PERCEPTION

THIRD EDITION

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CHAPTER TWELVE

Smell and Taste

Taste and smell are sometimes called the minor senses, probably out of respect for seeing and hearing. But this designation is arbitrary. Though people do rely heavily on their eyes and ears to guide their everyday activities, the "minor senses" provide crucially important information. The smell of smoke, for instance, can signal a dangerous fire, and the foul taste of spoiled food can prevent ingestion of harmful substances. In fact, many animal species depend almost exclusively on taste and smell to tell them about their world. The mole's very keen sense of smell, to take just one example, allows this animal to live in the dark, safe confines of underground burrows, with virtually no need for eyes. Although humans don't rely as much on taste and smell as do other creatures, we should not underestimate our capacity to use these senses to detect and recognize objects in the environment. In fact, one of the things you are likely to gain from reading this chapter is a healthy respect for your nose and tongue.

As we mentioned above, taste and smell are called the minor senses. They are also sometimes referred to by their technical names, "gustation" (from the Latin *gustare,* meaning "to taste") and "olfaction" (from the Latin *olfacere,* meaning "to smell"). Taste and smell are also sometimes lumped together as the "chemical senses" because the receptors housed in the nose and on the tongue register the presence of chemical substances. In this respect, chemical substances are analogous to light energy that strikes the photoreceptors of the eye. But, as this book has emphasized, you see objects, not light; by the same token, you taste and smell objects and substances, not chemicals. So from the standpoint of an organism concerned with its environment, the term "chemical senses" is a bit misleading. In fact, taste and smell serve precisely the same purposes as vision and hearing; all of them provide behaviorally relevant information about the environment.

Although all the senses work for one common goal, something sets taste and smell apart: the sensations arising from stimulation of the tongue and nose can take on a uniquely pleasurable, sometimes sensual, quality. Sunsets may look beautiful and symphonies may sound enrapturing, but their pleasures are less compelling than the aroma and taste of, say, freshly baked chocolate chip cookies. On the other hand, few sights or sounds are as repulsive as a really putrid smell or foul taste. When there's an annoying song on the radio, you can usually succeed in ignoring it. But try to ignore the stench of a stopped-up toilet. Similarly, just thinking about the taste of some food that made you sick once can nauseate you all over again. Thus in addition to their roles as sources of information, taste and smell wield a powerful emotional impact.

There is a sizable and growing body of data—both perceptual and physiological—concerning taste and smell, and in this chapter we shall discuss some of these findings. (Students interested in a more detailed survey are urged to consult the volume edited by Getchell, Doty, Bartoshuk, and

Snow, 1991.) We shall consider taste and smell separately, although the two are intimately intertwined. Let's begin with smell.

THE SENSE OF SMELL

Smells are with us all the time. From the aroma of your first cup of coffee in the morning to the smell of clean sheets as you doze off at night, you are awash in a sea of odors. Smells enhance the enjoyment of food (which is why appetite decreases when a cold stops up the nose). You can verify this for yourself. Compare the taste of a piece of apple and a piece of raw potato while holding your nose so that you cannot smell them—you'll be astonished to find that on the basis of taste alone, the two are very similar. Odors also influence the ways you spend your money. How often have you passed by a bakery and been enticed in by the smells wafting onto the street? It is said that some bakeries vent their ovens onto the sidewalk, purposely using the aroma of fresh bread to lure customers inside (Winter, 1976). Besides the natural smells of the bakery, some businesses also use artificially created odors to influence people's buying habits. For example, plastic briefcases are impregnated with leather scent to enhance their appeal to prospective buyers, and the market value of a secondhand car increases if it's been sprayed with "new car" smell. Real estate agents like to have a freshly brewed pot of coffee on the stove when a house is being shown, for the aroma is said to convey a sense of "home" to the potential buyer.

Besides the odors of foods, cars, and briefcases, other smells also influence people. TV commercials constantly remind us that we are ourselves an important source of odors and exhort us to buy products that will modify our existing body odors as well as create new ones. In this pursuit, vast amounts of money are spent every year. Such products include deodorants, perfumes, aftershave lotions, mouthwashes, and antiflatulence medications. Nonetheless, every individual continually gives off a unique though invisible cloud of smells. Your odors constitute a smell signature so distinctive that a trained scent-hound can trace your tracks amid the "noise" of odors from many other people. Only the scents of identical twins seem to confuse good scent-hounds (Kalmus, 1955). But these hounds are not the only creatures that can use scent for tracking. Some humans—the Botocudos of Brazil and members of some aboriginal tribes in the Malay peninsula—can hunt by following their prey's scent (Titchener, 1915). Though few people in industrialized societies perform similar feats, they do have some primitive abilities to use scents for distinguishing people from one another, as the following experiments document.

If you had to judge whether another person was male or female on the basis of smell alone, do you think you could? The answer appears to be yes. Patricia Wallace (1977) tested whether college students could discriminate male from female just by smelling a person's hand. While blindfolded, a student would sniff a hand held one-half inch from the student's nose. The male and female individuals whose hands served as test stimuli had washed thoroughly before the test session and then worn a disposable plastic glove for 15 minutes prior to testing, to promote perspiration. Wallace found that subjects could tell male from female hands, with over 80 percent accuracy. Wallace further found that female sniffers were better at the task than were male sniffers.

In addition to using the smell from sweaty hands, people can also accurately judge gender on the basis of breath odor. Working at the Clinical Smell and Taste Research Center at the University of Pennsylvania, Richard Doty and his colleagues had male and female judges (college students) assess the breath odor of student "donors" who sat on the other side of a partition (Figure 12.1). By inserting their noses into a plastic funnel, the judges were able to smell the breath of the donors, who were exhaling through a glass tube connected to the funnel. Donors had been instructed to refrain from eating spicy food the day before testing and were not permitted to wear any odorous cosmetic products. Most judges scored

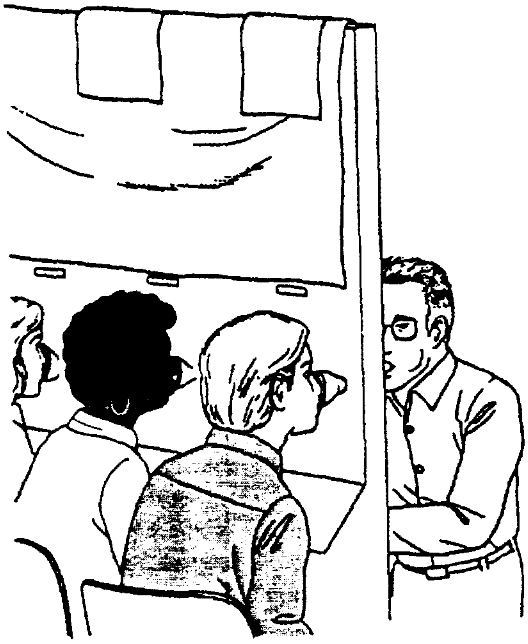


FIGURE 12.1 Setup for measuring gender identification based on breath odor.

better than chance (50 percent) at identifying the sex of the donor, and again female judges outperformed male judges (Doty, Green, Ram, and Yankell, 1982). Doty also had judges rate breath odors for pleasantness and intensity. The breath odors of men were rated on the average as less pleasant and more intense than the breath odors of females. In interpreting their results, Doty and his colleagues noted that fluctuations in reproductive hormones during a female's menstrual cycle cause changes in oral bacteria, which in turn can affect breath odor.

Probably the most remarkable example of acuity for body odor is the case described by William James (1890, vol. 1, pp. 509–510) of a blind woman who worked in the laundry of the Hartford asylum. She would sort the laundry of individual inmates on the basis of smell only, after the clothes had been washed. Less dramatic but impressive nonetheless is the performance of people in the dirty shirt study by Mark Russel, a British psychologist (1976). He had twenty-nine freshmen bathe with clear water and then don T-shirts that they wore for the next 24 hours, during which they used no perfume or deodorant. At the end of this period, the T-shirts were collected and individually placed in sealed containers. The same freshmen were now presented with three containers, one with their own shirt, one with the T-shirt worn by an unknown female, and one with the T-shirt worn by an unknown male. Of the twenty-nine people, twenty-two were able to pick out their own T-shirts—a level of performance well above chance. Moreover, twenty-two out of the twenty-nine were also able to identify which of the remaining two T-shirts belonged to a male and which belonged to a female. Male odors were described as "musky," whereas female odors were described as "sweet."

Besides aiding in identification of gender, odors also possess the remarkable ability to call up long-ago memories. A whiff of cedar triggers remembrance of the chest in which your grandmother kept her blankets; scent from a carnation vividly recalls your senior prom; and the smell of clove brings back memories of a dentist's office. Some people have developed a huge repertoire of odor memories and rely on them for their profession. Perfume makers, for example, can discriminate hundreds of aromas, many quite subtle. Astute physicians rely on the nose as a diagnostic tool, using a patient's odors as clues for detecting disease. In fact, any number of disorders have characteristic odors. Here are some examples: typhoid creates a smell like that of freshly baked, brown bread; yellow fever creates a smell like that in a butcher shop; and kidney failure creates a smell of ammonia. (For a complete table of diseases and odors, see Smith, Smith, and Levinson, 1982.)

It is well known that smell plays an enormously important role in the social lives of many animals. Indeed, mammals send and receive at least two dozen different types of odor messages (Doty, 1986), ranging from distress signals to age appraisal. For many animals, mate selection and identification are solely governed by odor. Typically, the females of these species will emit sensuous scents, called **pheromones,** from specialized glands, and these scents can be detected by potential mates. Among such species is the male cabbage moth, an insect whose antennae can sense minute concentrations of the scent released from a sexually receptive female cabbage moth many miles away (Lerner et al., 1990).

The understanding of chemical sex signals has allowed scientists to exploit other species's pheromones. For example, agricultural biologists use pheromones to control some harmful insects. With sex attractants as bait, unsuspecting harmful insects can be lured to their deaths in traps. Pheromones can also be exploited for the eating pleasure of humans. Certain female pigs are trained to hunt truffles, a fungus highly prized by many gourmets. These sows can sniff out truffles buried as much as a meter below ground, and once the truffles are located, the animals root furiously to unearth them. Why do sows expend all that energy, rooting so furiously for a piece of fungus? Truffles contain a chemical with a distinct, musk-like odor that is highly similar to the scent secreted by male pigs during mating behavior. So it appears that the sow's intense interest in truffles is sexually motivated (Claus, Hoppen, and Karg, 1981).

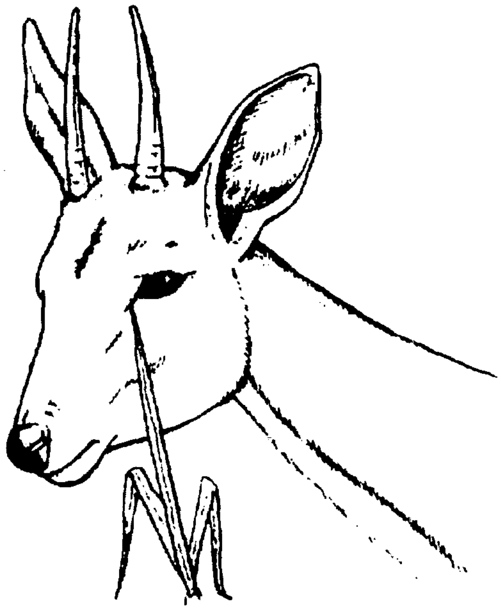
It is natural to wonder whether human sexual behavior is influenced by smell. Is there a pheromone for humans? Certainly the perfume industry would have us believe the answer is yes, but the evidence, while suggestive, is inconclusive. Case studies do disclose that people with serious smell disorders frequently report disinterest in sex (Henkin, 1982), but firm experimental data are lacking. What is clear is that odor signals play a role in the synchronization of menstrual cycles of women living in close contact on a prolonged basis (Graham and McGrew, 1980).

Besides promoting sexual arousal in animals, smells are often employed as defensive weapons. Everyone can testify to the rank odor of a skunk's discharge and can well apppreciate how that odor would ward off enemies (and friends as well). Numerous animal species also employ glandular secretions to mark their territories, often engaging in seemingly bizarre behaviors to ensure that their odor signatures are conspicuous (Macdonald and Brown, 1985). For example, the oribi (a deerlike animal) sticks blades of grass into a gland situated just below its eye, coating the grass with its scent (see Figure 12.2). Odors also guide animals in their search for food, whether it is the bee attracted to the fragrance of flowering plants or the vulture picking up the scent of a dead animal. In fact, the human reliance on eyes and ears to guide vital activities may be fairly unique, since many other animals depend primarily on their noses for such guidance. Indeed, if we were writing this perception book for a nonhuman audience, we'd have to revise it drastically. Instead of emphasizing seeing and hearing, the vast bulk of the book would have to address the most pressing concern of the nonhuman world—the sense of smell.

THE STIMULUS FOR SMELL

Let's start with the basics, asking what physical properties give various substances the power to evoke sensations of odor. As you'll see, the answers are complex. First, to be odorous, a sub-

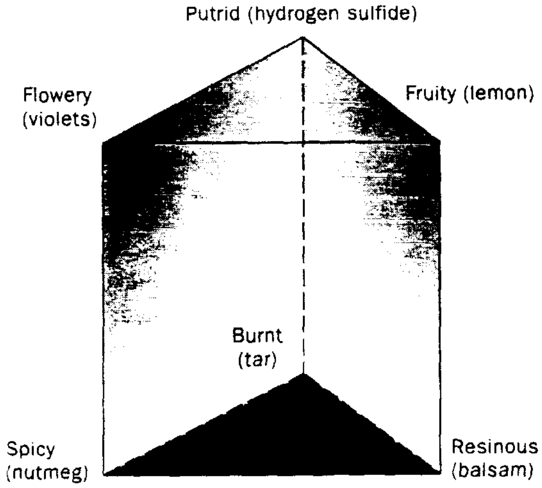
FIGURE 12.2 Drawing of an oribi coating a blade of grass with scent from its scent gland.



ilar in spirit to Newton's color circle. Henning's geometric model is meant to depict the "principal" odors from which all other odors can be generated. To determine the number of principal odors, Henning used two procedures. First, he instructed people to use verbal labels to describe various scents presented one at a time. Second, he gave people sets of odorous substances and instructed them to line up the substances according to the similarity of their smells (Gamble, 1921). In all, Henning tested well over 400 different odorous substances. Using these sets of judgments, Henning constructed a three-dimensional form—a triangular prism (shown in Figure 12.3)—whose surfaces were meant to reflect people's judgments of odor similarity. Particular odors corresponded to points on the surface of the prism, with nearby points corresponding to odors that were judged similar. Odors were confined to the surfaces and edges of the prism; its interior was considered hollow, meaning that points inside the prism were not used to describe an odor.

Odors near the corners of his prism seemed to Henning to have unique qualities—they could be described using a single verbal label (shown in Figure 12.3). To give you some idea of substances that evoke these six principal odors, we have included in parentheses a substance representative of each. Odors located other than at the corners of the prism (either on an edge or on the plane of one surface) could not be described using a single verbal label. But they could be described by some *combination* of principal qualities represented by the labels at the prism's corners. For example, the smell associated with pine was located along the edge midway between "Fruity" and "Resinous"—implying that the odor of pine possesses both of those qualities. Pine was located where it is on the prism because of its similarity to lemon and balsam. Similarly, the smell of garlic was located on the surface bounded by "Flowery/Fruity/Resinous/Spicy," implying that the odor of garlic possesses all four of those qualities. Again, garlic was placed at that point on the prism because its odor bears at least some similarity to the odors of violet, lemon, balsam, and nutmeg.

FIGURE 12.3 Henning's smell prism.



Henning's scheme purported to show how odors on the edges or surfaces of the smell prism resemble odors at the prism's corners. This does not mean, however, that a mixture of odors from the corners could produce odors on other parts of the prism. Although it is similar in smell to both balsam and lemon, pine cannot be synthesized by a mixture of those two. In fact, "the resulting odor tends to be a unique percept blend in which both components can be smelled" (Engen, 1982). In this sense, odor shares the analytic character of pitch perception rather than the synthetic character of color perception. For example, if you simultaneously sound a D and an F on the piano, you can hear the separate components in the chord; however, if you mix red and green lights, the result is a synthesis (yellow) in which each component's identity is lost.

Henning's model is appealing for precisely the same reason that Newton's color circle is appealing: both provide a simple, geometrical description of sensory experiences. The accuracy of geometric models is easy to test because they make clear predictions. However, in the case of Henning's smell prism, the predictions have not been confirmed, as William Cain (1978) documents. One major problem is that most people find it impossible to classify odors using just six categories—which implies that Henning may have underestimated the number of principal odors. Critics have also faulted Henning for using a small number of highly trained subjects and for eschewing quantitative analysis of his data. In defense of his procedures, Henning bragged that "the critical introspection of trained psychologists is more valuable than statistics taken on all the students in the University, and the statistical procedure, about which science in America has raved so much, has by no means the precision of a *qualitative* analysis" (Henning, 1916, from a translation by Gamble, 1921).

