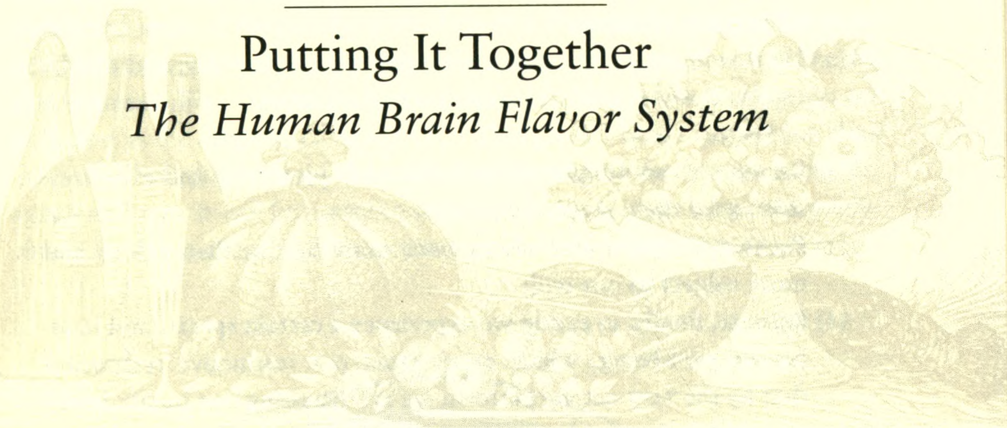
CHAPTER EIGHTEEN

Putting It Together

The Human Brain Flavor System



We have covered the main sensory and motor systems of the brain that are involved in generating the sensation of "taste," which we now recognize is really "flavor." We share these systems with other animals, but there are some big differences that characterize humans. We have fewer olfactory receptors, but we are much more adapted to retronasal smell, and we have much bigger brains, with many more brain areas and connections between them. And we have language. Our overall brain system for flavor therefore varies in quantitative terms from that of other animals, and qualitatively it has new capacities to create and elaborate the sensation of flavor. To recognize this, I will call it the *human brain flavor system* and claim that it is uniquely human.

That humans have a unique brain system for flavor was already predicted by Jean Anthelme Brillat-Savarin. In his book's early section "Pleasures Caused by Taste" (*taste* standing here for *flavor*, as we have often noted), he waxes eloquent:

> [T]aste as Nature has endowed us with it is still that one of our senses which gives us the greatest joy:
>
> (1) Because the pleasure of eating is the only one which, indulged in moderately, is not followed by regret;

(2) Because it is common to all periods in history, all ages of man, and all social conditions;
(3) Because it recurs of necessity at least once every day, and can be repeated without inconvenience two or three times in that space of hours;
(4) Because it can mingle with all the other pleasures, and even console us for their absence;
(5) Because its sensations are at once more lasting than others and more subject to our will;
(6) Because, finally, in eating we experience a certain special and indefinable well-being, which arises from our instinctive realization that by the very act we perform we are repairing our bodily losses and prolonging our lives.

And in the following section, "The Supremacy of Man," he writes:

> [O]f all the creatures who walk, swim, climb, or fly, man is the one whose sense of taste is the most perfect.
>
> The tongue of an animal is comparable in its sensitivity to his intelligence.

The idea that only humans experience pleasures that are perfect as opposed to those of other animals was a conceit of nineteenth-century thought, reflecting the conviction that humans are at the pinnacle of the animal world in whatever we do. Now in our post-Darwinian era we would characterize each animal in terms of its shared general properties through common or parallel lineages, and by those properties that are unique to it in finding its evolutionary niche. From this perspective, we would recast Brillat-Savarin's claims by saying that the human brain has specific capabilities that make the appreciation of flavor of unique importance in humans. Brillat-Savarin in fact hinted at this in writing: "[S]ince taste must not be weighed except by the nature of the sensation which it arouses in the center of life, an impression received by an animal cannot be compared with one felt by a man."

