

have the proper tools to settle the debate scientifically. While the exact date of domestication is still unknown, recent phylogenomic analyses comparing wild olive varieties to domesticated cultivars point to the first domestication event in the Levant region of Syria (same as wheat, incidentally), with domestication of all of the modern day cultivars radiating from this original domestication event.

**Why are olives important?** In ancient times, olive oil was hugely important for everyday life. Most everything was cooked in the stuff, and it was also used as fuel for lanterns, to make soap, for medicinal purposes, and, of course, to grease athletes up before wrestling matches at the gymnasium. Today, the purposes of the olive have changed a bit — besides the garnish for a martini, or a starter at a tapas bar, olives and olive oil make up a huge portion of the exports from Mediterranean countries. It's estimated that around 3 million tons of olive oil are produced every year worldwide. The US alone imports around 300 tons of oil per year. Olives are now cultivated all over the world — the climates of California and some places in South America have proven ideal for growing the trees. It's probably a good thing, too, that cultivation is spreading, since the health benefits of olive oil have triggered a huge growth in worldwide consumption. In the last 20 years, consumption of olive oil in the US has tripled, and is growing every year.

Several nations have established crossbreeding programs to create better and more profitable cultivars of olives, selecting for faster fruit maturation, pest resistance, smaller seeds, higher oil content, etc. It will be interesting to see to what extent modern breeding technology can improve upon millennia of domestication!

#### Where can I find out more?

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## Primers

# Multisensory flavour perception

Charles Spence

*"Eating is the only thing we do that involves all the senses. I don't think that we realize just how much influence the senses actually have on the way that we process information from mouth to brain."*

— Heston Blumenthal, Tasting Menu, The Fat Duck restaurant

*"Cooking is the most multi-sensual art. I try to stimulate all the senses."*

— Ferran Adrià, elBulli

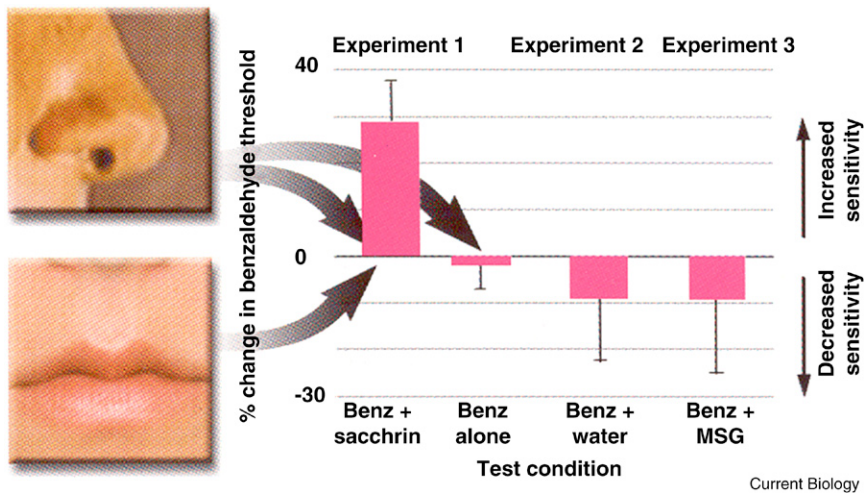
People often confuse tastes with flavours. Strictly speaking, taste perception refers to those sensations that are elicited by the stimulation of the gustatory receptors on the tongue — sweet, sour, salty, bitter and umami. Quite how many basic tastes we are sensitive to, and whether they are really 'basic', are hotly-debated questions in the field. A growing number of researchers now believe that metallic and fatty acid tastes deserve to be added to the list, while others have argued that there may be as many as 25 different basic tastes. It will be interesting to see whether the recent discovery of a 'gustotopic' map in primary taste cortex helps to resolve these conflicts in the coming years.

It is important to note, however, that we virtually never experience pure tastants in isolation. Rather, we mostly experience flavours, resulting from the combination of taste, retronasal olfaction (sometimes referred to as 'mouth smell', in contrast to orthonasal olfaction or 'sniffing') and trigeminal inputs. 'Fruity', 'meaty', 'floral' and 'burnt' are all flavour descriptors. Although it is difficult to arrive at a precise estimate of the relative contributions of taste and retronasal smell to flavour perception, a figure that one often sees quoted in the literature is that ~80% of what we commonly think of as flavour comes from the information

transduced by the olfactory receptors in the nose.

