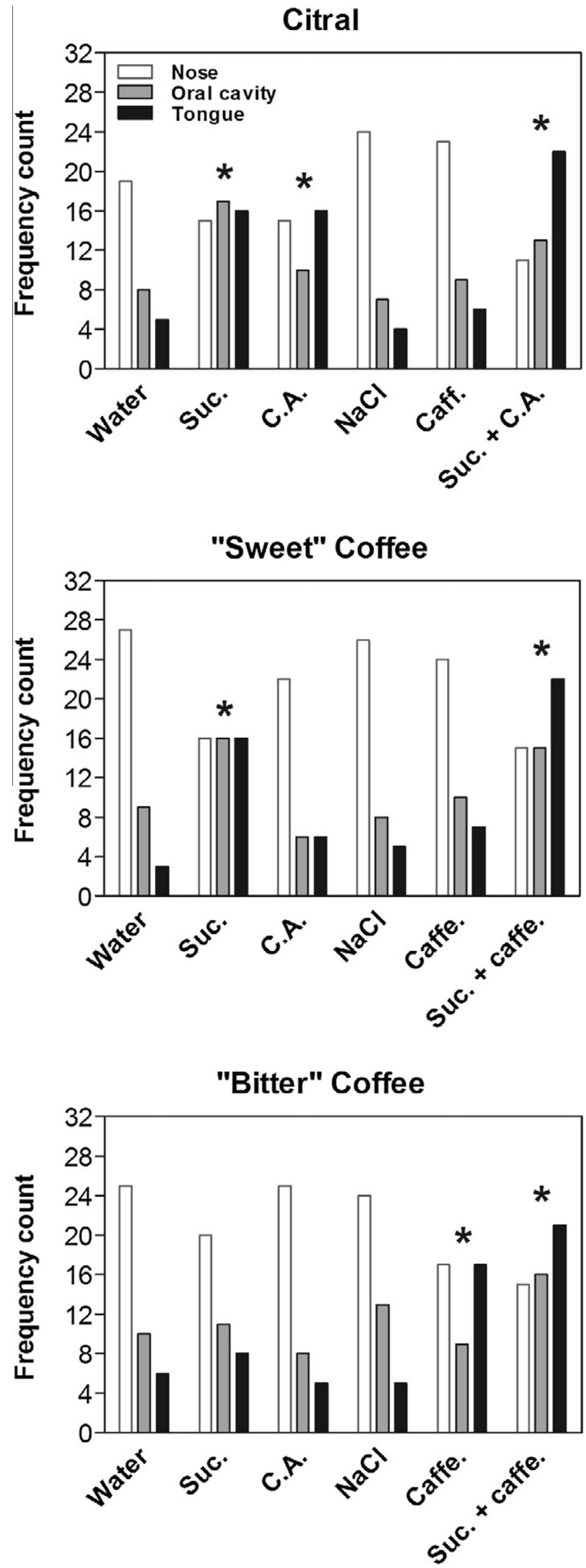

Fig. 5. Frequency of participants' responses in Lim et al.'s (2014) odour localization task for each odour-taste combination. (Suc. = sucose; C.A. = citric acid; NaCl = Sodium Chloride; Caffe. = caffeine). The participants reported no location, one location, or multiple locations in each trial. Asterisks indicates those conditions that are significantly different ($p < .0001$) from the baseline odour-water pair. [Figure reprinted from Lim et al. (2014) with permission.]

