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Review

What is the Relation between Chemosensory Perception and Chemosensory Mental Imagery?

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Abstract

The study of chemosensory mental imagery is undoubtedly made more difficult because of the profound individual differences that have been reported in the vividness of (e.g.) olfactory mental imagery. At the same time, the majority of those researchers who have attempted to study people's mental imagery abilities for taste (gustation) have actually mostly been studying flavour mental imagery. Nevertheless, there exists a body of human psychophysical research showing that chemosensory mental imagery exhibits a number of similarities with chemosensory perception. Furthermore, the two systems have frequently been shown to interact with one another, the similarities and differences between chemosensory perception and chemosensory mental imagery at the introspective, behavioural, psychophysical, and cognitive neuroscience levels in humans are considered in this narrative historical review. The latest neuroimaging evidence show that many of the same brain areas are engaged by chemosensory mental imagery as have previously been documented to be involved in chemosensory perception. That said, the pattern of neural connectively is reversed between the 'top-down' control of chemosensory mental imagery and the 'bottom-up' control seen in the case of chemosensory perception. At the same time, however, there remain a number of intriguing questions as to whether it is even possible to distinguish between orthonasal and retronasal olfactory mental imagery, and the extent to which mental imagery for flavour, which most people not only describe as, but also perceive to be, the 'taste' of food and drink, is capable of reactivating the entire flavour network in the human brain.

Keywords

flavour, olfaction, orthonasal, retronasal, taste

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1. Introduction

The vast majority of research on the topic of mental imagery in humans has been conducted in the visual modality (e.g., see Galton, 1880, 1883; Ganis, 2013; Kosslyn, 1994; Pearson, 2019). That said, mental imagery also operates in the other senses too, such as audition (e.g., Gissurarson, 1992; Halpern and Zatorre, 1999; Hubbard, 2013; Intons-Peterson, 1992; Oh et al., 2013; Reisberg, 1992; Zatorre et al., 1996), haptic touch (e.g., Gallace, 2013; Jeannerod, 1995; Klatzky et al., 1991), olfaction (Carrasco and Ridout, 1993; Crowder and Schab, 1995; Herz and Engen, 1996; Stevenson and Case, 2005; Zatorre, 1999), and taste (see Note 1) (e.g., Sauvageot et al., 2000). According to Bensafi et al. (2013, p. 77): "Olfactory and gustatory mental images are defined as short-term memory representations of olfactory or gustatory events that give rise to the experience of "smelling with the mind's nose" or "tasting with the mind's tongue". " (see also Kosslyn, 2003).

Until a few decades ago, however, many researchers still questioned the very existence of olfactory mental imagery (e.g., see Elmes, 1998; Elmes and Jones, 1995; Engen, 1982, 1987; Herz, 2000; Schab, 1991). For instance, Schab (1991, p. 242) claimed that: "There is no unambiguous empirical evidence supporting an ability to image odors", while Carrasco and Ridout (1993, p. 287) state that: "Whether a system of imagery for olfaction exists is currently an unsettled issue" (Note 2). Researchers have though, by now, managed to provide extensive psychophysical and cognitive neuroscience support for the existence of an 'inner nose' (e.g., Algom and Cain, 1991; Carrasco and Ridout, 1993; Levy et al., 1999a; Lorig and Roberts, 1990; Lyman, 1988; Lyman and McDaniel, 1990; though see also Crowder and Schab, 1995; Schifferstein, 1997).

Just as in the visual modality (e.g., see Kosslyn, 1994; Pearson and Kosslyn, 2015; Pylyshyn, 2003), there has also been some debate concerning the question of whether olfactory mental imagery is propositional (i.e., semantically-mediated) or depictive in nature (Rinck et al., 2009; Sugiyama et al., 2006 — cf. Koenig et al., 2000). Furthermore, some authors (e.g., Crowder and Schab, 1995; Elmes, 1998; Herz, 2000) have argued that it is not altogether clear whether the alleged odour images in previous research were perceptual or propositional in nature, that is, whether they were odour-like rather than verbal-like experiences. At the same time, however, other researchers have questioned the extent to which tacit knowledge and task demands may explain the data from a number of the mental imagery studies that have been published to date (Farah, 1988; Intons-Peterson, 1983; Pylyshyn, 1981; Schifferstein, 1997).

A large body of cognitive neuroscience research now suggests that visual mental imagery activates many (if perhaps not necessarily all) of the same brain areas as visual perception (e.g., Kosslyn et al., 1995; though see also Spagna et al., 2021). Intriguingly, however, the patterns of connectivity appear to operate in opposing directions — 'bottom-up' in the case of visual perception and 'top-down' in the case of visual mental imagery (see Dijkstra et al., 2017). For those interested in the chemical senses, it is natural to wonder whether the same story — namely, that imagery and perception activate the same network of brain areas — also describes the case of chemosensory perception and chemosensory mental imagery (in all its various guises, stretching from olfactory mental imagery through gustatory and flavour mental imagery; see also Royet et al., 2013).