Assuming that we take such a figure to be broadly correct, the curious thing is why it should be that we localize flavour to the oral cavity, rather than to the nose, where most of the information is transduced. The latest research suggests that this occurs because retronasal smell (not to mention taste) is ventriloquized to the location in the oral cavity where we experience the tactile stimulation associated with food and drink. That said, other researchers believe that the fact we attend to the mouth might also be important here. Either way, it is this phenomenon, known as 'oral referral', that gives rise to an integrated flavour percept (or Gestalt) which may, in turn, help to explain why it is that we so often confuse flavour with taste (given that this is where the taste buds are located). I have lost count of the number of times that people have contacted me complaining of their loss of taste, when, in fact, what they have actually lost is their ability to smell, often after a viral infection or car accident.

Smell (both orthonasal and retronasal) often combines with taste to enhance our perception of flavour. So, for example, in one classic study, Pam Dalton and her colleagues at the Monell Chemical Senses Centre in Philadelphia demonstrated that the ability to detect threshold levels of benzaldehyde (the distinctive cherry-almond aroma common to many Western desserts — think Mr Kipling's Bakewell Tarts!) sniffed in solution could be dramatically enhanced simply by placing a subthreshold drop of saccharin on the tongue (Figure 1). By contrast, placing a subthreshold amount of monosodium glutamate, or just water, on the tongue had no such effect. Note that these results were obtained with Western participants; in Japan, by contrast, monosodium glutamate appears to lower the threshold for benzaldehyde whereas saccharin does not, presumably because the sweet almond combination is not so common in Japanese cuisine, while pickled condiments that contain the monosodium glutamate/almond mixture are. Such results suggest that our brains learn to bind just those combinations of olfactory and gustatory stimuli that have been



**Figure 1.** The multisensory integration of taste and smell. The figure highlights the results of a series of experiments conducted by Dalton *et al.* (2000) demonstrating the integration of orthonasal olfactory and gustatory cues. When a sub-threshold saccharin solution was placed on the participant's tongue, a significant increase in olfactory sensitivity was observed, despite the fact that the taster had no odour, thus demonstrating the multisensory interaction of olfaction and taste. By contrast, holding a small amount of water in the mouth had no effect on olfactory thresholds, nor did holding a solution that contained monosodium glutamate. These latter results highlight the stimulus dependency (both olfactory and gustatory) of multisensory integration in human flavour perception, a result that has now been replicated in many other studies.

experienced together in the foods that we have experienced previously.

In fact, provocative research on the acquisition of flavour preferences suggests that flavour learning starts *in utero*. So, for example, French researchers have reported that neonates whose mothers consumed anise-flavoured food during pregnancy are more likely to orient toward the smell of anise after birth, while elsewhere it has been demonstrated that young children are more likely to eat carrots if their mothers happened to drink carrot-flavoured milk during pregnancy.

Dalton *et al.*'s (2000) experiments can be seen as one of the first studies of flavour perception in which the principles of multisensory integration, as uncovered by cognitive neuroscience studies of the multisensory integration of auditory, visual, and tactile stimuli in the laboratory, have been extended to the flavour senses. Another early example of the multisensory approach to the perception of food and drink comes from research by Zampini and Spence (2004) showing that potato chips could be made to taste 15% crunchier (and fresher) simply by manipulating the crunching sounds that a person heard when biting into such a dry foodstuff. These results, while

surprising to many food scientists (who rarely consider sound when thinking about flavour perception), make perfect sense when framed in terms of the extensive multisensory perception literature on sensory dominance.

#### Food colouring and its impact on multisensory flavour perception

Ever since the seminal observations of Moir in the 1930s, researchers have known that changing the colour of a food or beverage can change its perceived taste/flavour. So, for example, adding flavourless red food dye to certain white wines can convince consumers (both social drinkers and wine experts alike) that what they have before them is red wine, not white. Red food colouring also appears to be a particularly good inducer of sweetness. One suggestion here is that we may have internalized the environmental association between sweetness and redness in ripe fruits. But while a large number of such studies have demonstrated that changing the colour (both the hue and the intensity) can change the perceived flavour and the intensity of the taste (for example, its sweetness), many other studies have failed to demonstrate any such effect. So what is going on here?