the aroma of either bitter or sweet coffee or citral aroma Lim et al. (2014). At the same time, a tastant (bitter, sour, salty, or sweet; or on occasion, a combination of two tastants) was presented in solution to the participant's mouth. Once again, the participants had to localize the ensuing perceptual experience. In this case, the self-reported crossmodal congruency between the olfactory and gustatory stimuli (defined as *"the extent to which the two sensations are commonly experienced together in a food"*; or put another way, the ecologically validity of the stimulus combination) was found to modulate oral referral (see Fig. 5). The rated odour-taste congruency correlated positively with the extent to which the odour was referred to the mouth (r = 0.88–0.98). Specifically, citral aroma plus citric acid and/or sucrose gave rise to more oral referral (specifically to the tongue) than did the relevant aroma-water baseline combination; Greater odour referral was also seen for the "sweet" coffee odour when presented together with the sucrose and sucrose-plus-caffeine mixture (see Fig. 5, middle panel); meanwhile, the caffeine-plus-sucrose mixture increased odour referral in the case of the "bitter" coffee odour as compared to the caffeine alone condition. By contrast, when presented as an individual tastant, the bitter taste of caffeine was found to have no impact on the degree of odour referral to the mouth in the case of the "sweet" coffee odour; similarly, sucrose failed to influence the degree of oral referral for the "bitter" coffee aroma.

2.5. Interim summary

The results reported in this section can be taken to suggest, and in some cases demonstrate, that a number of factors modulate the oral referral of olfactory stimuli to the mouth: these factors include von Békésy's (1964) intriguing suggestion regarding relative stimulus timing, the intensity of the gustatory stimulus (though note that, as yet, this has only been demonstrated in the case of orthonasal olfaction; i.e., when looking at the location binding of orthonasal olfactory stimuli; Stevenson et al., 2011b), and the congruency between the olfactory and gustatory inputs (in the case of retronasal olfaction; Lim & Johnson, 2012; Lim et al., 2014; see also Green, Blacher, & Nachtigel, 2010).

Another factor that has not been mentioned yet, but which was considered by Murphy and Cain (1980) as relevant to oral referral concerns the role of specifically trigeminal inputs. However, as noted by Lim (in press), there is still far too little systematic research into the role of the trigeminal system in the oral referral illusion (not to mention in flavour perception research more generally) to draw any firm conclusions here. (Here, it is perhaps also worth noting that most non-trigeminal irritants odours are not food related, such as, for example, rose PEA; Schneider et al., 2009). As yet, the role of the congruency between taste/odour and tactile sensation in modulating oral referral has similarly not been investigated directly. As Lim and Johnson (2012, p. 520) note: *"It is yet to be seen whether variations in tactile stimulation can affect the degree of retronasal odor referral and more broadly whether incongruent tactile stimulation can disrupt or circumvent integrative mechanisms between tastes and odors."*

2.6. On the origins of olfactory-gustatory congruency

While the above-mentioned studies clearly demonstrate that the degree of crossmodal congruency modulates the oral referral of retronasal odours to the mouth, it leaves open the question of where exactly that congruency comes from. There is plenty of evidence to show (or suggest) that congruency, defined by Lim and Johnson (2012, p. 288) as *"a taste that commonly appears with an odor in foods"*, mostly (if not entirely) results from associative learning, following prior exposure to the component stimuli when presented together in flavour stimuli (e.g., Frank & Byram, 1988; Prescott, 1999, 2012; Prescott, Johnstone, & Francis, 2004; Stevenson, Boakes, & Prescott, 1998; Stevenson, Prescott, & Boakes, 1995). Indeed, a number of researchers have suggested that when the available sensory inputs approximate a food that is familiar to the observer then the perceptual system will attempt to bind those cues into a unitary flavour percept, object, or Gestalt. The result of this multisensory integration is then localized to the mouth. This view certainly fits within the broader notion that has been prevalent in the literature on multisensory perception for decades now that the brain strives to create and "*maintain a perceptual experience consonant with a unitary event.*" (Welch & Warren, 1980, p. 655; see also Spence & Chen, submitted). Intriguingly, though, the perceptual similarity between the olfactory and gustatory stimuli does not seem to play any role in orthonasal (and so, presumably, also retronasal) odour binding (see Stevenson et al., 2011a).