In this narrative review (Ferrari, 2015; Furley and Goldschmied, 2021), I examine the similarities and differences between chemosensory perception and chemosensory mental imagery. In the following sections, this question is addressed at a number of different levels (Finke, 1980), from phenomenology (i.e., based on introspection) through to perceptual/psychophysical interactions and behavioural similarities. The degree of overlap in terms of the underlying neural substrates is also assessed. Ultimately, it is argued that while there are many similarities between chemosensory mental imagery and chemosensory perception at these various levels, there are also a number of salient differences. Furthermore, it remains unclear as to whether a meaningful distinction can be made between orthonasal and retronasal olfactory mental imagery, and whether the entire flavour network in the human brain (Suen et al., 2021) is reactivated in the case of people mentally imagining the flavour of food and drink (see also Seubert, Ohla, Yokomukai, Kellermann and Lundström, 2015; Stevenson and Prescott, 1997).

2. Comparing Chemosensory Mental Imagery to Chemosensory Perception

2.1. Introspection: Individual Differences in the Vividness of Chemosensory Mental Imagery

The results of those studies that have used introspective reports to assess the vividness of people's mental imagery tend to suggest that visual images are experienced as most vivid, whereas olfactory and gustatory images tend to be least vivid (e.g., Ashton and White, 1980; Betts, 1909; Marsella and Quijano, 1974; Schifferstein, 2009; Sheehan, 1967; White et al., 1977 — see also Gilbert et al., 1998; Lawless, 1997; Lindauer, 1969; Royet et al., 2013; Young, 2020). Lawless reported that 25% of the participants whom he quizzed reported never having experienced olfactory mental imagery. When Brower and Brower (1947) asked participants to imagine the sight, sound, and smell of frying onions, 57% reported being unable to imagine the smell, whereas only

3% were unable to visualize it. When Lindauer (1969) repeated the test, all his participants could visualize frying onions, but 30% reported being unable to imagine the smell.

At the same time, however, the published research also suggests the existence of large interindividual differences in the ability to create (and/or the vividness of) olfactory mental images (Schifferstein, 2009; Sulfaro et al., 2024; Switras, 1978, 1979 — though see also Bensafi et al., 2005; and Takahashi et al., 2023; Zeman, 2024, on the emerging study of aphantasia) (Note 3). According to research from Fantin et al. (2022), age and gender may affect the vividness of people's olfactory mental imagery, at least when it is assessed by self-report. Meanwhile, another study reported that those individuals who are classified as good olfactory imagers (by questionnaire) sniffed odorants for longer and judged them to be more edible and familiar, thus suggesting a better semantic knowledge associated with odours (Rouby et al., 2009; see also Bensafi and Rouby, 2007; Stevenson et al., 2007). People sometimes appear to recruit visual cortex when they find themselves in the 'tip-of-the-nose' state — that is, visual imagery is seemingly recruited to help try and identify the source of (or name for) an odour (Qureshy et al., 2000).

In contrast to the well-documented individual differences in the vividness of olfactory mental imagery, far fewer studies have provided evidence relevant to addressing the question of whether such individual differences also exist in terms of people's ability to imagine basic tastes or flavours. The ability of people to imagine specifically oral trigeminal stimuli, such as, for example, the pungency of pepper (Spence, 2024) or ginger (Spence, 2023a), the burn of chilli (Spence, 2018), and/or the cooling of menthol have also received virtually no attention from researchers either (Simons and Carstens, 2008; Stevenson and Prescott, 1997). Meanwhile, studies of craving (a largely separate area of empirical research; see Kemps and Tiggeman, 2013) (Note 4) appear to suggest that these two modalities of mental imagery come close behind vision in terms of driving people's cravings. For instance, according to the results of one survey in which people were asked to assign percentages to each of five senses involved in an imagined food craving experience, vision (40%) scored top, followed by gustatory (31%) (Note 5) and olfactory (16%), with the senses of touch (10%) and audition (4%) apparently little used (Tiggemann and Kemps, 2005). The vividness of olfactory mental imagery responsiveness to food cues has also recently been established as a risk factor for weight gain due to its role in supporting craving (Perszyk et al., 2023).

Dou et al. (2018) reported that even when participants are instructed to try and suppress their mental imagery, food items (be they presented as orthographic stimuli or as drawings) nevertheless still involuntarily elicit olfactory (an effect in ∼40% of trials), taste (∼54%), touch (∼60%), and visual/auditory (∼79%) mental imagery. At the same time, some researchers have suggested that imagery training may facilitate people's ability to mentally imagine the flavour of food (Richardson and Patterson, 1986; see also Bensafi et al., 2013). As Stevenson and Case (2005, p. 244) note: "self-reports of olfactory imagery can resemble those obtained for actual perception".

2.2. Perceptual Interactions between Chemosensory Mental Imagery and Perception

Researchers have long been aware that visual imagery and visual perception interact as, for example, in the well-known Perky effect (Perky, 1910; see also Ishai and Sagi, 1995; Pearson et al., 2008) (Note 6). For instance, in her classic early study, Cheves Perky reported that those participants who had been asked to imagine coloured objects (such as a banana) on the wall of a pitch black room incorporated elements of a faint colour patch that had been surreptitiously back-projected onto the wall of the experimental chamber. This phenomenon subsequently came to be known as 'incorporation' — though see Craver-Lemley and Reeves (1992), for the suggestion that this may simply reflect nothing more than an attentional distraction effect. More recently, Berger and Ehrsson (2013; see also Berger, 2020) reported that perception and mental imagery interacted, such that, for example, imagining a visual stimulus in one location could lead to the ventriloquism of a sound that had simultaneously been physically presented from a different location. At the same time, however, in a number of these areas there is a question of discriminating between the mental imagery of a stimulus in a particular location, say, from merely attending to that location (or modality, Segal and Fusella, 1971 — see also Royet et al., 2013).