Research from the Crossmodal Research Laboratory (CRL) here in Oxford, conducted together with Givaudan (one of the world's largest flavour houses), has demonstrated that whether or not a given colour, added to a food or beverage, affects a person's taste/flavour perception depends critically on the meaning that the person associates with foods and drinks having that colour. So in the UK, for example, young consumers expect that a drink coloured blue (Figure 2A) will taste of raspberry, whereas Taiwanese consumers expect that such a drink will likely taste of mint (think Listerine). Consequently, one needs to know what expectations a consumer has in order to predict what it is they will likely experience when a particular colour is added to a given food or beverage in the marketplace. If the expectation and the experience are not too different from one another (say, expecting blackcurrant, while getting blackberry), then the consumer will likely report experiencing the 'expected' flavour (or something close to it). If, however, the flavour expectation and the flavour experience are very different (expecting blackcurrant, say, and getting beetroot) then a 'disconfirmation of expectation' response is likely, and the colour may have little effect on the experienced flavour.

At this point, it may be helpful to distinguish between those sensory cues that are constitutive of flavour (namely, retronasal olfaction, gustation, oral-somatosensory and trigeminal inputs), and those food-related sensory cues (such as visual, auditory, and orthonasal olfactory cues) that serve to generate flavour expectations. Both can be powerful drivers of the reported flavour experience.

Given the commercial opportunities associated with a better cognitive neuroscience understanding of the multisensory perception of flavour, it should come as little surprise that many of the big food/flavour houses (Nestlé, Firmenich, Givaudan, Unilever, and so on) are all investing, and some even publishing, in the area. Imagine, for example, the benefits to an international flavour house of knowing that they can lower the concentration of the typically more expensive aroma added to

a flavour by changing the amount of tastant (typically much cheaper) that is added, while still keeping the flavour profile delivered to their customer constant.

Another area of intense commercial interest currently revolves around seeing whether the consumer's brain can, in some sense, be tricked into perceiving tastes/flavours without the need to include all the unhealthy ingredients that so many of us seem to crave. There are also some interesting commercial opportunities here around exploiting genetic differences in taste perception. Some people have 16 times more gustatory receptors on their tongues than others. In a very real sense, then, we may well live in different taste worlds. While some of the most profound differences in taste perception involve certain bitter-tasting compounds, recent research has demonstrated that 'supertasters' are also more sensitive to the oral-somatosensory attributes of foodstuffs (for example, to the fat in a salad dressing), and possibly also to certain olfactory stimuli, while at the same time being less influenced by visual cues when judging taste/flavour. Interestingly, Gary Pickering and colleagues have just published a paper suggesting that wine experts, if not 'foodies', tend to be more sensitive to certain bitter tasting compounds than the rest of the population.

### The impact of cutlery, plateware and packaging

It is crucial to realize that the context in which we eat also has a profound impact on our experience of food and drink. So, for example, we have recently conducted a study at Ferran Adrià's experimental test kitchen (Alicia-elBulli Foundation in Spain) demonstrating that exactly the same dessert (a strawberry mousse) is rated as tasting 10% sweeter, and more than 15% more flavourful, not to mention being liked significantly more, when eaten from a white plate than when consumed from a black plate (Figure 2B). How best to account for such effects of plateware is proving to be a challenging ongoing research question. One plausible suggestion is that colour contrast might be part of the answer (that is, the red dessert may simply look redder when seen against a white background). What is certainly

