Keywords Olfaction/Gustation/Taste/Smell/Senses

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In this article...

- The anatomy of the nose and the nasal cavity explained
- An introduction to the olfactory apparatus and its physiology
- Why the senses of smell and taste deteriorate with ageing

The senses 3: exploring the interrelated senses of smell and taste

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Key points

The senses of smell and taste are closely linked

Odours are detected by olfactory receptor neurons in the nasal cavity

Neural pathways associated with the sense of smell connect to the hippocampus and amygdala, which is why particular smells can invoke vivid memories

Taste cells are located in the taste buds, which are found mainly in the papillae of the tongue

Ageing is associated with reductions in the acuity of taste and smell

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Abstract This is the third and penultimate article in a series exploring the human senses. It examines the senses of smell (olfaction) and taste (gustation). The sense of smell is reliant on olfactory receptor neurons, which are located in the olfactory epithelium of the nasal cavity, while taste relies on the detection of tastant molecules, which are dissolved in saliva. The first two articles in this series explored the nature of hearing and balance, and of vision.

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The sense of smell is reliant on specialised olfactory receptor neurons in the olfactory epithelium of the nasal cavity. Odorant molecules bind to receptors on the surface of these neurons, leading to the generation of a nerve impulse, which is relayed to the olfactory cortex; it is here that smells are perceived. Taste relies on the detection of tastant molecules, which are dissolved in saliva. Tastants bind to receptors on the surface of taste cells located in the taste buds; this leads to the generation of nerve impulses, which are relayed to the gustatory cortex where taste is perceived. Ageing tends to lead to both a diminished sense of smell and taste, which can contribute to loss of appetite in older people. Reductions in the acuity of smell and taste or even complete loss of these senses are a common feature of many pathologies including Alzheimer's disease, Parkinson's disease and Covid-19.

Sense of smell

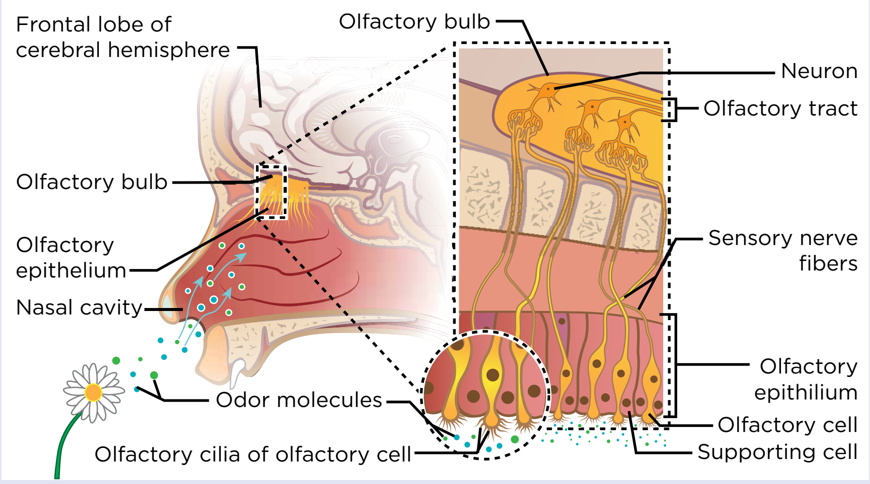
Structure of the nose and nasal cavity

The nose consists of cartilage covered by skin. Two openings termed the nares or nostrils allow air to be drawn into the nose during inspiration and directed into the nasal cavity behind. The nostrils contain coarse hairs, which act as filters, helping to prevent larger particulate materials, such as sand and other debris, from entering the airway. These hairs are associated with sensory nerve endings in the skin of the nostrils; when activated, such as through contact with debris or insects, a nerve impulse is generated and relayed to the conscious areas of the brain.

The nasal cavity is found immediately behind the nose with its lateral walls formed from the bone of the maxilla (upper jaw); it typically has a volume of around 6cm^3 and is lined by a mucous membrane. Anatomically, the nasal cavity is divided into a right- and left-hand side by the nasal septum. Functionally, each side of the nasal cavity has an inferior respiratory portion and a superior olfactory portion.

