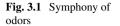
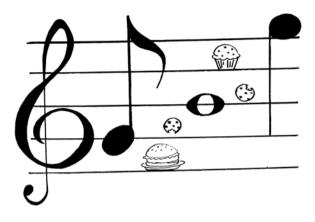
Chapter 3 Eat or Be Eaten

A Bittersweet Symphony of Food

A quiet symphony is heard in the background as I write in the corner of my favorite bakery. The music is a beautiful marriage of instruments; a blend of the soft sounds of oboes, violins, cellos, and the forcefulness of the brass instruments provides an inspiring atmosphere. If I concentrate on the music, a remarkable phenomenon occurs. Although the symphony as a whole continues, I can focus my hearing on the individual melodies of a single set of instruments within the song (Fig. 3.1). First, I concentrate on the soulful cry of the oboe, a sad melody that slowly climbs the scale. Next, I switch my focus on the French horns. This forceful staccato sound brings to mind a determined cavalry riding across a battlefield. The deep-voiced cellos sound like rolling thunder. Finally, I return to the symphony as a whole. Instead of listening to the individual voices of the instruments, I choose to integrate the individual notes of each instrument into the symphony and let the perfect harmony wash over me. Our auditory system processes stimuli in a very different way than our visual system.

The walls of the bakery are two toned: a dusty peach on top and a deeper red that starts right at the chair rail and continues on to the floor. My pumpkin muffin is a deep orange and my iced tea is a cool amber color. When I look around, I see only the single colors and, unlike the music, I cannot see the underlying individual colors that make the peach dusty or the pumpkin orange. Although I can see these many colors and their subtle shades, my eyes only have three different pigments (blue, green, and yellow). [Note that the three pigments do not correspond to the three primary colors blue, yellow, and red.] This is an interesting difference that is attributed to the overlap in the color sensitivity of the pigments and the relative distribution of pigments in our visual system. Pigments are those molecules located on the surface of the eye's photoreceptors that absorb the light and allow us to see color. As blue light enters my eye, the light is absorbed by a pigment. This pigment then changes its shape and excites the photoreceptors in my eye. These receptors pass this information on to other neurons and after a series of neuronal connections, my mind registers the color blue, all of which occur in milliseconds. I see far more colors than the basic three pigments in my eye, and that is because the different





colors essentially excite the pigments in proportion to their representation in the color. Almost like mixing paint at your local hardware store, a dab of red, three dabs of blue, and a half of yellow create a light purple color. For a simplistic example, imagine standing on the shore of a Caribbean island and looking out at the crystal clear sea. The ocean around these islands often appears blue-green in color. When one looks at the ocean, this light (half green and half blue) excites my greenabsorbing pigment and the blue-absorbing pigment equally. For our visual system, this method works quite well and allows us to perceive the subtle differences between shades of teal and sea foam. When green and blue light are mixed together, we perceive the scene as teal-colored light. Try as we might, we only see the color blue-green and we cannot perceive the original green and blue. The individual components are forever lost in the final color. This is a gestalt way of viewing colors. (Gestalt is a German word meaning shape or form and is encountered most often in the fields of neuropsychology or psychology. The concept is that the brain or mind conceives of a sensory stimulus as a whole rather than the all of the sub-elements. Think of the classic pointillist painting "A Sunday Afternoon on the Island of La Grande Jatte" by Georges Seurat. A gestalt approach to viewing the image would be to ignore the individual dots of paint and view the scene as a whole). Without years of training or highly sophisticated computer equipment, it is virtually impossible to tell which individual colors are mixed together to form the final product. Interestingly, our perception of odors and tastes is more similar to our auditory than our visual experiences.

As I entered the bakery, the aroma of the morning rolls and French roast coffee inundated my sense of smell. The bakery bombarded my nose with cinnamon, amaretto, sourdough, pumpkin, and French roast. I can sit back, taking in all the odors at once, like the sounds of a symphony, and form a "gestalt" of the bakery. Conversely, I can also analyze each of the odors and detect the individual scents. One of my favorite breakfast treats is a pumpkin muffin. As I bite into my muffin, a myriad of spices send me to paradise. Tasting beyond any individual flavors, I enjoy the totality of the muffin, the gestalt of pumpkin. With my second bite, I shift my focus instead to the individual tastes. First and foremost is the pumpkin itself.