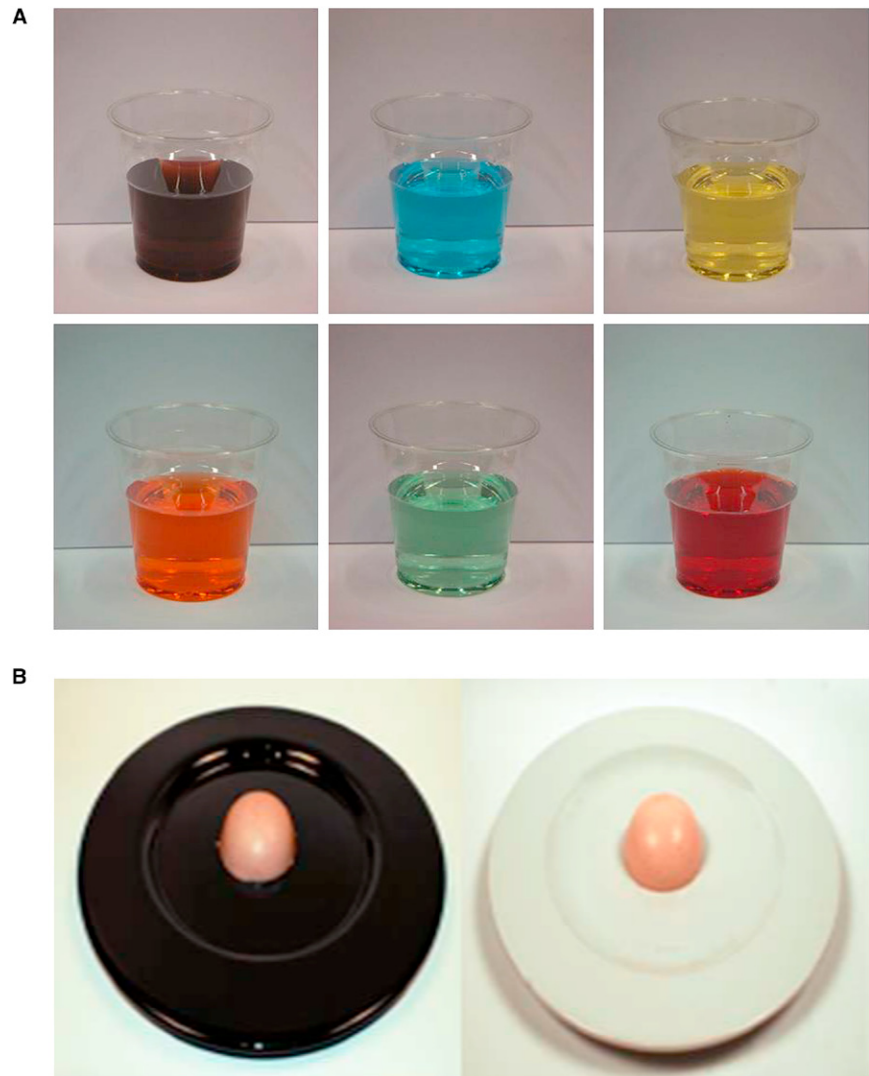


Figure 2. The influence of colour on multisensory flavour perception. Researchers have for many years known that changing the colour of a food or beverage can change its perceived taste and flavour. In much of our current research, we try to establish the specific taste/flavour expectations that are elicited by particular food colours (A). Recently, we have shown that the colour of the plateware can also change both people's sensory-discriminative and hedonic response to foods (B).

also true, however, is that we often associate particular visual cues — for example, packaging colour or shape, what is sometimes referred to as the 'image mold' — with particular taste/flavour properties/qualities. Indeed, this is the basis of much of branding.

A growing body of research now demonstrates that everything from the cutlery we eat with, through to the glassware we choose to drink from, can all influence both our sensory-discriminative and hedonic responses to a wide variety of real food and drink items. So, for example, the taste of food is influenced by the material from which the spoon used

for tasting is made (for example, gold, copper, zinc, stainless steel, or plastic). People also rate a variety of foods as tasting better, not to mention rating them as more filling/dense, if sampled with the aid of a heavier spoon, from a heavier bowl, or from a heavier yoghurt pot. Taken together, such findings suggest that consumers cannot help but transfer some of the associations that they have with all the peripherals (the product-extrinsic cues) to the food and drink itself.

