nature food

Review Article

https://doi.org/10.1038/s43016-022-00611-x

Odour hedonics and the ubiquitous appeal of vanilla

Received: 27 April 2022

Accepted: 6 September 2022

Published online: 18 October 2022

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Our food choices and consumption behaviours are often influenced by odour hedonics, especially in the case of those orthonasally experienced aromas (that is, those odours that are food-related). The origins of odour hedonics remain one of the most intriguing puzzles in olfactory science and, over the years, several fundamentally different accounts have been put forwards to try and explain the varying hedonic responses that people have to a wide range of odorants. Associative learning, innate and molecular accounts of odour pleasantness have all been suggested. Here the origins of the hedonic response to vanilla, which is one of the most liked smells cross-culturally, are explored. The history of vanilla's use in food and medicine is outlined, with a focus on its neurocognitive appeal. While vanilla is one of the most widely liked aromas, it is also rated as smelling sweet to most people. Food scientists are becoming increasingly interested in the possibility that such 'sweet smells' could be used to help maintain the sweetness of commercial food products while, at the same time, reducing the use of calorific sweeteners. Such an approach is likely to be facilitated by the low cost of artificial vanilla flavouring (when compared with the high and fluctuating price of natural vanilla pods).

Although the importance of the sense of smell has been downplayed by cognitive neuroscientists over the past 150 years or so[1], olfaction undoubtedly plays an important role in well-being[2,3] and interpersonal interactions/attraction[4,5]. It is our sense of smell that helps us to detect danger and off-taints in food and drink[6,7] and orthonasal olfactory cues also play a crucial role in food choice as well[8,9]. At the same time, however, olfactory stimuli are rarely experienced in isolation and are typically experienced in combination with other senses (for example, as when eating and drinking). That said, the role of olfaction in humans is probably supportive, rather than leading, especially given the ubiquity of visual dominance[10]. It should be noted here that visual cues have also been shown to dominate over our perception of the flavour of food and drink[11,12].

It has been suggested that all smell sensations carry an element of pleasure or pain and, indeed, hedonics may be one of the primary, or dominant, responses that people have to odorants[13–15]. In fact, the close link between emotion and olfaction is probably related to the shared neural substrates involved, including brain structures such as the amygdala, hippocampus, insula, anterior cingulate cortex and orbitofrontal cortex[16]. However, researchers seem to disagree with regards to the question of where such differences in odour hedonics originate. One argument is that our hedonic responses to odours are mostly acquired as a result of associative learning—that is, via previous experience with odours such as in the context of foods[17]: we learn to like the smell of vanilla because of the sweet taste with which it is so often paired in food and drink (even though the fermented vanilla pod itself tastes very bitter). Similarly, we learn to like the smell of coffee because of what it is normally associated with (that is, caffeine). And we learn to like the 'new car' smell[18–20], not because of anything unique about the molecular structure of the volatile organic chemicals per se, but because this olfactory stimulus happens to be associated with a highly rewarding experience[3]. Another explanation for our response to certain evolutionarily important odorants, such as those found in blood, is that they are innate, and probably preserved across species (ref. [21], compare with ref. [22]). One might at least consider the possibility that the sweetness that humans associate with floral

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scents represents such a food-related preserved response (see ref. [23] for other suggestions regarding our innate response to certain food odorants). However, according to an increasingly popular alternative account, olfactory pleasantness (at least in the case of unfamiliar monomolecular odorants) can sometimes be predicted on the basis of the structure of the molecular odorants themselves. According to Joussain and colleagues[24], this link between the physicochemical structure of an odorant and hedonics "may already be engraved" at the level of the olfactory receptor neurons in the olfactory epithelium. The question of the relationships between odour hedonics (and their origin) and food behaviour is of widespread interest given its relevance to food scientists, industry and so on. Furthermore, gaining a better understanding of the mechanisms behind the positive odour hedonics associated with vanilla and its strong connection with sweetness could help bias people's food choices and the food characteristics associated with preferential intake, and possibly also help to tackle the growing global obesity crisis[25].