2.7. On the dual-sensing of certain airborne molecules

As suggested by an anonymous reviewer of an earlier draft of this manuscript, it is perhaps also worth highlighting the fact that the chemosensory stimuli that we perceive, and label, as odorants, are ultimately merely just airborne molecules. Importantly, a subset of these molecules are detectable, and perceptible, by the gustatory system as well as by the olfactory system (e.g., see Chalé-Rush, Burgess, & Mattes, 2007; Wajid & Halpern, 2012; though see also Stevenson & Halpern, 2009). It would be interesting to know whether or not the magnitude of oral referral is larger in the case of such molecules. However, given how few odorants can be detected orally with the nose closed (i.e., when olfaction is prevented; see Spence et al., 2015), it can, I think, be argued that while this possibility should certainly be borne in mind, the dual sensing of airborne molecules, is likely a relatively rare occurrence in our everyday perception of flavour and hence of oral referral.[6]

2.8. Mathematical modelling of unification in multisensory flavour perception

In terms of its mathematical formalization, the congruency between olfactory and gustatory cues can perhaps best be conceptualized in terms of the 'coupling priors' incorporated in Bayesian causal inference models. Such models are undoubtedly becoming increasingly popular in the field of multisensory perception research (e.g., Ernst, 2007; Sato, Toyoizumi, & Aihara, 2007; Shams & Beierholm, 2010). The *prior* term (p_{common}) in Bayesian causal inference models, refers to *"how likely two co-occurring signals are to have a common cause versus two independent causes"* (Körding et al., 2007, p. 3). The Bayesian approach provides one means of formalizing different degrees of certainty regarding the unity (or unification) of two or more unisensory inputs as a continuous (rather than as a discrete) variable (e.g., Körding et al., 2007). It should, however, be noted that this approach is not without its critics (see Jones & Love, 2011; Murphy, 1993). Notably, some commentators worry that Bayesian models may do little more than simply re-express the cognitive account in mathematical terms. That said, such critics appear to be in the minority. I, for one, believe that the notion that olfactory-gustatory congruency can be captured, or formalized, in terms of coupling priors in Bayesian causal inference models will likely turn out to be a helpful way in

[6] One other potentially confusing case potentially comes from those flavours that are not perceptible as orthonasal odours. Solutions of ferrous sulphate may be one of the likely very few such examples. It has been argued that such solutions have little if any odour when sniffed orthonasally outside the mouth (Lawless et al., 2004). As Lawless, Stevens, Chapman, and Kurtz (2005, p. 193) put it, *'they are not effective orthonasal stimuli at the concentrations which evoke a strong retronasal smell'*. In this case, it would seem likely that an odorant is released in the mouth following a lipid oxidation reaction with saliva (Lawless et al., 2004).

which to conceptualize what is going on here. Should this be the case, it will, of course, be fascinating, in future research, to know a little more about how, and where exactly, such coupling priors (in the case of multisensory flavour perception) are represented neurally (cf. Rohe & Noppeney, 2015). However, note that even if we figure out where priors come from (e.g., are they all learned, or are some perhaps innate), that still leaves us with the more fundamental problem of why it is that the sense of smell is lost from our experience when tasting.

2.9. Oral referral and retronasal odour enhancement by taste

A priori, it might well have seemed reasonable to assume that olfactory-gustatory congruency would determine the magnitude of both oral referral and other examples of the multisensory integration of flavour stimuli, such as, for example, the retronasal enhancement of odour by taste. However, the latest evidence from Lim and her colleagues has now started to qualify this intuitive view in an interesting way (see Green, Nachtigal, Hammond, & Lim, 2012; Lim et al., 2014; Linscott & Lim, 2016). In particular, it turns out that while olfactory-gustatory congruency modulates both phenomena, the tastant (or combination of tastants; see Lim et al., 2014) also needs to have a nutritional signalling value in order for the latter to occur. In particular, Lim et al. have shown that the retronasal enhancement of odour by taste only occurs for nutritive tastants (namely sweet, salt, and umami, signalling the presence of sugars, electrolytes, and amino acids, respectively). By contrast, no such enhancement is seen for bitter and sour tastants likely indicating the presence of a less desirable attribute (e.g., poisons/potential toxins in the former case, and overripe or spoiled foods signalled by organic acids or low pH in the latter case; Scott & Mark, 1987; Scott & Plata-Salaman, 1991).[7] Interestingly, there is currently no evidence to suggest that the nutritional content of a tastant plays any role in oral referral.[8]