An excellent mixture of moistness and sweetness swamps my chemical senses. Although we often speak of taste when we consume foods, the majority of the perceptions we experience while eating arrive through our sense of smell. When food is in our mouth, odor signals travel through the back of our mouth to arrive at our nose. To test this yourself try the "plug the nose" experiments discussed in Chap. 1. (Since we psychologically integrate both odor and taste sensations, I will use the term smell as indicating both of these terms for the rest of this chapter.) Hints of spices add to the pumpkin flavor. Cinnamon adds a touch of sharpness, and a gentle kick comes from ginger. Nutmeg adds an earthy tone, and the coup de grace comes from a fine dusting of powdered sugar.

Imagine that a young baker in training has the opportunity to make the morning muffins. She dutifully mixes in the sugar, flour, eggs, butter, pumpkin, and other ingredients. Right when the spices are due to be mixed into the recipe, the phone rings and she forgets to add the ginger. From a nutritional point of view, the ginger-less muffin is equivalent to the other muffins. However, if I were to taste this new muffin, a different symphony of odors would find its way to my nose. I would recognize this new muffin as quite similar to the earlier version, but something would be amiss. If properly trained, I might be able to recognize that ginger was missing. Now, if my nose operated the same way as the visual system outlined above (as a gestalt only system), I would perceive the pumpkin muffin as something entirely new and different. One bite of my gingerless pumpkin muffin would send me back to the counter asking for a refund because the muffin in my hand is clearly not a pumpkin muffin. A gestalt-only view of the odorous world (as in our visual world) would tell me that this is not a pumpkin muffin—close yes, but not what I ordered.

In an evolutionary sense, why should it matter whether we can perceive pumpkin muffins as the individual components of pumpkin, nutmeg, ginger, and powdered sugar as opposed to the taste of the muffin as a whole? As human beings, we eat for both pleasure and purpose. However, for all other organisms the act of consumption serves the purpose of acquiring both needed nutrients and building blocks of life and the chemical energy needed to run the machinery necessary for life. With these two evolutionary purposes in mind, we can look at the role of smelling and tasting in a new light. Along with serving as the window to the wonder of well-cooked meals for humans, perhaps more importantly, smell provides other organisms with vital information about the nutritional quality of a meal. Our bodies utilize the sugar as a source of energy that is needed to run the daily functions of our body. My pumpkin muffin is an excellent source of sugar, probably more than my body needs. My gustatory system allows me to perceive the amount of sugar in the muffin independent from the kick of ginger or earthiness of nutmeg.

A more natural example originates from the ability to detect potentially harmful compounds, such as poisons. Poisons usually have a bitter taste. For these chemicals, our life and death rests in our ability to detect the presence of the poison independent of the other flavors in the food. How effective would our smell and taste system be if a small bit of poison could be masked with other chemicals found in food? This helps explain why the ability to perceive smells as both individual components and as a whole is a better system overall. Why and how did this system come to be?

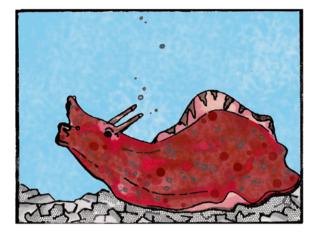
These questions cannot be fully understood until we see how organisms use their sense of smell and taste to effectively find food or avoid predation in nature. This chapter is about how organisms have evolved chemical signals that are used in one of most basic aspects of life: eating. How do organisms locate and identify food? How do they stop from becoming a meal for some other animal? As we shall soon see, organisms have very complex methods in which chemical signals are used to communicate to each other about food or even about potential predators to protect themselves from being eaten.