In this narrative historical Review, my particular interest is in trying to understand the origins of our hedonic response to the odour of vanilla (vanillin), which, at least according to the latest research, is one of the most liked smells cross-culturally at present[26]. Vanilla flavouring is very widely used by the food industry globally, and the link between odour and food preference as it relates to vanilla is an intriguing one. Later in this Review, I will take a look at how the emerging knowledge and insights can be applied in the future in a food science/commercial context[27].

The world's most liked smell

Arshamian et al. recently conducted a study of 225 individuals from nine diverse non-western cultures (including in several remote groups of hunter-gatherers and horticulturalists) in which the various groups of participants had to rank order ten odorants in terms of their hedonic ratings. The odorants, delivered from scented pens (thus minimizing any non-olfactory cues), were chosen on the basis of previous research from an urban sample in New York City[26] to cover a wide range of the hedonic spectrum. The odorants chosen were vanillin, linalool, eugenol, ethyl butrate, 2-phenylethanol, 1-octen-3-ol, 2-isobutyl-3-methoxypyrazine, octanoic acid, diethyl sulfide and isovaleric acid. Regardless of an individual's cultural background, vanilla was the most liked of the ten odorants tested. Odour valence ratings correlated strongly and positively across all cultures. In fact, only 6% of the between-group variance was explained by culture. This result is certainly consistent with the title of Rain's book claiming that vanilla is the world's favourite flavour and fragrance[27], although, of course, Arshamian and colleagues' findings fall far short of rigorously supporting such a claim empirically. Indeed, it is interesting to note how other researchers stress the chemical, biological and cultural considerations underpinning odour hedonics when considered in a global context[28]. Vanilla was found elsewhere to be a very popular aroma cross-culturally, coming in just behind banana, peppermint and lemon in a study of 22 aromas evaluated by 30 participants in each of 16 countries[29]. On the basis of their findings, Pangborn and her colleagues "concluded that degree of liking of food-related aromas varies across regions, probably due to differences in traditional food habits and availability of regional flavour sources"[29].

Cross-cultural differences in odour hedonics have also been reported by other researchers. For instance, a German–Japanese study of odour hedonics, which did not include vanilla amongst the 18 olfactory stimuli tested, highlighted a number of cross-cultural differences between these populations in the case of specific odorants such as (for example) dried fish, soybean and church incense[30]. The former two odorants were rated as much more liked amongst the Japanese participants, whereas the latter smell was liked more by the German participants[31]. As well as any cultural differences in people's odour preferences, some modest variation in the liking for seasonally appropriate odours has been reported in both Japan and Germany[32,33]. Furthermore, people's responses to isovaleric acid, one of the less pleasant odorants presented to participants in the study by Arshamian et al.[27], changes markedly depending on how it is described (that is ripe cheese versus sweaty socks)[34,35] (see also refs. [36,37]). Such results can presumably be taken to suggest that odour hedonics, at least for many real-world odorants, cannot simply be reduced to molecular structure[24,38–40]. Furthermore, a range of other factors have also been shown to exert an influence over odour hedonics (in general, that is, not specific to vanilla odour[41]): these include physiological factors (for example, gestation, menstrual cycle, satiety[42–44], gender[45,46], aging[47], certain pathological states[48]) and the chemical environment (drugs, smoking, and pollution).

The ambient aroma of vanilla has also been documented to exert an influence over people's mood and arousal[49]. More speculatively, it has been suggested that those companies wishing to reduce their customer's shock when sending out large bills should consider scenting them with vanilla as this might help to relieve stress and anxiety (E. Harris, C. Sengupta & A. Gray, unpublished manuscript). Elsewhere it was found that those individuals scented with vanilla, but not with camphor, were more likely to be successful in 'foot-in-the-door'-type procedures[50]. The scent of vanilla is apparently particularly popular amongst North American real-estate brokers[51]. Elsewhere, Hultén[52] documented a 65% increase in sales when a pleasant vanilla fragrance was released in the glassware section of an IKEA store over two weekends (compare with refs. [53,54]). Due to its relaxing effect, vanilla has also been suggested as a potentially beneficial scent in a healthcare setting[3]. According to Hoppough[55], Sony stores also pump in a scent that incorporates notes of vanilla[56]. Vanilla's sweet properties/associations could be used to influence perceived sweetness and thereby bias consumer food behaviour in a healthy direction. At the same time, however, and as we will see later, it has also been suggested that an ambient odour of vanilla may increase appetite (thus potentially biasing people to consume more).