Following Henning's work, other researchers have also tried to group odors according to qualitative similarities (for example, Crocker and Henderson, 1927). Most of these categorization schemes have started out by identifying a series of semantic descriptors to be used as odor qualities—descriptors such as "sweet," "flowery," "fruity," "burned," and so forth. Whatever odor categories may emerge, therefore, are constrained right from the start; they've got to conform to the specific descriptors chosen by the researcher in the first place. Moreover, there are reasons to question how reliably people can use verbal labels to describe their olfactory sensations (Davis, 1977). The constraints imposed by the descriptors, as well as the difficulty of using any label at all, would distort any classification scheme based on predefined verbal labels.

There is a technique, however, called **multidimensional scaling (MDS),** that sidesteps these problems. This technique was used by Susan Schiffman (1974) to study odor classification. Instead of using descriptor terms for various odors, a person merely compares different odors, numerically rating their similarity to one another. These similarity ratings are then used to place odors within a geometric framework called an odor space. Odors are arranged within the odor space in such a way that the distances separating odors reflect the rated similarity or dissimilarity of those odors. Odors rated as highly similar (such as cinnamon and ginger) would be placed near each other in an odor space, whereas odors judged to be dissimilar (such as vanillin and turpentine) would be located far apart (see the Appendix for a more detailed description of MDS; Chapter 13 gives another use of this technique). As you can see, the idea of an odor space is reminiscent of Henning's smell prism—both arrange odorous substances in a geometric form based on perceptual similarity. However, the rules for generating an odor space by means of multidimensional scaling differ from those used by Henning. In multidimensional scaling, objective numerical procedures create the geometric arrangement of odors; Henning used his own subjective impressions of data to create his geometric arrangement.

Besides objectivity, the procedures used in multidimensional scaling offer another advantage. The experimenter does not constrain the number of possible dimensions ahead of time; instead, statistical treatment of the similarity ratings determines the number of dimensions needed to place odors in the odor space. (You can think of the dimensions as axes defining the coordinates of a geometrical space, like the Cartesian coordinates used to define the two-dimensional space you're familiar with from plane geometry.)

In using multidimensional scaling, Schiffman found that just two dimensions adequately described the relations among a wide variety of odorous substances. Figure 12.4 replots some of the data from Schiffman's analysis. Look at the various odors in this odor space, and note their relative positions. You'll probably agree that the nearby entries smell more alike than do the widely separated ones. How can the two dimensions that Schiffman's work uncovered be interpreted? To answer this question, Schiffman examined the adjectives people use to describe the various odors she tested. She found that, from left to right in Figure 12.4, odors tended to shade from pleasant (such as vanillin) to unpleasant (such as hydrogen sulfide). It is not too surprising that one strong dimension of odor perception has this "hedonic" quality, for odors so often trigger either approach ("pleasant") or avoidance ("unpleasant"). From top to bottom, however, Schiffman was unable to find any systematic progression in the adjectives used to describe the odors. This finding suggests that this dimension of odor experience does not correlate with any simple psychological dimen-

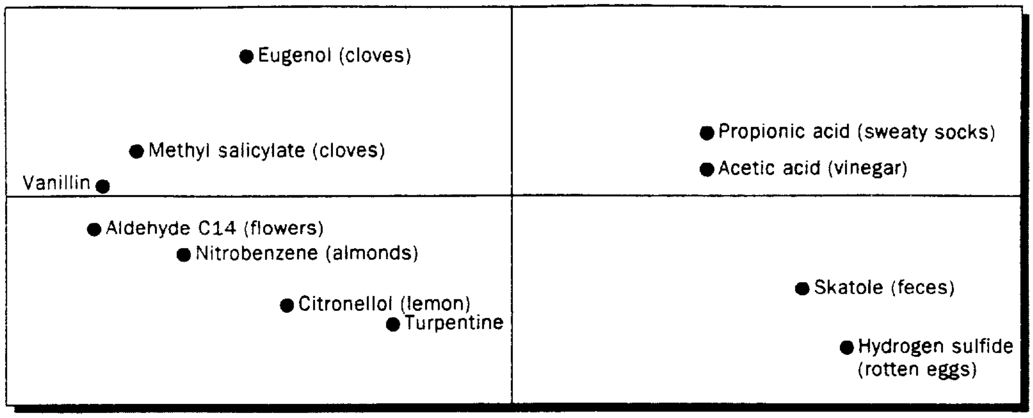


FIGURE 12.4 An odor space, showing the relations among various odors as defined by multidimensional scaling. (Adapted from Schiffman, 1974.)

sion for which there are linguistic descriptors. To what, then, might the ordering in the odor space correspond?

Schiffman (1974) asked whether perceptually similar odors might have some molecular property in common, such as the size or shape of the molecules making up the odorous substances. The discovery of molecular similarities among perceptually comparable odors might furnish important clues about how odorous substances affect receptor cells in the nose. Schiffman considered several molecular characteristics in an attempt to uncover what physical properties, if any, similar smells have in common. Examining the molecular shapes of various substances, she found no relation between the shapes of various compounds and the odors produced by those compounds. This finding, incidentally, contradicts a very popular theory of odor perception. John Amoore (1970), a noted olfactory scientist, proposed that a molecule's shape determines which receptor it is able to stimulate. This theory has been characterized as the lock-and-key model, since the molecule "unlocks" the receptor only if the shape of the molecule matches that of the receptor. According to this theory, molecules that look alike (in terms of the arrangement of their constituent atoms) should also smell alike. However, Schiffman's analysis fails to support this simple idea; she finds no relation between the shapes of molecules and the similarity of the odors they produce.

Besides molecular shape, Shiffman also examined a number of other chemical characteristics of compounds that smell alike, such as their molecular weight and their solubility in water. However, she found no single characteristic that could explain odor similarity. At the moment, then, the question of the relation between odor quality and molecular structure remains unanswered. Somehow it seems ironic that of all the senses, smell, nature's oldest and most primitive sense, has a stimulus that is one of the most complicated and baffling. This mystery, however, may be close to solution. It is now thought that promising clues concerning the nature and diversity of primary odor qualities may come from studying people with specific losses in odor sensitivity (Wysocki and Beauchamp, 1984). Called **anosmia,** this condition of odor insensitivity may be attributable to genetic deficiencies in the manufacture of olfactory receptor proteins (the importance of which we'll get to in a moment). To the extent that molecular receptor types are related to odor qualities, **specific anosmias** may reveal the diversity of olfactory receptor types.

Besides odor quality—the focus of Henning's model and Schiffman's MDS analysis—odor intensity, too, has been analyzed at the molecular level. Edwards and Jurs (1989) looked for common physical characteristics among dozens of different odorants all rated as equivalent in subjective strength. Among the most prominent of those characteristics were molecular weight and molecular configuration.

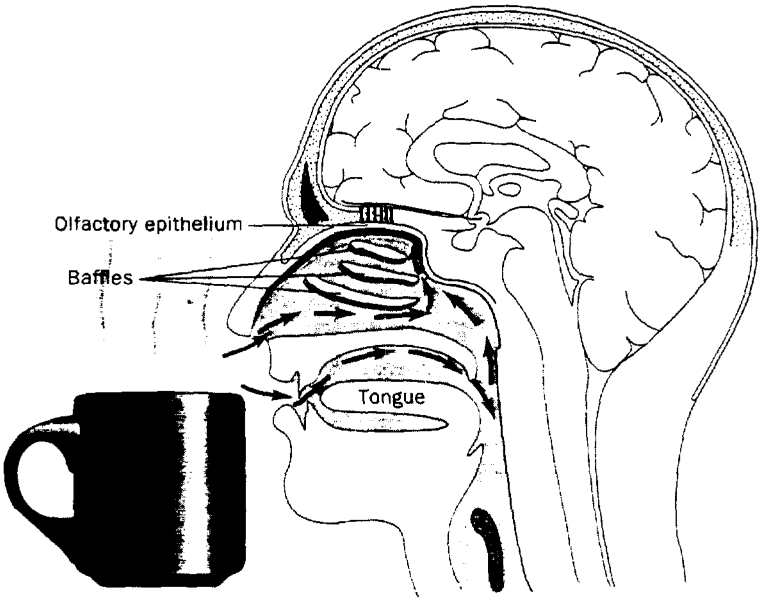
Before continuing the discussion of odor perception, we should next present the major components of the olfactory system, in particular the olfactory receptor cells that capture the volatile molecules from odorous substances. The properties of these receptor cells, after all, shape the world of smell.

THE ANATOMY AND PHYSIOLOGY OF SMELL

The stimulus for smell, as noted earlier, consists of airborne molecules, or vapors. The act of inhaling pulls these vapors into the nostrils and then circulates them through the nasal cavity, a hollow region inside the nose where the olfactory (smell) receptors are located (see Figure 12.5). Exhaling expels the vapors back into the air. Sniffing or more odorous vapors into the nose and speeds their circulation through the nasal cavity.* In this respect, sniffing is comparable to cupping your ear to help in hearing a faint sound. Sneezing, in contrast, represents a reflexive clearing of the nostrils, an action comparable to covering your ears to muffle a loud sound.

Odor-bearing vapors can also reach the nasal cavity through the mouth, circulating up the throat through a chimneylike passage leading to the smell receptors. Both routes, then—the nostrils and the throat—lead to the same place, the olfactory receptors in the nasal cavity. However, vapors from a substance in the mouth may smell

FIGURE 12.5 A cutaway section of a human head, showing the routes taken by air inhaled into the mouth and nasal cavity.



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* Optimum odor detection occurs when the odorant flows through the nose at a rate of about 30 liters per minute. Interestingly, whenever you try to sniff some odor in your environment, you produce this optimal flow rate without having to think about it (Laing, 1983).

different from the same vapors brought in through the nostrils. This odd disparity is described in Box 12.1 (p. 320).

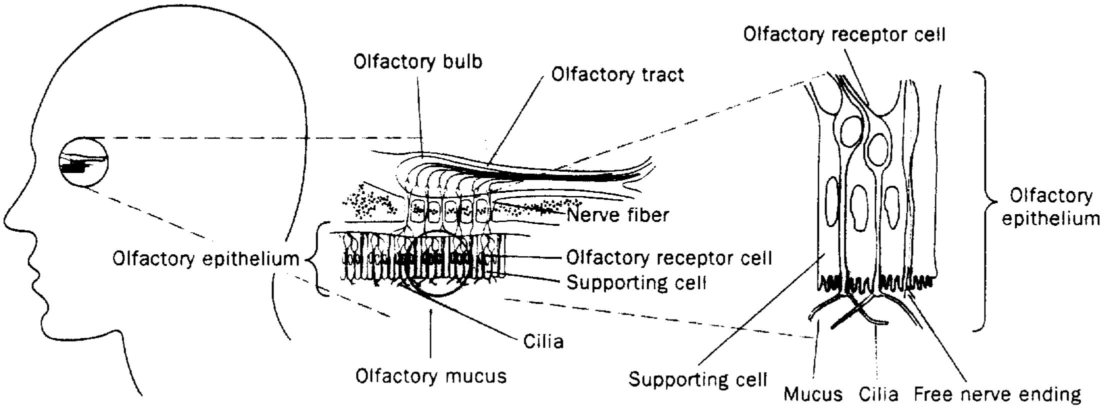
Most of the air entering the nostrils and mouth flows down the throat to the lungs. However, wisps of air do rise up into the nasal cavity, where they circulate around a series of baffles formed by three bones located in the nasal cavity (see Figure 12.5). As it circulates through this series of baffles, air is warmed and humidified, and debris such as dust is removed by tiny hairs lining the nasal cavity. The entire process has been likened to an air-conditioning system that improves smell acuity (Negus, 1956). As you can imagine, when your nose is congested, the passages of the nasal cavity are narrowed, limiting the amount of odorous vapors that can reach the smell receptors. This is why your sense of smell is dulled when a cold clogs up your nasal cavities. This clogging effect can be chronic in individuals with nasal polyps.

Actually, the two nostrils appear to work in alternating shifts, a phenomenon called the **nasal cycle.** At any given time, the mucous lining in one nostril is more engorged than that of the other nostril, narrowing the nasal passage and offering greater resistance to the inflow of air. This constriction of the nasal passage is under control of the autonomic nervous system and occurs, therefore, unconsciously. You can easily confirm the dominance of one nostril by holding a mirror just under your nose midway between the two nostrils—notice how the two pools of condensation (produced by exhalation) differ in size. Nostril dominance normally switches every 2 to 3 hours (Keuning, 1968), and there is evidence for increased brain activity in the hemisphere contralateral to the dominant nostril (Werntz, Bickford, and Shannahoff-Khalsa, 1987). Some have gone so far as to suggest that people plan their cognitive activities based on which nostril (and, hence, which side of the brain) is currently dominant (Shannahoff-Khalsa, 1986).

So far we've described how vapors are introduced into the nose and how they circulate inside the nasal cavities. Now let's consider how neural elements turn these vapors into the perception of an odor. The receptor cells that register the presence of odorous molecules sit on a patch of tissue called the **olfactory epithelium.** As you can see in Figure 12.5, the olfactory epithelium forms part of the ceiling of the nasal cavity. There are actually two patches of olfactory epithelium, one at the top of each nasal cavity. Each patch of tissue is about the diameter of a dime, but much thinner.

Figure 12.6 shows an enlarged drawing of an olfactory epithelium. Note that the structure labeled **olfactory receptor cell** is embedded in a layer of supporting cells. It is estimated that the

FIGURE 12.6 The olfactory epithelium (enlarged to show detail).



Box 12.1 *Is Olfaction a Dual Sense?*

Have you noticed that some foods smell almost repulsive before you get them into your mouth, but once you start eating them they are enjoyable? Certain strong cheeses, such as Limburger and Roquefort, are good examples of this disparity between odor and flavor. Yet what is referred to as "flavor" is largely the smell associated with the food as it is chewed. This is known from the fact that foods lose their flavor when olfactory cues are eliminated during eating (such as when you have a head cold). How is it, then, that the same food can generate two distinct odor experiences, depending on whether you are sniffing the food or eating it?

Paul Rozin at the University of Pennsylvania, thinks this happens because olfaction is a dual sense—that is, one used to acquire two sets of information: information about objects in the external world and information about objects within the mouth. According to Rozin (1982), these two types of information have different behavioral consequences. Airborne odors arriving through the nostrils can come from a host of objects and events—other people, animals, plants, fire, and so on—only some of which have anything to do with eating. Behavioral reactions to these odors depend on identifying the source of the odor. In this sense, olfaction serves the same interests as vision and hearing, identifying relevant objects and events in the environment. But olfaction's role changes during eating, after food has been selected and introduced into the mouth. Now odors become part of the flavor complex that also includes taste, temperature, and palatability. Rozin believes that these two different contexts (odor in the mouth versus odor out there) are registered by the olfactory nervous system and give rise to distinctly different perceptual experiences.

Rozin figured that if odor does indeed have different perceptual properties in the mouth versus outside the mouth, people should have trouble recognizing odor through the mouth if their previous experience with the odor was just through the nose. To test this hypothesis, Rozin came up with a set of unfamiliar odors and flavors by mixing together various exotic fruit juices and soups. He then taught blindfolded people to identify these various mixtures on the basis of their odors; each mixture was assigned a number for purposes of identification. Once these individuals had learned to do this, Rozin asked them to identify the same mixtures delivered directly to the mouth through a plastic tube. In this way, any contribution of odor inhaled through the nostrils was eliminated; odor information came entirely from aromas passing up the throat to the olfactory receptors. The results were clear—people made many errors in identifying the mixtures, and they reported that the flavors were impossible to recognize. Evidently, the same substance smells different, depending on whether it is in the external world or in the mouth. This would explain why you may dislike the flavor of things (such as coffee) that smell appealing and also why you can enjoy eating foods that smell foul. Without encouragement, most people would never get around to eating foul-smelling foods in the first place.

human nose contains somewhere between 6 and 10 million olfactory receptor cells. Dogs, in comparison, have about 200 million olfactory receptor cells, which probably accounts for their legendary ability to track the path of a person hours after the individual has trodden that path. Notice also in Figure 12.6 the structure labeled **free nerve ending.** Although these nerve fibers do not themselves give rise to odor sensations, they do significantly influence the perception of odors. We shall consider the role played by these nerve endings shortly, but for now let's continue focusing on the olfactory receptor cells.

There are a couple of things very special about olfactory receptor neurons that set them apart from receptors in the eye and ear. For one, olfactory receptor cells, unlike photoreceptors and hair cells, are genuine neurons, possessing all the paraphernalia of neurons—cell bodies, short dendrites, and long axons. Therefore, olfactory receptor neurons are able to perform two jobs at once: they transduce chemical stimulation into neural impulses, while at the same time carrying those impulses up to the brain along their axons, which make up the **olfactory nerve.** In vision, hearing, and taste, these jobs are assigned to different types of cells. This means, incidentally, that the only neurons in the brain that actually come in contact with the outside world are those located in the nasal cavity.

Even more remarkable, olfactory receptor neurons are constantly dying and being replaced (Graziadei, 1973; Moulton, 1974). Nowhere else in the central nervous system are neurons capable of reproducing. Once in place, neurons elsewhere in the brain are there for life; when those neurons die, the loss is irrevocable. But olfactory cells live for only about 5 to 8 weeks. As a result, the olfactory cells currently at work in your nose have been on the job no more than a few months at most, and already in your lifetime you've gone through hundreds of generations of olfactory receptor neurons. This turnover of neurons is all the more remarkable when you realize that as each new olfactory cell matures, its axon must grow an appreciable distance to reach its target site in the brain. And once there, each axon presumably must form connections that effectively duplicate those that were undone by the death of its predecessor—otherwise odors would not smell the same from one month to the next. Buck (1992) discusses several possible means by which this amazing developmental feat might be accomplished.

