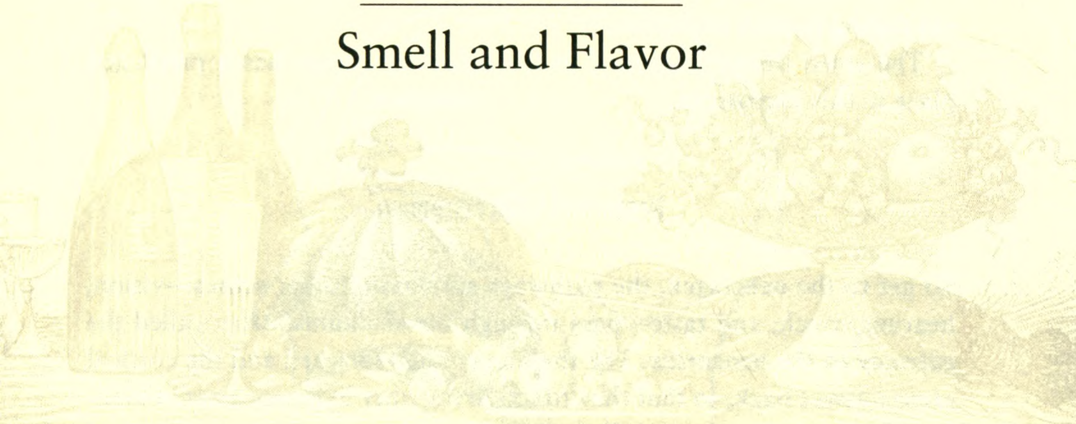
CHAPTER TWELVE

Smell and Flavor



We have seen that the olfactory cortex begins the task of creating the brain's representation, not of individual smell molecules, but of "smell objects" representing the food we are consuming. What more is needed? The main need is someone to "read" the smell object in a way that gives it meaning in a human context. This requires the neocortex, in evolutionary terms the newest type of cortex, that dominates the mammalian brain.

The increase in the area of the neocortex in primate and human evolution has produced many different cortical areas. These areas are of three main types. First are the areas that connect with the sensory and motor pathways below. These are called the *primary sensory and motor areas*. They are relatively large in the human in order to carry out the initial processing of sensory input and the final control of movements at the neocortical level. Second are the *association areas*, specializing in elaborating the properties of a given sense—for example, in vision there are areas for elaborating the processing of signals about color, movement, and faces—and coordinating motor acts. Finally, there are *higher association areas*, which are concerned with creating our highest mental faculties. These include language—both the areas related to interpreting language and those related to producing speech—and higher cognitive functions such as reasoning and planning ahead. These areas multiply the representations of our sensory and motor worlds. They also multiply the number of connections between areas. In addition, each area generates internal states that further abstract those worlds. The attributes that we consider human depended on a great expansion of these cortical areas during human evolution.

The smell image fashioned in the olfactory cortex has a privileged place in this expansion.

Neocortical Smell Perception

To get to the neocortex, the pathways subserving other senses—vision, hearing, touch, and taste—pass through the thalamus, often called the *gateway to the neocortex*. The thalamus sends forward and the cortical areas answer back, so that they function together in a coordinated manner. These other sensory pathways are located in the middle and back of the brain.

For smell it is different. The olfactory cortex sends a small number of fibers to the thalamus; but as shown in figure 7.1, most go directly to a special area called the *orbitofrontal cortex* (*ofc*) because it is situated just above the orbits of the eyes in the most anterior (prefrontal) part of the brain. It is shown in relation to the rest of the brain in figure 12.1.

The prefrontal cortex is regarded as the peak level of the primate and human brain, containing the circuits that subserve most of our highest human cognitive functions mentioned earlier. Astonishingly, the output from the olfactory cortex is aimed precisely at this highest level.

The sense of smell is therefore uniquely privileged in several ways:

1. It has a direct input to the prefrontal cortex.
2. It gets there through a short path involving only three neurons: olfactory receptor cells, mitral cells, and olfactory cortical pyramidal neurons.
3. Its area is situated in the heart of the part of the brain that makes us human.

The significance for neurogastronomes is clear: the volatile molecules released from everything we eat are so important that they are evaluated quickly at the highest level of the human brain.

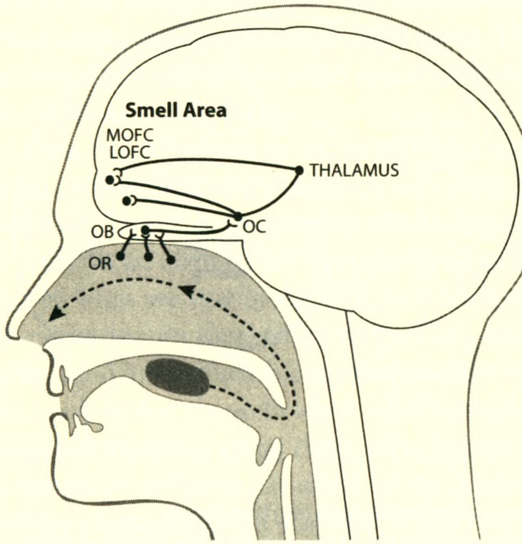


FIGURE 12.1 The human smell system

OR = olfactory receptor cells; OB = olfactory bulb; OC = olfactory cortex; MOFC = medial orbitofrontal cortex; LOFC = lateral orbitofrontal cortex.