The history of vanilla

The phenomenal global popularity of vanilla, both as a flavouring and as an ambient fragrance, is surprising given the origins of this aroma in nature[57,58]. The vanilla orchid originated in Mexico, growing naturally in the Veracruz region of Papantla, where the exclusive pollinator of this orchid is the *Melipona* bee[59]. In 1836, Charles Francois Antoine Morren travelled to Mexico in the hope of discovering the secret of how to produce vanilla beans[60]. While studying a vanilla orchid one day, Morren apparently observed a Mexican *Melipona* bee landing on a vanilla orchid. He watched the bee lift a protective hood-like membrane covering the throat of the orchid before disappearing inside. The bee collected its pollen and left the orchid before flying on to the next flower and repeating the process. Surprisingly, unlike European orchids, the flower did not wither away, but produced a pod instead[59].

Vanilla flavour and functions

Originally, the flavour of vanilla was obtained from vanilla beans, the seed capsules of *Vanilla* spp. plants, which are now known to be native to tropical rainforests located from Mexico to Brazil[61,62]. In recent years, vanilla orchids have been cultivated extensively in tropical areas such as Madagascar and Indonesia, with cultivation on Reunion Island beginning in around 1819[63,64]. Crucially, vanilla beans have no vanilla flavour on harvesting. They only acquire their characteristic flavour after curing, which involves repeated drying and fermenting of the beans[65]. Vanilla flavour, in other words, only develops as a result of fermentation of the vanilla pod[63,66]. The orchid genus *Vanilla* (Family: Orchidaceae) consists of 110 species, three of which are cultivated for their flavour-related commercial value (*Vanilla planifolia* Jacks. ex Andrews, *Vanilla tahitensis* J. W. Moore and *Vanilla pompona* Schiede, Family: Orchidaceae[63,67]). Originating in Central America, vanilla was also used as a flavouring agent. The Spanish first brought it to Europe from Mexico in around 1520[63]; but the absence of the appropriate insect pollinator meant that no vanilla pods were grown in Europe[63].

Vanilla was originally used medicinally in Mesoamerica[68], and only later did it come to be used as a sweet flavouring. Indeed, it was the stomach-settling properties of vanilla that led to its incorporation into Coca-Cola during the 1920s[27,68]. Contemporary research has proposed a number of pharmaceutical benefits of vanilla (for example, in fighting cancer[69–71]). Furthermore, like many herbs and spices, vanillin has been shown to help preserve food by inhibiting the activity of food spoilage yeasts, thus functioning as a highly effective antimicrobial agent[72,73] (note that vanilla is considered a spice[74]). In the thirteenth century, Aztecs mixed cured vanilla pods with copal to scent their temples during sacred rituals, while the green bean was used medicinally (for example, to treat venomous insect bites and heal wounds[27]). Bythrow[68] writes that: "the Aztecs and Totonacs knew that they had discovered a sacred plant in the vanilla orchid. Keeping their cultivation strategies a secret, early Americans utilized vanilla in their medicinal and culinary practices and introduced the Spanish conquerors to the sweet bean". Given that fermented vanilla pods actually taste very bitter, it is an intriguing question as to when the aroma of vanilla first became associated with sweetness. Interestingly, vanillin is also unusual in that it is one of the very few odorants that has been shown to activate human bitter taste receptors TAS2R14, TAS2R20 and TAS2R39[75]. According to Bythrow[68], Europeans historically valued vanilla for its flavour, its lore as a love potion and its medicinal uses. It would certainly be interesting to know whether, in the ancient world, cured vanilla pods also smelled sweet to people, or just pleasant/relaxing[76–78].