Over the last 30 years or so, various researchers have investigated whether chemosensory mental imagery interacts with chemosensory perception. For example, Carrasco and Ridout (1993) conducted two studies, one with a set of 16 largely familiar olfactory stimuli (such as chocolate and leather) presented to participants in pairs. Another group of participants merely imagined pairs of odorants. In both cases, the participants had to rate the degree of similarity between various pairs of olfactory stimuli. Multidimensional scaling (MDS) suggested that three-dimensional solutions with similar stimulus dimensions, such as fruitiness, strength, and familiarity, defined the psychological space of both imagined and perceived odours, hinting at the similarity between imagery and perception at this level (see also Sugiyama et al., 2006).

Algom and Cain (1991) reported similar interaction patterns for perceived and imaginary mixtures of odorants. A couple of years later, Algom et al. (1993) studied perceptual and mental mixtures of odour and taste. They used taste–smell interactions to study olfactory mental imagery. The participants in their study were either presented with tastant–odorant mixtures (sucrose and orange), or asked to construct these mixtures mentally (note that both groups had previously been familiarized with the mixture constituents). The participants' task was to rate the intensity of presented or imagined mixtures. Both perceived and mentally constructed mixtures (of different concentrations of sucrose and orange) revealed the same, approximately additive, pattern of (multisensory) integration. These results were therefore taken to show that imagined smells interact with both imagined and perceived tastants in the same way as real perceived smells do.

By contrast, when Schifferstein (1997) studied sucrose–citric acid mixtures, mixture suppression was observed when tastants were actually combined, while a very different pattern of results was observed when participants merely imagined what a mixture of tastants would taste like. The latter results would appear to suggest that the phenomenon of mixture suppression does not operate when people imagine mixtures of basic tastes. Indeed, such results led Schifferstein to question whether Algom et al.'s (1993) earlier results might have reflected people's tacit knowledge of olfaction and gustation rather than the consequences of olfactory plus gustatory mental imagery being combined. However, to the extent that mixture suppression is a phenomenon that reflects interactions taking place at the taste receptor level, rather than centrally (cf. Bell et al., 1987, for a receptor-level explanation of odour mixture suppression), Schifferstein's results should perhaps not come as such a surprise.

Stevenson and Prescott (1997) reported a study in which the participants had to make judgements concerning the sweetness, sourness, and intensity in memory (i.e., using gustatory mental imagery) or with combinations of sucrose and citric acid that were actually presented. Participants' performance in the imagery and perception conditions was equivalent. Debriefing revealed some explicit knowledge about the way such mixtures interact (cf. Schifferstein, 1997). In a second experiment, Stevenson and Prescott investigated the relationship between such explicit knowledge and performance on the memory task. The participants once again made the same ratings, but sampled, on separate days; (1) capsaicin alone, (2) a flavoured, sucrose–citric acid solution and imagined adding capsaicin, (3) the solution alone, and finally (4) the solution with capsaicin. Performance was equivalent across the semi-mental and real mixture conditions. In particular, only sweetness was suppressed. Intriguingly, however, debriefing of the participants revealed that they thought that all of the tastes and flavours had been affected by capsaicin, thus arguing against Schifferstein's tacit knowledge account in this case (see also Cain and Algom, 1997).

The evidence that has been published to date demonstrates that imagined chemosensory stimuli (such as imagined odours and imagined basic tastes) can interact with the perception of actual olfactory and gustatory stimuli (see Spence, 2023b, for a review). Odour-induced taste enhancement (OITE) has been observed in response to a remembered/imagined olfactory stimulus (see

Djordjevic et al., 2004a,b). For instance, the presentation of a strawberry odour has been reported to enhance the perceived sweetness of a sucrose solution whereas the presence of a soy sauce odour enhanced the perceived saltiness of a solution of sodium chloride instead. That is, the presence of an odour enhanced participants' perception of the congruent taste (where congruency is determined by the cooccurrence of the taste and smell in foods; Spence, 2022). A similar, but rather limited effect was also documented with odours that were merely imagined: that is, imagined strawberry enhanced perceived sweetness of water solutions, and imagined soy sauce enhanced the perceived saltiness of weak sodium chloride solutions. In other words, imagined odours can induce changes in perceived taste intensity that are comparable in kind to those elicited by perceived odours.

Djordjevic et al. (2004a) reported that simply imagining a ham odour was sufficient to reduce people's ability to detect sucrose in solution when compared to their performance when instructed to imagine strawberry odour, or when no odour imagery instructions were provided. Note that the latter two conditions gave rise to an equivalent level of performance, thus arguing that it was imagining the incorrect odorant that selectively impaired performance (i.e., rather than imagining the correct odorant somehow facilitating it). In this study, significant effects were reported for both the perception and imagery conditions. Meanwhile, Djordjevic et al. (2004c) demonstrated that olfactory imagery enhanced poeple's ability to detect a congruent odourant, whereas visual imagery did not. In this case, the participants were presented with two bottles, one with no odour, and the other with a threshold level concentration of phenyl ethyl alcohol (PEA, which smells like roses) and citral, a substance that smells like lemons, and had to try and identify the bottle that contained the aroma.