3.1 The Paradox of Being Delicious and Avoiding Predation

If there is a predator, such as a fox, hawk, or even an insect, there must be a prey, be it rabbit, mouse, or oak tree. If you are the predator, this interaction can be a very positive thing, but if you are the prey, this event is another story. Within this dichotomy is the understanding of the basis for all predator-prey interactions. Predators are constantly under selective pressure to have more efficient ways of detecting, locating, and catching prey. Sharper eyes, better ears, and faster legs are just some of the ways in which predators improve. Along this same vein, prey are also constantly adapting to avoid getting caught-better camouflage, faster muscles, or more potent defenses. This has been called an "evolutionary arms race," harkening back to the Cold War era when the United States and USSR were in a race to produce the most military arms. As one side, say the predator gets faster, the prey must also pick speed or risk extinction. As the prey develops better camouflage, the predators develop sharper eyes to detect their hidden prey. Upon closer inspection of this arms race, the fittest prey, the younger and stronger, typically always have a slight advantage over the predators. As the old saying goes, "The fox is only running after its lunch, whereas the rabbit is running for its life." Meaning, that if the fox makes a mistake, the fox only goes hungry until the next rabbit appears. However, if the rabbit makes a mistake, the rabbit has made a fatal error. Some of the more obvious developments in the arms race, faster legs or sharper talons, are some of the least interesting aspects of this story. A far more interesting story lies in the chemical arms race. One of the more fascinating examples of a chemical adaptation to avoid predation occurs deep on the ocean floor.

Mollusks are a group of organisms that include snails, oysters, clams, and mussels. Each member of this group of organisms has an organ called the mantle. The mantle produces the hard calcium shell that we envision when we think of the many mollusks that find their way onto our dinner plates. The shell is an excellent example of an antipredator adaptation and confers upon clams and oysters adequate protection against the many different predators in the ocean. Although all organisms within the group called mollusks have a mantel, not all of them have a shell as protection against the harsh undersea world. Some, like the squid, have internalized their shell, while others, like the sea slugs and some of the cuttlefish, squid and octopi, have abandoned the shell altogether.

Fig. 3.2 Sea hare



Without a hard shell, a mollusk must develop other methods of protection from would-be predators. Cuttlefish use a complex system of color changing organs, called chromatophores, to camouflage themselves. Octopi have the ability to both crawl along the ocean floor or, if need be, to quickly propel themselves by creating a powerful water jet. We are all probably aware of another antipredator adaptation of the octopus: its famous ink. If harassed by a predator, the octopus releases ink into the face of the attacker in order to confuse and blind them. Under this cloak of darkness, the octopus jets away to freedom. This system is a wonderful example of an evolutionary adaptation to solve a specific problem. The ink and jet system works well for the octopus. Yet for one of its cousins, the sea hare, the jet system has a single design flaw. For this system to work, the animal must have the ability to quickly swim away during the confusion created by the ink. The poor sea hare does not have this ability. They are named not for their rabbit-like movement patterns but for their diet, which consists of seaweeds and sea lettuce, and to two sensory structures that stick up off of their head-like rabbit ears (Fig. 3.2). What if you are a sea hare, a relatively slow-moving animal confined to the two-dimensional world of the ocean floor? If you are one of these nice, soft, and delicious mollusks, why would you rid yourself of a hard shell? How do you avoid becoming a predator's lunch? In spite of the sea hare's shell-less body, there appears to be no predator that makes its living eating this sea hare. A number of benthic crustaceans, namely lobsters and crabs, have been known to enjoy a sea hare or two from time to time, and sea anemones will consume sea hare when they get the chance. However, the sea hare (Aplysia sp.) is not a main staple in the diet of any animal species. The answer lies in chemicals.