The aroma of cured vanilla beans now includes descriptors such as sweet, vanillin, floral, prune/raisin, spicy, woody and tobacco-like[79]. That said, I would be tempted to question Bythrow's[68] assertion (quoted above) that the vanilla bean was perceived as sweet when it was first introduced to the Spanish conquistadors; my intuition is that this bitter-tasting bean may only have become sweet to the majority of the population once Coca-Cola introduced vanilla to its medicinal tonic in the 1920s. According to Rain[27], vanilla remained part of the American pharmacopoeia until 1916 for stomach distress, and hysteria and as a nerve stimulant. Here, though, it's interesting to note that Thomas Jefferson is credited with first adding a vanilla pod to ice cream[80]. Jefferson apparently returned from France in 1789 with his chef—newly trained in making frozen desserts. In Philadelphia in 1791, Jefferson sent to France for 50 vanilla bean pods, implying that this was already a popular flavouring.

The Aztecs are most often cited as the first culture to use and domesticate vanilla to flavour their drink of choice, *chocolat*[68]. Chocolate was originally served as a bitter liquid, mixed with spices or corn puree. While it is not known whether it was Cortes who brought vanilla back to Spain, the flavour began to appear in Spain shortly after his conquests[27]. After its arrival in Europe in the sixteenth century, sugar was added and it became popular throughout society—first among the ruling classes and then among the common people[81,82]. Sugar was presumably only widely combined with vanilla in chocolate drinks once the price of sugar had declined[83–86]. Similarly, one only sees the formerly very expensive vanilla appearing in French perfume recipes and store inventories around the start of the nineteenth century[87].

Contemporary production of vanilla flavouring

Vanilla beans containing the flavour and their solvent extracts are 'natural vanilla flavour', whereas synthesized aroma compounds such as vanillin contained in vanilla beans and its analogue ethyl vanillin are 'synthetic vanilla flavour'[88]. The key structural feature of vanillin, the main compound responsible for the characteristic flavour of vanilla, is the vanillyl (3-methoxy-4-hydroxyphenyl) group. Synthetic pure vanillin lacks complex flavour notes, and thus cannot replace vanilla in high-quality products. Although customers typically prefer non-synthetic flavours, non-synthetic vanilla extract is approximately 200 times more expensive than its synthetic counterpart[63,89], in part because it is one of the most labour-intensive crops to grow worldwide[65,90]. As a result, vanilla pods are expensive, with the price fluctuating sometimes unpredictably according to current political and climatic conditions. This price instability is one of the reasons for the shift to artificial vanilla flavour or pure vanillin by many in the food and beverage industry. Demand for cured vanilla pods, over 16,000 metric tonnes in 2015[91], exceeds supply by as much as ten to one. With the high prices and the inability of non-synthetic vanilla production to meet the global demand for the vanilla flavour, the focus for many in the flavour industry has turned to pure vanillin.

Contemporary popularity of vanilla

Vanillin, the key compound that gives rise to the distinctive scent of vanilla is now used widely in foods such as cola-type beverages and ice cream[89], sugar cookies, puff pastries and butter creams[68]. The vanilla flavour from pods tends to be used for high-quality products such as expensive chocolates and luxury ice creams[92], which account for approximately 75% of the total vanilla plant flavour used. Long associated with dessert, vanilla is the second most expensive spice, just behind saffron, according to Bythrow[68], due primarily to the extensive processing required. Other major uses include cola-type beverages and baked foods[89]. Indeed, there is plenty of evidence to suggest that the aroma of vanilla tends to enhance the sweetness of whatever foodstuff it is added to[93,94]. It has recently been proposed that the addition of the sweet aroma of vanilla might prove to be an effective strategy in terms of sugar reduction[95]. In recent years, numerous different research groups have become interested in cross-modal approaches to sugar reduction[96–99]. The results of one study revealed that a 25% sugar reduction in yoghurt with 0.2% vanilla (or strawberry) flavour added did not affect the sweetness, as shown in temporal profiles, and hedonic ratings[95]. That said, the study reported that vanilla flavours such as vanillin seem to have appetite-enhancing effects[88], suggesting that the presence of this odorant might actually lead to an increase in people's consumption instead[100,101].