Taken together, therefore, the evidence that has been published to date highlights a number of similarities between chemosensory mental imagery and chemosensory perception (e.g., Algom and Cain, 1991; Algom et al., 1993; Baird and Harder, 2000; Carrasco and Ridout, 1993; Djordjevic et al., 2004a,b,c, 2005; Stevenson and Prescott, 1997), as well as a few putative differences (e.g., Barker and Weaver, 1983; Osaka, 1987; Schifferstein, 1997).

3. Behavioural Similarities: Sniffing and Salivating in Response to Imagined Stimuli

Overt eye movements seen while people imagine particular visual stimuli have been shown to match those expected were people to be actually looking at a perceptual image (e.g., Laeng and Teodorescu, 2002). Such findings have been taken to highlight the behavioural similarities that exist between visual mental imagery and visual perception (see also Laeng and Sulutvedt, 2014).

Researchers have also reported an overlap between perception and imagery in the case of people's olfactory behaviours. In particular, people tend to inhale when imagining odours (Bensafi et al., 2003) (Note 7). What is more, they sniff (inhale) more deeply when imaging a pleasant odour (e.g., chocolate) than when imagining an unpleasant one (e.g., urine; Bensafi et al., 2003). Meanwhile, Bensafi et al. (2007) reported that hedonic-specific activity in piriform cortex during odour mental imagery appears to mimic that seen during olfactory perception

At the same time, blocking people's nostrils has been shown to reduce the vividness of olfactory mental imagery in a group of individuals with a high olfactory mental imagery ability (Arshamian et al., 2008). Blocking participants' noses so as to prevent sniffing reduced the emotional impact of the olfactory mental image and made the imagined quality of pleasant odours less distinct from unpleasant odours. Kleemann et al. (2009, p. 1) summarized their findings by suggesting that: "We conclude from our results that olfactory perception and olfactory imagery both have effects on the human respiratory profile and that these effects are based on a common underlying mechanism" (Note 8).

In terms of gustatory responses (or behaviours), people tend to salivate when eating sour-tasting foods, such as a lemon, or even seeing lemons being sliced and/or other people biting into sour foods, such as (a slice of) lemon (see Spence, 2011, for a review). Furthermore, simply imagining tasting something sour has also been shown to lead to salivation. For instance, Winer et al. (1965, p. 876) verbally suggested to their participants that a solution that participants had in their mouth (which was a pure tastant, either citric acid or sucrose dissolved in water) to: "Disregard the actual taste of the solution you are using and vividly imagine, trying as best you can, all during the collection interval, that the solution is a strong, sour/sweet solution (like the one you tasted earlier)". The results provided some (albeit weak) evidence to suggest that verbal suggestion had a measurable impact on parotid secretion rate in response to the actual gustatory stimuli. In particular, introducing the suggestion that water was sour and that citric acid was tasteless, effectively elevated and depressed the rate of parotid secretion (see also Jenkins and Dawes, 1966; White, 1978; Wooley and Wooley, 1973).

However, a somewhat different pattern of results was reported by Drummond (1995). In the latter study, 24 participants both imagined, and actually tasted, something sour on one side of their tongue. Increased parotid salivation was observed in both cheeks during the actual unilateral gustatory stimulation, with a greater response documented on the stimulated side than contralaterally. However, although the participants were able to imagine the sour taste more clearly after having actually experienced it, salivation did not increase significantly during the imagery trials (either before or after exposure to the sour taste). In fact, salivation during the imagery condition actually decreased below baseline after exposure. More recent research has though demonstrated that vivid visual mental imagery of what a desirable food smells like can give rise to an increase in salivation (Keesman et al., 2016; Krishna et al., 2014 — though see also Wang et al., 2017).

Taken together, therefore, the evidence in terms of observable behavioural responses to chemosensory mental imagery once again shows both a number of similarities (Bensafi et al., 2003, 2005, 2007; Jenkins and Dawes, 1966; Kleemann et al., 2009; White, 1978; Winer et al., 1965; Wooley and Wooley, 1973) as well as a few differences (Drummond, 1995). While the majority of the research has tended to focus on participants imagining ambient odours (such as ham, strawberry, or soy sauce), or basic tastes (such as sour or sweet), one might expect to find that people would exhale through their noses, and/or engage in some sort of masticatory behaviours (i.e., over-and-above simply salivating), when mentally imagining the taste/flavour of food. However, we are not aware of anyone who has reported on this directly/explicitly. In their excellent and very thorough review of olfactory imagery from a couple of decades ago, Stevenson and Case (2005) highlight the fact that at least two separate sensory systems, taste and smell, are involved in eating and drinking. They write that “The distinction between taste and smell is an important one for two reasons: First, many participants regard eating and drinking as involving only taste stimuli and do not understand the role of smell. This perception has been exploited in some imagery experiments. Second, several of the studies described below involve both taste and smell, so it is important to bear in mind that these are separate sensory systems”. (Stevenson and Case, 2005, p. 245).

4. Cognitive Neuroscience of Chemosensory Perception/Mental Imagery

The cognitive neuroscience research that has been published over the last quarter of a century or so has identified a number of neural substrates involved in various aspects of chemosensory perception. The question to be addressed in this section of the review concerns the extent to which the same areas are also involved (i.e., activated) in the case of chemosensory mental imagery. The anterior insula and frontal operculum (AI/FO), known as the primary gustatory cortex (though see below for other discrete regions within the insula that might also deserve this label), receive direct projections from the ventroposterior medial nucleus of the thalamus, and project to the orbitofrontal cortex (e.g., Börnstein, 1940; Frey and Petrides, 1999; Shenkin and Lewey, 1944; Small, 2010; Small et al., 1999). Intriguingly, taste-specific representations have been discerned in human insular cortex (IC) and the overlying operculum (Chikazoe et al., 2019).