Some people believe that this cyclical turnover of cells may have something important to do with reduced sensitivity to an odor following prolonged exposure to that odor, a phenomenon well documented in the environmental health literature (Ahlstrom et al., 1986). But, in order to appreciate how this might come about, you'll need to know a little more about the structure of the olfactory receptor neurons, in particular the parts that actually extend into the mucous lining of the nose.

From the short, dendritic end of each olfactory receptor cell extends a clump of several **cilia**—thin, hairlike structures suspended in a thin layer of mucus that coats the surface of the nasal cavity. The receptor sites for olfaction are imbedded in the membrane of these cilia; to reach the receptor sites, molecules of odorant must pass from the inhaled air into the mucus layer. In this effort, odorants may have some help from olfactory binding protein (Snyder, Sklar, Hwang, and Pevsner, 1989; Anholt, 1991). Olfactory binding protein, as its name implies, has a chemical affinity for a great many different odorants. It traps and concentrates odorous molecules, ferrying them into the mucus and thence to the receptor sites. This process is illustrated schematically in Figure 12.7. Although some details remain to be nailed down, it's almost certain that the actual receptors are long protein molecules that snake back and forth through the ciliary membrane.* The odor-

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* Olfactory receptor proteins, of which more than a hundred different varieties have been identified, are members of a large family of receptors, all of which (1) crisscross the membranes of host cells exactly seven times, and (2) employ the same basic mechanisms for initiating signals in those host cells. This superfamily of receptors includes the protein portions of rod and cone pigments, and many chemical receptors in the brain, including those for serotonin and dopamine (Shepherd and Firestein, 1991; Buck 1992).

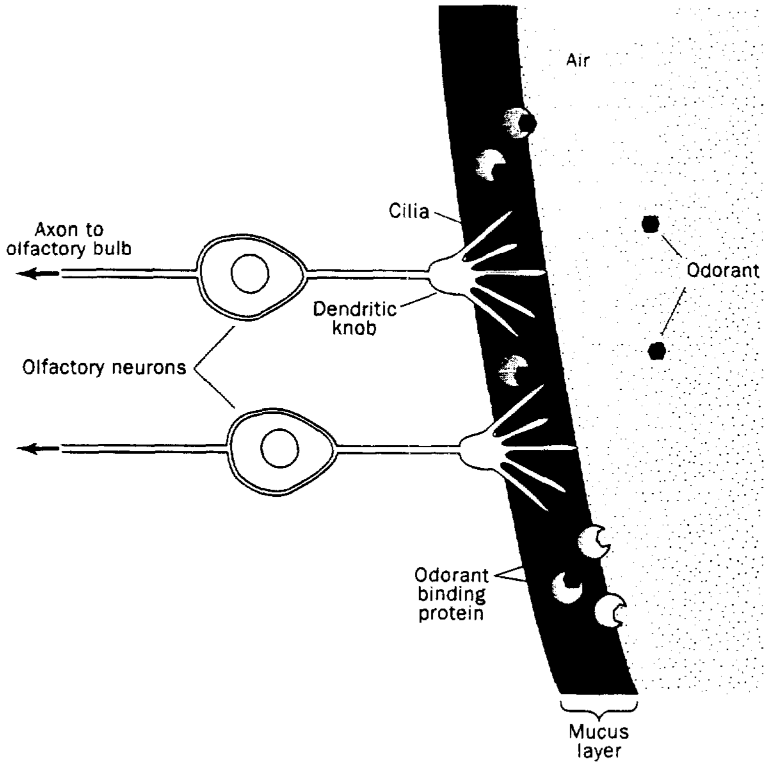


FIGURE 12.7 Odorants received at the olfactory epithelium are picked up by specialized proteins and transported to receptor sites on the cilia. (Adapted from Levitan and Kaczmarek, 1991.)

ant molecules bind to specific sections of the receptor proteins embedded within the ciliary membrane. Binding of the odorant to the receptor triggers a series of molecular events that, in rapid succession, calls into play several different intermediaries located within a cilium (Lindner and Gilman, 1992). The last of the intermediaries is an enzyme that triggers electrical changes in the cell, probably by binding to specific proteins that form the outer membrane of the cilia.

Different olfactory receptor neurons presumably have different receptor proteins, making them differentially responsive to various odorants. Lancet (1986) provides a thorough summary of the evidence favoring the existence of olfactory receptor proteins. According to this protein hypothesis, specific anosmias are attributable to the absence of specific receptor proteins. Temporary anosmia (a temporary, reversible loss in odor sensitivity) would occur whenever the cilia are damaged, as they are by certain toxic chemicals and by some drugs. Once new cilia grow, odor sensitivity returns.

These ideas about odor transduction are controversial, and much remains to be learned about the specifics. For instance, it's not known whether one olfactory receptor neuron houses just a single type of receptor protein or several different proteins. Setting aside these uncertainties about sensory transduction, let's turn to the question of neural coding of odor quality. How are the various qualities of odor represented in the firing patterns of neurons of the olfactory system? What neural responses make it possible for us to distinguish, say, the smell of lemons from that of limes?

Neural Coding of Odor Quality by Olfactory Fibers. You've already learned something about how qualitative (as contrasted with intensive) aspects of a stimulus are represented in other senses. Recall from Chapter 9 that each fiber in the auditory nerve responds to some range of frequencies, giving the strongest response to one particular frequency. Likewise, each fiber in the optic nerve prefers contours of a particular size and, for some, a particular color. Again, the preferred size or color varies from fiber to fiber. In those modalities, then, different subcategories of sensory fibers carry information about different sensory qualities. As a group, olfactory nerve fibers (the axons of the olfactory receptors) do *not* behave in this discriminating, specialized fashion. The vast majority of olfactory nerve fibers respond to a whole host of different odors, some of which bear no qualitative similarity to one another (Kauer, 1991). To be sure, individual fibers don't indiscriminately respond to all possible odors; there must be, and is, some degree of response specificity. But the range of effective odorants is quite large for any given nerve fiber; there is nothing resembling the specialization evident in auditory and visual nerves. Consequently, olfactory fibers individually can signal that some odorous substance is present, but they cannot provide unequivocal information about the identity of that substance. It has been reported that a small fraction of olfactory nerve fibers respond to only a limited set of odorous substances (Gesteland, 1978), but it is arguable whether these few fibers provide sufficient information about the identity of particular odorous substances.

So, the olfactory nerve, by and large, does not treat an odorant as some combination of basic components each separately registered by specialized cells. Nor, for that matter, does there appear to be anything in the olfactory fibers resembling the center/surround antagonism characteristic of visual receptive fields, and there is nothing comparable in the olfactory epithelium to the tonotopic organization of the basilar membrane and the auditory nerve. Simply stated, nature seems to have worked out a unique form of sensory coding within the olfactory system, and to understand more about that code, we must direct our attention to the next couple of stages of processing, the olfactory bulb and the olfactory brain.

The Olfactory Pathways. The previous discussion focused on the olfactory epithelium and the receptor neurons embedded in that tissue. The rest of the olfactory system consists of the **olfactory bulb** (which receives all the input from the olfactory nerve) and the **olfactory brain** (a cluster of neural structures receiving projections from the olfactory bulb). Structurally, the olfactory bulb bears a superficial resemblance to the retina, in that it has several layers of cells laterally interconnected (see Figure 12.8A, p. 424). On the basis of the response properties of neurons in the bulb, however, it is clear that the two structures—retina and olfactory bulb—function quite differently.

For one thing, the incoming axons from the olfactory epithelium activate neurons in the receiving stage of the bulb rather diffusely (those "second-order" neurons receiving this diffuse afferent input are concentrated in clusters called *glomeruli*). There is not, in other words, any kind of topographic, spatial map of the epithelium onto the bulb. There is, though, enormous convergence at this anatomical stage—it is estimated that there are 1,000 receptor cell axons for each second-order neuron in the bulb. Consequently, very weak neural signals, originating in many different olfactory neurons and carried by olfactory nerve fibers, can be summed within the bulb to create reliable responses to minute concentrations of an odorant (Duchamp-Viret, Duchamp, and Vigouroux, 1989).

It is generally believed that odor quality is coded by the spatial *pattern* of neural activity across the entirety of the olfactory bulb (Freeman, 1991; Kauer, 1991)—an idea reminiscent of the explanation of the tilt aftereffect given in Chapter 4. In

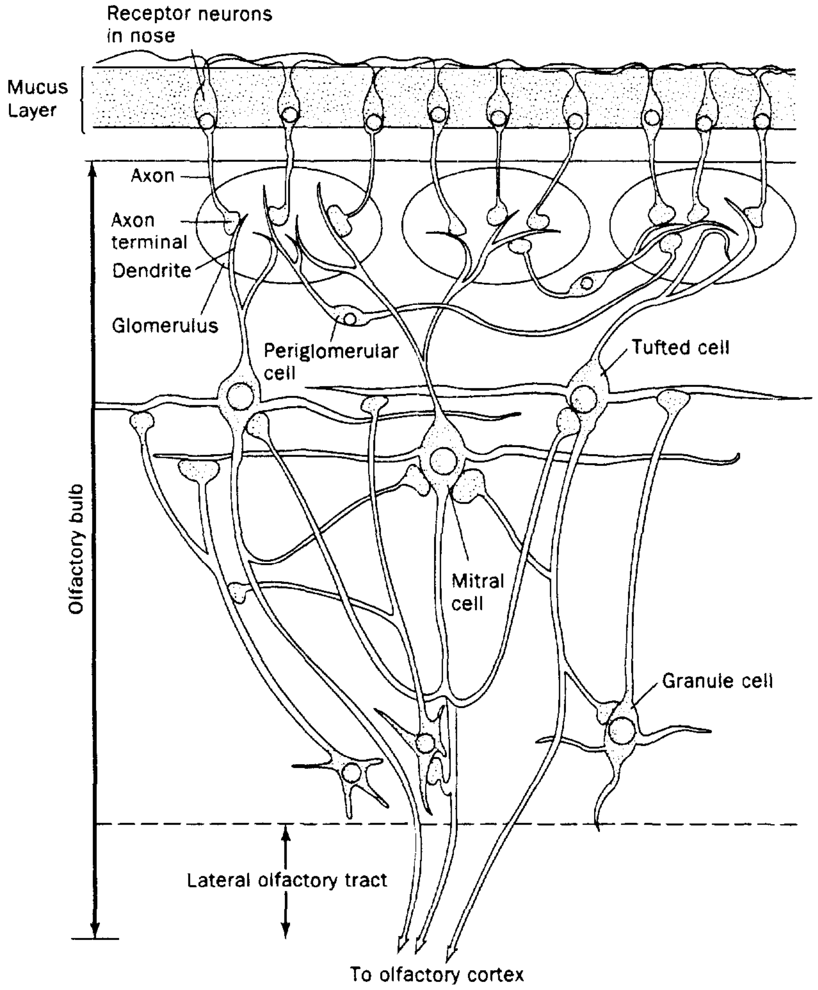


FIGURE 12.8A A schematic drawing of the multiple layers of the olfactory bulb.

this view, virtually all neurons in the bulb contribute to the registration of odor quality; there are no specialized neurons that signal, say, the fragrance of a rose. Support for this view comes from studies in which a map of neural activity was created using the 2-deoxyglucose technique described on page 20 in Chapter 1. (That technique involves the uptake of a radioactively labeled chemical that selectively concentrates in brain regions high in metabolic need.) Different odorants produce characteristic, reliable patterns of metabolic activity within the bulb, but these patterns are rather globally distributed over the structure and are not confined to local clusters of cells (reviewed by Holley, 1991).

Activity of neurons in the olfactory bulb is also shaped by two other important aspects of an odorant. First, neural activity varies throughout the phase of the inhalation cycle, being greatest at the end of each inhalation. And second, neuronal activity in the bulb depends on the level of emotional arousal; if an animal is hungry, thirsty, sex-

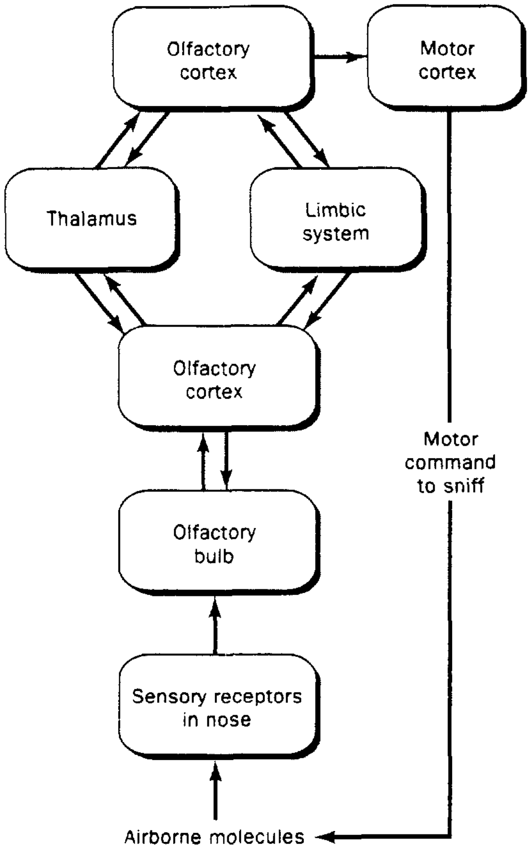


FIGURE 12.8B A flow diagram of the pathway constituting the olfactory system.

ually aroused, or fearful, neural responsiveness is enhanced.

If a given odor is indeed represented by a particular global "map" of neural activity within the bulb, we would expect destruction of parts of the bulb to disrupt this map and, hence, impair odor perception. It is remarkable, therefore, that several studies find normal olfactory performance in animals with rather massive lesions of the olfactory bulb (Holley, 1991). Those studies focused mainly on detection and discrimination, not more refined aspects of odor perception such as identification of or memory for odors.

The output from the olfactory bulb is carried by axons from several, morphologically distinct classes of cells within the bulb. Those axons project to the olfactory cortex in the frontal lobe which, in turn, communicates with several other areas of the brain, including subcortical structures in the limbic system (see Figure 12.8B). This latter connection is noteworthy, for the limbic system, which is phylogenetically quite old, is involved in emotional responses. It is thought that the emotion-evoking capacity of odors—and the ability of emotion to affect smell as strongly as it does—arises from two-way links between the olfactory and limbic systems.

Studies of the physiological properties of neurons in the olfactory cortex are few in number. To date, efforts to identify some type of odortopic organization in the cortex (that is, an organized map of different odors represented by different neurons) has failed (Greer, 1991). It is known, though, that people with damage to this region of the brain can have difficulty detecting and/or identifying odors (see review by Richardson and Zucco, 1989), indicating that those regions are critically involved in the processing of olfactory information. As described above, any given type of odorant molecule usually evokes a broadly distributed, characteristic pattern of activity within the olfactory bulb. Of course, the air we ordinarily breathe carries numerous odorous molecules associated with different odor sources. So, the olfactory cortex is receiving from the bulb a complicated pattern of activity associated with this montage of odorant molecules. Researchers are just beginning to grapple with the problem of how the olfactory portions of the brain extract the appropriate invariant response from what must be a fluctuating and unpredictable background of neural responses triggered by the other odorants that are present (Hopfield, 1991).

Neural Representation of Odor Intensity. The previous section focused on odor quality—the difference, for example, between the odor of a banana and the odor of peanut butter. Another dimension of odor perception, of course, is the intensity of a given odor. Odor intensity depends on the concentration of the airborne molecules along with the amount of odorant actually reaching the receptors in the olfactory epithelium. (A given concentration is going to smell weaker when your nose is stuffed up.) Not surprisingly, the nervous system registers information about concentration in the firing rate of neurons responsive to an odor: weak odors elicit fewer neural impulses than strong odors. This property seems to hold at all levels of the olfactory system, from the receptor cells to the cortex. To complicate the picture, though, people can experience changes in the *quality* of an odorant (even chemically pure ones) with changes only in intensity (Gross-Isseroff and Lancet, 1988). So, odor intensity and odor quality are not independent dimensions.

* * *

This overview of the olfactory system sets the stage for considering the perception of odors.

ODOR PERCEPTION

Odor Detection. It is often said that the human sense of smell is rather dull compared with that of other species such as the dog (Moulton, 1976). Although this is true, the human nose is remarkably sensitive nonetheless. For instance, people can detect ethyl mercaptan (a foul-smelling substance) in concentrations as minute as 1 part per 50 billion parts of air. This performance rivals that of the most sensitive laboratory instruments available for measuring tiny concentrations of molecules. Such sensitivity is all the more impressive when you realize that only a small fraction of the odor molecules in this minute concentration actually reaches the olfactory receptors in the top of the nasal cavity. During normal breathing, only about 2 percent of the odorous molecules entering the nostrils actually make it to the receptors; the remaining molecules are absorbed by the lining inside the nose.