Ultimately, the question has to be why the flavour of the fermented bean of this obscure (not to mention, hard to pollinate) orchid originating in Mexico has become such a highly liked and dominant flavour and fragrance globally in recent centuries. A secondary question is when exactly did this bitter-tasting cured vanilla pod come to be associated with sweetness (compare with ref. [75]).

Explaining odour hedonics

Having documented the global popularity of vanilla (both as a flavouring, and as an ambient fragrance), I now turn to explaining its ubiquity in terms of the acquired, innate and molecular accounts of odour hedonics that were mentioned earlier (compare with ref. [24]).

Predicting odour hedonics for unfamiliar monomolecular odorants

Our response to a variety of unfamiliar volatile aromatic chemicals may be predicted on the basis of the structure of the molecules themselves. When the number of distinct olfactory notes ascribed to a range of 411 monomolecular odorants was assessed[102], both expert and non-expert participants perceived structurally more complex monomolecular odorants as having a larger number of olfactory notes. Functional magnetic resonance imaging has revealed that more structurally complex odorant molecules tend to give rise to a larger number of descriptions, and evoke greater activity in the dorsal anterior cingulate gyrus than do simpler odorants[103]. The latter brain area is responsible for odour-related verbal and lexical processing, and for resolving cognitive conflict—perhaps associated with competing odour descriptors.

The pleasantness of an unfamiliar odour tracks, or at least correlates weakly with, the size of the molecule. In a study by Kahn and colleagues[14], 185 participants took part in one of seven experiments involving some subset of 144 monomolecular odorants and 16 mixtures that were rated on a range of (perceptual) dimensions. Elsewhere, hedonic judgements of chemical compounds were positively correlated with molecular size/weight, meaning that larger molecules tended to be rated as more pleasant[104]. The correlation between molecular weight and olfactory pleasantness for novel monomolecular odorants has also been documented[105] (compare with ref. [24]).

It would seem that more complex monomolecular odorants give rise to perceptual experiences that involve a larger number of describable olfactory elements (or notes) and are also rated as more pleasant. Although the correlation between physicochemical properties of individual volatile odour molecules and odour hedonics in the case of unfamiliar monomolecular compounds is significant, it is not particularly strong[14,104]. As such, the associative learning (or acquired/hedonic) account of why we like the smell of particular volatiles that we happen to be very familiar with (such as vanilla) may, in most everyday circumstances at least, explain more of the variance than a purely molecular account (compare with refs. [106–108]).

The crowd-sourced DREAM (Dialogue for Reverse Engineering and Methods) Olfaction Prediction Challenge utilized a large olfactory psychophysical dataset to develop machine learning algorithms to predict the sensory attributes of molecules on the basis of their chemoinformatic features[109]. Intriguingly, the resulting models accurately predicted odour intensity and pleasantness, as well as successfully predicting 8 among 19 rated semantic descriptors (garlic, burnt, spices, fish, sweet, fruit, flower and sour). That said, the psychophysical data were collected from just one cultural group, and none of the models did a particularly good job of accounting for differences at the level of the individual observer. Relevant to the theme of this Review, the 'bakery' olfactory descriptor could be predicted on the basis of the similarity of a given molecule to vanillin or ethyl vanillin.

