*Brain, Behaviour and Cognition Series*

# THE NEUROPSYCHOLOGY OF SMELL AND TASTE

G. Neil Martin

Psychology Press

# THE NEUROPSYCHOLOGY OF SMELL AND TASTE

Smell and taste are our most misunderstood senses. Given a choice between losing our senses of smell and taste, or our senses of sight and hearing, most people nominate the former. Yet our senses of smell and taste have the power to stir up memories, alter our mood and even influence our behaviour.

In *The Neuropsychology of Smell and Taste* G. Neil Martin provides a comprehensive, critical analysis of the role of the brain in gustation and olfaction. In his accessible and characteristic style he shows why our senses of smell and taste do not simply perform basic and intermittent functions, but lie at the very centre of our perception of the world around us. Through an exploration of the physiology, anatomy and neuropsychology of the senses, the neurophysiological causes of smell and taste disorders, and their function in physical and mental illness, G. Neil Martin provides an accessible and up-to-date overview of the processes of gustation and olfaction.

*The Neuropsychology of Smell and Taste* provides a state-of-the-art overview of current research in olfactory and gustatory perception. With sections describing the effect of odour and taste on our behaviour, and evaluating the contribution current neuroimaging technology has made to our understanding of the senses, the book will be of interest to researchers and students of neuropsychology and neuroscience, and anybody with an interest in olfaction and gustation.

**G. Neil Martin** is a Chartered Scientist and a Fellow of the Royal Society of Arts. As Director of the Human Olfaction Laboratory at Middlesex University, his research covers human olfaction and the effect of ambient odour on behaviour. He has written over a dozen books on psychology and teaches courses in neuropsychology, biological psychology, forensic psychology, health psychology and integrative medicine. He received his PhD in psychophysiology from the University of Warwick.

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*G. Neil Martin*

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# SERIES PREFACE

From being an area primarily on the periphery of mainstream behavioural and cognitive science, neuropsychology has developed in recent years into an area of central concern for a range of disciplines. We are witnessing not only a revolution in the way in which brain–behaviour–cognition relationships are viewed, but also a widening of interest concerning developments in neuropsychology on the part of a range of workers in a variety of fields. Major advances in brain-imaging techniques and the cognitive modelling of the impairments following brain injury promise a wider understanding of the nature of the representation of cognition and behaviour in the damaged and undamaged brain.

Neuropsychology is now centrally important for those working with brain-damaged people, but the very rate of expansion in the area makes it difficult to keep up with findings from the current research. The aim of the *Brain, Behaviour and Cognition* series is to publish a wide range of books that present comprehensive and up-to-date overviews of current developments in specific areas of interest.

These books will be of particular interest to those working with the brain-damaged. It is the editors' intention that undergraduates, postgraduates, clinicians and researchers in psychology, speech pathology and medicine will find this series a useful source of information on important current developments. The authors and editors of the books in the series are experts in their respective fields, working at the forefront of contemporary research. They have produced texts that are accessible and scholarly. We thank them for their contribution and their hard work in fulfilling the aims of the series.

Chris Code and Glyn W. Humphreys
University of Exeter, UK and University of Birmingham, UK
Series Editors

# PREFACE

In 1892, Henry's arguably more creative brother, William James, wrote this withering assessment of two of our oldest senses and other physiological phenomena: 'Taste, smell, as well as hunger, thirst, nausea and other so-called "common" sensations need not be touched on… as almost nothing of psychological interest is known concerning them' (William James, 1892, *Briefer Course Psychology*).

Picking up the baton, Sir Victor Negus in 1958, not to be outdone in terms of complete collapse of motivation and interest, wrote: 'the human mind is an inadequate agent with which to study olfaction, for the reason that in Man the sense of smell is relatively feeble and not of great significance'.

Given this largely unreceptive and, frankly, arctic view of these senses, even the most charitable soul would not view it as a positive augur for a book on both. For a start, there might not be enough material to fill it. Second, the material may be of epiphenomenal interest only. Smell and taste, it might be argued, are minor senses, of occasional sensory interest constituting a pleasurable distraction but performing intermittent basic, perfunctory functions that are too elementary and quotidian to warrant sophisticated neuropsychological inspection. Some of this is true. Given a choice between losing the senses of smell and taste, or the sense of sight or hearing, people would normally nominate the former, rather than the latter. We rely on the dominant senses more; this is why they are dominant. We are no longer quadripedal and do not rely on our chemosenses to navigate, to mate, to make ingestive decisions, to influence behaviour and so on, in the way we did before we became bipedal, serendipitously noticing the air was fresher and cleaner above ground (odours are heavy; they like the ground or bottom floor).