The IC receives multimodal sensory inputs including gustatory, visceral, thermal, and pain *via* the sensory thalamus. However, despite its designation, the gustatory area in the IC involves a relatively small percentage (10%) of gustatory neurons. In fact, the majority of the population responds to jaw and mouth movements. The IC does, however, have dense reciprocal connections with the amygdala, in which 7% of the neurons respond to gustatory stimuli. Additionally, some gustatory information is sent directly to the orbitofrontal cortex (OFC), designated as the secondary gustatory cortex. The OFC is believed to process the identification of food, and to represent information concerning satiety and food preference. Recalling the taste of food has been reported to give rise to an asymmetric prefrontal cortex activation (Okamoto et al., 2011 — see also Okamoto et al., 2006).

Neuroimaging research from Levy et al. (1999b) indicated that the brain regions activated for mentally imagined tastes are consistent with those for actual taste perception. However, using the technology available at the time, it was simply not possible to distinguish the regional brain localization for salt or sweet taste memories. However, the story has now changed, given the dramatically higher field-strength scanners (7T) that have become available for research in recent years and which offer much better spatial resolution (see below). In a functional magnetic resonance imaging (fMRI) study, Japanese volunteers were instructed to think about pickled plums (*umeboshi*), a traditional Japanese food with a strong and sour taste (Kikuchi et al., 2005). A significant increase in neural activation was documented in the right insula, the bilateral opercula, the bilateral orbitofrontal cortices, and the left Broca's area. Although activation in the primary gustatory area (insula) was very weak and detected only unilaterally, the pattern of neural activation was nevertheless similar to that observed during taste perception. Here, it is interesting to note that like in a number of other studies, the objective existence of chemosensory mental imagery (specifically mentally imagining tastes) is taken to come from activation of the relevant brain areas rather than necessarily from the introspective reports of the participants involved (see also Djordjevic et al., 2005). As the authors themselves put it: "If the cerebral activation pattern during concentration on strong-tasting foods is similar to that of taste perception, we may assume that the human brain has the potential for taste imagery. In particular, the aim of their functional magnetic resonance imaging (fMRI) study was to investigate whether the cerebral activation while participants concentrated on strong-tasting food was similar to that of taste perception" (Kikuchi et al., 2005, p. 281) (Note 9).

There are two other points to make about Kikuchi et al.'s (2005) intriguing study. First, the participants were not explicitly asked to mentally imagine the taste (or flavour) of sour plums. Rather they merely looked at three pickled plums while repeating the phrase: 'Pickled plums are sour' in Japanese to themselves. So while the participants stated that they could produce taste imagery, it is unclear whether they actually did so while they were lying in the brain scanner. Second, the researchers were unable to rule out the impact of salivation, either on brain activity, or on the possibility of imaging the taste of this strong-tasting food (Note 10). Note here that other research has demonstrated that simply reading the word ‘cinnamon’ activates olfactory brain regions (González et al., 2006), while reading the word ‘salt’ can activate gustatory brain regions (Barrós-Loscertales et al., 2012 (Note 11) — see also Pomp et al., 2018).

Turning now to the case of olfaction, Wiesmann et al. (2001, p. 237) note that: “Olfactory information is projected from the olfactory bulb to the primary olfactory cortex, which is composed of the anterior olfactory nucleus, the olfactory tubercle, the piriform cortex, the amygdala, the periamygdaloid region, and the entorhinal cortex. From there, the primary olfactory cortex projects to secondary olfactory regions including the hippocampus, ventral striatum and pallidum, hypothalamus, thalamus, orbitofrontal cortex, agranular insular cortex, and cingulate gyrus” (see also Boot et al., 2024).

Primary piriform cortex (PC) is typically activated when non-experts try to imagine an odour (e.g., Djordjevic et al., 2005; Kettenmann et al., 2000; Levy et al., 1999a). That said, Royet et al. (2013) have argued that the neural activity that has been reported in the PC where non-experts try to imagine olfactory stimuli might have other causes, such as the neural activity that is associated with sniffing, attention/expectation, and/or other top-down influences, and crossmodal associations (Karunanayaka et al., 2015). Sniffing also results in PC activation, perhaps linked to somatosensory stimulation that is caused by airflow through the nostrils (Koritnik et al., 2009; Sobel et al., 1998).

A meta-analysis of human neuroimaging studies conducted by McNorgan (2012) identified a number of brain areas that were modality-specific, as well as several others that were modality-general (see also Daselaar et al., 2010; Olivetti Belardinelli et al., 2004 — see Note 12). In particular, overlapping brain regions that were activated during olfactory mental imagery and olfactory perception included the primary olfactory cortex, anterior cingulate cortex, hippocampus, insula and superior parietal lobule. Olivetti Belardinelli et al. (2009), meanwhile, reported greater activity of sensory–specific cortices in high- *vs* low-vivid participants for visual, gustatory, kinesthetic, tactile, and the somatic modalities, but not for either auditory or olfactory imagery. Mental imagery generation in different modalities activates sensory-motor areas (Palmiero et al., 2009). Research from Han et al. (2022) suggests that different neural strategies may sometimes be used by those individuals who are high *vs* low in olfactory mental imagery abilities (by self-report questionnaire). The latter group had stronger brain activation of the supplementary motor area and the superior frontal cortex. Variation in the activation levels and connection strength between olfactory areas has also been reported by Bensafi et al. (2013).