Here, though, it should be noted that the majority of scents that we come across in daily life actually consist of several tens or even hundreds of different volatiles. In fact, some of the most desirable flavours (for example, the flavours of good-quality wine or coffee) may contain well over 1,000 distinct volatile compounds[110–113]. Even though only a small proportion of these are likely to be perceptible consciously, and hence contribute to the unified aroma/flavour percept[23,114], the majority of natural odours are composed of a multitude of volatiles, unlike the monomolecular olfactory stimuli used in the majority of studies. According to research, somewhere between 40 and 80 volatiles contribute to the complex natural flavour of vanilla[63,115–117]. Perhaps unsurprisingly, natural vanilla is considered a complex flavour[118] (although see ref. [112]). It is relevant here to note that attempts to predict the pleasantness of odour mixtures have thus far been restricted to binary combinations of one pleasant and one unpleasant odorant. In particular, researchers have reported that they were able to predict the perceived pleasantness of binary mixtures of two odorants (three of which were pleasant and three unpleasant), with pleasantness ratings falling in between, and dependent on the relative concentration[119]. In this case, the prediction was based on the pleasantness of the elements weighted by their respective perceived intensities.

Innate responses to evolutionarily important odours

In a few cases, it has been suggested that our response to evolutionarily important odorants may be innate or hardwired. This suggestion has been made, for example, with regard to volatile chemical *trans*-4,5-epoxy-(E)-2-decenal, which is found in mammalian blood. Its presence tends to induce postural avoidance, increases physiological arousal and enhances visual perception of affective stimuli in humans. The presence of this odorant would seem to serve as an alarm signal across species[21]. That said, there would be little reason to suspect that vanilla, or vanillin, would be associated with such an innate response.

Associative learning and the response to vanillin

Familiarity breeds liking (as in the 'mere exposure' effect[120–123]). Our early preference for umami and sweet tastes might thus be the result of exposure to amniotic fluid and breast milk, which both apparently have these as dominant tastes (ref. [124]; see also refs. [125–127]). On the challenge of knowing whether the detection of olfactory stimuli in water should be described as tasting or smelling, see Parker and Stabler[128]. It is important to note that after birth, classical conditioning can modify olfactory preferences[129,130]. That said, the preference for the taste/flavour of breast milk declines before adulthood for most of us (although there was a short-lived trend for breast-milk ice cream[131–133]).

It would certainly seem relevant here to consider the influence of early exposure to vanilla in flavourings of foods on later liking[134]. Vanillin, one of the odorants used in the study by Arshamian et al.[26] also happens to be present in human breast milk, depending on the mother's diet (it is also present in artificial breast-milk formulations[135–138]). Various beneficial effects on infant health and immune response have been associated with the consumption of breast milk[139], including the transfer of various taste/flavour preferences from the mother to her offspring. The flavours of alcohol and garlic have, for instance, been shown to pass to the breast milk from the mother's diet[140–142]. However, it is also important to note here that changes in the odour of the mother's breath or sweat may also impact a baby's weaning behaviour, and both may exert an influence on the baby's subsequent feeding behaviour.

Vanilla was also apparently added to milk formula for newborns and small babies for decades in Germany[143] (see also ref. [134]). Mennella and Beauchamp[137] note, in passing, how "some authorities have recommended that vanilla be added to formulas intended for infants beginning the weaning process, reportedly for both its flavoring properties and its ability to provide variety to the bottle-fed infant's otherwise 'bland' diet ... And finally, vanilla-flavoured pacifiers (Ross Laboratories, Inc.) are currently being distributed in some hospitals"[137]. These authors also write that: "these data support the hypothesis that flavors, either consumed by the mother and transmitted to her milk or added to formula, are detected by the infant and serve to modulate feeding. They also suggest that experience with a flavor in milk alters the infant's responsiveness to that flavor during subsequent feedings. It is hypothesized that under the natural condition of breast-feeding, infants become familiar with the flavors consumed by their mothers, and such experiences may impact on later food and flavor acceptability and choice"[137] (see also refs. [144–147]). Indeed, long ago, Steiner[148] observed that newborns exhibited a 'smiling' expression accompanied by sucking and licking movements when exposed to the smell of vanilla. On the flip side, however, when Soussignan and colleagues addressed the same question using butyric acid (rancid butter smell) and vanillin odours, they found that while butyric acid induced more facial expressions of disgust than smiles in newborns (65% versus 33%), the smell of vanillin induced as many facial expressions of disgust as smiles (33% versus 33%)[149]. Bear in mind here, as stated earlier, that vanillin is one of the very few odorants capable of activating the human bitter taste receptors[75].