Olfactory sensitivity varies greatly from odor to odor. For example, the substance mentioned above, mercaptan, can be detected at a concentration 10 million times less than that needed to smell carbon tetrachloride, a liquid sometimes used in dry-cleaning fluid (Wenger, Jones, and Jones, 1956). Because people are so sensitive to mercaptan, it is added to natural gas, itself odorless but toxic, to warn of gas leaks (Cain and Turk, 1985). One account of this remarkable sensitivity assigns a crucial role to a substance we mentioned earlier, olfactory binding protein (Snyder, Sklar, Hwang, and Pevsner, 1989). This protein, which is found only in nasal tissue, is created by a gland that is located toward the very rear of the nose. A duct carries the protein toward the tip of the nose where, every time you inhale, molecules of the protein are mixed into the incoming air. The protein in the newly inspired air traps molecules of potential odorants and carries these bound molecules to the olfactory receptors. Olfactory binding protein is very well suited to enhance sensitivity: the protein has at least some affinity for virtually all odorants. Moreover, though only a few odorants have been studied so far, the protein has greatest affinity for odorant molecules to which the human nose is most sensitive.

Besides molecular properties, odor sensitivity also depends on a number of other factors, including time of day, age, and gender. In particular, people are generally able to detect weak odors better in the morning than in the evening (Stone and Pryor, 1967); elderly people are less sensitive than young adults (Cain and Gent, 1991; Schiffman, 1983); and females are more sensitive, on average, than males (Koelega and Koster, 1974). Because of these age and gender differences in smell acuity, some people may be put off by body odors that others are not even aware of. Your own experiences in social settings probably confirm this observation. Your experiences may also lead you to believe that your sensitivity to odors increases when you are hungry. But this belief is questionable—some experiments say yes (Schneider and Wolf, 1955); others say no (Furchtgott and Friedman, 1960). Consistent with popular belief, however, smokers are less sensitive to odors than are nonsmokers (Ahlstrom et al., 1987). This dulled odor sensitivity is also found in nonsmokers who live or work with individuals who are heavy smokers (Ahlstrom et al., 1987).

Odor Identification. Having bragged about the sensitivity of the human nose, we must qualify what we mean by "sensitivity." The remarkable performance described above refers to the ability to *detect* the presence of a faint odor, not the ability to *identify* the odor. In fact, at near-threshold concentrations, people can smell an odor but not tell what odor they are smelling. The following experiment illustrates this point (Engen, 1960). When given three empty test tubes and a fourth test tube containing an extremely dilute odor, people can accurately select the tube that "smells different" from the others. But using the same set of stimuli, people make many errors when instructed to pick the test tube that contains some named odor ("pick the tube containing menthol"). So people behave as if they have two thresholds, one for detecting the presence of an odor and a second, higher threshold for identifying what that odor is.

For some odorous substances, part of the identification problem may stem from their bistability: such substances can elicit either of two different qualitative experiences, and these fluctuate over time. (A visual example of bistable perception is the young woman/old lady ambiguous figure shown in Figure 4.23.) For instance, the compound dihydromyrcenol (which is related to turpentine) sometimes has a citruslike odor and other times a woody odor. Lawless, Glatter, and Hohn (1991) were able to bias people's descriptions of this substance by also having the people smell an odorant that was unambiguously woody (for example, pine) or unambiguously citruslike (for example, lemon oil). After smelling citrus, people said the ambiguous compound smelled woody; after smelling the woody odor, the compound smelled like citrus. This shift in perception is not attributable to sensory adaptation, for it did not matter whether the unambiguous stimulus was sniffed before or after sniffing dihydromyrcenol. This context-dependent change in odor identification could be exploited for creative menu planning using dishes with multiple aroma components, such as curried chicken. And when serving wine, it is possible to make a fruity wine such as a German Reisling have either an acidic or a floral bouquet, depending on the accompaniment.

Most odorous substances, though, elicit unique odor qualities regardless of context. Still, individuals differ greatly in their ability to identify odors—to attach a label to the odor of a substance. Odor identification has been measured in two large studies, one a sample of 1,955 people ranging in age from 5 to 99 years (Doty et al., 1984) and the other involving a survey of more than a million readers of a popular magazine (Wysocki, Pierce, and Gilbert, 1991). Conclusions from those two studies were in agreement. Overall, females are significantly better at odor identification than are males, and the best performance is exhibited by individuals ranging in age from mid-twenties to late forties (see Figure 12.9). Some people beyond their sixties show marked impairments in the ability to identify odors, which may explain why elderly people sometimes complain about the blandness of food; after all, smell is an essential component in the enjoyment of food. It should be noted, though, that odor identification performance is much more variable among the elderly: some people in their seventies or older perform as well as middle-aged individuals.

Besides age and gender, there are other important determinants of olfactory performance. Tobacco smoking impairs the ability to identify odors, as the graph in Figure 12.10 documents: the longer the history of smoking, the greater the number of errors on a standardized odor identification test (Frye, Doty, and Schwartz, 1989). Fortunately, cessation of smoking promotes recovery. Ambient air quality, too, affects odor perception. Individuals working in plants manufacturing vaporous chemicals may exhibit long-term impairments in olfactory identification (Schwartz et al., 1989), and people living in cities with poor ambient air quality have difficulty identifying at least some odors compared with matched samples of people from cities with generally better air quality (Wysocki, Pierce, and Gilbert, 1991).

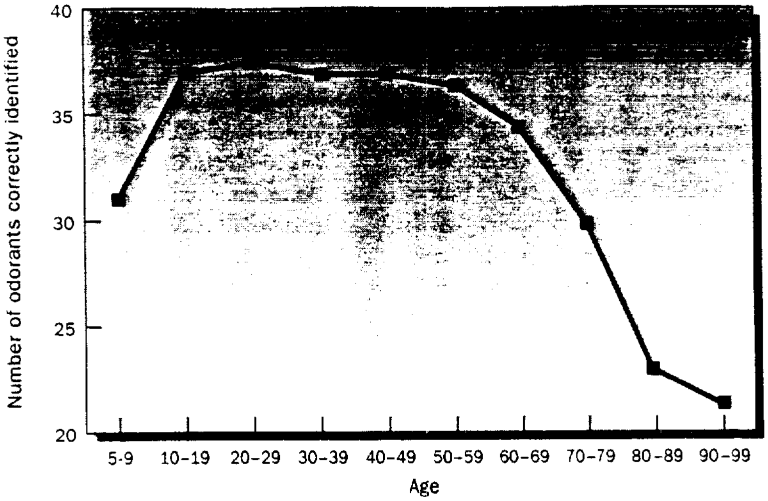
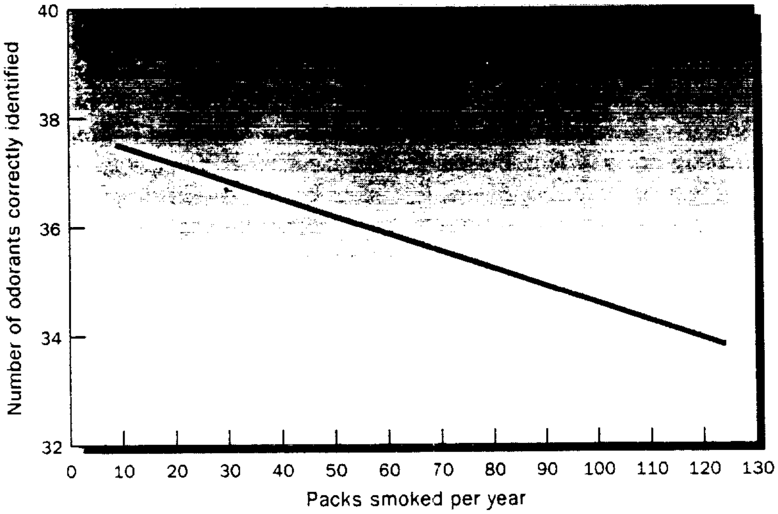


FIGURE 12.9 Ability to identify odors varies with age.

These deficits associated with smoking and with air quality may be related to structural changes at the receptor sites on the olfactory cilia, which become altered with chronic exposure to particular odorants.

Murphy and Cain (1986) have found that blind adults are significantly better at odor identification than comparably aged sighted individuals. Perhaps, then, odor identification should be thought of as a skill that can be sharpened with the enforced practice required without vision. Indeed, even in sighted individuals, practice with feedback improves the ability to identify odors. Desor and Beauchamp (1974) tested people's ability to name

FIGURE 12.10 Ability to identify odors is impaired by cigarette smoking.



thirty-two common odorous objects contained in individual opaque jars. After sniffing the jar, the person guessed what the object was and rated the familiarity of the odor. Some smells—such as coffee, paint, and banana—were readily identified and were also rated as highly familiar. Other smells—including ham, cigar, and crayon—were incorrectly identified by most people; these odors were also rated as less familiar. Desor and Beauchamp then went through the series again, this time providing people with the correct answer when they made errors. With this practice, everyone was able to learn to name each of the thirty-two odors correctly. Furthermore, the same people were trained on an additional set of thirty-two new odors, and with practice they were able to identify all sixty-four odors with few errors.

Although practice improves odor identification, it does not help everybody to the same degree. For example, practice seems to benefit females more than males, as Figure 12.11 shows. The graph summarizes results from an experiment where Cain (1982) asked male and female college students to identify each of the eighty common odorous stimuli listed in the figure. Each person went through the set of stimuli several times, with feedback provided after every trial. Students of both sexes improved with practice on this task, but the females consistently outperformed the males on just about every odorous stimulus. Each bar in Figure 12.11 summarizes identification performance for a particular stimulus. Stimuli in the upper portion of the figure (for instance, coffee) were readily identified, whereas stimuli toward the lower portion (such as cough syrup) were difficult to identify. Unshaded bars indicate female superiority at identifying that odorant, whereas shaded bars indicate male superiority. The length of the bar denotes the size of the sex difference in

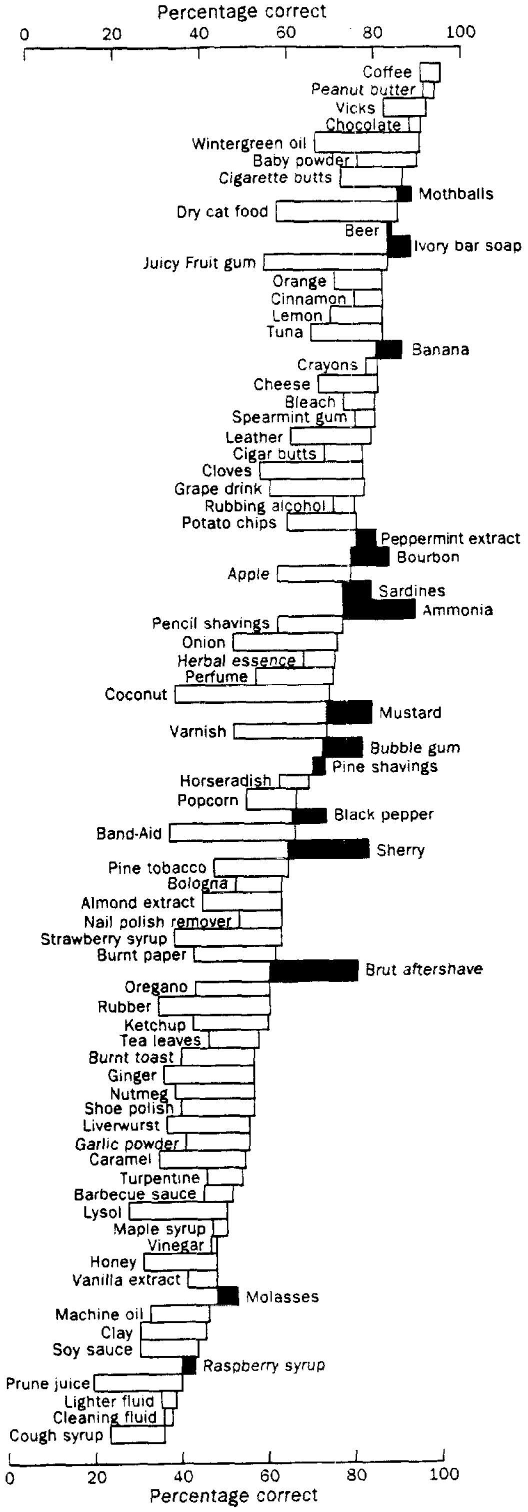


FIGURE 12.11 Odor identification performance for eighty common stimuli, arranged from top to bottom in order of ease of identification. Unshaded bars indicate the superior ability of female subjects to identify a particular stimulus; shaded bars indicate the superior ability of male subjects. (Redrawn with permission from Cain, 1982.)

odor identification. For instance, males were much better than females at identifying Brut aftershave lotion, but only marginally better at identifying the smell of mothballs. Females were much better than males at identifying coconut, but only slightly better at identifying peanut butter. As the overwhelming number of unshaded bars indicates, females are generally better at this task than are males, a point made above. The origin of these sex differences is not yet known; nonetheless, it is clear that both sexes do benefit from practice.

Next on our list of important determinants of odor identity is stimulus salience. This is dramatically demonstrated by the abilities of mothers to recognize their newborns by smell alone after less than 1 hour of postnatal exposure to the infant (Kaitz, Good, Rokem, and Eidelman, 1987); this olfactory link between mother and infant occurs in a variety of species besides humans, and there is evidence that this adaptive reaction coincides with structural and neurochemical changes in the olfactory bulb (Kendrick, Levy, and Keverne, 1992). Newborn infants, too, apparently rely heavily on olfaction to recognize their mothers. Porter (1991) provides an excellent review of findings on the role of odor perception in mother-infant relationships. Related to this issue, Schaal (1988) has reviewed the literature on the development of olfaction in infants and children, concluding that from birth onward, infants are quite good at detecting and discriminating odors. What does seem to change, according to Schaal, are infant's hedonic reactions to odors—it may take several years for children to develop aversions to some odors that all adults judge to be offensive.

Related to salience is the influence of familiarity, which also has an impact on the ability to name an odor. Older individuals, though generally poorer at odor identification than young people, *do* show superior recall for substances that have been in use over a long period of time. For instance, older adults have little trouble recognizing the smell of vinegar and coffee, odorants that older persons have been exposed to since youth. In comparison, epoxy and hair conditioner stump older adults but not youngsters (Wood and Harkins, 1987). At the other end of the age continuum, newborn infants exposed for about a day to an artificial odorant preferentially orient to that odorant two weeks later when it is paired with a novel one (Davis and Porter, 1991). This olfactory familiarization probably underlies infants' ability to recognize their mothers by smell.

But if experience with odors starts from day one, why are we relatively poor at identifying them, even odors we've experienced over and over? Of course, odors are typically associated with information from other senses, information that unambiguously identifies the source of those odors. For instance, a citruslike aroma is usually accompanied by the sight of a lemon. But in odor identification tasks, people have only the sense of smell to go on, and even healthy, young females may get fewer than half the items correct. Now, the problem isn't one of discrimination: people find it easy to judge correctly whether two odors are "same" versus "different"—the problem involves naming individual odors. In other words, the link between odors and their verbal descriptions is inherently weak (Engen, 1987). This inability to name a familiar odor has been aptly termed the **tip of the nose** phenomenon (Lawless and Engen, 1977)—a variation on the phrase typically used when one blocks on a term or a name. If the problem is indeed one of retrieving odor names from memory, prompting with clues as to an odor's identity should help. And it does. Several researchers (Davis, 1981; Zellner, Bartoli, and Eckard, 1991) have found that merely providing people with a color name related to an odor (such as "yellow" when lemon was being sniffed) is sufficient to trigger correct identification.

Odor Concentrations. Besides having characteristic qualities, odorous substances also vary in the intensity of those qualities. Intensity, as you could guess, depends on the concentration level of odorous molecules. A common misconception about the sense of smell concerns people's alleged poor ability to judge differences in odor concentrations. Until recently, it was generally thought that people require about a 25 percent difference in odor concentration before they can tell that one sample of an odor is stronger than another sample of that same odor. (This implies that a bouquet of five flowers would smell no stronger than a bouquet of four flowers, since they differ by only 20 percent.) Compared with vision and hearing (where difference thresholds are on the order of 10 percent), this represents dull sensitivity indeed. However, William Cain (1977) has shown that this dismal performance does not reflect an inferiority on the part of the olfactory nervous system; instead, the poor performance stems from moment-to-moment variability in the amount of odorous vapor delivered to the olfactory receptor cells. Remember, only a small fraction of these vapors actually reach these cells. Taking account of variability in effective odor concentration, Cain found that concentration differences as small as 7 percent are discriminable. This places the nose in the same league with the eye and the ear as a judge of intensity differences. (Thus if their fragrance was delivered through Cain's apparatus, five flowers *would* smell stronger than four.)

Remember the description of magnitude scaling, in Chapter 10 and in the Appendix, where people assigned numbers to sounds according to their loudness? Comparable scaling measurements have been made of perceived odor intensity. As with loudness, odor intensity grows as a power function of concentration. Although the values vary from odor to odor, many odors give exponents in the neighborhood of 0.6, indicating that perceived odor intensity grows somewhat gradually relative to increasing concentration. For example, doubling odor concentration produces only about a 50 percent increase in perceived intensity, not 100 percent (the value associated with an exponent of 1.0). As a result, a bouquet of ten flowers will not smell twice as strong as a bouquet of five flowers; to smell twice as strong as five flowers, a bouquet would have to consist of seventeen flowers. Intensity ratings can be affected by color. Zellner and Kautz (1990) found that some odorous substances smell stronger when the sniffed liquid substance is colored (for instance, red, in the case of strawberry). Evidently, simple conditioning cannot explain this finding, since enhanced odor intensity was found even with inappropriate color/odor combinations (for instance, red lemon).