### Atmospherics and flavour perception

Even the atmosphere of the environment has been shown to





Figure 3. The ‘Sound of the sea’ seafood dish, as served at Heston Blumenthal’s The Fat Duck restaurant. The dish comes to the table with a pair of headphones hanging from a conch shell.

have a surprisingly large effect on our taste and flavour experiences. So, for example, Daniel Oberfeld and his colleagues in Germany found that white wine (tasted from black tasting glasses) was liked more when either red or blue, rather than white or green, ambient lighting was used in a winery on the Rhine. Subsequent laboratory experiments showed that participants rated a white Reisling as tasting significantly sweeter under red lighting than under green or white lighting. Not only that, but people said that they would be willing to pay significantly more for the wine tasted under red lighting than under white lighting. Elsewhere, researchers have reported that people who like strong coffee tend to drink more of it under brighter ambient illumination conditions, whereas those who prefer weaker coffee tend to drink more under dimmer illumination. Red-and-white table-cloths and Italian flags festooned on the walls, not to mention a dash of Pavarotti singing opera over the loudspeakers, can all impact on the perceived ethnicity of a dish too.

In fact, it turns out that the auditory aspects of the atmosphere are at least as important as the visual in determining our experience of the taste and flavour of food and drink. Take Andy Woods and his Unilever colleagues’ recent finding that loud white noise (similar to what one might be subjected to on an airplane) reduces the perceived intensity of salt and sweet tastes. Meanwhile, here at the CRL, we have conducted research together

with Heston Blumenthal (of The Fat Duck restaurant in Bray) showing that people rate seafood as tasting significantly better, but no more salty, when listening to the sounds of the sea rather than some other soundtrack. Such findings have now made their way into the signature dish on the tasting menu at The Fat Duck, the ‘Sound of the sea’ seafood dish (Figure 3).

What is generating a huge amount of interest currently is research on the synaesthetic matching of tastes and flavours to sounds and music (not to mention shapes). So, for example, together with the The Fat Duck research kitchen, we have recently demonstrated that you can bring out the bitterness in a bittersweet toffee simply by playing a soundscape having a lower pitch. Meanwhile, the sweetness of the very same food can be slightly, but significantly, enhanced by playing a soundscape with a higher pitch. The reason why sweetness should be associated with higher pitched sounds and bitter tastes with lower pitched sounds might perhaps originate in the different facial expressions (and hence vocal expressions) that neonates make in response to the presentation of sweet and bitter tastes on their tongues. It remains a question for future research to determine whether such synaesthetic matches explain why it is that playing certain pieces of music (for example, *Just Can’t Get Enough* by Nouvelle Vague) have been reported by Adrian North and others to bring out specific notes (such as ‘zingy and refreshing’)

in wines, and presumably they also do so for other foods.

### Conclusions

As this brief tour of the burgeoning cognitive neuroscience literature on multisensory flavour perception has hopefully made clear, there is far more to flavour perception than merely what happens on the tongue. By applying the cognitive neuroscience insights from the study of multisensory integration of the spatial senses (of vision, hearing, and touch), researchers, not to mention food companies and flavour houses, are currently furthering their understanding of many of the key factors underlying the multisensory perception of flavour. But what should hopefully also be apparent from this Primer is that, in order to really understand the experience of flavour, one needs to move beyond the traditional definitions of flavour (as captured by the International Standards Organization (ISO 5492, 1992, 2008) definition of flavour as a “*Complex combination of the olfactory, gustatory and trigeminal sensations perceived during tasting. The flavour may be influenced by tactile, thermal, painful and/or kinaesthetic effects.*”). One needs to incorporate the latest findings concerning flavour expectancy, and a whole host of contextual/ atmospheric effects that have traditionally been ignored by food scientists, but which the latest research suggests can end up having a very dramatic impact on the flavour experiences of real consumers under ecologically-valid testing conditions.

To conclude, it is worth noting that, even if one is not interested specifically in flavour perception, one cannot avoid the fact that, as the eminent biologist J.Z. Young (1968, p. 21) noted some years ago: “*No animal can live without food. Let us then pursue the corollary of this: Namely, food is about the most important influence in determining the organization of the brain and the behavior that the brain organization dictates.*” Indeed, some of the most dramatic changes in brain activity can be seen when a hungry participant is presented with appetizing food images and aromas while lying passively in the brain scanner.

