The essence of the human condition?
Lorenzo Stafford on our ancient and under-appreciated sense of smell

Olfaction, our sense of smell, is among our oldest, having its origins in the rudimentary senses for chemicals in air and water. Yet it is sometimes seen as something slightly comical, a poor relation to its younger sensory neighbours. From the ancient Greeks to the present day, this humble sense has been derided as vague, bastard, ambiguous. Although Nietzsche praised the animalistic nature of smell for its ability to further understanding without the need for language, others, including Freud, thought it relatively unimportant and mainly a reminder of our animal origins (Le Guérer, 2002).

One reason for this view is our inability to ‘abstract’ odours. You cannot reflect on an odour linguistically; you cannot move it into some mental workspace and manipulate it to the same extent as you can for sound and vision. Connected to this are differences in our ability to recreate or re-experience odours. In Perfume: The Story of a Murderer (Suskind, 1985), the author describes an individual who not only has the ability to actually smell them again, but to ‘actually smell them upon recollection’. Sounds easy? Then try this: Close your eyes and visualise any famous painting (e.g. Mona Lisa, Van Gogh’s Sunflowers); move around the image in your mind, reflecting on an odour linguistically; you cannot ‘abstract’ odours. You cannot.

It seems a paradox, then, that calling an odour to mind is so difficult yet if we smell a certain odour it can trigger intense emotions and associated memories that can literally overwhelm us; far more than other senses. How many of us have experienced the situation where, years after an affair, we are randomly presented with the same odour of the perfume really was! I normally find that the vast majority of people find sound and vision far more intense and easier to manipulate than they do the odour. We can easily see the red strawberry, imagine the pink inner flesh, and yet to recreate the smell in our mind is extremely difficult. Now we can appreciate just how unusual Suskind’s protagonist really was!

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It seems highly probable that odours have such effects due to the fact that all of the senses, the olfactory cortex is proximal to the main memory centre of the brain (hippocampus), and also the closest to the emotional centre of the brain (amygdala). One example of the emotional intensity of odours comes from a preliminary study we completed, where we had participants simply smell a variety of essential oils (including rosemary, lavender, cedar wood), rate them on various dimensions and detail what sort of memories/emootions they associate with each odour (Stafford et al., 2009). Even in the confines of a relatively contrived lab setting, we found some odours induced quite vivid memories, where for instance rosemary (a eucalyptus-based odourant) evoked memories of vapour rub and ‘being cared for’. Jasmine reminded some of ‘Nanas house’, whilst cedar wood of ‘church at Easter’; the latter is a damp woody smell, but to connect this not only to ‘church’ (assume wooden pews), but in a possibly damp time of year, seems very apt.

Further experimental work has also supported this by demonstrating that the emotional intensity of odour-associated memories is greater than those memories cued by sound/visual, though there are no differences in the amount remembered (Herd, 1997). So, it is not that odour-associated memories are remembered any better than those memories related to other senses; in fact the rate of forgetting is initially steeper for odour-associated memories. However, following this, the rate of forgetting is relatively flat (Herz & Engen, 1996). Other differences in olfactory memory include differences in the ‘reminiscence bump’. memories from our past are more accurately recalled from around adolescence, but odour-associated memories are strongest from earlier in our lives, typically between 6 and 10 years of age (Chu & Downes, 2000). Differences such as these have made researchers wonder whether a separate memory store exists for odours.

**Smell and taste**

One aspect of olfaction that is frequently overlooked by people is its central role in our enjoyment of food. Back in the late 1980s, whilst backpacking around Thailand I ‘tasted’ my first hot and sour soup (Tom yum kai), which even to this day was a turning point in my own sensory history. I say ‘tasted’ but in fact the majority of flavours experienced in the mouth are due to the olfactory, retinalonal system of odours detected in the mouth. Think about it: we perceive only five tastes (sweet, bitter, sour, salty, umami), but around 1000 olfactory receptors, each having its own specific molecular receptive range, allow us to perceive a virtually infinite number of odourant mixtures. When you consider the kinds of ingredients in this fine soup (including lemon grass, coriander), there is no way it could be fully appreciated by taste alone. With our ability to perceive so many different flavours, and the opportunity to learn to associate these to unique foods, it is small wonder the flavour industry is so lucrative.