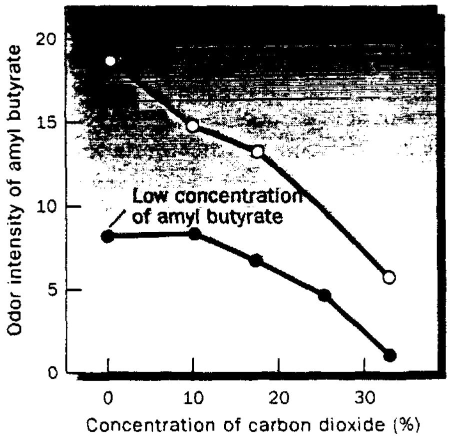
Is discrimination of odor concentration useful? Suppose you walk into your house and smell some foul odor. You can't see where it's coming from, so you have to rely on your sense of smell to guide you to the source. You move around trying to locate where the smell becomes stronger. Since odor concentration varies with distance, this strategy will ultimately bring you to the source.

While tracking the odor, you might also sniff, thereby pulling more of the odorous vapors into your nose. Shouldn't that perceived odor intensity vary depending on the vigor of the sniff? A deep sniff, after all, pulls more odorous vapors into the nose than does a weak, shallow sniff. And since more odorous molecules will be available for stimulating the olfactory receptors, the resulting smell seemingly should be stronger the deeper the sniff. Yet this may not always happen—some investigators have reported that odor intensity remains constant regardless of the vigor of a sniff (Teghtsoonian, Teghtsoonian, Berglund, and Berglund, 1978). This finding is especially surprising since when sniffs are produced artificially, by blowing odorous air into the nose, perceived intensity *does* depend on the rate of air flow (Rehn, 1978). Why would artificial sniffs and natural ones have different effects on perceived odor intensity? After all, with both types of sniffs the flow rate of the odorant varies comparably. According to Teghtsoonian, Teghtsoonian, Berglund, and Berglund (1978), the olfactory system may recognize when the increase in flow rate results from a natural sniff, and it may then calibrate the perception of intensity to take this factor into account. These investigators have dubbed the phenomenon **odor constancy,** since perceived strength of an odor remains constant despite variations in flow rate. You can see the similarity between this phenomenon and shape constancy (Chapter 5), color constancy (Chapter 6), and size constancy (Chapter 7). In all these instances, perception of objects in the world remains constant despite changes in the energy impinging on the receptors. We should note in passing that others have suggested alternative mechanisms by which odor constancy may be achieved (Laing, 1983).

The Common Chemical Sense. While on the subject of odor concentrations, we should note that most odors judged pleasant at moderate concentrations lose some of their attractiveness at high concentrations. This is why a salesclerk in a cosmetics department always urges customers to allow a dab of perfume time to dilute before smelling it. One reason intense odors can be overpowering has to do with the free nerve endings in the olfactory epithelium (a look back at Figure 12.6 will refresh your memory). Those nerve endings are chemical-sensitive cells stimulated by just about any volatile substance of moderately high concentration; they make up what is known as the **common chemical sense.** It is the common chemical sense that is responsible for the *feeling* that accompanies certain "smells"—such as the coolness of menthol or the tingle in your nose when you burp. Even the crisp, invigorating "smell" of fresh mountain air (which itself has no odor) comes from stimulation of the common chemical sense by ozone in the air. In fact, just about any volatile substance can elicit this "feeling" in the nose if the concentration of that substance is high enough. In the case of some substances, stimulation of the common chemical sense produces a burning sensation that causes you reflexively to hold your breath and turn your head away from the source of stimulation. Those of you who have inhaled ammonia fumes know what this feeling is like. Incidentally, cigarette smokers are less sensitive to stimulation of the common chemical sense; for them, the inhaled concentration of an irritating substance must be about 25 percent higher, as compared with nonsmokers, to elicit a reflexive change in breathing pattern (Cometto-Muniz and Cain, 1982). Elderly people, too, show reduced sensitivity to nasal irritants that stimulate the common chemical sense (Stevens and Cain, 1986) and, as you might guess by now, males are less sensitive than females (Garcia-Medina and Cain, 1982). Some people have totally lost their common chemical sense, from damage to the trigeminal nerve carrying information from the nose's free nerve endings to the brain. In these individuals, harsh chemical substances elicit *no* reaction when inhaled.

The common chemical sense serves as a warning system to signal the presence of potentially irritating substances. However, its operation is not limited to dangerous concentration levels; in fact, even at safe levels of stimulation the common chemical sense influences the perception of odor, as an experiment by Cain and Murphy (1980) demonstrates. In their study, people sniffed amyl butyrate (a fruity-smelling substance) and rated the perceived intensity of the odor. Mixed in with the odorant were various amounts of carbon dioxide. (Carbon dioxide is a gas that does *not* stimulate olfactory receptors but *does* stimulate the free nerve endings in the nose. Hence it has no odor; but because it stimulates the common chemical sense, it elicits a pungent sensation when inhaled.) Cain and Murphy wanted to know whether stimulation of the common chemical sense would influence people's judgments of odor intensity. Some of the results from their experiment are summarized in Figure 12.12; the vertical axis plots the perceived odor intensity of the amyl butyrate

FIGURE 12.12 Stimulation of the common chemical sense (carbon dioxide) affects perceived odor (amyl butyrate).



and the horizontal axis shows the concentration of the odorless carbon dioxide. Note that increasing the concentration of carbon dioxide, which itself could not be smelled, reduced the perceived intensity of the amyl butyrate. Even though the actual concentration of amyl butyrate remained constant, its smell changed from pleasant and fruity (at low levels of carbon dioxide) to pungent and irritating (at high levels of carbon dioxide). People also rated how irritating the "smell" seemed. As expected, higher concentrations of the odorless carbon dioxide gas were judged more irritating. However, the pungency of the carbon dioxide was lessened when more amyl butyrate was mixed in with it. We see, then, that the interaction between odor and the common chemical sense works both ways, with each influencing the perception associated with the other. Clearly, the common chemical sense adds an important ingredient to your experience of odorous substances.

Turning back to the topic of odor perception, let's consider "anosmia," a term referring to a loss in the ability to perceive odors.

Disorders of Smell. Deficiencies in hearing and seeing are usually easy to detect because people depend so much on sight and sound to guide their everyday activities. Deficiencies in odor perception, in comparison, can go unnoticed. Though hard to imagine, some individuals are completely unable to distinguish odorless, pure air from strong concentrations of odorous substances. One frequent cause of this "odor blindness," or anosmia, is a blow to the head (Varney, 1988); in such cases, the anosmia often proves to be temporary, suggesting that the olfactory receptors or their axons had been damaged (recall that these neurons can regenerate). Anosmia may also be acquired from inhaling caustic agents such as lead, zinc sulfate, or cocaine. These, too, are believed to injure the olfactory receptors, which is why recovery of smell sensitivity often occurs after ingestion of the caustic agent ceases. Reduced odor sensitivity and identification performance are also observed in patients with Alzheimer's disease (Rezek, 1987). In these patients, impaired odor perception probably results from degeneration of neurons in the olfactory epithelium (Talamo et al., 1989). Schiffman (1983) reviews the various causes of anosmia.

Sometimes anosmia does not involve a total loss of the sense of smell but is instead specific to particular substances. In these cases, a person shows normal sensitivity to some odors but abnormally poor sensitivity to others. These are the specific anosmias we mentioned earlier, and they are more common than you might think. For example, 3 percent of the U.S. population have trouble smelling the odor of sweat, 12 percent have diminished sensitivity to musky odors, and 47 percent have trouble smelling the odor of urine (Amoore, 1991).

Losing one's sense of smell can have serious consequences. Individuals with acquired anosmia often claim that eating is no longer pleasurable, and these people show a loss of both appetite and weight (Schechter and Henkin, 1974). There is even speculation that anosmia may dull one's sexual drive (Bobrow, Money, and Lewis, 1971). This possibility is not entirely farfetched. As mentioned in the beginning of the chapter, animals rely very heavily on odor to motivate and guide their sexual behavior. And certainly, the large sums of money spent on perfume, not to mention the erotic nature of many perfume commercials, suggest a connection between the nose and sexual behavior.

Before leaving our discussion of disorders of smell, this is a good place to mention **odor hallucinations**—the experiencing of odors for which there is no physical stimulus. Odor hallucinations are sometimes associated with brain tumors (Douek, 1974); they are also a common complaint of people diagnosed as mentally ill (Rubert, Hollender, and Mehrhof, 1961). But don't assume that odor hallucinations necessarily indicate brain damage or mental illness. People sometimes describe sensing strange, metallic odors when they have the flu or other viral diseases (Schiffman, 1983). This effect is thought to result from a virus's having damaged cells in the olfactory epithelium. In any event, you needn't become immediately alarmed when you experience some olfactory hallucination; it is often difficult to distinguish real odors from imaginary ones, since the source of an odor may not be obvious. How many times have you searched your house trying to discover where that "funny smell" was coming from?

Adaptation to Odors. Imagine walking into the lobby of a movie theater and smelling the aroma of fresh popcorn. Driven by this lovely smell, you stand in line to buy some, but by the time you reach the counter, the aroma has faded considerably. This exemplifies how exposure to an odor decreases sensitivity to that odor—a phenomenon called **odor adaptation.** Certain occupations depend crucially on odor adaptation—sewer workers, for instance, can carry out their jobs without being bothered by the stench of their surroundings. Odor adaptation also means that people cease to be aware of their own body odors or of the odors permeating their immediate surroundings. It was Freud (1930/1961) who observed that ". . . in spite of all man's developmental advances, he scarcely finds the smell of his own excreta repulsive, but only that of other people's" (p. 54). Thus, sometimes one must rely on others for information about self-odor, a widely exploited theme in deodorant, mouthwash, and soap commercials.

Odor adaptation has been studied in the laboratory, and the results confirm what experience suggests (see Halpern, 1983). Following even prolonged exposure to an odor, one never *completely* loses the sensitivity to that odor. Instead, its perceived intensity steadily decreases with continued exposure, eventually falling to about 30 percent of its initial level (Cain, 1978). (This is why some people can "tolerate" wearing an overpowering amount of perfume or aftershave—their noses have adapted to the strong fragrance that others wince at.) If an odor's concentration is weak to begin with, it may be impossible to detect that weak odor following adaptation to a strong concentration of the same odor.

Recovery from exposure to an odor takes just a few minutes unless the adaptation odor was quite strong, in which case an hour or more may be required for complete recovery (Berglund, Berglund, Engen, and Lindvall, 1971). There is also anecdotal evidence for an ultra-long-term adaptation effect, whereby individuals develop a chronic insensitivity to odors common to their work environment. Even when they report to work first thing in the morning, they fail to smell odors that visitors readily sense. The adaptation of these workers carries over from one day to the next. At the same time, these individuals exhibit normal sensitivity for odors not peculiar to their workplace; so they have not completely lost their sense of smell. Moreover, upon returning to work following a short vacation, they are initially able to sense the odors that their colleagues on the job cannot sense; after a few days on the job, however, they again become insensitive to those odors. Gesteland (1986) has speculated that these long-term losses in odor sensitivity may be related to the growth processes in the olfactory receptor cells that we described earlier. Perhaps chronic exposure to a limited set of odors affects receptor cells responsive to that set of odors, and several weeks away from that environment are needed to allow the spoiled cells to be replaced with fresh ones.

This explanation of long-term adaptation probably does not apply, however, to short-term adaptation, where brief exposure to an odor temporarily lessens your sensitivity to it. In this latter case, the process responsible for adaptation probably occurs within the brain, not in the nose. One reason for believing this is that you can adapt one nostril to an odor (keeping the other one closed) and then measure a loss in odor sensitivity using just the unadapted nostril (Zwaardemaker, 1895, cited in Engen, 1982). Since this nostril was closed during adaptation, the olfactory receptors associated with the nostril must have received no stimulation. Nonetheless, your perception of odors introduced into this nostril are still dulled, indicating that the process underlying the loss in sensitivity occurs in the brain, not in the receptor cells. However, the physiology of postreceptor adaptation is poorly understood.

So far we have considered situations where the perceived strength of an odor is reduced by prior exposure to strong concentrations of that same odor. In some cases, though, a temporary loss in sensitivity to one odor can be produced by exposure to a different odor—a phenomenon called **cross-adaptation.** As you might expect, odors that tend to smell alike (such as nail polish remover and airplane glue) usually show a large degree of cross-adaptation: exposure to one reduces your sensitivity to the other. If you spend several minutes sniffing perfume samples at the cosmetic counter, don't be surprised if the fragrance you're already wearing seems temporarily to have worn off; sniffing perfumes similar to your own has lessened your sensitivity to the one you're wearing. Dissimilar odors, in contrast, do not influence each other nearly so much (Moncrieff, 1956). Thus sniffing perfume samples will not subsequently affect your ability to appreciate the aroma of coffee.

You can experience cross-adaptation by performing the following simple experiment. First, take a sniff of a lemon and get an idea of the intensity of its aroma. Now hold a spoon of peanut butter close to your nose for a minute or so, adapting to its smell. Then quickly take another whiff of the lemon—you will find the lemon's fragrance just as strong as before. Next adapt for a minute to a lime held under your nose, and then again sniff the lemon. This time you will find the lemon's fragrance noticeably weakened. A lesson to learn from this exercise is that your appreciation of food during a multicourse meal depends on the order in which the foods are served. This is particularly true for foods with similar aromas. For instance, cheese with a strong, overpowering smell (such as Roquefort) should not be served before one with a more delicate aroma (such as Gouda).

Initially, it was hoped that cross-adaptation would provide a method of odor classification. Presumably, odors stimulating the same receptors should exhibit maximum cross-adaptation, whereas odors stimulating different receptors should show little or no cross-adaptation. Although this sounds reasonable, the results are confusing. In particular, cross-adaptation is sometimes asymmetrical: adaptation to odor A may strongly influence your perception of odor B but adaptation to odor B may exert hardly any effect on the smell of odor A (Cain and Engen, 1969). This outcome seems to indicate that cross-adaptation is not strictly due to receptor adaptation. Moreover, odors that exhibit marked cross-adaptation sometimes bear no resemblance to each other chemically. Cross-adaptation, like short-term adaptation in general, then, does not appear to result from fatigue of the olfactory receptors.

Odor Mixtures. Besides being subject to cross-adaptation, different odors can affect one another when mixed together in inhaled air. In fact, this occurs quite commonly, as the following examples illustrate. Most meals consist of a bouquet of aromas that when properly mixed can generate a very pleasing experience. Mixing fragrances is the essence of the perfume maker's job; it is also a concern of people who bathe only with a soap that will complement their cologne. Odor mixture also underlies the success of commercial air fresheners sold to cover up house odors. In effect, these products exploit the ability of one odor to mask another by "swamping" the offensive odor with an even stronger pine or floral scent. These products should be distinguished from true deodorizers, which act by actually removing odorous molecules from the air or by preventing the production of odorous molecules in the first place (the mechanism employed in some underarm deodorants).

As indicated before, the nose seems able to sort out and identify the various odors that are in a mixture. This is why you can identify many of the food ingredients that went into some complex dish simply from the smell of that dish. In this sense, the nose's behavior resembles the ear's ability to single out one pitch from a musical chord; the nose does not behave like the eye, which sometimes loses track of the individual hues making up a mixture. However, a person's judgments of an odor mixture cannot be predicted on the basis of the simple addition of the two components. For instance, two different odorants of moderate intensity may not sum to yield an intense mixture; this failure of additivity is termed **mixture suppression,** and its physiological basis is not well understood (Derby, Ache, and Kennel, 1985; Laing, 1988). (For a full discussion of odor mixture, see Engen, 1982.)

Odors and Memory. Even when people cannot identify some odor, they are often able to say with confidence whether or not they have smelled it before—which suggests that odors can reach back into memory (see Box 12.2, pp. 438–439). For Helen Keller, who was blind and deaf from infancy, smell was

> *a potent wizard that transports us across thousands of miles and all the years we have lived. The odors of fruits waft to me in my southern home, to my childhood frolics in the peach orchard. Other odors, instantaneous and fleeting, cause my heart to dilate joyously or contract with remembered grief. (1908, p. 574)*

Odors can be potent reminders of the past—they effortlessly call up memories (Schab, 1991). But can memories call up odors? The answer seems to be no. Most people have great difficulty *imagining* what an odor smells like, even a very familiar one. Can you, for instance, conjure up the smell of a rose? Of course you recognize its fragrance when you actually encounter a rose, but recalling such a smell seems very difficult. Isn't it odd that one can readily hum tunes in one's head, can vividly picture a scene in the mind's eye, but cannot recreate in the mind a remembered smell? Perhaps, during the course of evolution, the sense of smell became fully developed before consciousness came on the scene. And perhaps, as a result, the olfactory system does not have access to the neural machinery needed to imagine odors consciously in the absence of the objects that normally evoke them. But emotional arousal seems quite able to trigger odor memories, probably from the intimate connections between the olfactory system and the limbic system. The so-called "smell of fear" may have neurologic reality. On these speculative notes we'll end our discussion of smell and move on to its sister sense, taste.