In the years to come, we will need to do everything we can to help preserve the enjoyment in food and drink of the growing elderly population suffering from a loss of their gustatory and olfactory perception, two senses which are critical to flavour perception, but for which there are no prosthesis (akin to hearing aids and glasses used to compensate for auditory and visual loss). There is also hope that our growing cognitive neuroscience understanding of multisensory flavour perception may help the food companies to deliver healthier foods to the marketplace, that taste just like they always did, but which contain less of the unhealthy ingredients (such as sugar, salt, fat and carbonic acid). One development that would likely help further our understanding would be to develop a predictive mathematical account of the relative contribution of each of the senses to multisensory flavour perception in terms of Bayesian decision theory.

Eating and drinking are among life's most enjoyable experiences. It is about time that cognitive neuroscientists took the study of multisensory flavour perception more seriously.

#### Further reading

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## Nutrient sensors

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Elucidating the cellular and molecular basis of nutrient metabolism and regulation of feeding has become a major focus in scientific research over the last twenty years. Because of the increasing number of overweight and obese people in western and other societies, research efforts have initially been directed towards the basic metabolic processes that regulate nutrient uptake of cells and organ systems. One of the major goals of this research is to better understand the physiological and molecular processes that are disrupted or deregulated in various diseases, including diabetes, obesity, metabolic syndrome and heart disease. But research efforts have expanded to include the neural and molecular underpinnings of feeding behavior. It has become apparent that a central role in nutrient metabolism and, by extension, the regulation of feeding behavior, is the sensing of different classes of nutrients. Our goal is to provide an overview of what is currently known about nutrient sensors both in mammals and the invertebrate model system *Drosophila melanogaster*.

#### What are nutrients?

Nutrients can be divided into two main classes, macronutrients and micronutrients. Macronutrients, which include carbohydrates, amino acids and fat, serve as energy sources, as well as structural components that are essential for growth and development and are required at regular intervals. Micronutrients are needed only in small amounts but nevertheless are essential for the function of cells and organ systems. They include approximately 10 vitamins and 20 minerals, each having specific roles. Many vitamins and most minerals serve as co-factors for enzymes, but others have more specialized roles. For example, iron is an essential component of heme, the pyrrole structure of hemoglobin, and some vitamins have hormone-like functions (Vitamin A and D) or serve as antioxidants (Vitamin C and E). Finally, water and some minerals (sodium, potassium, chlorine) are also necessary for most animals in large quantities

and on a daily basis, albeit they are not necessarily considered to be 'nutrients'. Yet, they are all required to maintain cells and organs in optimal and healthy conditions.

Nutrient sensors are molecular/cellular machines that respond to a specific nutrient component. The focus of this primer will be on sensors that detect and monitor nutritious components with caloric value (sugars, proteins and fat). Yet, it should be noted that water, salts and micronutrients are likely to be monitored internally by specific sensors as well, even though we know little about how these substances are sensed and whether this sensing affects physiology and behavior. With the exception of salts, there is no evidence that water or micronutrients are sensed by our primary taste sensory organs or internal sensors, although insects have water-sensing neurons and are able to taste water. Regardless, a caloric nutrient sensor — in its most basic form — may be described as a protein that specifically detects a macronutrient and then induces a response in that cell, ultimately leading to changes in the distribution of the nutrient or the animal's feeding behaviour. These sensors can function as detectors of nutrient flux via metabolic pathways within cells or as extracellular detectors of nutrients. A prime example of the first category would be internal glucose sensing by the pancreas, which monitors changes in glucose concentration via ATP levels in the pancreas, which then leads to release of insulin or glucagon as a signal of glucose levels. Examples of the second kind of nutrient sensor include taste receptors, which sense nutrients before they are internalized and transmit information about nutrient identity to the brain. This broad definition for nutrient sensors is appropriate, especially because recent studies have revealed that numerous taste receptors are expressed internally, where they detect nutrients prior to or even after absorption by the gastrointestinal system. Indeed, in several cases, it has been shown that taste receptors in the gut have important postingestive roles that affect not only physiology and metabolism, but also feeding behavior. The connectivity of hormonal and neural pathways (*i.e.* the different nutrient sensing organs: taste system, intestine, pancreas, liver, adipose and the brain) suggests extensive