3. Attention and flavour binding in oral referral

The phenomenon of flavour binding (e.g., Green, 2002; Small & Green, 2011; Stevenson, 2009, 2014) appears to make it much more difficult for people to covertly direct their endogenous attention (Spence, 2014) selectively to just one element of an integrated flavour Gestalt (e.g., Delwiche, 2004; Small & Green, 2011; Spence, 2015a; Stevenson, 2009, 2014) – what some have chosen to call a "flavour object" (e.g., Lim & Johnson, 2012). Indeed, this inability to pull apart sensations through the endogenous direction of attention has also been noted by Smith (2013). Furthermore, research from Ashkenazi and Marks (2004) demonstrates that people find it difficult to attend voluntarily to olfactory stimuli once they have been localized to their mouth. Stevenson (2014) highlights two ways of thinking about what might be going on here: either attention might involuntarily "default" to the mouth and "taste" (this is what Stevenson calls "binding by ignorance"), or alternatively, taste and smell might come to constitute a common attentional channel that is directed to the processing of those stimuli experienced as originating in the mouth, in effect, as Stevenson puts it becoming one sense (see also Auvray & Spence, 2008).

One of the important questions lurking in the background here concerns whether the multisensory integration that gives rise to oral referral occurs early or late in human information processing – that is, whether attention effects occur prior to, or after multisensory integration (cf. Helbig & Ernst, 2008). However, this is by no means a simple question to answer given how closely interconnected attention and multisensory integration are (see Talsma, 2015; Talsma, Senkowski, Soto-Faraco, & Woldorff, 2010, for reviews), thus making it a particularly challenging matter to try and discriminate between them, even under the optimal of testing conditions (which is certainly not the case of flavour).

Further complicating matters here, the recent observation that mislocalization phenomena, such as evidenced by the audiovisual ventriloquism effect, can also be elicited by imagined visual stimuli, raises its own challenges (Berger & Ehrsson, 2013). That is, merely imagining a visual stimulus has been shown to capture the perceived location of a physically presented auditory stimulus. Given such results, one might well wonder whether merely imagining a taste, or flavour object (Hollingworth & Poffenberger, 1917; Chapter 11; Olivetti Belardinelli et al., 2009), could also lead to the oral referral of olfactory stimuli, no matter whether they happen to be presented orthonasally or retronasally. More generally, though, it should be noted that it is also not always so easy to distinguish the effects of attention on perception from those of mental imagery (see Segal, 1971, 1972; Segal & Fusella, 1970, 1971).

In conclusion, the fact that attention is normally directed to the mouth, either in an endogenous (i.e., voluntary), or exogenous (i.e., stimulus-driven) manner (see the earlier discussion of gustatory/attentional capture) as a result of tasting a flavourful stimulus would appear to be key to the phenomenon of oral referral. Attention that is presumably directed by knowing that a stimulus is touching the tongue or sides of the mouth. One of the key contrasts between oral referral and ventriloquism, then, is that in the latter, at least in the classic case, people are aware of two kinds of stimuli, visual and auditory. They are just not aware of how one is influencing their perception of the other, or that capture is taking place. The odd thing about oral referral is that people don't seem to realize that smell is involved in their in-mouth perception of what they are eating or drinking. The attentional capture is of something not recognized as present or misclassified/misperceived as a taste. The suggestion is that congruent combinations of olfactory and gustatory stimuli make it more likely that attention is focused on a common flavour object that is localized to the oral cavity by touch, whereas with incongruent combinations of stimuli there is less chance of binding taking place, and hence less oral referral. The challenge, though, as is so often the case when talking about attention, is knowing how to crystallize (or operationalize) its role neurally.[9]