THE SENSE OF TASTE

We say of food, "This tastes good" or "I like the taste of that." But taste determines not only how much we like or dislike some food but also whether we will eat it at all. In effect, the tongue and mouth (assisted by the nose) are designed to ensure that nutritious substances are eaten while noxious ones are not. Living in a civilized environment, one seldom needs to rely on taste to gauge edibility—if the grocer sells it or the restaurant serves it, we assume it must be safe to eat. Taste serves mainly to define our preferences among a large group of commercially available edible foods. Still, taste provides a bounty of perceptual experiences and therefore deserves to be studied.

Technically, the term "taste" is used to refer to sensations caused when various substances dissolved in saliva penetrate the taste buds on the tongue and surfaces of the mouth. If you were to drop a pinch of sugar onto the tip of your tongue, the resulting sensation would constitute what most people call "taste." But when you actually eat something, you learn much more than this about the substances in your mouth—besides taste, you have an immediate appreciation of the food's temperature, texture, and consistency (Gibson, 1966). All these sources of information combine with the substance's taste to form a complex of sensations that is known as **flavor.** Although the remainder of this chapter is concerned with the taste component of flavor, keep in mind that these other sources of information also contribute to one's enjoyment of food.

In our discussion of taste, we shall follow the same general outline used in the section on smell: we'll describe the stimulus for taste, consider the question of taste categories, provide a brief overview of the anatomy and physiology of the gustatory system, and then take up the question of taste sensitivity. Finally, we'll explore the interaction between taste and smell.

THE STIMULUS FOR TASTE

To be tasted, a substance must be *soluble:* it must dissolve upon contact with saliva. This is why you cannot tell the difference between a plastic spoon and a stainless steel spoon simply on the basis of their taste—neither material will dissolve in saliva. Moreover, food seems tasteless when saliva is not present in the mouth, because it represents the vehicle for transporting taste solutions to the receptors within the tongue and mouth. The salivary glands, incidentally, produce in the neighborhood of 25 ounces of fluid in one day, most of it while one eats. Some food substances, particularly those containing citric acid, promote copious salivary secretion, whereas others, including glucose, are less effective. Besides aiding in digestion, saliva contains ingredients that prevent erosion of teeth enamel and eliminate bacteria in the oral cavity. In chemical composition, saliva closely resembles salt water, although the sodium content of saliva varies from one person to the next (Bradley, 1991). It is claimed that you can actually detect this difference in sodium content when you taste someone else's saliva (Bartoshuk, 1980), but we'll leave it to the intellectually curious to confirm this claim.

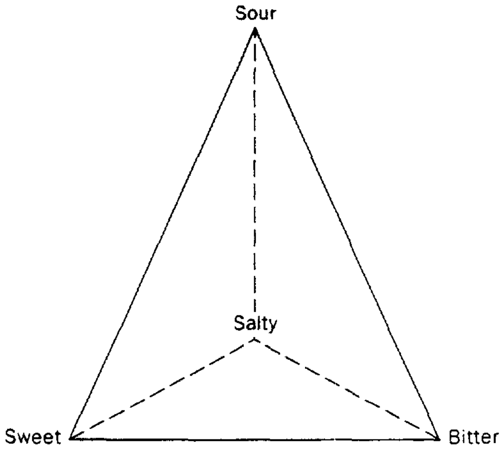
THE CLASSIFICATION OF TASTES

Nowadays it is widely believed that tastes can be grouped into four distinct categories: sweet, sour, salty, and bitter. However, this particular idea is still controversial. Earlier lists of the basic taste qualities contained more entries. For example, Aristotle believed there were seven basic tastes, the four listed above plus pungent, harsh, and astringent. In the centuries following Aristotle's time, new tastes were added to the list (such as viscous and fatty), whereas others were dropped (Bartoshuk, 1978). It wasn't until the early part of the nineteenth century that the list dwindled to the four categories most people are now familiar with. The person who formalized the four-taste idea is Henning (1916), the same man who was responsible for the odor classification scheme shown in Figure 12.3. Once again, Henning relied on geometry to present the relations among the various taste categories. In this case his model, shown in Figure 12.13, took the form of a tetrahedron, with each of the four taste qualities located at one of the four corners.

Henning wanted his geometrical model to emphasize the unity of the four taste qualities; he emphatically rejected the idea that these four taste qualities could be *separately* experienced in any complex mixture of tastes. More recently, however, Donald McBurney (1974) has argued that one *can* pick out and judge the relative contributions of these four primaries, or "basics," as he calls them. He believes this is possible because the tongue analyzes substances into these four distinct categories. Other taste experts disagree with the idea that there are genuinely separate taste qualities. Two of these notable opponents, Susan Schiffman and Robert Erickson (1980), have questioned much of the evidence for the existence of distinct taste primaries. Besides challenging this evidence, Schiffman and Erickson have also performed their own experiments on this topic. Let's consider the results from a couple of their studies.

Schiffman (whose work on odor categories we described earlier) used multidimensional scaling to analyze people's ratings of taste similarity. (Recall that this procedure establishes the number of dimensions required to account for similarity rat-

FIGURE 12.13 Henning's taste tetrahedron.



Box 12.2 *Smell, Taste, and Literature*

Languages have limited vocabularies for describing smell and taste experiences. Though it's fairly easy to describe what you see and what you hear, smell and taste are another matter (Bedichek, 1960). This works a special hardship on authors who must communicate their character's smell and taste experiences. Fortunately, good writers rise above the apparent limitations of language. When you read a work in which smell and taste play a key part, you are reminded how important these "inarticulate senses" really are. To illustrate, let's consider some samples of writing in which authors have managed to give these inarticulate senses a voice of their own.

Smell can evoke memories long-buried and obscure; the same thing can happen in the case of taste. Probably the best-known literary description of this phenomenon comes from Marcel Proust's *Swann's Way*. In the book's overture, the narrator muses that it's impossible to recapture one's past merely by trying to think about it. True recapture requires that you reexperience the *sensations* that you felt originally. And he then goes on to provide an eloquent example of this idea. While he is visiting her, the narrator's mother sees that he is cold and gives him a cup of tea and some little cakes called *petites madeleines*. Without thinking, he drinks some of the tea, into which cake crumbs have fallen. Immediately, he finds himself overcome with an "all-powerful joy," but he doesn't understand why. Then it strikes him: the taste was one he had experienced years before, as a young boy in the little French village of Combray.

> *In that moment all the flowers in our garden and in M. Swann's park, and the water-lilies on the Vivonne and the good folk of the village and their little dwellings and the parish church and the whole of Combray and of its surroundings, taking their proper shapes and growing solid, sprang into being, town and gardens alike, from my cup of tea. (Proust, 1928, p. 58)*

Since the next 200 pages of Proust's novel deal with his remembrances of things that happened in Combray, the entire novel actually springs from the taste of those few tea-soaked cake crumbs. What a powerful jolt to the memory!

One lesson from Proust is that any writer who wants to create truly convincing and complete lives cannot ignore smell and taste. James Joyce (1922/1934) understood this as well as any writer of the past 100 years. In his masterpiece, *Ulysses*, Joyce frequently used smells to reach into the minds of various characters. You may know that various episodes in *Ulysses* emphasize different organs of the human body, with the so-called Nausicaa episode highlighting the eye and the nose. This episode takes place just after sunset on a June evening in 1904. Leopold Bloom, the middle-aged Dubliner around whose comings and goings the book revolves, is walking along the beach, trying to clear his head. Bloom finds himself attracted to Gerty MacDowell, a young girl who's sitting on some rocks near the beach. Although they never even speak, Bloom is infatuated. When she leaves, Gerty waves her perfumed handkerchief at Bloom. The scent reaches Bloom, triggering thoughts of Gerty and of his wife, Molly, too:

Wait. Hm. Hm. Yes. That's her perfume. Why she waved her hand. I leave you to think of me when I'm far away on the pillow. What is it? Heliotrope? No, hyacinth? Hm. Roses, I think. She'd like scent of that with a little jessamine mixed. Her high notes and her low notes. At the dance night she met him, dance of the hours. Heat brought it out. She was wearing her black and it had the perfume of the time before . . . Mysterious thing too. Why did I smell it only now? Took its time in coming like herself, slow but sure. Suppose it's ever so many millions of tiny grains blown across . . . Clings to everything she takes off. Vamp of her stockings. Warm shoe. Stays. Drawers: little kick, taking them off. Byby till next time. Also the cat likes to sniff in her shift on the bed. Know her smell in a thousand. Bathwater too. Reminds me of strawberries and cream. (Joyce, 1922/1934, p. 368)

Another great writer with a special appreciation of the chemical senses was Jonathan Swift (1827/1945), the eighteenth-century English satirist. In one of his books, Swift paints a dramatic portrait of adaptation to the smells of a highly unusual environment. In the fourth and final journey related in Gulliver's Travels, Lemuel Gulliver finds himself marooned on an island ruled by the noble Houyhnhnms, a race of intelligent, honest, socially advanced horses. The island is also populated by a nasty, degenerate breed of barbaric humanlike creatures, Yahoos, whom the Houyhnhnms shun and whom Gulliver abhors. After living very happily among the horselike Houyhnhnms for more than 3 years, learning their language and developing great admiration for their culture, Gulliver must leave the island and return to England and the home and family that he had once loved. In Gulliver's words:

As soon as I entered the House, my Wife took me in her Arms, and kissed me, at which having not been used to the Touch of that odious Animal for so many Years, I fell in a Swoon for almost an Hour. At the time I am writing it is Five Years since my last Return to England: *During the first Year I could not endure my Wife or Children in my Presence, the very Smell of them was intolerable, much less could I suffer them to eat in the same Room. To this hour they dare not presume to touch my Bread, or drink out of the same Cup, neither was I ever able to let one of them take me by the Hand. The first Money I laid out was to buy two young Stone-Horses which I keep in a good Stable, and next to them the Groom is my greatest Favourite; for I feel my Spirits revived by the Smell he contracts in the Stable. My Horses understand me tolerably well; I converse with them at least four Hours every Day. They are Strangers to Bridle or Saddle, they live in great Amity with me, and Friendship to each other. (Swift, 1726/1890, p. 331)*

These literary tidbits give you some idea of how writers of varying backgrounds and literary significance have worked with smell and taste. These samples are a reminder of how impoverished one's own perceptual world would be without these "inarticulate senses."

ings.) Her analysis disclosed that taste judgments could *not* be contained within a "taste space" defined by just four components. (Henning's tetrahedron is one possible taste space utilizing four components.) Schiffman obtained evidence for more than four components even when taste judgments were obtained from anosmic individuals. Because these people could not smell, Schiffman could be certain that the extra dimensions uncovered in her analysis were not the product of olfaction. This led her to conclude that four primaries are inadequate to account for the entire range of taste (Schiffman and Dackis, 1975).

Robert Erickson approached the notion of taste primaries in a different way. He presented people with taste solutions consisting of one or more of the so-called primary tastes and asked those people to judge whether they perceived "one" or "more than one" taste quality. For comparison, Erickson asked for the same judgment about auditory tones presented either alone or in a chord. As expected, a single tone was always judged as one, whereas multiple tones were always judged as more than one. This merely confirms the analytical nature of pitch perception: identification of one tone is possible in the presence of another. The results with the taste solutions were quite different. Solutions composed of a single component were sometimes judged as more than one, whereas multicomponent solutions were sometimes judged as one. Moreover, people were often unable to identify whether a mixture contained a particular component, even when they could reliably identify that component in isolation. For instance, quinine (a bitter-tasting substance) was easily recognized on its own; but when mixed with sucrose (which, of course, is sweet), the quinine in the mixture was unrecognizable. These findings led Erickson to conclude that complex tastes are *not* analyzed into primary components but instead take on their own, unique quality, which may give little hint of their ingredients (Erickson, 1982).

This issue of taste categories is by no means settled (see, for example, McBurney and Gent, 1979). Taste researchers are reluctant to give up the idea of four primaries, for good reasons. In particular, some progress has been made in identifying chemical similarities among substances belonging to the same taste group (Beidler, 1978). Establishing the molecular basis of taste quality is a goal that taste experts have been striving toward for decades. Abandoning the categorization scheme that has guided this search would be a bitter pill to swallow. For the moment we'll set aside the question of primaries and proceed to a less controversial topic, the neural mechanisms of taste perception.

THE ANATOMY AND PHYSIOLOGY OF TASTE

The Taste Receptors. Let's begin by taking a tour of the tongue and the inside of the mouth. The tongue itself consists of muscle covered with mucous membrane. To picture the terrain under study, take a careful look at your tongue in a mirror. Notice that it is covered with little bumps. These bumps are called **papillae** (from the Latin *papula,* meaning "pimple"). When viewed from the side (see Figure 12.14), they resemble regularly spaced columns separated by channels. The walls of the papillae are lined with tiny structures, called **taste buds,** that are shaped like garlic bulbs. These taste buds house the receptor cells responsible for registering the presence of chemical substances. Not all the papillae scattered over your tongue contain taste buds—those in the center of the tongue have none, which is why food confined to this area has no taste. The center of the tongue is analogous to the blind spot in the eye: both are devoid of receptors. There's another parallel. Under normal conditions, you don't notice the blind spot since the brain fills in that gap; similarly, you don't notice the tongue's "blind spot." In fact, taste sensations appear to originate from the mouth's entire surface, including from regions that have no receptors (Todrank and Bartoshuk, 1991). Moreover, when the brain's taste information from an entire side of the tongue is blocked by a virus, there is no subjective change in the daily experience of taste (Pfaffmann and Bartoshuk, 1989, 1990).

Taste buds are not restricted only to the

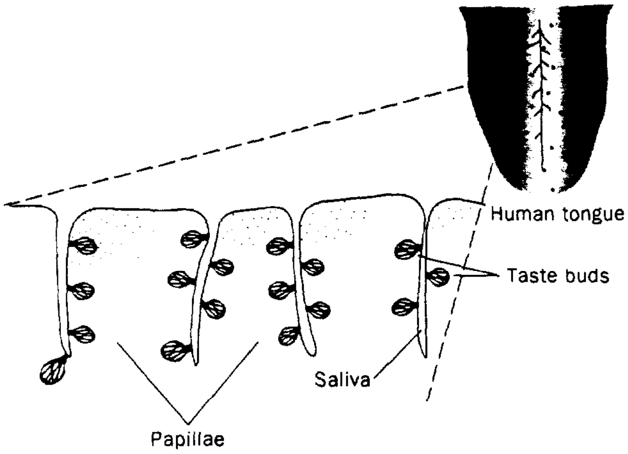


FIGURE 12.14 A side view of the tongue's papillae.

tongue: taste buds, absent the papillae, are located in the roof of the mouth, inside the cheeks, and in the throat. Some animals have structures similar to taste buds on parts of their bodies other than the tongue and inside of the mouth. Fish, which live in a watery equivalent of saliva, have taste receptors scattered over the surface of their bodies; and some insects have them on their feet, enabling them to taste the surfaces they walk over.

Human papillae that do contain taste buds have anywhere from several hundred buds down to just a single bud (Bradley, 1979), with a grand total of something like 6,000 taste buds distributed throughout the inside of the "average" mouth. We stress average, because the total number of buds varies dramatically among individuals. One count from the tongues of healthy, college volunteers revealed a fourteenfold difference with the sample (Miller and Reedy, 1990). Moreover, the students with taste bud counts toward the top of the distribution rated taste solutions of a given concentration as more intense than did students from the bottom of the distribution of taste bud density.

Developmentally, infants start out life with relatively few taste buds, but during childhood the number steadily increases to the numbers cited above. Around age 40, the trend reverses and the overall number of taste buds declines (Cowart, 1981). This decline in the taste bud population may account for the well-documented loss of taste sensitivity in the elderly (Schiffman, 1983).

Like the olfactory receptors, taste buds are constantly degenerating and being replaced by new ones (Beidler and Smallman, 1965). The life expectancy of an individual taste bud is only about 10 days. Hence throughout your lifetime there is a continuous, rapid turnover within the large population of taste buds. Unlike olfactory cells, however, taste buds are not true neurons, meaning that they do not have axons that project to the brain. In a moment, we'll see how taste information is carried to the brain; for now, though, let's take a closer look at an individual taste bud.