The neural mechanisms underpinning olfactory mental imagery can apparently also be activated by verbal descriptors [‘floral bouquet’; e.g., in the context of scent marketing (Meng et al., 2020); as well as by non-figurative visual cues (Hossu et al., 2024)]. Importantly, however, odour coding in human PC is category-specific (Howard et al., 2009), meaning that olfactory information processing does not break down odour objects into specific features, like colour, motion, and shape (as has been documented in the visual modality, say).

Viewing pictures of appetizing foods appear to activate the gustatory cortices for taste and reward, namely the right insular/opercular and left OFC (Simmons et al., 2005). Research from Avery et al. (2021) demonstrated that the IC activity when viewing images of foods can be decoded by the inferred taste quality associated with those foods. In fact, subsequent research from Avery et al. (2023) suggests that there may be a common neural code for representing imagined and inferred tastes. The participants in the latter study were presented with the words ‘SUGAR’, ‘SALT’, ‘LEMON JUICE’ and ‘WATER’ and were instructed to “imagine to the best of your ability that someone has placed a spoonful of that substance on your tongue” (Avery et al., 2023, p. 6). In another task, the same participants saw images of dominantly sweet, salty, and sour foods. High-field fMRI revealed that imagined tastes elicited activity in the bilateral dorsal mid-insula which was reliably similar to that elicited when viewing images of food with the corresponding dominant taste quality, thus suggesting a common neural code for representing taste quality regardless of whether explicitly imagined or automatically inferred when viewing food.

However, while the involvement of chemosensory cortical areas in mental imagery does indeed suggest that those mental images are depictive or perceptual in nature, one possibility that should be considered is that imagined and experienced tastes or smells may be represented in those same regions using a different format, or at the least within different neural populations. Avery et al. (2021, 2023) attempted to address this issue of format by using cross-task decoding analyses. Avery et al. (2023) used just such an analysis in order to demonstrate that the mid-insula activity evoked by the mental imagery of taste and the activity evoked by viewing food pictures shared a common format. By contrast, when the same type of analysis was performed in Avery et al.’s (2021) study, the results suggested that while they both activate that same mid-insula region, respondes to food pictures responses and those of experienced tastes (which were delivered during scanning) did not appear to share a common format.

Japanese researchers prompted sweet, sour, salty, and bitter-tasting foods by presented words (e.g., ‘lemon’) or else pictures of foods dominantly associated with those basic tastes. Participants were instructed “to recall the taste of the presented food or beverage” (Kobayashi et al., 2004, p. 1273). During the perception task, orange, apple, grapefruit and grape juice were delivered to the participants’ mouths. The left insula was predominantly activated when participants engaged in gustatory mental imagery. The middle and superior frontal gyri were also involved in the generation of gustatory ‘hallucinations’, but were not activated by gustatory perception. Kobayashi et al. went on to suggest that these regions in the frontal cortex may mediate the ‘top-down’ control involved in retrieving gustatory information from long-term memory storage. The suggestion was that the source of the top-down signals may be in middle and superior frontal gyri, and that these signals may affect the neural activities in the insula, orbitofrontal, and precentral gyri. A few years later, magnetoencephalography (MEG) research from Kobayashi et al. (2011) demonstrated that the PFC was indeed activated prior to the IC when the participants in their study engaged in gustatory mental imagery (Note 13) — what the authors describe as “the “top-down” modulation of taste perception” (Kobayashi et al., 2011, p. 1).

4.1. Unanswered Questions Concerning the Mental Imagery of Flavours

What happens neurally when people image the flavour of food and drink (assuming, that is, that that is something they are able to do)? In terms of multisensory flavour perception, superadditive opercular activation in response to congruent food flavour is mediated by enhanced temporal and limbic coupling (Seubert et al., 2015). One would therefore imagine that flavour mental imagery should also give rise to enhanced coupling between these brain areas (see also Suen et al., 2021). However, we are not aware of anyone who has conducted a similar analysis to that reported by Seubert et al. but for imagined odours, tastes, and imagined flavours. One might also want to know about the cortical processing of pungent trigeminal stimuli, such as, for example, delivered by chilli, black pepper, or ginger (see Spence, 2018, 2023a, 2024). Note that trigeminal inputs are included as part of flavour perception by many, if not necessarily all, researchers (ISO, 1992/2008). Relevant here, Japanese researchers have reported that tasting and ingesting capsaicin (the pungent active that gives chilli its burn) activates the ventral part of the middle and posterior short gyri (M/PSG) of the insula which is known as the primary gustatory area (though see below on the several regions within the insula that have been described as the primary gustatory cortex), suggesting that capsaicin is recognized as a taste (Kawakami et al., 2015). One might also wonder whether chemesthetic oral experiences which are in some sense metameric (cf. Ravia et al., 2020), such as of heat or cooling, which may be delivered by thermal or chemesthetic stimuli, recruit the same network of brain areas when participants directly perceive *vs* merely imagine such complex chemosensory stimuli.