The human brain flavor system can be thought of as containing two stages. The first stage is the sensory systems that feed into it, which we have covered so far. These transform the individual sensory representations into the combined sense of flavor. The second stage is the action systems that draw on the full capacity of the human brain systems that generate and control our behavior. The systems we have considered in the previous chapters are collected in the diagram of figure 18.1. This gives a better impression than the individual diagrams of the extensive amount of the human brain devoted to flavor. It will be useful to summarize this sensory stage as a preparation for explaining the action system in the following chapters.

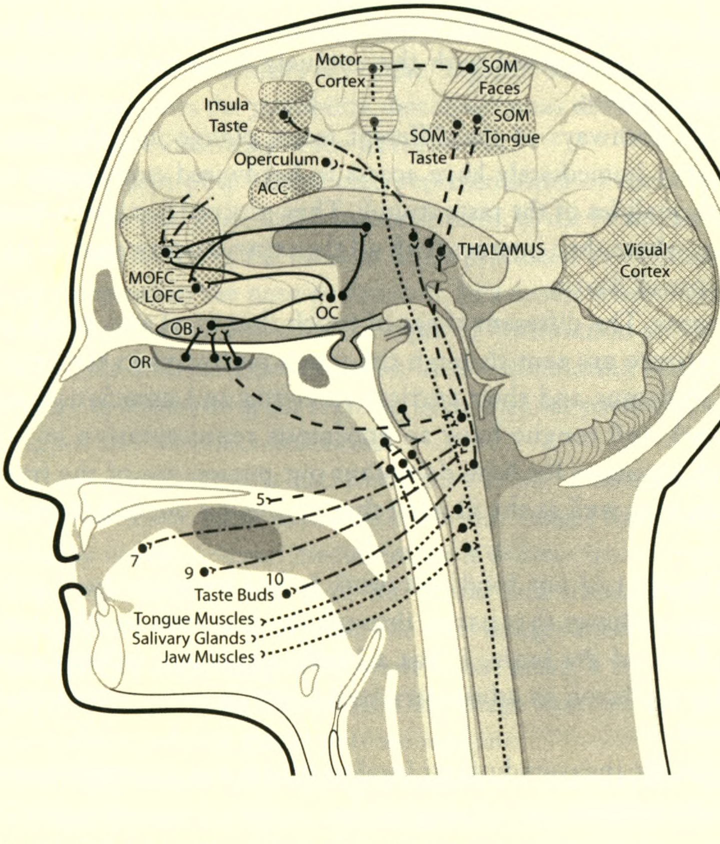


FIGURE 18.1 The human brain flavor system summarized from previous figures

Abbreviations are the same as those in the previous illustrations of the different systems. ACC = anterior cingulate cortex; SOM = somatosensory cortex.

(Adapted from G. M. Shepherd, Smell images and the flavour system in the human brain, *Nature* 444 [2006]: 316–321)

Flavor Perception System

As we have seen, the human brain flavor system begins with the five senses receiving their stimuli in their receptors and converting them into neural representations:

- *Smell.* Among these inputs, smell is unique in going directly to the olfactory cortex in the forebrain limbic system, where it forms distributed memories of the smell stimuli represented as odor objects. Within the limbic system the smell objects therefore have direct access to brain systems for memory and emotion. The olfactory cortex further projects to the orbitofrontal cortex at the front of the brain, where it connects to the highest centers concerned with the uniquely human capacities for judgment and planning.
- *Taste.* The pathways of the different tastes plunge into the brain stem, where they immediately have access to hardwired expressions of the emotional qualities of the taste stimuli. They proceed further to their cortical areas, where they interact with all the other sensory representations at the core of flavor.
- *Mouth-sense.* The different types of touch that food and liquid in the mouth activate are sent through the touch pathways in the brain stem to the thalamus and their cortical receiving and association areas. The mouth and tongue have an enormous representation in the cortex, which accounts for how dominant our perception of the food in our mouths is as well as the illusion that its smell is coming from its taste.
- *Sight.* The sight of our food and drink before we consume it activates the visual pathway that passes through the thalamus to the visual areas at the back of the brain. It has a highly significant influence on how we judge its flavor, as advertisers well know in enticing us to eat what they produce.
- *Sound.* Finally, the sound of our food as we eat it is an integral part of the flavor experience.