Humans' Big Olfactory Brain

Maybe this direct pathway would not matter so much if the human sense of smell was not very important. Let us deal with the popular impression that humans have smaller olfactory brains than other mammals.

The bigger the brain, the more elaboration of sensory and motor representation can occur. This reaches its peak in the neocortex, the richest medium yet designed in animal life for elaboration of our sensory, motor, and internal worlds. It is usually assumed that the great overgrowth of the neocortex is related to the dominant role of vision in the lives of primates and humans. However, much of this great expansion of processing machinery is also available for the other senses as well, including smell. The main message of this book is that, despite the declining numbers of receptor genes, the brain processing mechanisms of the smell pathway, culminating in the neocortex, *bestow a richer world of smell and flavor on humans than on other animals.*

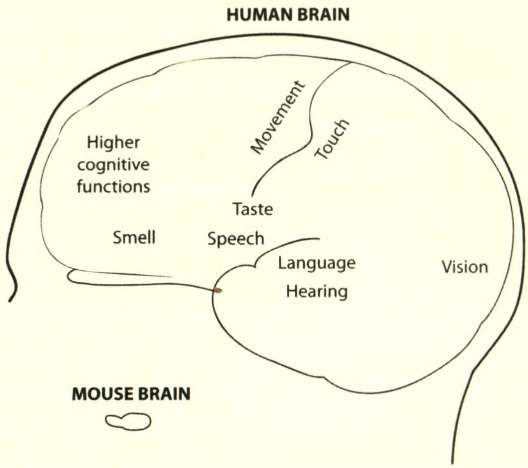


FIGURE 12.2 The human brain compared with the mouse brain for relative size
The diagram shows the locations of different brain systems related to different functions and behaviors.

This point can be made by comparing the mouse brain and the human brain. Because the two brains are usually illustrated at the same size, the olfactory bulb and orbitofrontal cortex of the mouse appear to be very large in relation to those of the human. However, this is where a picture, although it may be worth a thousand words, is worth the wrong words. If we show, as in figure 12.2, the two brains in their true sizes, the olfactory bulb of the human is actually nearly as big as the entire mouse brain, and the orbitofrontal region is huge by comparison. The conclusion is clear: the smell pathway has been maintained in size in the human, whereas the amount of brain to process the signals in that pathway has increased enormously. Much of neurogastronomy is about what this increased brain power can do to carry out enhanced processing of its smell and flavor input.

Unique Information Processing and Connectivity

What is there about this patch of neocortex that enables it to contribute a much enhanced human meaning to the smell image, in the form of a smell object arriving from the olfactory cortex?

There are two main possibilities. One is that its construction enables it to carry out enhanced processing of the smell input. The second is that its increased connections with other brain areas go far beyond what has been available to the olfactory cortex.

First, how is this "new" cortex constructed? It is thicker, because it represents a kind of doubling of the single layer of the simple olfactory cortex into two thick layers, containing more subvarieties of pyramidal cells and interneurons. In both layers the pyramidal cells have an organization similar to what we saw in the olfactory cortex: axon branches that feed back excitation on themselves and other pyramidal cells, and that also activate inhibitory interneurons to cause feedback and lateral inhibition. The result is that the individual basic operations, of boosting and recombining inputs and shaping them with inhibitory interneurons, appear to be similar in principle to those in the olfactory cortex, but greatly expanded in complexity. In addition, there is a new population of small *stellate* (star-shaped) cells, which serve (among other functions) as an internal relay for the sensory input coming either directly from the olfactory cortex or indirectly from the thalamus.

So we see again the principle that each stage of processing in the smell pathway is carried out by a new and more powerful type of processing mechanism.

Second, what about the connections? Recall that the connections of the olfactory cortex consisted of the input from the olfactory bulb and the output to the orbitofrontal cortex. The olfactory cortex is a region dedicated to processing the odor image from the olfactory bulb and outputting it to the orbitofrontal cortex. The olfactory cortex does have output connections to other parts of the brain besides the orbitofrontal cortex, but the only connections to the neocortex are the direct ones to the orbitofrontal cortex. In contrast, the orbitofrontal cortex has critical connections with many other parts of the neocortex.