It is, though, possible to imagine that attending to the flavour of food might not necessarily activate exactly the same network of brain areas activated as when actually tasting food, given that people consider the flavour of food and drink to originate from the oral cavity, and explicitly and ubiquitously refer to it as ‘taste’ (see Auvray and Spence, 2008; Prescott, 1999; Spence et al., 2015), due to the phenomenon of oral referral (Small, 2010; Spence, 2016). It is further worth noting that our attention is typically directed to the oral cavity while eating (i.e., when savouring the ‘taste’ of food; Spence, 2019; Stevenson et al., 2011), not to the nose where the majority of the information is actually transduced (see Spence, 2015). Relevant here, modulation of early gustatory cortex (IC and frontal operculum), and perceptual enhancement has been reported a result of attention being directed to taste (e.g., Marks and Wheeler, 1998a,b; Spence, 2019; Veldhuizen et al., 2007; Zelano et al., 2005, 2011).

Finally, here, and coming from a rather different research direction, Barron et al. (2013) assessed the neural changes in the hippocampus and medial prefrontal cortex that were associated with exposure to a novel combination of flavours/ingredients, i.e., such as avocado and raspberry smoothie or tea jelly. In this case, the researchers concerned were interested in the question of whether the co-activation of multiple relevant memories might provide a training signal to the valuation system that allows the consequences of new experiences to be imagined and acted on. However, it would seem at least worth considering whether the performance of such a task might require the manipulation of mental imagery for flavour.

4.2. *Interim Summary*

Taken together, the cognitive neuroscience research on the neural substrates of chemosensory perception and chemosensory mental imagery appear to show a great deal of overlap in terms of the networks of primary and secondary areas that are involved, though with the patterns of connectivity seemingly reversed — bottom-up in the case of chemosensory perception and top-down in the case of chemosensory mental imagery. The research that has been published to date has primarily focused on taste (or perhaps flavour — Note 14) and olfaction (presumably orthonasal olfaction, but as has been mentioned the distinction between orthonasal and retronasal olfaction has not been developed for the case of mental imagery in quite the way that it has been in the case of chemosensory perception; e.g., Rozin, 1982; Small et al., 2008; Wilson, 2021). As such, it will be intriguing to find out whether a similar pattern emerges when multisensory flavour mental imagery is compared to multisensory flavour perception (cf. Nanay, 2018). Finally, here, another aspect of our multisensory experience of food and drink that is often very important concerns mouthfeel. While mental imagery questionnaires have recently started to incorporate questions about this attribute of food experience (Note 15), it would be interesting to know more about the degree of overlap in terms of the relevant brain areas in the case of both perception and imagery.

One important point to consider here concerns the involvement of chemosensory cortical areas in chemosensory mental imagery. Multiple studies that have been discussed thus far claim to have documented activation of the primary gustatory cortex. However, closer examination reveals that those studies appear to point to different areas of the insula, such as the AI/FO (dorsal anterior insula; e.g., Small, 2010; Small et al., 1999), the dorsal mid-insula (Avery et al., 2021, 2023), and the ventral anterior insula in Kawakami et al. (2015). As pointed out by a helpful reviewer, a large body of research on the functional organization of the insula shows that these regions have different functional roles across a variety of cognitive tasks (for instance, see Kurth et al., 2010), and differential connectivity to the wider brain (e.g., Cauda et al., 2011; Kelly et al., 2012). As such, it does not seem likely that these different areas have equal claim to the designation of ‘primary gustatory cortex’. This obviously bears on the question of the involvement of these areas in chemosensory mental imagery. This point is likely to be especially relevant when it comes to flavour mental imagery, given that two of these insula regions (ventral anterior and dorsal mid-insula) have elsewhere been implicated in the integration of taste and smell to produce flavour (see Seubert et al., 2015; Small, 2012).

5. Experience/Expertise and its Effect on Chemosensory Mental Imagery/Perception

The chemical senses also an area where expertise is known to exert a profound influence. At the perceptual level, Sezille et al. (2014) assessed the hedonic appreciation and verbal description of a range of pleasant and unpleasant odours in untrained, trainee cooks, flavourists, and perfumers. They reported no group level differences in hedonic ratings for pleasant and unpleasant odours. On a verbal level, smell descriptions were richer and did not refer to pleasantness in experts compared to untrained participants who used terms that referred to the odour sources (e.g., candy) accompanied by terms referring to odour hedonics (see also Gilbert et al., 1998). Perfumers, as a representative category of olfactory experts (Gilbert et al., 1998), are significantly better at olfactory imagery (in terms of generating vivid imagery) than novices.

Olfactory experience has been found to induce functional reorganization in brain regions involved in odour imagery in perfumers (Plailly et al., 2012)

(Note 16). Perfumers exhibit both cortical and functional changes in the primary and secondary olfactory areas (Delon-Martin et al., 2013). Specifically, expert perfumers exhibited less activation in the hippocampus and PC during olfactory imagery as their level of expertise increased (presumably because less effort is required to generate the olfactory images). As a group, perfumers showed an increase in grey-matter volume in the bilateral gyrus rectus/medial orbital gyrus (GR/MOG), an orbitofrontal area that surrounds the olfactory sulcus. Additionally, grey-matter volume in the anterior PC and left GR/MOG was found to be positively correlated with experience in professional perfumers. These findings led Delon-Martin and colleagues to conclude that the extensive olfactory knowledge acquired as a result of prolonged olfactory training leads to the structural reorganization of olfactory brain areas. According to Royet et al. (2013), the strength of connection between areas may also vary as a function of the level of expertise of odour experts. Here, it is interesting to note that when perfumers create a olfactory mental image, the right middle frontal gyrus, a key region in the neural signature of retrieval strongly co-activated with olfactory and memory regions but not in non-experts (Lepage et al., 2000). Intriguing changes have also been reported in the case of expert wine-tasters (e.g., Carreiras et al., 2024).