One of the questions I find most interesting is how the multiple sensory pathways indicated in figure 18.1 interact to create the flavor we sense.

Multisensory integration occurs when the cell responses in a region to two or more stimuli at the same time are more than the addition of the individual responses. This is a property called *supra-additivity*. It can occur in cells in several regions when congruent (complementary) stimuli are delivered simultaneously.

The behavioral response is a perception of flavor from the combined senses, such as taste and smell stimuli when they are congruent. Congruency is a property that is learned, presumably involving the mechanisms in the olfactory cortex that projects to the orbitofrontal cortex and through it to the other regions such as the insula and anterior cingulate gyrus. Maria Veldhuizen, Kristen Rudenga, and Dana Small at the John B. Pierce Laboratory and Yale University suggest that the fact that the "supra-additive responses in these regions are experience-dependent strongly supports the possibility that these areas are key nodes of the distributed representations of the flavor object."

The concept of a "distributed representation of the flavor object" is useful. This distributed activity constitutes, in the brain, an internal "image" of the flavor of the food or drink produced by stimulating the sensory receptors in the nose and mouth. Just as the sensors are distributed in the body and gather different types of information about the food, so the brain's internal representation of the stimulating object arises from activity in different brain regions, each with its particular combination of input and output connections.

These considerations lead to the idea of an "internal brain image" of the flavor object. Ideas about such internal images have long been dominated by vision. A visual mental image is distinct from the sensory visual image that is projected onto the retina and transmitted through the thalamus to the visual cortex. The two images meet somewhere in the primary and secondary association visual areas, a zone referred to as a *buffer.* This is where the bottom-up image that we see with our eyes meets the top-down image that we imagine.

"Mental images" are usually considered within a given modality, such as visual images (as when one imagines a visual object that one examines from different angles). Other examples are "smell images" as mental images (as when one imagines a smell), "auditory images" (as when one imagines a song), and even "motor images" (as when one imagines a willed movement). The idea of "odor imagery" has received support from studies of human brain scans by M. Bensafi and Noam Sobel and their colleagues. These examples of internal mental states depicting the imagined object seem intuitively reasonable, and in fact can be related to actual sites in the brain. In the case of vision, there is evidence that the buffer between external and internal images is located in the visual cortex.

This "pictorial" view represents the most widely accepted concept of mental images. Stephen Kosslyn, at Harvard University and now at the University of California, Berkeley, has been a leading advocate of this majority view. An alternative minority view is that our internal "image" is not in a literal pictorial form but rather in a "propositional" form that is more appropriate for representing the action that the image engenders.

In this discussion we are extending the idea of a mental image from one that is limited to within a brain area devoted to one modality, such as the visual cortex, to one being distributed among several different brain areas representing multiple modalities. A consensus is emerging that simultaneous activation by a food of a common set of regions, including the *orbitofrontal cortex, anterior insula and overlying operculum, frontal operculum, and anterior cingulate gyrus*, constitutes the distributed representation in our minds of a flavor object. We can express this by saying that the "simultaneous supra-additive learned activity in these regions constitutes a flavor image." This perceptual image makes up the neural representation of a remembered flavor.