However, a life without either is like sight without colour or like somatosensation experienced through rubber gloves. These senses are considered unimportant because we take them for granted and we do rely on them to an extraordinary casual degree – the reason we do this is because they very rarely go wrong (one noteworthy example notwithstanding). Myopic or presbyopic individuals can wear glasses to correct their degenerating lenses, the tone-deaf can cope with this inconvenience, a person with a headache will find the slightest noise an irritation that tips into unbearability. But because the senses of smell and taste – the invisible senses – perform so well day to day, we only notice major impairments in their function when these impairments affect us badly. The most ersatz example is the common cold where individuals famously misattribute the failure to perceive food flavour to the inability to taste (rather than the inability to smell, which is what occurs). Food flavour is predominantly olfactory, not gustatory.

We also underestimate how efficient these senses are. Our sense of smell is more effective than a smoke detector. According to Engen (1982), we can recognize odours within 0–3 seconds of encountering them, and at a distance of between 1–2 m (one of the reasons why olfaction is more productively and creatively studied by psychologists than gustation. The Japanese Sanitation Centre noted that we (humans) can detect the malodorous isoamyl mercaptan (a variant of which is added to odourless propane gas to make it pungent) at 0.77 parts per trillion (Nagata and Takeuchi, 1990). Cain (1977) concluded that our noses are more sensitive than a chromatograph. We can probably detect ethyl mercaptan (which is added to gas) at around 1 part per billion (Whisman *et al*., 1978), the equivalent, as Yeshurun and Sobel note (2010), of three drops in an Olympic Swimming Pool. It is probably not on the basis of little understanding that Brillat-Savarin had argued that the nose 'acts as the first sentinel, crying out, "Who goes there?"' We also have very low detection thresholds for certain odours such as d-limolene and ozone (Cain *et al*., 2007), a phenomenon considered in more detail in Chapter 1. In short, our sense of smell – for a sense we appear not to rely on or which we regard as being of little significance – is very effective. Less gloriously, the external agent of this sense bequeathed to psychology one if its more colourful legacies. Emma Eckstein, a patient of Wilhelm Fliess – the otolaryngologist of orgon machine fame – suffered severe nasal bleeding after the removal of a nasal pack that had been left in her nasal cavity after surgery (the surgery itself was spuriously recommended for the interruption of nasal neurotic reflexes, whatever they might have been). Following this, Fliess dreamed about the 'after care', a somnolence that subsequently led to Freud's musings on the nature of dreams.

Smell and taste serve a vital purpose: they are essential for stopping us from killing ourselves, not only by detecting noxious odours, a mephitic alarm that saves us, but by preventing us from ingesting material that can harm us (rotten or spoiled food). These senses also interact with the largest cranial nerve, the trigeminus, which adds another dimension to behavioural life – this somatosensory nerve mediates the heat-delivery of a chilli, the tear-evocation of an onion and the jolting assault of ammonia. It adds another survival dimension to the panoply of chemosensation – the stimulation of the trigeminus activates the same fibres and substances implicated in the experience of pain. Combined with this survival role is another that allows us to derive feelings of pleasure or disgust from objects, environments and people. Scent is an effective person-repellant and attractor. As McBurney (1986), echoing Brillat-Savarin earlier, put it when describing the utility of the chemosenses:

> I argue that smell and taste are first and foremost our gatekeepers for ingestion and monitors of social behaviour. Their principal task, therefore, is to answer these questions: 'What is that stuff in my mouth (or about to go in my mouth)?', 'Do I like it?', and (for odour) 'Who is that and what do I want to do about him or her?'

At a psychological, but no less interesting level, scents in the environment affect our behaviour in ways of which we are barely conscious. Exposure to pleasant odour is associated with increases in charitable behaviour (Baron, 1997), better anagram formation (Baron and Thomley, 1994), increased emotional experience when reading literature (Cupchik and Phillips, 2005), changes in brain electrical activity associated with attention (Martin, 1998), reduced visual vigilance (Gould and Martin, 2001), improved verbal recall (Herz, 1997), reduced anxiety in women waiting for dental surgery (Lehrner *et al.*, 2000), increases in pain perception (Martin, 2006) and increased accurate recall of memories of events experienced years previously (Aggleton and Waskett, 1999), amongst other effects.