The connection between our sense of smell and feeding behaviour has been known for some time, with neural projections from the olfactory cortex to the hypothalamic feeding centres of the brain. Less clear, particularly in humans, is the full extent to which the olfactory cortex is involved in eating behaviour. One way of examining this question is to see whether differences in hunger state predict contrasts in olfactory sensitivity to food- and non-food-related odours. Olfactory ‘sensitivity’ is a term usually applied to the measurement of ‘threshold’, the lowest concentration of an odour that can be reliably detected. (The two other main measures of olfactory ability are ‘discrimination’, where a person is presented with three odours, two of which are the same, and the task is to state which one is different; and ‘identification’, where a person smells a range of common odours and has to identify each one from a list of alternatives.) In the threshold test, participants are blindfolded and given a sample of the target odourant at the strongest concentration, to familiarise themselves with the odour. In one version of the test, they are then presented with three odours, two of which are blanks, and the task is to state which one is different. A correct response results in representation of the same triplet (in a different order) and is repeated until a mistake is made, which then results in the next (stronger) concentration step being presented. Using this threshold method researchers (Albrecht et al., 2009) found that olfactory sensitivity to a non-food odour did not vary between low and high hunger states. However, for a food-related odour, olfactory sensitivity was highest – from a list of alternatives – in the lowest concentrations of the odourant – following a satiating meal rather than before; that is, in a ‘low’ rather than ‘high’ hunger state. This was surprising, as we might intuitively think that detecting food-associated odours would be better when we are more hungry. Since pleasantness ratings for the food odour decreased following a satiating meal, it could be that a better sense of smell plays a role in regulating food intake by rejecting foods we no longer need.

In an era of increased worldwide obesity, one obvious application of the above research is to understand if olfaction plays any sizeable part in the condition. This interest has been peaked by two pieces of evidence. First, that a number of hormones including leptin play a central role in controlling food intake (Hellstrom...
et al., 2004). Second, the evidence from animal work establishing a link between pre-ingestive feeding behaviour and leptin receptors in the olfactory cortex (Getchell et al., 2006). By extension, these studies suggest that olfaction is more involved in food consumption than previously thought.

Given this, it is perhaps surprising that few studies have examined the relation between obesity and olfactory function in humans. In our own study (Stafford & Welbeck, 2011) we found that compared with individuals low in body mass index (BMI), those with high BMI were better at detecting the food odour, with larger differences in the satiated state. This suggests that for individuals with a propensity to gain weight, having a heightened sense of smell following a meal may not in fact aid in the control but instead help sustain food intake.

Nevertheless further work is required in this area using clinical samples before stronger claims can be made.

'Smelling' across the lifespan
Are we born with innate likes/dislikes for certain odours, or are these acquired (learned) behaviour? Fascinating research suggests it is a mixture of the two. One study presented three-day-old infants with pleasant (vanillin) and unpleasant odours (butyric acid, which smells of rancid butter) and measured typical facial responses (Schaul et al., 2002). Although these odourants produce clearly distinct facial responses in adults, in these infants the pattern was rather mixed, with no clear facial differences in smiling/disgust to the pleasant odour, though there were a higher number of disgust versus smiling responses to the unpleasant odour. This strongly suggests that avoidance of odours associated with disgust might be innate, whereas odours connoting something positive (encouraging approach behaviour) need to be learned. This also links to a study which found that compared to those adults who were breast-fed as infants, those bottle-fed with vanilla-flavoured milk, preferred the taste of vanilla-flavoured ketchup (Haller et al., 1999). This indicates both that positive tastes/odours are learned behaviour, and that early taste/olfactory experiences play a role in influencing later food preferences.

More recent work examined the influence of culture on this subject, testing young French residents (mean age: 23 years) of Algerian French (AF) and European French (EF) origin. They found that the AF group preferred the odour of mint to that of rose, with no corresponding differences in the EF group (Poncelet et al., 2010). The researchers also investigated chemosensory event-related potentials (CSERPs). ‘P2 amplitude’ is theorised to be involved in the emotional tone of an odour, whilst ‘P2 latency’ is thought to reflect differences in experience, development and age. In the study, the researchers found longer P2 latencies to the odour of mint for the AF versus EF group. Since mint is frequently consumed in tea in North African cultures, these findings suggest the plasticity of the brain in response to the early experience of particular foods, moulding later olfactory preferences.