One species of the Californian sea hare, *Aplysia californica*, has further developed another ingenious anti-predation ink method for dealing with its predators; a mechanism that was quite unexpected. Just as its cousin the octopus, the Californian sea hare can also produce ink—in fact the sea hare produces two different types of ink. One ink is produced and secreted from the purple gland, appropriately called the

purple ink, while the other secretion is produced from the opaline gland which produces a gooey, whitish substance (opaline ink). Researchers have known for years that the purple ink is released when the sea hare is harassed, similar to the octopus. Instead of producing a cloud of confusion to allow the sea hare to escape, the purple ink is smelled by the potential predators, such as a sea anemone, and produces a "bad taste" in their mouth, which seems enough to discourage further tastes. If a sea anemone happens to swallow the sea hare before the secretions are released, the anemone will promptly spit out the sea hare due to the bad taste.

The old saying "You are what you eat," illustrated in the catfish example about body odors and dietary choices in Chap. 1, is just as relevant here too. The sea hare does not produce most of the bad tasting chemicals itself; rather the chemical is acquired from the hare's preferred meal of red seaweed. Californian sea hares found in areas without red seaweed lack the reddish color common among sea hares and also lack the ability to produce purple ink. In addition, a sister species of the Californian sea hare, Aplysia viccaria, lacks the preference for red seaweed and lacks the distasteful purple ink, but produces small quantities of white ink (of unknown function) in its place. The production of anti-herbivory chemicals is fairly common in plants and algae. A number of organisms have developed a tolerance to these anti-herbivory chemicals-an acquired taste. Upon eating the plant or algae, these organisms sequester the compounds to use as their own anti-predation shields. If the collection and use of anti-predatory chemicals was the only mechanism of chemical signals used by the sea hare, this use of odors would hardly be unique and unexpected. But the Aplysia story has an interesting twist found in the opaline substance. The story begins with one of the sea hare's predators, the spiny lobster.

To fully appreciate the depth of deception and communication that occurs between Aplysia and the spiny lobster, a basic understanding of the olfactory abilities of the lobster is necessary. For that, we turn to the work of P.M. Johnson and Dr. Charles Derby at Georgia State University. Dr. Derby and his numerous colleagues have tried for years to understand how animals differentiate between smells. His laboratory has been instrumental in learning whether organisms smell as a gestalt or as a compilation of individual odors. The primary focus of their study has been the spiny lobster. When we think of creatures with amazing abilities of smell, the bloodhound and shark often pop into our minds. Stories abound about the tracking abilities of bloodhounds and most of us have heard of the shark's ability to detect a drop of blood in a million liters of seawater. These examples are unimpressive when compared to the lobster's capabilities. Instead of a single nose, lobsters have at least 13 pairs of appendages sensitive to aquatic odors. Dogs and sharks have millions of receptors in their nose, while lobsters have millions of receptors on a single appendage. Lobsters can learn and track odors just as well as bloodhounds, and there are several studies showing that lobsters can detect a drop of odor in a million times a million liters of seawater.

Let us return to our sea hare and spiny lobster story. The sea hare certainly could not out run the lobster, so using an ink cloud for confusion would not work. With so many highly sensitive chemoreceptors, one would think that the lobster would succumb to the sea hare's distasteful purple ink, but the sea hare does not use the purple ink. While studying the lobsters in Bermuda, P.M. Johnson and Charles Derby witnessed a novel approach to the use of antipredator chemicals. When attacked by a spiny lobster, the sea hare again releases two types of chemical secretions: the liquid purple ink and the gooey opaline substance. Once the lobster encounters the opaline, the spiny lobster begins a frenzied consumption of the opaline ink. Consuming the mass of opaline, the lobster acts as a child in a candy shop and devours the opaline. During this feeding frenzy, the sea hare slowly crawls away to freedom and to safer feeding grounds. The purple ink, although released in concert with the opaline ink, appears to have no effect on the spiny lobster. Why would the lobster settle for the meal of ink and let the tasty sea hare crawl away? The sea hare has developed the key chemical or chemicals to trigger the feeding reflex of the spiny lobster. Maybe the gooey nature of the opaline provides the lobster with the feeling of having just consumed a meal. The sea hare manipulates the lobster's own sense of smell to fool the lobster into believing that a savory meal is at hand. In this way, the sea hare survives to see another day.