The psychological effects of exposure to odour have also been demonstrated outside the laboratory, in applied contexts such as the workplace (Sakamoto, *et al.*, 2005). Mental concentration levels have been reported to be higher during exposure to the odour of lavender but not jasmine (Sakamatoto *et al.*, 2005) whereas participants who slept in the presence of jasmine odour performed cognitive tasks more rapidly and reported being more alert after waking (Raudenbush *et al.*, 2003). The odours of peppermint, jasmine, ylang-ylang 1, 8-cineole and menthol appear to have no beneficial effect on reaction time (Ilmberger *et al.*, 2001), but respondents' ratings of these odours as positive or negative did influence reaction time: odours rated as positive were associated with faster reaction times (Ilmberger *et al.*, 2001).

The behavioural effects of malodour are more stereotypically predictable. Malodour has strong historical and medical associations with ill-health, especially disease and infection ('malaria', for example, literally means 'bad air' and was the name given to conditions arising from the inhalation of noxious fumes emanating from Roman marshes; Martin, 1996). Malodour is also an environmental hazard: it is the major source of public complaints to local government authorities in the US and Europe (Nicell, 2009). Exposure to it is associated with significant increases in ill-health and psychological annoyance, leading to a seriously impaired quality of life, stress, insomnia, eye irritation, nausea, headaches, irrational behaviour and anorexia (Nicell, 2009; Sucker *et al.*, 2009). Laboratory studies have found that exposure to unpleasant odours increases pain perception (Martin, 2006; Villemure *et al.*, 2006) and the stereochemical, androstenone (described in Chapter 1), has also been associated with increased perception of pain, especially in women (Villemure and Bushnell, 2007). Frequency, intensity, duration, offensiveness and location are all important factors that determine the strength of people's responses to environmental malodour.

Increases in an individual's negative mood are significantly associated with exposure to a foul-smelling odour. Across their lifespan, people remember unpleasant odours better than pleasant ones (Larsson *et al*., 2006) and these odours are detected more quickly than pleasant odours (Boesveldt *et al*., 2010). The likeability of faces decreases in the presence of malodour administered at below-threshold levels (Li *et al*., 2007). Participants exposed to an unpleasant smell are more inclined to rate strangers that are similar to themselves more positively than they would dissimilar strangers (Rotton *et al*., 1978). Rotton (1983) reported that women who rated paintings and black and white photographs in a room polluted with ethyl mercaptan gave significantly lower scores of 'well-being' to the photographs and judged the pictures to be less professional and less worthy (but no less tasteful) than did participants in an unpolluted room. These participants also reported lower feelings of pleasure and levels of arousal than participants in the air-conditioned room. The longer the exposure to the malodour, the less the pleasure taken in completing the task. Participants detect fewer proof-reading errors in a polluted room but detect more when moved to an unpolluted room. Participants taken to an unpolluted room and asked to solve a series of puzzles, the first and second of which were insoluble (a measure of frustration) attempted fewer puzzles after a previous, 30-minute exposure to the malodour. Malodour, therefore, is a highly instrumental sensory stimulus, capable of directing emotion, thought and behaviour.

The behavioural effects of scent have been more comprehensively studied than the effects of taste because taste is the briefer sensation and is generated only for one purpose: the detection and appreciation of food inside the mouth. While we do habituate quickly to scent, we have, to some degree, more control over and exposure to its spatial distribution and its uses – we use it to deodorize, to make us attractive, to repel, to freshen, to relax and so on. (None of these could apply to taste specifically, the measurement of responses to which have been mainly physiological in nature or limited to the study of psychophysics and valence/pleasure.) The maximum field of influence of scent, therefore, is greater.

Unlike the naming of tastes (where we are moderately competent), our naming of odours is notoriously bad. Of the tens of thousands of odours we can detect, we can name very few accurately. As chemicals, these odours should not surprise us with their problematic linguistics. When sitting in the garden, we do not comment on the fragrance of the phenyl ethyl alcohol, while admiring the verdant source of the isobutyl methoxypyrazine as we nibble our peeled amyl acetate, stopping occasionally to sip thiourine with ethanol, while avoiding the scent of isovaleric acid from discarded footwear. Instead, we use descriptors. We say that something smells or tastes like a referent, even though this referent is nothing more than chemistry and chemistry that interacts with our olfactory and gustatory systems to provide the unitary percept we are familiar with. So, we enjoy the scent of a rose, and of freshly mown grass, of a banana, and the taste of gin with tonic, and avoid malodorous feet – the names, the psychology, we give to the chemistry.