Figure 12.15 (p. 442) illustrates what an individual taste bud looks like under the microscope (buds are too small for the unaided eye to see). Each bud contains an average of fifty individual taste receptor cells, arranged within the bud like the cloves of a garlic. Sprouting out of the end of each taste receptor cell is a slender, threadlike structure called a *microvillus*. A clump of these threads juts into a tiny opening in the wall of the taste bud. It is contact between taste solutions and these microvilli that triggers an electrical potential in the receptor cell. Sensory transduction at these sites involves a cascade of complicated membrane events, some similar to those occurring in olfac-

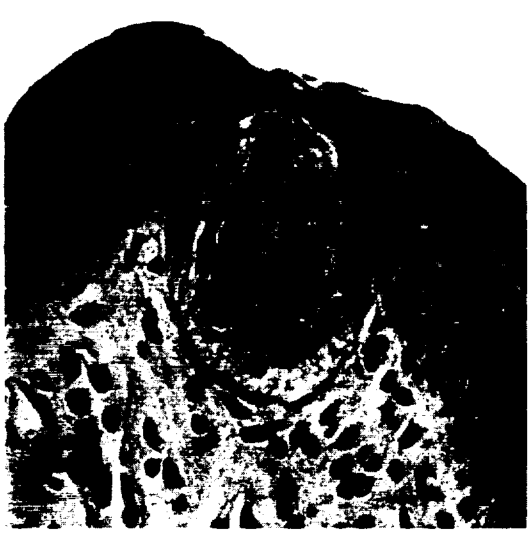


FIGURE 12.15 An individual taste bud. (Photograph courtesy of Dr. Inglis Miller.)

tory transduction (Roper, 1992). Those events differ for the various prototypical taste solutions, and it appears that a single receptor may possess the relevant membrane machinery for several of those solutions. In addition, neighboring taste cells appear to be electrically coupled via intermediary neurons, an arrangement that would promote lateral interactions among receptors. Although the function of these connections is unknown, comparable kinds of circuitry in the retina serve to sharpen differences in activity between neighboring neural elements (Ratliff, 1965). Mucous secretions from supporting cells in the taste buds carry the solution away from the vicinity of the taste bud. This cleaning action is analogous to that described in the case of the olfactory epithelium. But because the tongue's rinsing process is relatively slow, aftertastes can linger after you have swallowed or spit out what was in your mouth.

Back inside a papilla, the taste receptor cells make contact with nerve fibers innervating the tongue. Remember that taste receptors themselves do not have axons to send messages to the brain; like photoreceptors, they must pass their messages on to neurons that in turn carry neural impulses to higher centers. Taste buds in the tongue and mouth are innervated by no less than three distinct cranial nerves, and the same taste bud may be innervated by more than one nerve (Keverne, 1982). We'll not go into which nerves innervate which regions of the tongue and mouth; but keep in mind that taste information arrives at the brain over several different communication lines. Moreover, these communication lines are hooked to a population of receptor cells whose members are constantly dying and being replaced.

So far we've considered the tongue's receptors. Can we relate the responses of specific receptors to specific taste qualities? For decades, textbooks gave the mistaken impression that particular taste sensations were dependent on different regions on the tongue. It was customary to show a "tongue map" with sweet on the tip, salty on the front edges, sour along the edges toward the back of the tongue, and bitter on the midline of the back. But those maps apply only to the ability to identify very weak solutions: different regions of the tongue are differentially sensitive to weak concentrations of the four tastes (Collings, 1974). At higher concentrations any of the four taste sensations can be elicited from any place on the tongue. Moreover, several different distinct taste qualities can be evoked by applying different substances to a single papilla (McCutcheon and Saunders, 1972). So, taste qualities are intermingled over the tongue and cannot be uniquely identified with taste buds at particular locations.

Having looked at the taste receptors, let's now consider how messages generated by those receptors are represented in nerve fibers carrying information from the taste receptors to the brain.

The Taste Pathways. Individual taste fibers exhibit a low, sustained discharge even when no taste substances are on the tongue. When such a substance is introduced, a fiber's activity increases by an amount that depends both on the nature of the substance and on its concentration (Erickson, 1963; Ogawa, Yamashita, and Sato, 1974). With respect to the nature of the substance, most individual fibers respond to several different taste substances—for instance, one particular fiber might respond to both acids and salts.* If individual fibers are indeed not selective for a particular taste, an individual fiber cannot unambiguously specify a certain taste quality. How, then, could the brain know which taste substance was actually present? This question of uniqueness coding in taste is, you will recognize, reminiscent of the same issue in olfaction.

Years ago Carl Pfaffmann (1955) proposed that taste quality is represented in the *pattern* of activity across a population of taste fibers. This **cross-fiber theory** of taste quality has also been championed by Erickson (1968, 1984). Of course, for such a pattern theory to work, taste fibers must respond better to some substances than to others—if they responded to the same extent to *all* taste substances, the cross-fiber pattern of activity would be equivalent for all substances as well. In fact, although most neurons in the taste system are responsive to several taste stimuli, each responds best to a particular taste substance (Frank, 1973). These neurons, in other words, respond selectively to different taste substances. This selective response within a given fiber means that information about taste quality may be coded by the pattern of activity within an ensemble of fibers, as the cross-fiber theory requires (Di Lorenzo, 1989).

Besides differing in quality, the tastes of substances also vary in intensity, depending on the concentration of the substance. Let's consider, then, how taste intensity might be represented within the taste fibers. Most taste experts believe that intensity is signaled by the level of activity within individual fibers, since firing rate increases with the concentration of the stimulating solution. Moreover, if the same solution remains present on the tongue for several seconds, a fiber's activity quickly decreases from the level initially evoked to a somewhat lower one. You might suspect that this drop in neural activity explains why your sense of taste is dulled by repeated sampling of the same food or drink. However, this can't be the entire story, for adaptation of taste sensations may take anywhere from several seconds to a few minutes. Instead of adaptation, the decreased response of taste fibers probably serves a specific function—getting the tongue ready for new tastes. We'll explain why this is important.

Recall that taste judgments allow you to gauge the edibility of food. Taste judgments can be made with astonishing speed: you can identify the taste of what you're eating within the first second of tasting it (Kelling and Halpern, 1987). So after this initial identification, it's less important to continue tasting what you've been tasting than it is to get ready for new tastes. And getting ready for new tastes requires letting the activity in the nerve fibers settle back to a level where they can once again signal the presence of a new substance. Neural adaptation of the kind exhibited by nerve fibers thus makes detection of these changes in taste quality possible (Ludel, 1978). This property of adaptation is particularly important in such sensory modalities as taste, where one fiber may carry information about several different stimulus qualities.

Fibers carrying taste information from the tongue project via several nuclei to two different regions of the brain, with these two regions mediating different aspects of taste perception. One region, the insular cortex, is buried in a region between the temporal and parietal lobes; it is the taste analogue to the visual cortex and the auditory cortex. The conscious experience of tastes presumably arises from activity within this area of the brain, as evidenced by the losses in taste perception occasioned by damage to it (Pritchard, 1991) and by elicitation of taste sensations when it is electrically stimulated in awake humans undergoing brain surgery (Penfield and Faulk, 1955). Still, the percentage of neurons in the insular region responsive to taste stimulation is small; the majority of neurons are activated by chewing or by tactile stimulation of the inside of the mouth.

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*You should be aware that some people now believe the taste fibers to be more selective than previously thought. If correct, the activity in a single fiber could uniquely specify taste quality (Bartoshuk, 1980).

Nor is there evidence for any sort of topographic arrangement of taste-sensitive neurons by preferred substance (Smith-Swintosky, Plata-Salaman, and Scott, 1991).

The other taste region of the brain constitutes part of the limbic system, whose importance in emotional reactions we mentioned earlier during the discussion of smell. People who have *only* this subcortical pathway intact cannot identify taste substances verbally but still show characteristic facial reactions to sour and bitter solutions. These subcortical taste areas, then, appear to register at least some behaviorally relevant information about taste. It is speculated that this subcortical taste center mediates learned taste aversion, a phenomenon covered later in this chapter.

Finally, keep in mind that taste, besides chemically analyzing substances entering the mouth, must be responsive to the internal, nutritional state of an organism. Selective deprivation from, say, salt leads animals to seek out substances that contain an abundance of that ingredient. It is not surprising, perhaps, to learn that activity levels in gustatory neurons are modulated by appetite (Scott and Plata-Salaman, 1991). The neural pathways mediating this modulation remain unknown.

SENSITIVITY TO TASTE

Detection and Identification. The variation in taste sensitivity across the tongue (Collings, 1974) has already been mentioned. Now we shall consider some other factors that influence the ability to taste substances in weak concentrations. Actually, right at the limit of sensitivity, where the presence of a substance is barely detectable, it is very difficult to identify a taste (McBurney, 1978). Try the following experiment to confirm this point. Fill three identical glasses with equal amounts of water. (The water should be at room temperature.) Place a few grains of sugar in one and a few grains of salt in another and stir both thoroughly. Don't add anything to the water in the third glass. While you keep your eyes closed, have a friend hand you each glass, one at a time. Take a sip from each and see whether you can pick out the one containing plain water—to do this requires merely *detecting* that the other two contain "something." Next, try to pick the glass containing sugar and the one containing salt. This task requires *identifying* the tastes; if you were sufficiently frugal in the amounts you added to each glass, this task should be difficult, if not impossible. Realizing that you can succeed just by guessing, see how many times you are correct over a series of ten trials. For this demonstration to work, you may need to use less salt than sugar in producing the solutions. The reason is that a salt solution can be detected at one-third the concentration necessary for the detection of sugar, when the solutions are at room temperature.

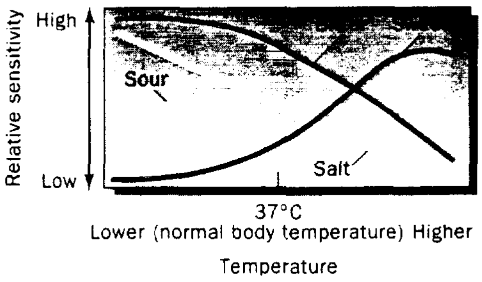
For most people, the highest sensitivity is to bitter, so if you were to repeat the taste detection test using quinine, you'd have to add just a minute quantity to the water. Some people, however, have difficulty tasting bitter substances. For example, the chemical phenylthiocarbamide (PTC) tastes quite bitter to about two-thirds of all Americans, whereas the remaining one-third are barely able to detect any taste at all from PTC. The same is true for other substances, including 6-*n*-propylthiouracil, known as PROP. In all these substances, atoms of nitrogen, carbon, and sulphur are linked in a particular structure. Studies of families show that sensitivity to the bitterness of PTC or PROP is genetically determined. Individuals to whom PTC doesn't taste bitter ("nontasters," we can call them) have two recessive genes for this trait; those who are sensitive to the bitter ("tasters") have one or two dominant genes for the trait. (Inexpensive paper strips impregnated with PTC are readily available from science supply firms; you might want to purchase some to test yourself and friends.)

Neither PTC nor PROP are commonly found in food, so the inability to taste them is inconsequential. However, Linda Bartoshuk and her colleagues have found that tasters and nontasters also show reliable differences in their judgments of the bitterness of common substances (Miller and Bartoshuk, 1991), including saccharin (an ingredient in many diet sodas) and caffeine (one of the bitter ingredients in coffee). In fact, the caffeine in a typical cup of coffee is not perceived as bitter by nontasters, although it is by tasters (Hall, Bartoshuk, Cain, and Stevens, 1975). This means, then, that a cup of black coffee will taste more bitter to some people than to others. Perhaps individuals who add lots of sugar and cream to their coffee are PTC tasters trying to tone down a degree of bitterness that nontasters never even experience. Again, we are reminded that not all individuals share the same perceptual experiences. Instead, each person lives in a perceptual world that is constrained by the workings of his or her individual sensory nervous system.

In the taste tests suggested above, we specified that the water should be at room temperature because taste sensitivity varies markedly with temperature. Moreover, different taste substances are not equally affected by temperature, as illustrated in Figure 12.16. Note that bitter substances become more difficult to detect at higher temperatures, whereas sensitivity to sweet increases with temperature. Think what this tells you about the effect of temperature on the taste of various foods and drinks. For instance, wine advertisements that urge you to serve their product well chilled may be trying to hide its sweet taste, a common fault with cheap, immature wines. The variations in sensitivity shown in Figure 12.16 also underscore an important rule for cooking: if you season food on the basis of taste, the final seasoning should be done only after the dish has reached serving temperature.

Is there anything to the adage that your ability to taste is better when you're hungry? From the results of one study (Moore, Linker, and Purcell, 1965), the answer appears to be no—if by "ability to taste" one means detecting very weak solutions. The study did find, though, that taste sensitivity was better in the afternoon than in the morning, which may explain why people *think* their sense of taste is keener when they're hungry. Another misconception about taste concerns the dulling effects of smoking on a person's sensitivity to taste. Here, too, the evidence is to the contrary—regular smokers are just as good as nonsmokers at correctly identifying taste solutions (McBurney and Moskat, 1975). Why, then, are former smokers always claiming that food tastes better after they have quit? Remember that flavor consists of several mouth-related sensations, taste being just one. Perhaps the reformed smoker's enhanced pleasure from food comes from one of these other sources. For example, smokers are less able to appreciate the pungency of odors (Cometto-Muniz and Cain, 1984), and pungency is a sensation produced by a number of spices used in cooking (Rozin, 1978).

FIGURE 12.16 The effect of temperature on taste.



As in the case of odor identification, it has been found that females are better at taste identification than males (Meiselman and Dzendolet, 1967). Though the reasons for female superiority are not yet understood, there seems no doubt that females are better equipped with respect to taste and smell to appreciate food.

Discriminating Taste Intensity. So far we've focused on various aspects of the ability to detect and identify different solutions. Now let's consider how good people are at judging differences in concentration of a single taste substance—another kind of judgment needed in the preparation of food. To get some idea of the difficulty of such judgments, you should try a modification of the taste experiment used to introduce this section. This time fill three large glasses with clear water and place one teaspoon of sugar in the first glass, one and one-quarter teaspoons of sugar in the second, and one and one-half teaspoons of sugar in the third. After stirring, have someone else rearrange the glasses so that you don't know which is which but the other person does. Now try to rank them in order of sugar concentration. This task measures your ability to judge differences in taste concentration.

Although the problem has not been thoroughly studied, available results indicate that people require about 15 to 25 percent difference to be able to judge that one solution is stronger than another (McBurney, 1978). On the basis of these numbers, you should be just barely able to pick out the weakest of the three sugar solutions but will probably be unable to discriminate between the remaining two. The fact that people can discriminate concentration changes in the neighborhood of 15 to 25 percent has implications for cooking: to improve a dish's taste by adding more of some ingredient, add just enough to increase the total amount by about 25 percent each time. This will ensure that you don't suddenly add too much.

Taste Adaptation and Modification. Outside the taste laboratory, people rarely ingest substances in very weak, near threshold concentrations, and moreover, hardly ever are those substances encountered in isolation. When you eat, your palate is typically bathed in a complex of taste substances. So it is of interest to study how the taste of one substance is influenced by the presence of other substances. Such influences can take two forms: (1) the taste of a substance may be weakened by prior exposure to that same substance—the familiar process of **adaptation;** and (2) the taste of a substance may be altered in quality by another substance—a process called **taste modification.**

Let's start with adaptation. You can demonstrate taste adaptation for yourself in the following way. Fill four glasses with equal amounts of water. Now take a freshly sliced lemon and carefully squeeze one drop of juice into one glass, two drops into the second, and the remaining juice into the third (this is the adaptation solution). Thoroughly stir all three solutions. Keep the fourth glass free of lemon—it should contain water only. In this demonstration you should be aware which glass is which (you may want to number them). Now take a sip of the first solution, the one containing a single drop of lemon juice. You should be able to detect a slightly sour taste (sour is the predominant taste of pure lemon juice), especially in comparison with the neutral taste of water only. Next sip the two-drop solution and compare it with water only. As it is twice as strong, this solution should taste more sour than the one-drop one, and certainly different from water only.

Now adapt your tongue to sour—take enough of the concentrated solution into your mouth to cover your tongue. Don't swallow it; instead, roll it around in your mouth for about 30 seconds, and then spit it out. Now once again sip the two dilute solutions, again comparing them with water only. You should find that the sour taste of both is considerably weaker—perhaps too weak to distinguish from the taste of water only. Wait a few minutes and then repeat this part of the test. You'll find that your sensitivity recovers rather quickly.

This demonstration merely confirms that taste—just like vision, hearing, and smell—shows adaptation. As pointed out in the previous section, this decline in taste sensitivity cannot be caused entirely by the reduced responsiveness of taste fibers; the time course of fiber adaptation is much too short to account for the adaptation of taste sensations. This latter form of adaptation must take place along one of the neural pathways discussed earlier, but exactly where is a mystery (see Gillan, 1984).

Suppose you had adapted to a strong solution of *salt* water and then were tested on the dilute solutions of lemon. Recall that cross-adaptation provides a way to test whether different substances stimulate the same neural elements (look back at page 435 to refresh your memory about the logic of the procedure). You would find that adaptation to salty has essentially no effect on your ability to taste sour. The same would be true if you were to adapt to sweet and then test your sensitivity to sour. In general, cross-adaptation works only when the adapting substance is similar in quality to the test substance (McBurney and Gent, 1979;

Bartoshuk, 1974). Thus you'd find your sensitivity to dilute solutions of lemon temporarily reduced if you were first to eat a sour pickle, since these two share the quality, "sour." The quality "bitter" seems to be an exception to this rule: sensitivity to bitter substances can be reduced by adaptation to a different taste, sour (McBurney, Smith, and Shick, 1972). In all, though, the results from cross-adaptation studies generally point to the existence of distinct taste qualities.

Modification, the second form of taste interaction, occurs when exposure to one substance subsequently alters the taste of another substance. Several of these so-called "taste illusions" have been described by Bartoshuk (1974; Bartoshuk et al., 1969). One that might be familiar to you involves fresh artichokes—after eating this delicacy, people find that other foods and drinks, including plain water, tend to have a sweet taste. (Actually, this is but one example of taste aftereffects involving water; Box 12.3 describes others that you can easily experience.) Another intriguing taste illusion is produced by the leaves of the *Gymnema sylvestre* plant, found in India and Africa. Eating the leaves or drinking tea made from those leaves temporarily abolishes the sweet taste of sugar. In fact, following exposure to *Gymnema sylvestre,* sugar crystals on the tongue are indistinguishable from grains of sand; salt, in contrast, retains its taste—proof that *Gymnema sylvestre* doesn't simply wipe out the entire sense of taste.