6. Conclusions

The study of chemosensory mental imagery has proved particularly challenging because of the profound individual differences that have been reported in the vividness of, for instance, olfactory mental imagery (e.g., Arshamian and Larsson, 2014; Djordjevic et al., 2004c; Gilbert et al., 1998; Zhou et al., 2022). At the same time, the majority of those researchers who have attempted to study people's mental imagery abilities for taste (gustation) have actually mostly been studying flavour mental imagery. Nevertheless, there exists a body of human psychophysical research showing that chemosensory mental imagery exhibits a number of similarities with chemosensory perception. Furthermore, the two systems frequently interact with one another (see Spence, 2023b, for a review). In this narrative historical review (Ferrari, 2015; Furley and Goldschmied, 2021), the many similarities between chemosensory perception and chemosensory mental imagery at the introspective, behavioural, psychophysical, and cognitive neuroscience levels in humans are highlighted, as well as the differences, such as there are.

The latest neuroimaging evidence show that many of the same brain areas are engaged by chemosensory mental imagery as have previously been documented to be involved in chemosensory perception. That said, the pattern of neural connectively appears to be reversed between the 'top-down' control of chemosensory mental imagery and the 'bottom-up' control seen in the case of chemosensory perception (Kobayashi et al., 2011). However, as shown by the research published by Avery et al. (2021, 2023), just because the same neural areas are activated that does not mean that the format for imagined and perceived chemosensory stimuli is necessarily always the same. At the same time, however, there remain a number of intriguing questions. For instance, it is currently unclear to what extent it makes sense to try and distinguish between orthonasal and retronasal olfactory mental imagery. It also remains unclear whether mental imagery for flavour, which most people not only describe but also perceive to be the 'taste' of food and drink, is capable of reactivating the entire flavour network in the human brain (e.g. including retronasal olfaction). These, then, both represent intriguing areas for future research in the study of chemosensory mental imagery.

Notes

1. Though, as we will see later, taste typically refers to people imagining flavours rather than basic tastes.
2. One also needs to be sensitive to the suggestion that an investigator's intuitions and introspections about imagery, in particular the vividness of their own mental imagery experience, may shape their theoretical views (see Reisberg, Pearson and Kosslyn, 2003). In other words, rather than simply accepting the fact that there may be some profound individual differences in the vividness of olfactory mental imagery, researchers with presumably weak olfactory mental imagery typically appear to assume that those whom they study must experience the world similarly.
3. Köster (2002) uses the term 'olfactorise' to mean 'the capacity to imagine smells'.
4. It is sometimes hard to know the extent to which flavour mental imagery is actually involved when the participants in cravings studies are instructed to: "Imagine you are eating your favourite food" (Harvey et al., 2005).
5. Though, what people describe as gustatory most likely actually refers to flavour mental imagery.
6. Though note that in the case of the latter two studies this is more retaining an image in memory than the spontaneous generation of something from within, as in the original Perky (1910) effect.
7. But not when mentally imagining a visual stimulus.

8. Looking to the future, it would be interesting to know whether olfactory mental imagery could be harnessed to deliver some of the well-being benefits that exposure to actual pleasant ambient odours has been shown to have (Boot et al., 2024; Bromberg and Schilder, 1934; Spence, 2020; Weber and Heuberger, 2008; see also Schlintl et al., 2022).
9. One can see such a position as responding to the scepticism expressed by some researchers about the meaning, or usefulness, of questionnaire data (see Ahsen, 1995). Or, as Crowder and Schab (1995, p. 94) once succinctly put it: “experience is not evidence”.
10. As the authors note: “Most Japanese people salivate just on looking at pickled plums because of their long familiarity with this sour food”. (Kikuchi et al., 2005, p. 281).
11. Areas activated in response to reading taste words included the anterior insula, frontal operculum, lateral orbitofrontal gyrus, and thalamus among others. Given that these areas comprise the primary and secondary gustatory cortices, the researchers concluded that the meaning of taste words is grounded in distributed cortical circuits reaching into areas that process taste sensations.
12. This, note, is one of the very few studies that describes odours and flavours (i.e., rather than tastes).
13. The participants in this study were asked to recall the taste (sweet, sour, bitter, or salty) of flavourful stimuli (five stimuli were associated with each taste, as per the authors’ earlier study).
14. Note here that what is described as mental imagery for taste (or gustation) is really more likely to be mental imagery for flavour, given that something like 75–95% of what people think of as taste really comes from the sense of smell (see Spence, 2015).
15. Hazebroek and Croijmans (2023), for instance, recently conducted a study assessing the strength of people’s mental imagery for the aroma, mouthfeel, and taste of coffee.
16. Note that at the other extreme, those suffering from olfactory loss show a decline in activity in olfactory areas that correlates with the duration of the loss (Flohr et al., 2014).

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