This book aims to describe, review and discuss the contribution of psychology and neuropsychology to our understanding of smell and taste. Chapter 1 provides an introduction to the senses and describes the ways in which psychology and chemosensory science measures our responses to these stimuli. An understanding of how olfaction and taste is measured is important (not least because the subsequent chapters refer to the specific functions measured and the tests and techniques used). Equipped with this information, the bulk of the book will be better understood.

Chapter 2 considers some of the individual differences that exist in these senses, particularly sex and age. There are also modality-specific individual differences (such as supertasting and specific anosmia for androstenone). As these have implications for our understanding of both senses, these specific eccentricities are described there.

The book assumes very little in the way of prior knowledge of the brain and neurophysiology, apart from the basics. Chapters 3 and 4 describe and review the current knowledge of the neurophysiology and anatomy of chemosensation (Chapter 3), and how electrophysiology and neuroimaging have helped advance the understanding of the cerebral basis of olfactory and gustatory perception (Chapter 4). The emphasis in the book is on human neuropsychology but, as with all areas of psychology, it is informed by animal research – and much of what we understand of the initial stages of olfactory processes has been derived almost exclusively from animal work. Therefore, animal work is cited to inform understanding of human function. Given the significance of odour and taste to humans – compared with other species – however, these data are described circumspectly.

Chapter 5 continues the pure neuropsychological theme by describing disorders of smell and taste, the effect of degenerative disease on olfactory function and the effect of particular psychiatric disorders on smell and taste perception.

Finally, Chapter 6 brings together the material in the previous chapters to examine the neuropsychological basis of flavour – one of the largest remaining challenges for neuropsychology and chemosensation. It is, possibly, an impossible challenge. This chapter also examines the interaction between smell and taste and other modalities, such as vision, somatosensation and audition. Flavour is the sum of this interaction.

This book would not have been possible without the support of several people. First, and importantly, Chris Code and Glyn Humphreys, who were gracious enough to see the merit of this entry to their *Brain, Behaviour and Cognition* series and commission the manuscript; George Mather and Jamie Ward, who were kind enough to comment on the original proposal for Psychology Press; and Phil Jerrod, Laura Elllis and Becci Edmondson at Psychology Press for their advice, patience and good humour. For permissions to use figures, their enormous help and their encouragement for the book, a Brobdignagian thank you to Jessica Albrecht, Ivan Araujo, Thomas Bitter, Douglas Braaten, Warrick Brewer, Jelena Djordevic, Richard Doty, Diego Luis Garcia Gonzalez, Chris Hawkes, David Kareken, Don Katz, Alan Mackay-Sim, Paul Moberg, Claire Murphy and Bruce

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If you would like to write to me with comments and feedback about the content of the book, my email address is n.martin@mdx.ac.uk (or tweet @thatneilmartin).

# ABBREVIATIONS

| | |
|---|---|
| ACC | anterior cingulate cortex |
| AD | Alzheimer's Disease |
| AML | ascending method of limits |
| AMTL | anteromedial temporal lobe |
| AON | anterior olfactory nucleus |
| B-SIT | Brief Smell Identification Test |
| CN | cranial nerve |
| CNS | central nervous system |
| DAT | Dementia of the Alzheimer Type |
| DBS | deep brain stimulation |
| dlPFC | dorsolateral prefrontal cortex |
| DT | dopamine transporter |
| EEG | electroencephalography |
| EP | evoked potential |
| EPI | Eysenck Personality Inventory |
| ERP | event-related potential |
| fMRI | functional magnetic resonance imaging |
| fNIS | functional near-infrared spectroscopy |
| ISI | inter-stimulus interval |
| KS | Kallmann's syndrome |
| LGN | lateral geniculate nucleus |
| LOT | lateral olfactory tract |
| LPOFC | lateral prefrontal orbitofrontal cortex |

| | |
|---|---|
| MCI | mild cognitive impairment |
| MEG | magnetoencephalography |
| MRI | magnetic resonance imaging |
| MTLE | medial temporal lobe epilepsy |
| NA | nucleus accumbens |
| NST | nucleus of the solitary tract |
| OB | olfactory bulb |
| OCD | obsessive–compulsive disorder |
| OE | olfactory epithelium |
| OEP | olfactory evoked potential |
| OFC | orbitofrontal cortex |
| PBN | parabrachial nucleus |
| PD | Parkinson’s Disease |
| PET | positron emission tomography |
| PFC | prefrontal cortex |
| PMC | primary motor cortex |
| POC | primary olfactory cortex |
| PTA | primary taste area |
| PTC | primary taste cortex |
| rTMS | repetitive transcranial magnetic stimulation |
| SOC | secondary olfactory cortex |
| SS | single staircase |
| SSS | sensory-specific satiety |
| TBI | traumatic brain injury |
| UPSIT | University of Pennsylvania Smell Identification Test |
| VBM | voxel-based morphometry |
| VMPN | ventroposteromedial nucleus |