Another, equally exotic taste modifier comes from the *Synsepalum dulcificum* bush. Popularly called "miracle fruit," the berries from this bush impart an intensely sweet taste to even the sourest foods, such as lemons. Moreover, this sweetening aftereffect lasts about an hour after eating just a small amount of miracle fruit. This could provide a novel way to reduce your intake of sugar—you could fool your tongue into believing that food was sweet without adding sugar. Although it's not known exactly how miracle fruit works, it is known that it alters the responsiveness of taste fibers (Brouwer et al., 1983). Following exposure of the tongue to miracle fruit's active ingredient, fibers normally responsive to sweet substances but not to sour ones develop a temporary sensitivity to sour. In other words, these nerve fibers temporarily behave as though sour were sweet. After about an hour, these fibers return to their normal state, once again ignoring sour. Recall that an hour is also about how long the taste illusion persists. Incidentally, the sweet taste caused by miracle fruit can be abruptly abolished by tasting *Gymnema sylvestre,* the leaf that destroys the taste of sugar. Here's an interesting case where one illusion can be used to combat another.

There's one taste modifier that everyone is familiar with: toothpaste. You've probably had the annoying experience of finding that the taste of your morning fruit juice has been ruined because you had just brushed your teeth. This cross-adaptation occurs because toothpaste contains an ingredient that temporarily reduces the sweetness of sugar while making the acid in the juice taste extra sour (Bartoshuk, 1980).

Taste Mixtures. So far our discussion has focused on altering one taste by exposure to another. Next, let's consider what happens when two or more taste substances are mixed together (which occurs routinely whenever one cooks). Everyone knows that it's possible to tone down the taste of one substance by adding another—this is one reason why people add sugar to coffee, to mask its bitter taste. This reduction of one taste sensation by another is called **taste suppression,** and it seems to be a general property of taste mixtures (Bartoshuk, 1975; Gillan, 1982). But what do taste mixtures actually taste like? Is taste analogous to color vision, where two component hues (for instance red and green) can create an entirely new hue (yellow)? Or is taste more like hearing, where two tones played together still maintain their individuality?

The answer to this interesting and important question is not clear. McBurney (1978) maintains that new qualities are not produced by the mixture of taste components. According to this view, lemon juice with sugar added may taste both sour and sweet; but it won't taste salty or anything else new. This outcome is reminiscent of the situation

Box 12.3 *The Taste of Water: An Aftereffect*

You would probably agree that water doesn't seem to have any particular taste, aside from the faint mineral taste found in tap water. Yet by adapting your tongue to different substances, you can make water take on various distinct tastes. This phenomenon—"water taste"—is somewhat similar to the negative color afterimages described in Chapter 6. In the case of water, however, the taste aftereffect is not organized in an opponent fashion. This will become apparent when you perform the following experiment.

Obtain a bottle of distilled water for this experiment, for distilled water has no mineral taste whatsoever (you should confirm this for yourself). Pour a glass full of distilled water—this will be the test stimulus. Next, fill three other glasses with water (the tap variety will do) and add a teaspoon of salt to one, a teaspoon of lemon juice to the second, and a teaspoon of sugar to the third—these are the adaptation stimuli. Be sure each is well stirred. Begin by taking a sip of the distilled water, just to remind yourself what "no taste" tastes like.

Now take a mouthful of the salty solution and roll it around in your mouth for about 30 seconds. At the end of this adaptation period, spit out the salty water and take a sip of the distilled water. The previously tasteless liquid will now have a noticeable sour or bitter taste. Once this aftertaste has worn off, such that distilled water again has no taste, adapt to the sour (lemon) solution for 30 seconds. Now you will find that the same distilled water tastes faintly sweet. After this taste aftereffect has worn off, adapt to the sweet solution. This time distilled water will take on a sour taste.

Can you see the similarity between this taste aftereffect and the negative color afterimages you experienced when you looked at Color Plate 10? In the case of color, a white surface took on the hue that was dependent on the adaptation color. In the case of taste, the distilled water plays the same role as the white surface—both represent a neutral stimulus that becomes temporarily "shaded" by adaptation. There is, however, a real difference between colored afterimages and water taste aftereffects. With color, adaptation obeys an opponent rule: adapting to red makes white look green, whereas adapting to green makes white look red; blue and yellow are comparably related. With taste, adaptation is not reciprocal: adaptation to salty makes water taste sour, but adaptation to sour makes water taste sweet, not salty. Similar nonreciprocal aftereffects are found in the case of bitter (which you can most easily produce using unsweetened quinine water). Bitter makes distilled water taste sweet, but as you experienced, adapting to sweet makes distilled water taste sour, not bitter. All this implies that taste does not involve opponent process mechanisms such as those implicated in color vision (McBurney, Smith, and Shick, 1972). It also implies that the taste of water must be changing all the time during the course of a meal, since you are constantly adapting your tongue to different taste substances. Even the salt in your own saliva can act as a mild adaptation stimulus. Because you've adapted to your own saliva, when you sip distilled water it may appear to have a slightly sour taste.

in hearing, not color vision. Schiffman and Erickson (1980), however, report that sometimes a mixture will produce an unexpected taste, one not usually associated with the taste of any of the components. Such a result would be in line with the behavior of color vision, not hearing.

How does one unravel these seemingly contradictory observations? Part of the problem stems from the inherently subjective nature of these perceptual judgments. In effect, people must "introspect" on their taste sensations, decomposing the mixture into constituents. (To see how difficult this is, try analyzing the tastes evoked by each dish in your next meal.) Introspection, however, is not a simple task, and it is subject to all sorts of extraneous influences, such as the instructions given to people. As an alternative, people could be asked to "construct" a taste mixture that matches the taste(s) of a solution mixed by the experimenter. Such an experiment would be analogous to the metameric color-matching experiments described in Chapter 6. However, to perform such a taste-matching experiment requires having some idea of what components should be provided for the mixture. And this brings us back to the question raised at the outset—the question as to the existence of basic taste qualities. At present, this question represents the fundamental issue in taste research, and until it is resolved, we'll have to be content enjoying what we eat without knowing exactly what we are tasting.

TASTE PREFERENCES

Liking and disliking are not usually thought of as natural properties of sensory stimulation. There seems to be nothing inherently sad about the color blue, for example. Taste may be an exception, however. People can reliably rate various tastes along a dimension of "pleasant/unpleasant," and one person's ratings are very likely to agree with another's. Bitter is usually judged "unpleasant," whereas sweet, at least in low concentrations, is rated "pleasant." Such judgments are called **taste hedonics** ("hedonic" is derived from the Greek word meaning "pleasure"). Some taste experts believe that these hedonic qualities stem from biological factors governing food selection. Organisms ranging from insects to primates, humans included, crave sweet substances. This may be adaptive, since sugars are easily detected nutrients common in plants (Ramirez, 1990). Bitter is typically associated with toxic substances, which would explain why nearly all animals show an aversion to bitter substances. In fact, some plants and animals have capitalized on this universal aversion by evolving a bitter-tasting skin themselves, a characteristic that wards off potential predators (Gittleman and Harvey, 1980).

Earlier we mentioned that sensitivity to certain bitter substances, including PROP and PTC, varies with one's genetic makeup. This genetic heterogeneity produces a corresponding heterogeneity in preferences for particular foods. Generally, tasters are more finicky in their food preferences, expressing dislike for a greater number of foods (Fischer, Griffin, England, and Carn, 1961; Glanville and Kaplan, 1965). Anliker, Bartoshuk, Ferris, and Hooks (1991) summarize this body of work, noting that adults with normal bitter sensitivity tend to avoid certain strong-tasting foods, including sauerkraut, turnips, spinach, and strong cheese. Anliker and her colleagues also extended these observations to the preferences of tasters and nontasters among young children, aged 5 to 7 years. Although food preferences are governed by many factors, including social, moral, and cultural ones (Rozin, 1990), genetic differences in taste sensitivity have a clear influence as well.

With the mention of social and cultural influences on food preference, we should note that a natural aversion to bitter can be overcome, as evidenced by the almost universal enjoyment of such substances as beer, coffee, and quinine water. And just as natural aversions can be conquered, unnatural ones can be *acquired* (Garcia and Koelling, 1966; Garb and Stunkard, 1974). Extreme nausea following ingestion of some food is a sure bet to cause an animal to reject that food the next time it is available. This phenomenon, called **con-**

ditioned taste aversion, is an extremely potent method for discouraging predators from disturbing farm animals such as chickens and sheep. One meal of sheep meat laced with lithium chloride (a chemical that induces violent nausea) will dissuade a coyote from going near the source of that meat in the future. By the same token, one night of heavy indulgence in whiskey is enough to discourage a person from ordering whiskey sours in the near future.

Although sweet tastes are usually thought of as pleasant, extremely sweet food or drink can be unpleasant. Howard Moskowitz has studied how hedonic ratings vary with the concentration of various substances. He finds that for sweet substances, pleasantness increases with concentration up to a point, after which the substance becomes more and more unpleasant. This transition point Moskowitz (1978) calls the *bliss point*—the concentration yielding the highest hedonic rating. As you might expect, young children have a higher bliss point than do adults, which explains why advertisements for highly sweetened breakfast cereals are aimed primarily at the Saturday morning television audience. Contrary to expectation, however, some obese individuals actually have a lower bliss point than do people of normal weight (Grinker and Hirsch, 1972), although this finding does not hold for all sweet substances (Drewnowski, Grinker, and Hirsch, 1982).

Besides concentration, a food's color can also influence how much people like its taste. One clever study (Duncker, 1939) had people rate the taste of white chocolate and brown chocolate, and they did this while either blindfolded or not. With their eyes open, people judged the white chocolate as weak in taste, whereas the blindfolded group liked it just as much as the brown chocolate. The same pattern of results has been found for fruit-flavored beverages and cake (DuBose, Cardello, and Maller, 1980). The food industry, aware of the influence of color on taste perception, often adds color to products. Margarine, for instance, is naturally very pale but is dyed yellow to mimic the color of real butter. Likewise, orange food coloring is added to many orange juice products, and this strategy improves the flavor scores of these products (see Pangborn, 1960). To convince yourself of the potent effect color has on taste perception, just add green food coloring to milk and see how it tastes.

Related to the issue of taste preference is **sensory-specific satiety,** the reduction in the pleasurable sensory quality of a particular food as it is being eaten (Rolls, 1986). Suppose a moderately hungry person rates the pleasantness of the taste, smell, and texture of some food. Now, following this initial rating, imagine the individual gets a meal that includes the previously rated food, and immediately following the meal the person again rates the food's pleasantness. The postmeal ratings will be lower than the premeal ratings, even though the food itself has not had time to be digested. Evidently it is the sensory quality of the food itself, not its nutritional consequences, that produces the reduced hedonic response to the food. Moreover, this satiety effect is specific to the food items consumed during the meal—foods that were not eaten do not lower their pleasantness (Ross, Van Duijvenvoorde, and Rolls, 1984). The specificity of satiety means that relatively more food may be eaten during a meal that consists of many different foods served over several courses. Understanding sensory-specific satiety may shed light on eating disorders such as bulimia (Drewnoski, Bellisle, Aimez, and Remy, 1987), the condition where an individual engages in an eating binge followed by fasting or self-induced vomiting. Rodin, Bartoshuk, Peterson, and Schank (1990) have found that bulimic patients continued to rate sweet substances as pleasant even after ingesting a healthy dose of glucose dissolved in water; nonbulimics, in contrast, found the sweet substance less pleasant after ingestion of glucose. Rodin and her colleagues speculate that bulimics may engage in food binges because they fail to experience a reduction in its pleasantness during the course of eating.

The general topic of taste preferences is a fascinating one; there is much interesting material that cannot be presented here for lack of space. Those interested in that topic should consult Rozin's (1979) comprehensive chapter; in addition, there are several informative articles on cross-cultural studies of taste perception and preference (Johns and Keen, 1985; Bertino and Chan, 1986).

THE INTERACTION BETWEEN TASTE AND SMELL

Several times in this chapter we have stressed the role played by odor in what we usually think of as taste. Holding your nostrils closed while you eat dramatically demonstrates this role. One study (Mozel et al., 1969) found that the ability to identify food substances is severely hampered when odor perception is eliminated. In this study, twenty-one familiar substances were individually liquified in a blender and dropped onto a person's tongue from an eye-dropper; the person's task was to name the food. The results are summarized in Figure 12.17, which shows the percentages of people tested who could identify each of the twenty-one substances. The shaded bars give the results when the odor of the solution could be smelled; the unshaded bars give the results when odors were blocked from reaching the olfactory epithelium. Obviously, smell improved performance greatly. In fact, for several very familiar substances, including coffee, garlic, and chocolate, correct identification was impossible without smell.

There is something paradoxical about odor's contribution to taste: when odor is added to a substance that is being tasted, people do not report that its smell has increased in strength, they say instead that its *taste* has increased (Murphy, Cain, and Bartoshuk, 1977). Demonstrate this for yourself—begin eating with your nostrils held closed; then release them. Opening your nostrils means that odor will be added, but instead of experiencing this addition as smell, you will find that it is taste that has become stronger. In other words, taste and smell blend into a single experience, and this combined experience is typically referred to as "taste." One of the skills that "taste" experts develop is the knack of attending to the odors of the food or drink they are sampling. If you've ever watched a serious wine taster at work, you know what we mean. First of all, wine tasters prefer to evaluate wine when it is close to room temperature, so that the odorous vapors are more abundant. To further promote the release of vapors, a taster will swirl the liquid around in the glass and will then deeply inhale the vapors with the nose placed right at the mouth of the glass. This odor information alone is often sufficient to identify the particular wine being sampled. Be-

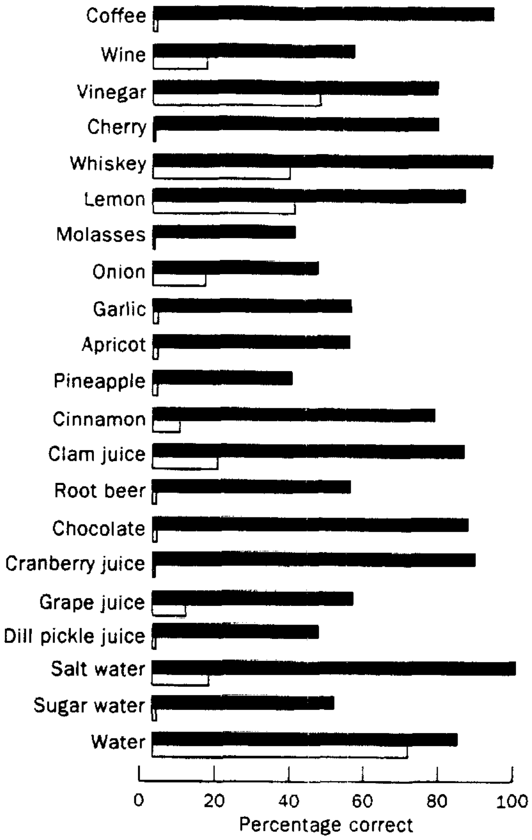


FIGURE 12.17 The percentages of subjects who could identify a substance dropped onto their tongues when they could smell the solution (shaded bars) and when they were prevented from smelling the solution (unshaded bars). (Adapted from Mozel et al., 1969.)

cause wines vary along several dimensions, wine discrimination has become a popular vehicle for studying perceptual learning, the enhancement in perception brought about by practice (see, for example, Owen and Machamer, 1979). In fact, entire books have been written on the sensory evaluation of wine (Kramer, 1989).

SUMMARY AND PREVIEW

This examination of the "minor senses," olfaction and gustation, brings us to the end of our survey of seeing, hearing, touch, taste, and smell. You should now have a more complete appreciation of how marvelously sensitive human beings are to the noisy, odorous, light-reflecting, tasty objects that make up their world. And you should likewise appreciate that this world is defined by the human sensory nervous system—other species with different nervous systems live in a world different from ours. The environment offers an abundance of opportunities for perception; whether one capitalizes on those opportunities depends on having receptors and brain mechanisms to register and process sensory information. Understanding perception requires studying *what* there is to be perceived (the environment as a source of stimulation) and *how* the process is implemented (the mechanisms of perception).

As stressed throughout these chapters, perception serves to guide thought and action. This means, therefore, that your perceptions of the world can be influenced by what you intend to do or what you are thinking. You've seen in this chapter and others that the evidence from your senses is often supplemented by evidence from other sources, including what you have learned about the world during previous encounters with it. In the final chapter, then, we shall consider the role of knowledge in perception and the role of perception in such complex activities as reading.

KEY TERMS

adaptation
anosmia
cilia
common chemical sense
conditioned taste aversion
cross-adaptation
cross-fiber theory
flavor
free nerve ending
mixture suppression
multidimensional scaling (MDS)
nasal cycle
odor adaptation
odor constancy
odor hallucinations
olfactory brain
olfactory bulb
olfactory epithelium
olfactory nerve
olfactory receptor cell
papillae
pheromones
sensory-specific satiety
specific anosmias
taste buds
taste hedonics
taste modification
taste suppression
tip of the nose