Flavor Action System

This, then, is the first part of the flavor system, the part that produces the perception of flavor. What we do with that perception—how it engages our behavioral responses—is the second part. I call this the *flavor action system*. The true extent of the human flavor system is revealed in the network of regions and connections that reflects the power of the greatly expanded human brain to give full meaning to the flavor image and elicit characteristically human behaviors. The left side of figure 18.2 indicates the sensory systems we have already discussed. The right side of the figure indicates the main parts of the brain that mediate these behaviors. As with the representation of the sensory systems in figure 18.1, this diagram

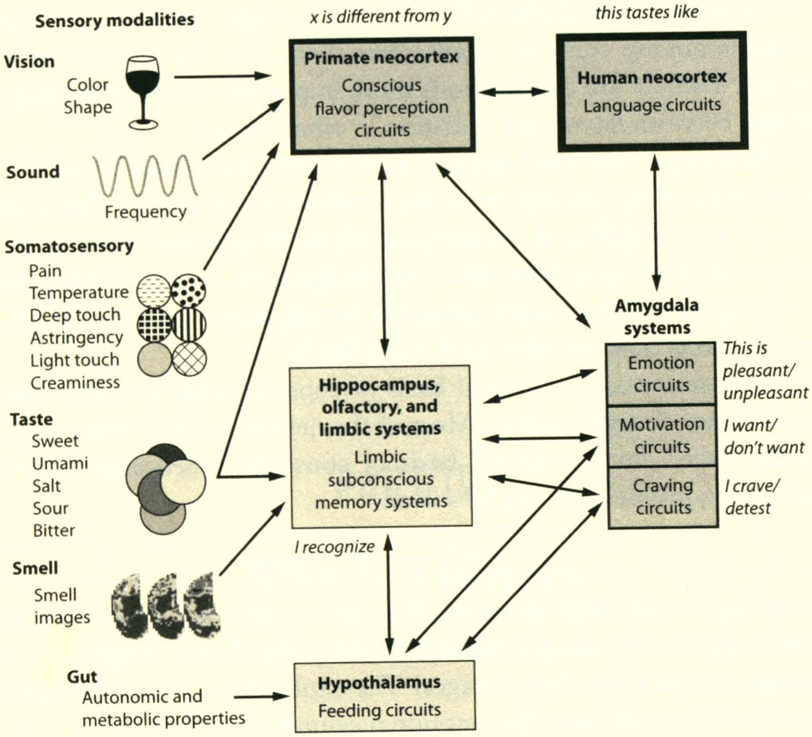


FIGURE 18.2 The human brain flavor system shown as a flow diagram
(Adapted from G. M. Shepherd, Smell images and the flavour system in the human brain, *Nature* 444 [2006]: 316–321)

shows the great extent of the human brain devoted to the action systems of flavor. The chapters that follow will consider each of these systems.

• *Emotion*. All mammals have brain systems for emotion. In humans, these are highly developed in size and in their extent of interconnectedness. As a result, our emotions expand from those related directly to the flavor sensation to engage regions involved in all aspects of our mental life.

• *Memory*. All mammals also have brain systems for memory, and they are very good; the memory of an elephant is legendary. In humans there are many regions of the brain for the memories laid down by the flavor system to engage. This is illustrated by the iconic tale of Proust and the remembrance brought about by the flavor of a madeleine biscuit.

• *Decisions*. One of the hallmarks of our bigger brains is our power to decide among complex alternatives that affect the present and the future. Nowhere are the decisions more important than in choosing the balance between flavor and nutrition in what we eat.

• *Plasticity*. What our brains do affects what our brains become. This dependence of our brains on activity reflects the plasticity that is built into our neural cells and connections. We need to know how our flavor preferences have long-term effects in changing the flavor system itself.

• *Language*. Humans are unique in having language, and this ability greatly affects how we sense and judge flavor.

• *Consciousness*. The neural basis of consciousness is a hot topic in neuroscience and philosophy. Most of the debate is about what we consciously "see," but the neural basis of conscious smell and flavor are challenging problems yet to be solved.

Let us begin with this question: Why do we like the flavors we like? What explains the close coupling between the flavor images and the pleasure we get from these images? The explanation lies in the connections that are made with the emotional centers of the brain.