3.1. Oral referral: a novel kind of multisensory interaction

Oral referral represents, at least according to the argument outlined here, a potentially novel kind of multisensory interaction, one that leads to a reassignment of the sensory modality that the observer thinks of as having being stimulated (Rozin, 1982;

[7] In terms of the neural underpinnings of such multisensory interactions that are contingent on the nutritional significance of the taste (or tastes), Rudenga Green, Nachtigal, and Small (2010) have demonstrated preferential communication between the anterior ventral insula and the feeding network of the human brain when a nutritive tastant is present in the mouth (see also Seubert, Ohla, Yokomukai, Kellermann, & Lundström, 2015). Given that, by contrast, the magnitude of oral referral is unaffected by the nutritional signalling value of the tastant(s), Lim and colleagues' results therefore suggest that different kinds of multisensory integration of chemical sensory cues are likely influenced by different factors (Lim et al., 2014).

[8] While I am not aware of anyone having attempted to assess the hedonic response to aroma-taste mixtures as a function of the extent of oral referral (cf. Lim et al., 2014; Linscott & Lim, 2016), one could certainly imagine why it would make sense to find nutritious flavour objects rewarding from a Gibsonian perspective (de Araujo & Simon, 2009; Gibson, 1966; see also Auvray & Spence, 2008; Prescott, 2012; Small & Prescott, 2005).

[9] It should, perhaps, be noted here that this conclusion differs somewhat from that put forward by Stevenson and his colleagues. Their conclusion is that the more attention-demanding the tastant, the more orthonasal location binding, while the greater the attention-demanding capacity of the odorant, the less orthonasal location binding that would be seen (Stevenson et al., 2011a, 2011b; see also Stevenson, 2012b). Problematic here, in terms of the attentional account, the less congruent or harmonious the olfactory and gustatory combination, the more attention that may be devoted to resolving what exactly one is tasting.