The primary role of the respiratory portion is to condition the air breathed in; it begins the processes of warming, cleaning and humidifying the air before it passes into the lungs. The respiratory portion has three prominent bony ridges termed

Fig 1. **The nasal cavity and olfactory apparatus**



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conchae. These function to create a turbulent air flow, which slows air movement. This allows efficient warming as the air passes over the highly vascular mucosal lining of the nasal cavity. The mucosa of the respiratory portion is composed of a ciliated pseudostratified epithelium, which is kept moist by a thin layer of mucus. This mucus will trap any small particulates such as dust and bacteria. The coordinated, wave-like motions of the cilia sweep contaminated mucus towards the back of the pharynx (throat), where it is swallowed before entering the sterilising acid environment of the stomach (Fig 1).

The olfactory apparatus and the physiology of olfaction

The superior portion of the nasal cavity is dedicated to olfaction; it is lined by the olfactory epithelium, which is responsible for detecting the odours present in inhaled air (Fig 1). The olfactory epithelium covers the inferior portion of the cribriform plate (part of the ethmoid bone) and is where the olfactory receptor neurons (ORNs) are located. These ORNs are responsible for the sense of smell and are found sandwiched in between supporting cells along the length of the epithelial layer (Cantone et al, 2017). ORNs are specialised bipolar neurons, which have multiple cilia extending from their distal ends. Each ORN has between three and 50 cilia, which reside in a thin layer of watery mucous covering the olfactory epithelium. Odorant molecules entering the nasal cavity dissolve in the mucus and bind to receptors (also known as odorant binding proteins), which are embedded in the cilia.

The binding of odorants to receptors activates a cyclic adenosine monophosphate (cAMP) second messaging pathway. This initiates the depolarisation of the ORN and the generation of an action potential (nerve impulse). It has been estimated that there are around 400-1,000 specific odorant receptor proteins. Each distinct smell may be attributed to a single odorant molecule or, more commonly – such as when a particular food is cooking – a combination of multiple odorant molecules.

Although the human sense of smell is poor in comparison to many animals, such as dogs and cats, many people can still differentiate up to 10,000 distinct smells, with each smell having a characteristic profile of odorant molecules. Humans are estimated to only have 5-10 million ORNs compared with dogs, which have around 220 million (Castillo, 2014). The incredible canine sense of smell is routinely used to detect illicit drugs, locate missing people and more recently, in medicine, as a potential screen for diseases including certain forms of cancer, and bacterial and viral infections, including Covid-19 (Otto et al, 2021).

Unlike most other neurons, ORNs have a relatively short lifespan of around 30 days and require continual replacement. Basal cells within the olfactory epithelium retain the ability to divide rapidly; these function as stem cells, and differentiate into new ORNs (Tesileanu et al, 2019).

ORNs are unmyelinated neurons with their axons extending through the bony cribriform plate (Fig 1); action potentials pass along the axon of the ORN before being relayed to the olfactory bulb, which is located above the superior portion of the cribiform plate (Attems et al, 2015). Despite what is shown in many textbooks, there are actually two olfactory bulbs, with one located above the right side of the nasal cavity and one above the left side. The olfactory bulbs contain specialised intermediary neurons called mitral cells, which are involved in processing information from multiple ORNs. Modified olfactory information is then relayed to the brain through the olfactory nerves (cranial nerve number I). The olfactory bulbs are thought to act as filters, masking information about many common background odours while enhancing the transmission of new or key odours. Destruction of the olfactory bulbs leads to diminished or complete absence of the sense of smell (anosmia).