Generally speaking, our sense of smell begins to decline in our mid-thirties, with a sharper fall from around 55 years onwards (Hummel et al., 2007). Interestingly, the age-related differences are more marked in threshold measures of olfaction compared with discrimination or identification. So, perceiving very small concentrations of odours is particularly difficult as we age, whereas the ability to differentiate and identify odours at stronger ( supra-threshold) concentrations declines less rapidly.

However, age-related falls in olfactory function are certainly not experienced by everyone, with many elderly people having similar scores to much younger individuals; which suggests that it may not be age per se that causes decreases in our sense of smell but some other factor associated with the ageing process, such as neurodegenerative disease. This links well with research highlighting that chronically low olfactory function can be an early marker for neurodegenerative diseases such as Alzheimer’s and Parkinson’s disease.

One study found that from an initial cohort of individuals with loss of olfactory function, after four years, 7 per cent were diagnosed with idiopathic Parkinson’s disease (IPD) and 13 per cent had more general IPD associated abnormalities (Haehner et al., 2007). Although at first glance, these percentages do not seem particularly high, when they are compared against a prevalence of IPD in the general population of 1.6 per cent and 1.8 to 2.6 per cent in the elderly, they suggest that olfactory loss can be an important early indicator of such conditions. More astonishingly, one recent study completed olfactory identification tests in a large group of elderly individuals and monitored them over a period of time. Those with impaired olfactory function were 36 per cent more likely to die than those with better olfactory function (Wilson et al., 2011). Surprisingly, this figure remained even after controlling for a range of other health-related factors (including cardiovascular, physical activity and depression). The authors theorise that the link between olfactory function and higher mortality is connected to a higher likelihood of neurodegenerative disease.

Olfaction and art
Setting up experiments in the area of
olfaction certainly present some challenges, and given the closeness of art and science it is unsurprising that trying to create olfactory art is just as problematic. Some years ago, on a visit to Tate Liverpool, I came across a rather unusual exhibit. A whole level had been given over to an audio installation with head-high speakers arranged in a circle, each apparently representing a male chorister. Though initially sceptical on what the work might add to the music itself, I found myself captivated by an incredibly rich and moving journey through the music. Yet I find it difficult to conceive of a comparatively moving art piece directly connected to our sense of smell. Perhaps, like many of us, I find the idea of being confronted with odours in a gallery space vaguely unpleasant and incongruent with art appreciation, which is precisely the restriction lamented by artists trying to work in this medium (Jones, 2009). This is entirely consistent with what I have said about the marginalisation of olfaction. The roots of this can also be traced on a developmental level, where very young children laugh and joke around the subject of smell without strong embarrassment, which changes with age and culture. One interesting prediction from this is that young children might well appreciate art emitting odours more than adults! Nevertheless, artists have found some ingenious ways to explore olfaction. One individual whose full-time job is actually researching olfaction in moths (Manduca Sexta) recorded the brain activity of one of his subjects; 32 neurons in one part of the brain responding to a range of related odourants. He then converted these electrical signals into music with specialist software, allowing different instrument assignment. The result (see www.as.wvu.edu/daly/music.html) is a surprisingly melodic experience!

Apart from art installations, literature has long been intimate with our sense of smell, which is likely due to the change of medium to the printed word and the greater focus on linguistic association. The most commonly referenced author to our sense of smell is Marcel Proust and his classic work Remembrance of Things Past, with a spine tingling extract given below: When nothing else subsists from the past... after the people are dead, after the things are broken and scattered... the smell and taste of things remain poised a long time, like souls... bearing resiliently, on tiny and almost impalpable drops of their essence, the immense edifice of memory.

Final thoughts
I started this article with our sense of smell being a somewhat poor relation to vision and audition. Hopefully, I have demonstrated that the study of olfaction is an interesting and worthwhile pursuit, leading to real insights about human and animal behaviour and, dare I say it, the human condition.

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