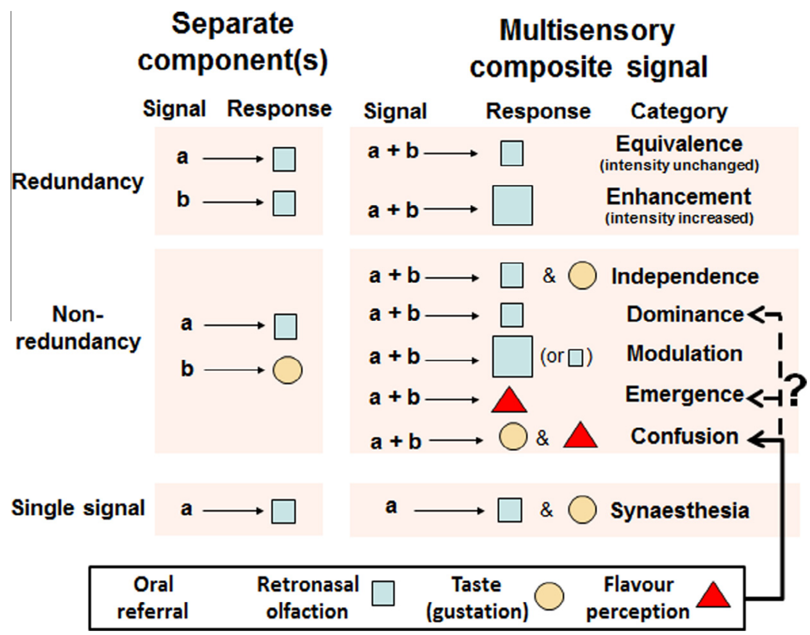

Fig. 6. Classification of the different types of multisensory interactions. adapted from Bremner, Lewkowicz, & Spence, 2012, in turn adapted from Partan & Marler 1999). Bremner et al. included multisensory syneasthetic percepts given the widespread interest in the topic since the publication of Partan and Marler's original paper. Here, I have added an additional row – Confusion. The argument being that oral referral may represent the only example of such modality confusion that has been reported in the literature to date. Note also that confusion cannot be subsumed within any of the other types of multisensory interaction that have been outlined previously. [That said, an argument can be made that what is really at stake here is actually Emergence, namely the emergence of a new modality that is flavour. Alternatively, one might think of it as an example of dominance. See text for details.]

Spence et al., 2015). As such, oral referral goes well beyond other illusions, such as the McGurk effect (McGurk & MacDonald, 1976) and/or the ventriloquism illusion (Alais & Burr, 2004; Caclin et al., 2002; Jackson, 1953), where we can be aware of both modalities even if not of how they interact. While there may be a change in the nature of the observer's perceptual experience in the case of the latter two illusions (specifically a change of the identity of what is said, or of the location where the sound is perceived as coming from), the observer is unlikely to be confused about which of their senses have been stimulated, or used to perceive the stimulus configuration that has been presented to them.

By contrast, it can be argued that oral referral reflects a qualitatively novel kind of multisensory interaction because it is one of the only examples from the entire published literature on multisensory perception of a situation in which the observer is confused about the modality/sense by which we are having a particular perceptual experience (Lim & Johnson, 2012; cf. Larsen, McIlhagga, Baert, & Bundesen, 2003). As such, "Confusion" should perhaps be added to the list of interaction types that have been outlined by researchers so far (see Fig. 6).[10] That said, one might also be tempted to think of it as an example of Emergence (of a new flavour modality) or perhaps even of Dominance when people report taste to the exclusion of olfaction (e.g., as when we say that we have lost our sense of taste when suffering from a blocked nose, or in those situations where the tastant is too dominant – so salty or sour, say, that you can't attend to, or get, the other flavour components).

3.2. Experiencing taste/flavour outside the mouth

One of fundamental constraints on multisensory flavour perception is that flavours are only ever experienced as originating in the oral cavity. This might seem all the more strange given the growing body of evidence showing the existence of taste receptors in the gut, and in a variety of other inaccessible locations (e.g., Finger & Kinnamon, 2011; Finger et al., 2003; Trivedi, 2012). Last year, Michel et al. (2014) demonstrated that taste/flavour experiences can, at least under certain conditions, be mislocalized outside of the mouth. These researchers conducted a version of the now-famous rubber hand illusion (see Botvinick & Cohen, 1998), using a rubber tongue instead of a rubber hand. The participants in these studies had to stick their tongue out, and insert their face inside a mirror box. By means of the latter contraption, it was possible to make it look as if the rubber tongue was the participant's own. Next, the participant's own tongue was stroked out of sight by the experimenter with a Q-tip, while another Q-tip was seen synchronously stroking the rubber tongue. In other words, the participants saw the fake tongue being stroked at the same time as they felt their own tongue being stroked. After a relatively short interval, many of the participants reported experiencing the fake tongue as their own. Having established the basic illusion, Michel and colleagues went on to investigate the consequences of dropping a few drops of lemon juice onto the fake tongue. Intriguingly, a few of the participants reported experiencing a sour taste on their own tongue. Given what we have seen here, it would be interesting, in future research, to determine whether the oral referral of olfactory, and not just taste, stimuli, could be mislocalized to the