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# 1

# SMELL AND TASTE

## An introduction to the psychology of chemosensation

### 1.1 Unique features of smell and taste

Smell and taste are chemosenses, that is, they are sensory systems that respond to chemical stimulation and whose chemical stimuli bind to receptors to create a sensation. Both are two of the most neglected and unusual in the sensory panoply in that each exhibits features that uniquely and dramatically separate it from the dominant senses of vision and audition, and even somatosensation. For example:

- Olfaction is the only sense with receptors directly exposed to the environment;
- Humans have an ability to detect hundreds, if not thousands, of different odours but only five or so tastes. However, the same humans are notoriously poor at identifying such odours;
- There is no agreed classification system for odour; there is more agreement for taste;
- Unlike vision, hearing and touch there is no olfactory dimension that relates stimuli to sensation; it has no predictable frequencies nor limited spectra (Mackay-Sim and Royet, 2006);
- Also unlike vision and audition, the olfactory system requires a third of the genome; vision requires three genes; audition requires a structure that develops from genes coding for other aspects of development (Mackay-Sim and Royet, 2006);
- The olfactory cortex has three layers, unlike most other sensory cortices;
- Taste and smell receptors regenerate every sixty days – thus, our current chemoreceptors did not exist two months ago;
- Smell is probably the most manipulable and confusable of the senses: people can be convinced that an odourless substance is odorous or that they are smelling something they are not;
- Taste is invariably confused with smell although smell provides the greatest contribution to food flavour;

- Olfactory dysfunction may be a better marker of risk of degenerative disease (e.g. Alzheimer's Disease (AD)) than more conventional neurophysiological or clinical measures.

Formally, smell is known as olfaction and taste as gustation and the chemicals that stimulate each sense are called odorants or tastants. In the case of gustation, sensation is produced by the interaction between the tastant on the tongue and the depolarization that occurs in the taste bud field it stimulates. In the case of odour, the molecules are inhaled via the external nares (nostrils) with the air that carries them, and are processed, via transduction, by the olfactory apparatus at the top of the nose and beyond (Chapter 3 describes this pathway and process in detail). An odorant is an odour compound which means that it is volatile (and, therefore, evaporates quickly) and hydrophilic and lipophilic (it can dissolve in oil and water). However, the sense of smell also delivers olfactory information from another source of respiration, other than external: from inside the mouth.

## 1.2 Orthonasal and retronasal breathing

Typical olfactory perception involves two types of breathing – orthonasal and retronasal. With orthonasal breathing, odour molecules enter the anterior or external nares, travel through the nasal cavity and are transported to the olfactory apparatus at the top of the nose and onward to the cortex. Retronasal breathing occurs in the oral/buccal cavity where odorants stimulate the posterior or interior nares of the pharynx (the receptors here are called nasopharyngeal receptors and are supplied by two cranial nerves (CNs), neither of which are olfactory), and travel to the olfactory apparatus and the olfactory receptors at the top of the nose (Burdach and Doty, 1987). It is this process that creates food flavour.

A fruit juice inserted into the mouth and rolled on the tongue while the nose is pinched shut, will be almost impossible to identify, although the identification of the juice's taste (that it is sweet or sour) will be relatively unaffected. However, if the nostrils are released, identification of the juice will be almost immediate because the internal nasopharyngeal receptors have been stimulated by the odour molecules released by the tastant and these molecules have stimulated the epithelium retronasally, via the back of the mouth. The failure of retronasal perception is the reason why when individuals suffer colds and the 'flu, they claim to be unable to taste food. What they actually mean is that they cannot smell the food – they can easily determine whether the food tastes salty, sweet and so on if pressed. What they are unable to do is identify the flavour (and, therefore, the food). The reason for this inability is the impairment in retronasal perception of odour. In this sense, therefore, the sense of smell is both an exteroreceptor and an interoreceptor. Unless we are ingesting, the exteroreceptive function is the most common and important, 'giving warning of enemies and other noxious things and guiding the animal to mates, food and other desirables' (Herrick, 1933). There are also psychophysical differences between orthonasal and retronasal breathing. Thresholds for odours are lower in the former and odours may be perceived more intensely (Voirol and Daget, 1986), especially