Scenting a breastfed infant's toy with vanilla leads to increased behavioural interaction (that is, increased looking and reduced vocalization) compared with an unscented toy or one that had been scented with ethanol[150]. Haller and colleagues conducted an intriguing questionnaire study of 133 people (aged between 12 and 59 years of age) visiting an exhibition in Germany[134]. The researchers asked whether the participants had been breast or bottle-fed as a newborn. The participants were then given tomato ketchup, and tomato ketchup adulterated with a very low level of vanillin, and asked which they preferred (note that the food chosen was one in which vanillin would normally not have been experienced, hence implying that any preference changes that were observed must have been attributable to the presence of vanillin, rather than to a previously familiar combination of ingredients). Intriguingly, the results revealed that those who reported having been bottle-fed as a baby ($N = 30$) preferred the ketchup that

https://doi.org/10.1038/s43016-022-00611-x

had been adulterated with a low level of vanillin (66.7% versus 33.3% for original), whereas those who had been breastfed as a small child (N = 103) preferred the unadulterated ketchup instead (70.9% versus 29.1% for the adulterated version).

A growing body of research now shows that we come to acquire a liking for those flavours in breast milk that our mothers consumed during pregnancy[135,151]. Schaal et al. conducted an intriguing study of 24 neonates born to mothers who either had or had not consumed anise flavour during pregnancy. The babies born to anise-consuming mothers showed a stable preference for anise odour immediately after birth and on day four. By contrast, those infants born to non-anise-consuming mothers displayed aversion or neutral responses instead. In recent years, a number of programmes have started to encourage pregnant mothers to consume carrot-flavoured milk and so on, to increase the likelihood that their offspring will consume these vegetables after birth[152–154]. What such findings suggest is that we acquire a liking for that which we are exposed to during our early taste/flavour experiences[155]. Vanilla flavouring is ubiquitous and, crucially, the flavour passes to breast milk as well as often being added to formula milk, and even to pacifiers.

Molecular versus perceptual accounts of olfactory perception

It is also important to consider whether the key volatile, vanillin is also present as one of the volatiles in other sweet-flavoured foods[23]. Indeed, it is unknown whether it is the physical presence of a specific volatile or its perception that is key to driving the odour-induced taste enhancement, and odour hedonics. Given that the prediction of perceptual responses to combinations of odorants is still challenging (to say the least), it is unclear whether it is the physical presence of a specific volatile, or the perceptual properties of the volatile mixture, that are key to determining learning/behaviour/hedonics. Note that, in this regard, humans are very different from mice, say, which are able to decompose odour mixtures into their component parts[156–158]. Much the same conclusion (that is, a perceptual account, emerges) from studies of flavour pairing, where shared compounds have proved to be a poor predictor of the pleasantness of the combination[159,160]. Instead, it is matching (or possibly contrasting) the perceptual qualities of the component stimuli, which may well be made up of several tens or hundreds of different volatile molecules, that is key to creating great-tasting flavour combinations.

One of the peculiar features of vanilla is that its psychophysical curve is particularly flat. Indeed, when Moskowitz and his colleagues evaluated the hedonic character of 32 odorous molecules as a function of the concentration of the stimulus, vanillin was found to be one of the few molecules that showed a psychophysical response pattern with almost no relationship between the intensity of the stimulus and the pleasant nature of the odorant[161]. That is, vanillin was rated as pleasant regardless of the concentration (that is, low, medium or high) at which it was delivered, unlike what is typically seen for the majority of odorants. It is interesting to speculate whether this peculiarity might be linked to the fact that vanillin is one of the few pure olfactants (that is, with no trigeminal component[162–165]). That said, contemporary research seems to show that ethyl vanillin is a TRPA1 agonist[166]. At the same time, however, it is worth noting that little is known about the neural processing of the reward value of vanilla odour[167,168].