Figure 12.3 shows how all the sensory pathways send projections from their neocortical areas to the orbitofrontal cortex. This means that the cells in the orbitofrontal cortex potentially are able to combine their olfactory inputs with inputs from all the other sensory systems that are stimulated by food in the mouth. They can also have interactions with other parts of the neocortex that are involved in other types of behavior. Chief among these are the *amygdala*, involved in emotion, and parts of the *prefrontal*

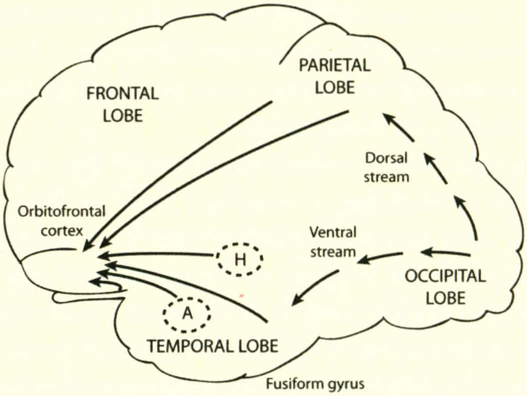


FIGURE 12.3 Many brain regions connect to the orbitofrontal cortex
H = hypothalamus; A = amygdala.

cortex, involved in flexible learning and in decisions about rewards. These are all capabilities that are necessary in judging flavors within the context of different senses in the mouth, different behavioral states such as whether we are hungry or satiated, and making decisions about whether a flavor is attractive or not, capabilities that are discussed further in later chapters.

Creating Smell

Given this smell pathway, how does it create the perception of a smell? Here we encounter a problem. Understanding the earlier stages of the olfactory pathway very effectively uses studies of laboratory animals such as rodents because there is a close resemblance between these stages in rodents and humans. However, in the case of the orbitofrontal cortex, these are two small areas in the rodent, whereas in the monkey and human they are relatively large, reflecting the much greater importance of neocortical processing of the olfactory input. We therefore have much less information about basic physiological properties of neocortical processing of smells than in other stages of the olfactory pathway. Our understanding at this level depends on studies of monkeys with cell recordings and of humans with functional imaging.

Work on this problem began in earnest in the 1970s with recordings from cells in the monkey by Sadayuki Takagi and his colleagues in Japan, showing that at successive stages in the olfactory pathway, from olfactory bulb to olfactory cortex to orbitofrontal cortex, the cell responses became more finely tuned to specific molecules. Then in the 1990s, a series of studies from the laboratory of Edmund Rolls at Oxford University showed how cells in the orbitofrontal cortex could respond to different combinations of tastes and smells. The advent of functional brain imaging in humans supported and extended these results. Out of these and subsequent studies, several important principles have emerged, which may be summarized as follows:

1. Some cells are tuned specifically to odors. These appear to represent the image of the smell object at this level and may constitute the neural basis of conscious smell perception.

2. Most cells do not respond to changes in odor intensity (in contrast to cells in the olfactory bulb and the olfactory cortex).

3. Some cells respond to both odors and taste stimuli. This can be called *sensory fusion.* It is not a property found in olfactory cortical cells and therefore appears to be the first step in creating the combined perception of flavor. (It has also been speculated that these combined responses could represent "sensory synesthesia," the unusual condition in which a person uses a term from one sense to describe a perception in another—as, for example, when a particular odor smells "blue.")

4. Some cells respond preferentially to pleasant smells, and others to unpleasant smells. The pleasant-responding cells tend to be localized in the medial part of the orbitofrontal cortex, and the unpleasant-responding ones tend to be in the lateral part of the orbitofrontal cortex, as shown with cell recordings and also with functional brain imaging. This separation is not seen at lower levels in the smell pathway.

The evidence that smells at this high level are arranged by the brain along a single axis, from pleasant to unpleasant, is summarized by Morten Kringelbach and Kent Berridge in their recent book *Pleasures of the Brain.* It is strongly supported by a theoretical approach of Noam Sobel and his colleagues in Israel, who believe that in this arrangement the complicated multidimensional nature of odor molecules is reduced to the unidimensional nature of odor objects. This attribute of smell is in turn one of the key attributes of the perception of flavor, a *quality axis* that obviously is not present in the senses themselves. In practical terms, when we consume our food and drink, we are not only detecting and discriminating among them, but also arranging them along our personal axis of pleasantness and unpleasantness. We will see that this applies to tasting wines, even by experts (chapter 24).

5. The qualities of pleasant and unpleasant are in turn reflective of their reward value, which we all know from our own flavor experience, and can be demonstrated in a monkey. We also know that we can change our preference from acceptance to rejection—for example, depending on whether we are hungry or full. Changing from acceptance to rejection of a smell can also be demonstrated in a monkey; it is known as *reversal learning*. Orbitofrontal cells are the first in the olfactory pathway to show this critical property of higher-level processing. It is an indication of how important smell is to flavor, because preferences for different smells can be learned and unlearned. It can be presumed that this, together with differences between smell receptors, is the basis for the development of preferences for smells by different cultures as well as the development of different individual preferences within a culture.

In summary, as Rolls states: "The . . . olfactory cortex represents the identity and intensity of odour in that activations there correlate with the subjective intensity of the odour, and the orbitofrontal and ACC [anterior cingulate cortex] represent the reward value of odour, in that activations there correlate with the subjective pleasantness of odour."

With smell perception at its core, we next consider the contributions of the other sensory systems in building the unified perception of flavor.