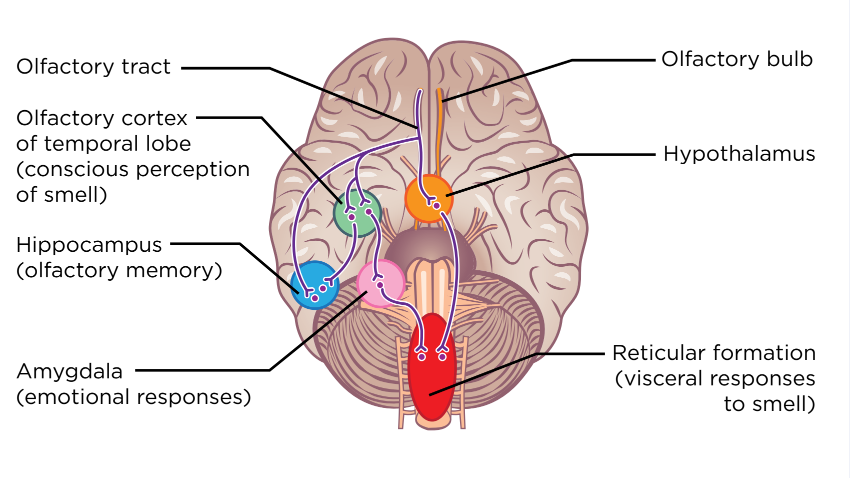
Interestingly, not everyone has olfactory bulbs. MRI scans show that olfactory bulbs are absent in around 0.6% of all women and 4.25% of left-handed women. Despite this absence, these women show an acute sense of smell; this suggests that an olfactory bulb may not be essential to olfaction in all people (Weiss et al, 2020).

Brain regions involved in olfaction

Following processing in the olfactory bulbs, neurons carry olfactory information to several regions of the brain (Fig 2):

- The olfactory cortex: located in the cerebral cortex, close to the lateral sulcus (Sylvian fissure) that separates the frontal and temporal lobes. This region of the brain is responsible for the conscious perception of odours (VanPutte et al, 2017);
- Hippocampus: this region of the brain is part of the limbic system, which is well developed in most animals and crucial to primal survival instincts. The hippocampus plays a key role in encoding long-term memories. Certain odours can invoke powerful memories from our past, for example, the smell of cinnamon, oranges or pine needles may bring back memories of childhood Christmases, or the smell of antiseptic may invoke memories of a hospital stay. Indeed, research indicates that our sense of smell is more intimately linked to memory than any of our other senses (Khamsi, 2022);
- Amygdala: this is also part of the limbic system and is primarily involved in emotional responses. In humans, odours can provoke powerful emotional responses; the smell of excrement or vomit, for instance, can elicit feelings of disgust. Emotional responses to smells develop early; indeed breastfeeding babies will move towards the unique smell of their mother's breast. The amygdala and hypothalamus often work in tandem,

Fig 2. **The olfactory pathways in the brain**



with smells not only triggering memory but powerful emotional responses, for example, the smell of a dental surgery in adulthood may trigger fear experienced in childhood (Kadohisa, 2013);

- Hypothalamus and reticular formation: these regions of the brain are intimately involved in regulating the autonomic nervous system (ANS) and play a key role in visceral responses to smells. In animals with an acute sense of smell, the odour of a nearby predator will commonly both elicit fear and activate the sympathetic branch of the ANS, triggering a fight or flight response. In humans, the smell of food cooking, particularly when we are hungry, will lead to the activation of the parasympathetic branch of the ANS, stimulating the production of saliva and gastric juice to prepare the mouth and gastrointestinal tract for receiving food (Fine and Riera, 2019; Kadohisa, 2013).

Sense of taste (gustation)

Our sense of taste is intimately linked to our sense of smell. Olfaction is essential to allow us to perceive many of the subtle flavours of the food we eat; this allows us to enjoy the process of eating and encourages adequate calorific intake. Initially, it is the visual and olfactory senses that allow us to judge the quality of the food we choose to put into our mouth, but it is taste which will ultimately determine whether that food is chewed and swallowed. Taste allows us to detect overly salty food or food that may have spoilt; it also allows the detection of some noxious and potential toxic materials that have been placed in the mouth (Briand and Salles, 2016).

Currently, humans are thought to be able to recognise five distinct primary tastes. These are:

- Sweet;
- Sour;
- Bitter;
- Salty;
- Umami (savoury).

Recently, it has been suggested that we also have the ability to recognise a sixth taste, which is associated with the fatty acids of fat-rich foods (Melis and Barbarossa, 2017).