[10] Such classification schemes are obviously not without their own controversy: If one pursues the line forwarded by Stevenson and others (Stevenson, 2014; see also Auvray & Spence, 2008), that oral referral is linked to the emergence of a flavour sense, then perhaps what we have is the emergence of a new sense as much as a confusion between inputs. That said, the flavour modality could itself still be a novel, or at least relatively rare, occurrence of emergence. The reason being that one of the only multisensory phenomena that have been put forward, thus far, as an example of emergence is the phoneme perceived in the case of the McGurk effect (see Partan & Marler, 1999, p. 1273). What is perceived (e.g., "da"), is qualitatively different from either of the speech stimuli that would be perceived under conditions of unisensory auditory or visual stimulation (i.e., the auditory phoneme "ba" or a face seen articulating "ga"). However, one might argue that it is really just an example of modulation, but one that just so happens to occur on a phonemic continuum that has clear categorical boundaries. Now, it is unlikely that this kind of meaty philosophical issue is going to be resolved in a footnote! Nevertheless, it is my hope that laying out a classification scheme such as that presented in Fig. 6, will at least help to draw attention to the issue, of how exactly to classify oral referral in the scheme of multisensory interaction types.

seen tactile stimulation on the (fake) tongue. However, given the various lines of evidence reviewed here, it has to be said that such a form of olfactory referral would seem unlikely. Nevertheless, the results of Michel et al.'s research do hint at the possibilities associated with capturing, or referring, perceptual experiences associated with the chemical senses, outside the strict confines of the oral cavity. Given the relations between odour and texture (e.g., Bult, de Wijk, & Hummel, 2007), and the texture congruency with taste and flavour, there is undoubtedly room for much more research here.

4. Conclusions

Ultimately, understanding the phenomenon of oral referral is key to gaining a better understanding of multisensory flavour perception (see Lim & Johnson, 2011, 2012). Oral referral has been likened, by some researchers, to the ventriloquism effect (Auvray & Spence, 2008; Todrank & Bartoshuk, 1991), but as we have seen here, the two phenomena may be importantly (i.e., qualitatively) different. This difference resides in the confusion that people experience concerning which of their senses have actually been stimulated, and what component of their perceptual experiences they should attribute to each one of their chemical senses (Shepherd, 2012). Oral referral is, then, both a fascinating empirical and theoretical phenomenon, and a fundamental feature of multisensory flavour perception in humans. Its occurrence is key to understanding the everyday confusion (between taste and smell) that is present in the world of flavour perception (Lim & Johnson, 2011, 2012; Rozin, 1982; Stevenson et al., 2011a,b; see also Lawless et al., 2003).

In summary, the intensity of the gustatory stimulus (at least in the case of orthonasal olfaction; Stevenson et al., 2011b), and the congruency between the olfactory and gustatory inputs (in the case of retronasal olfaction; Lim & Johnson, 2012; see also Green et al., 2010) would appear to be key modulatory factors. By contrast, the nutritional value of the tastant does not seem to affect oral referral, thus contrasting with what is seen in the case of retronasal odour enhancement by taste. Furthermore, and perhaps surprisingly, the phenomenological similarity between the odorant and tastant is also seemingly irrelevant, at least as far as orthonasal location binding is concerned (Stevenson et al., 2011a). While no evidence supports the early suggestion that oral referral reflects oral-somatosensory capture, attentional capture by salient gustatory cues, or an inability to voluntarily attend to olfactory stimuli once they get integrated into flavour objects located in the oral cavity, does seem to be important (Stevenson et al., 2011a). The latter possibly attributable to the emergence of a unitary flavour modality (Stevenson, 2014; see also Auvray & Spence, 2008). Whatever the most appropriate explanation, though, people appear to find it especially difficult to attend selectively to olfactory stimuli following their oral referral to the mouth (e.g., Ashkenazi & Marks, 2004; see also Stevenson, 2014).

Having demonstrated the robustness of the empirical phenomenon, and having established a number of key modulatory factors, it will be interesting in future research to try and figure out where, and how, oral referral occurs, or is represented, neurally (cf. Spence, 2015c), and how best to model it, most likely in terms of Bayesian decision theory.

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