3.2 Advertising the Home-Cooked Meal

Mornings in the bakery always seem to bring the most intense periods of writing for me, but just as all good things must end, my initial writing frenzy begins to wane after a couple of hours. Finishing my breakfast, I pack up my computer and walk to my office. To get there, I walk about 20 minutes from the middle of town to the eastern edge of campus. Bowling Green is a small town of about 30,000 residents and, by far, the largest economic mainstay in town is the university. Being a university town, the majority of downtown businesses are bars, restaurants, coffee shops, and bakeries. I estimate that nearly half of the businesses along my walking route sell food or drinks.

Passing the numerous restaurants, I notice that each of them has a unique way of advertising their latest food or drink offerings. Given the diversity of interests and people at the university, it is most likely that each of these establishments has its own clientele base. The first place that I pass is an old fashioned, greasy-spoon diner. Outside is a 1960s classic sign saying "Hamburgers, Chili and Fries" with each of the words highlighted by a circle of blue neon. Open late night, this is a favorite spot for post-party fare.

Next, I pass by one of the more recent additions to the center of town: a Mexican restaurant with an ad for "half-priced margaritas during happy hour." Right next to the Mexican restaurant is a small coffee shop with a sign describing their latest soup creations and different types of coffee roasts. Further down the road is a restaurant from a national chain claiming "The best buffalo wings in town." All of these restaurants are using carefully chosen words to evoke vivid mental images of delicious food, exquisite drinks, and rich desserts in order to draw the potential customer to their particular establishment. Some of the more modern signs also include mouthwatering pictures of the treats that can be found beyond the doors that beckon.

Just like the restaurants in my hometown, nature has its own dining establishments. In a fashion similar to the restaurants' financial dependence upon drawing in many customers, the restaurateurs of the natural world (i.e., flowers) must also entice potential diners to sample their offerings. In the natural world, there are no billboards, neon signs, or flashy words (as we know them) in which to market a potential meal to hungry animals. These restaurants that I am referring to are the world's flowers, and the potential patrons are the host of organisms that visit flowers to obtain nectar and other valuable resources. Instead of using a written language or neon sign, they advertise their offerings just as effectively using the language of smell.

Flowers provide nutritious meals for nature's diners in a couple of ways. During spring and summer, they produce sweet nectar for the many insects, bats, birds, and small mammals that inhabit the flower's neighborhood. Nectar is pure energy in the natural world and is highly coveted. During the fall, those same flowers that provided the sweet nectar now offer nature's dessert, fruit, before the harsh winter sets in. There are no free lunches in our world or in the world of nature. Just as I had to pay for my morning muffin and tea, nature's patrons must also pay the flowers for providing nutritious meals. As the meal takes two different forms, nectar and fruit, so too does the payment.

During the springtime, flowers produce nectar not just to feed others but also as a way to aid in their own reproduction. Although they are sexually reproducing organisms, being stationary means flowers need help in getting the male and female reproductive parts together. This process is called pollination and occurs when the male gamete, the pollen, is delivered to the female reproductive organ, the ovary. To reach the ovary and accomplish the goals of sexual reproduction, the pollen hitches a ride on the legs of insects, the backs of mice, or feathers of birds as they visit the flowers to dine on the nectar. These animals, called pollinators, then travel from flower to flower depositing the male gametes near the flower's ovaries. As they visit multiple flowers, the pollinators involuntarily pick up and deposit male gametes on the various flowers along their route.

In the fall, those flowers that were successfully pollinated in spring produce fruits, such as apples, pears, and cherries. The fruits are really just external houses for the seeds of the plant. During the fall, the fruit ripens, falls from the plant, and, once the fleshy part decays, leaves behind a seed that will hopefully mature into another plant. Landing and growing right next to your mother is not necessarily a good place to be if you are a seedling plant. Your mother may shade you from sunlight and stunt your growth, the roots of the parent plant may inhibit the seedling's own root growth, as well as other potential problems that accompany growing next to a fully mature plant. The seed is now faced with the same problem as the immobile male gamete described above. How do the fruits and the enclosed seeds get dispersed far enough away from the parent plant? Here again, the plant uses the services of another suite of animals. In the case of small berries, birds will often consume the berry whole, which leaves the seed undigested and traveling with the bird. Once the seed passes through the digestive tract of the bird, the seed is excreted and deposited some distance away from the parent plant. Other fruits are consumed, moved, and deposited in similar fashion by small mammals, such as mice, voles, and bats. This results in their seeds being dispersed away from the parent plant. Nature's pollinators serve to help plants reproduce and the fruit consumers help by dispersing the seeds.