Genetic determinants of responses to olfactory stimuli

Before closing this section, it is important to note that genetically determined individual differences play an important role in determining our liking for certain odorants/flavours[169]. In the case of coriander/cilantro, for example, the same molecule smells pleasantly citrusy/herbal to one section of the population, but unpleasantly soapy to another section of the population[170–172]. Androstenone is another chemosensory stimulus that delivers very different perceptual and hedonic responses as a function of an individual's genetic make-up[173]. One should probably also consider the incidence of anosmia to vanilla that affects roughly 1% of the population[174,175]. Such specific anosmias[176–179] are likely to influence odour hedonics too[180].

Given that we live in different taste worlds, it is clearly important to identify those flavours that are most widely liked to bias food choice. While the smell of vanilla has been identified as one of the most widely liked aromas[26], it is also described as smelling sweet. Food scientists are becoming increasingly interested in the possibility that sweet smells such as vanilla could be used to maintain the sweetness of commercial food products while, at the same time, reducing the use of calorific sweeteners[26]. At the same time, however, it has also been suggested that vanilla aroma may also encourage consumption[88]. Such an approach is likely to be facilitated by the low cost of artificial vanilla flavouring (when compared to the high and fluctuation price of vanilla pods).

Conclusions

Recently, Arshamian et al. documented the cultural independence of hedonic responses to a range of familiar odorants, such as vanilla[26]. It is tempting to think that such observations reflect a molecular basis for odour hedonics[14,181]. However, it is important to note that the majority of such claims (that is, for the molecular basis of olfactory pleasantness) appearing in the literature have been based on predicting people's responses to unlabelled monomolecular odorants that are often novel/unfamiliar[102,104,109], thus effectively eliminating the marked effects of learning/semantics that have been documented so frequently. The recently discovered existence of olfactory 'metamers' that have a different molecular structure but smell indistinguishable also argues against an unmediated molecular account of odour pleasantness[182].

Arshamian and colleagues[26] concluded that: "our data do not, however, adjudicate between learned versus innate explanations of odor pleasantness perception. Global regularities in odor perception could indicate common and shared experiences across all human groups. Infant data from diverse cultural contexts could adjudicate between these possibilities, although even here there are challenges since the fetus is already being enculturated into a specific chemical environment."[26] (compare with ref. [183]). There is little reason to consider an innate account as providing a plausible explanation for the ubiquitous preference that has been demonstrated for vanilla. When it comes to familiar odorants, the associative learning/conditioning is more likely to play a key role in determining valence[107,184]. As such, one would expect cultural differences depending on how/when a given odorant is experienced during development[185]. However, it is important to stop short of inferring from this that a molecular account can explain odour hedonics. Clearly, as we have seen, the molecular structure of these volatile compounds is important in helping to understand people's responses to unfamiliar monomolecular odorants, but the globally positive hedonic response to vanillin is more likely to be associative/familiarity-based. Meanwhile, the explanation for why trigeminal odorants are typically rated as unpleasant is presumably physiological in origin.

Of the more than 25,000 varieties of *Orchidaceae* (orchids are the most prolific member of the angiosperm family[186]), it is the pod from the vanilla orchid that nowadays flavours so many of our foods and drinks, not to mention scenting our homes, and many home and personal care products as well[187]. According to the research that has been reviewed here, vanilla is probably so universally liked not because of its molecular structure per se, but because of ubiquitous early exposure (it is one of the odorants that passes to breast milk)—not to mention in a historical context its antimicrobial, medicinal and anxiety-relieving properties[68,188,189]. Furthermore, it has been suggested that the bitter-tasting vanilla pod may only have taken on sweet properties when Europeans started to drink sweetened chocolate after vanilla's arrival in Europe in the sixteenth century (see refs. [190–192] on the biological and cultural role of sweeteners).

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Competing interests

The author declares no competing interests.

Additional information

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Peer review information *Nature Food* thanks Moustafa Bensafi and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

https://doi.org/10.1038/s43016-022-00611-x