The tongue and taste buds

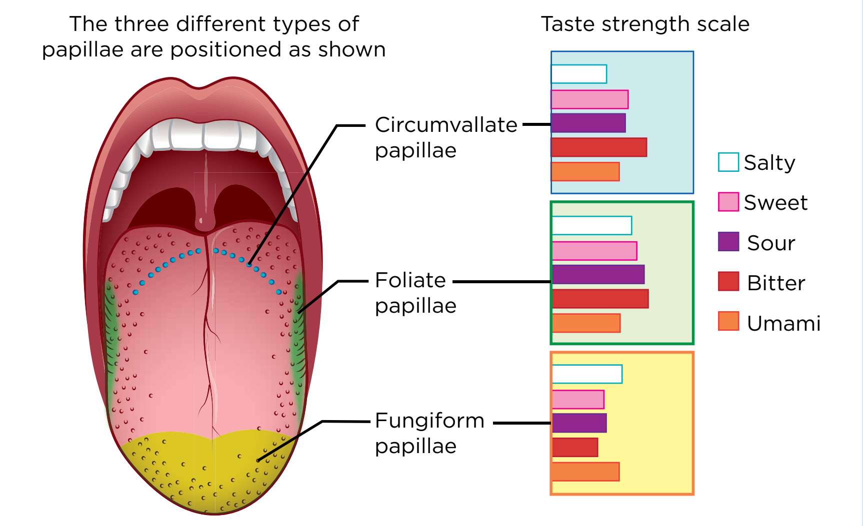
Taste buds are the primary sensory organs involved in detecting flavours in food. It has been estimated that humans have around 9,000 taste buds. Most are located on the tongue, with smaller numbers on the soft palate, pharynx and epiglottis.

The vast majority of taste buds are found in the tongue papillae; these are small, raised protrusions of the tongue epithelium (Fig 3). Three major types of gustatory papillae are present on the human tongue. The circumvallate papillae are the largest and found in a crescent-shaped arc towards the back of the tongue; each of these contains more than 100 taste buds. Foliate papillae (resembling leaves) are located in the middle, lateral portions of the tongue; these are smaller and typically house around 100 taste buds each. The front portion of the tongue is the location of the most numerous of the gustatory papillae. These are termed fungiform papillae since they are mushroom-shaped with each containing around four taste buds (Spence, 2022).

Each taste bud (Fig 4a) consists of around 50 taste cells (gustatory cells) (Fig 4b), together with supporting cells and basal cells. As with the olfactory receptor neurones, the taste cells in the taste buds have a relatively short lifespan (around 8-12 days) and are continually replaced by the actively dividing basal cells, which rapidly differentiate into new taste cells.

In addition to the three gustatory papillae, the tongue contains large numbers of filiform (thread-like) papillae. These do not contain taste cells but touch receptors that allow the tongue to determine the texture of the food. The filiform papillae are also predominantly responsible for giving the tongue its rough surface texture and help the surface of the tongue to grip and manipulate food during the process of mastication (Feng et al, 2014).

Fig 3. **Tongue papillae**



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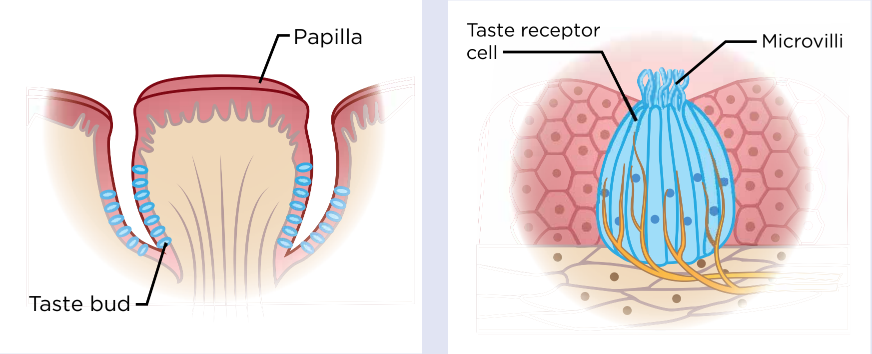
It was for many years thought that different portions of the tongue responded to the five primary tastes. However, the traditional taste map of the tongue, which was taught in schools and is still found in many basic biology textbooks, is now recognised as being inaccurate since it is now understood that all regions of the tongue can recognise the five major tastes (Fig 3) (Spence, 2022).

Fig 4. **Papilla, taste buds and taste receptor cells**



4a. Taste buds line the sides of each papilla and comprise taste receptor cells

4b. Taste receptor cells – these contact tastants in saliva via fine projections called microvilli

The physiology of taste

The chewing (mastication) of food is essential to taste; chewing grinds up and mixes the food in the mouth, allowing flavour molecules, termed tastants, to become dissolved in the saliva. The aqueous medium of saliva acts as a medium to transport the tastant molecules into the papillae where they can interact with the taste buds. Each taste cell has tiny membrane extensions termed microvilli (Fig 4b), which vastly increase the surface area of the cell. These microvilli have receptors on their surface, which the tastant molecules bind to. The binding of tastants with their corresponding receptors initiates depolarisation of the taste cell and the generation of an action potential (nerve impulse). Taste cells relay their action potentials to secondary neurones via chemical synapses.

Gustatory information from the tongue is relayed to the brain through three cranial nerves:

- The facial nerve (cranial nerve VII): carries information from the front two thirds of the tongue originating from the foliate and fungiform papillae;
- The glossopharyngeal nerve (cranial nerve IX): carries information from the posterior portion of the tongue originating from the circumvallate papillae;
- The vagus nerve (cranial nerve X): carries information from taste buds in the epiglottis.

These three nerves carry taste information initially to the solitary nucleus in the medulla oblongata of the brain stem, before it is relayed via the thalamus to the gustatory cortex in the frontal lobe of the cerebral cortex (Fig 5). It is the gustatory cortex that is ultimately responsible for decoding information from the taste buds, which allows the conscious perception of flavours (VanPutte et al, 2017).

The link between taste, smell and other senses

It has been estimated that between 75% and 95% of our sense of taste actually comes from our sense of smell. Even though this often-repeated claim has been questioned (Spence, 2015a), few would argue that the ability to fully taste food is intimately linked to our sense of smell. This becomes readily apparent when we suffer from a productive, catarrhal head cold, which impairs both our sense of smell and taste.

Today it is recognised that information from our senses of taste and smell, together with sensory information related to temperature and the "feel of the food" in the mouth, are integrated by the brain to produce the broad palate of flavours that we are capable of perceiving (Prescott, 2015).

Additionally, information from the visual and auditory senses can influence perception of food flavours (Spence, 2015b); for this reason, many high-class restaurants and Michelin-star chefs take great care over how food is presented on the plate and the ambient sounds that their diners are exposed to.

Changes to the senses of smell and taste

Many things can compromise the senses of smell and taste. A reduced sense of smell is referred to as hyposmia, while anosmia is the term used to describe a complete loss of the sense of smell.

The effects of ageing

Both our sense of smell and taste diminish with advancing years. Olfactory receptor neurons decrease in number into middle and old age, with around half of people aged 65-80 and three quarters of those aged over 80 having demonstrable loss of olfactory acuity (Nigam and Knight, 2017). Since smell is so intimately associated with taste, food can taste bland and the enjoyment of eating food can be diminished; this can lead to loss of appetite, inadequate food intake and subsequent weight loss.

Age-related loss of smell can also mean that noxious airborne chemicals are not perceived. Indeed, older people are recognised as being disproportionately affected by gas poisoning (Nigam and Knight, 2017). The sense of taste can also be compromised by reduced saliva production in older people and a gradual loss of taste cells. Perception of sour and bitter tastes appears to be the most severely impaired, but decline in detection of sweet and salty tastes are also reported (Alia et al, 2021). Worryingly, a reduced sense of smell and taste may lead to older people adding excessive amounts of salt to their food to make it more palatable. This has the potential to exacerbate pre-existing health problems such as hypertension (Nigam and Knight, 2017).

Pathologies associated with loss of smell and taste

Covid-19

One of the common characteristic symptoms of Covid-19 infection is significant impairment of the senses of smell and taste, which can reduce the enjoyment of food. Anosmia was reported in up to 80% of Covid-19 patients infected with early strains of the virus (the Alpha strains), with 11.8% to 35.5% of patients displaying anosmia without any other clinical symptoms (Ahmed et al, 2022). Many mechanisms have been proposed for the causes of anosmia in Covid-19 patients, including nasal obstruction, rhinorrhoea, oedema of the olfactory mucosa and direct olfactory epithelial damage. Currently, the exact cause is not fully understood, but appears to be most likely caused by viral infection

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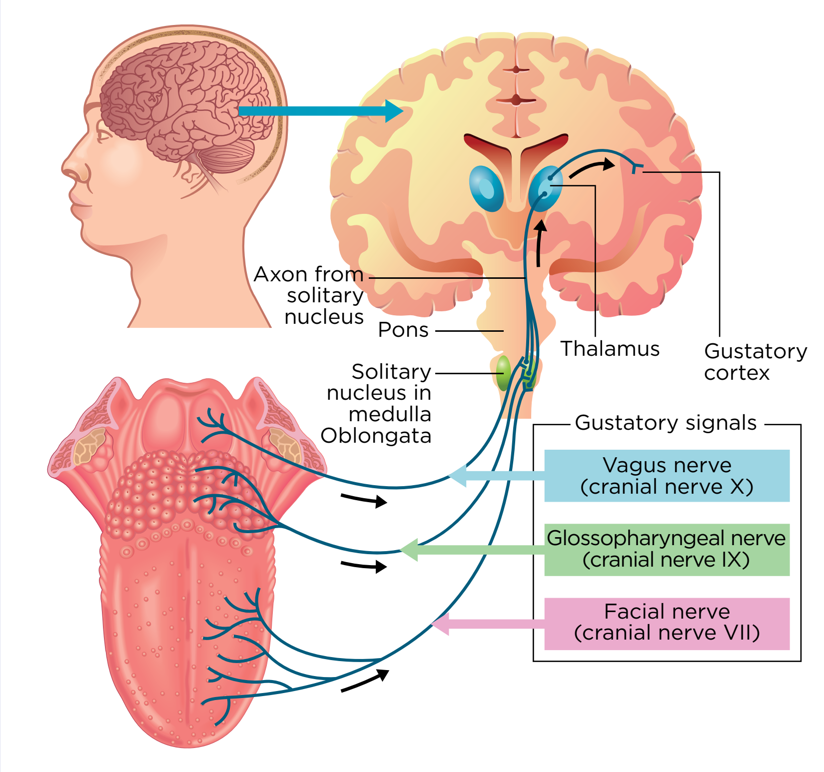
Fig 5. **The taste (gustatory) pathways**



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of the supporting cells and olfactory receptor neurons (Ziuzia-Januszewska and Januszewski, 2022).

Changes to the sense of smell and taste can deprive a patient of the pleasure of eating, which can have major psychological, social and physiological effects. Anosmia has been associated with food aversion, reduced social interactions, anxiety, depression, malnutrition and anorexia. Most patients will begin to regain their sense of smell after a few weeks, but around 5% of people infected with Covid-19 still report smell and taste dysfunction six months later (Boscolo-Rizzo et al, 2022).

In addition to Covid-19, hyposmia and anosmia are associated with many other pathological conditions (Boesveldt et al, 2017). These include:

- Chronic sinonasal disease;
- Upper respiratory tract infections;
- Head trauma;
- Neurodegenerative diseases including Parkinson's and Alzheimer's disease.

Help for patients with anosmia

Patients with hearing loss can be prescribed hearing aids, those with visual defects can make use of prescription glasses and a variety of visual aids, yet currently there are no widely available devices available to help with deficiencies in the senses of smell or taste. However, the Covid-19 pandemic has led to an explosion of research in this area. The use of intranasal steroid sprays has been shown to marginally improve olfaction by helping to resolve Covid-19-induced inflammation of the olfactory epithelium. Olfactory training involves asking patients to 'sniff and identify' several different odours, commonly rose, cloves, eucalyptus and lemon for 15 seconds twice a day over several months. Currently, this is the only intervention which has evidence of efficacy following post-infectious olfactory dysfunction (Boscolo-Rizzo et al, 2022). Undoubtedly, the research emerging from helping patients with Covid-19-induced anosmia will lead to more refined future treatments for patients with general taste and smell deficiencies.

> *"Research indicates that our sense of smell is more intimately linked to memory than any of our other senses"*

Conclusion

This article has examined the anatomy, physiology and neural pathways associated with the interrelated senses of smell and taste. We have provided a brief overview of how these senses tend to decline with advancing age and highlighted some of the pathologies that are associated with changes to smell and taste. In our next, and final, article in this series we will explore the sense of touch. **NT**

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