Probably because of our interest in fruit and flowers, this story of pollinators and dispersers is one of the best-studied and well-understood aspects of biology. For years, amateurs and professional biologists have watched bees, moths, and bats visit and revisit flowers and have marveled at the specialized characteristics that both the flowers and pollinators have adapted. Although floral odors are long known to play a role in the flower/pollinator relationship, only recently have the specific roles of smells and pollinator behavior been deciphered thanks to advances in chemical analysis techniques.

Even those of us who pay little attention to flowers recognize the tremendous diversity in flower shapes, sizes, smells, and blooms. Some flowers bloom in the spring while others wait until summer or even late fall. There is a vast range of sizes from the tiny little bluebell flowers, no bigger than the nail on your pinky finger, to the enormous Titan flower that was mentioned in Chap. 1. There are also distinct differences in fragrance. Some flowers have little noticeable smell, while others have powerful odors that can linger for days. All of these flowers have evolved with a single purpose: sexual reproduction for the plant. But why does such a vast diversity exist to serve a simple single purpose?

The answer lies in the specific relationship between flowers and their pollinators and the need for very specific communication. Just as one would not expect to walk into the United Nations General Assembly and be able to communicate to everyone in a single language, the various animals that act as pollinators also require a range of languages that each of them can understand. Thus, we find that some flowers speak a general odor language and target as many different pollinators as possible while others speak a very specific odor language that is aimed at a single species of pollinators. The wealth of information about this story is large, and a full explanation is beyond the scope of this book. (I suggest that those interested in a deeper explanation look at some of the references at the end of the book.) However, I can select a couple of the more interesting stories to demonstrate that flowers do have a language of smell and that they are capable of multilingual communication to different animals. The flowers, like the restaurants of my home town, are targeting their advertising to a very select clientele.

Pollinators come in many different forms, many of which are insects. You are probably familiar with the honeybees and bumblebees that frequent the gardens around our homes. In addition to these insects, beetles, ants, moths, butterflies, flies, and wasps are among the more common insect pollinators. Of course, some of these groups of insects, particularly the bees, are more important to the flowers than other groups. Among the noninsect pollinators, there are bats, lizards, hummingbirds, and even some small terrestrial mammals like mice. With such a diverse group of pollinators, what kind of scents have the flowers evolved to communicate that a meal is at hand?

One method is for the flower to develop a large array of smells where each smell targets a specific group of pollinators, signaling that the flower is ready and open for business. A single flower could produce the entire array of fragrances and broadcast

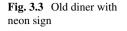
those fragrances to any pollinator within smelling distance. Each different fragrance would be analogous to an electronic "open for nectar" sign that flashes between English for the bees, Spanish for the moths, French for the beetles, German for the butterflies, Japanese for the bats, and a multitude of other languages. We know quite a bit about these molecules that signal "open." One of the leaders in this research area is Dr. Rob Raguso at Cornell University. Well aware of the abundant work on bees and flowers, Dr. Raguso looked elsewhere for a suitable model to apply his unique combination of chemistry and behavior. He found that model in moths. Unlike bees, which fly almost exclusively during the day, moths fly at night as well. What makes working with moths particularly interesting is the absence of the beautiful floral colors during the nighttime flights of moths. Without the ability to see colorful flowers at night, moths and other nighttime pollinators must rely on the presence of chemical cues to guide their search to ready and waiting flowers.

Many of the flowers that are pollinated by night moths generate a compound called linalool. Linalool is not a very complex or complicated molecule and is the signature smell associated with white, night-blooming flowers that are almost exclusively pollinated by moths. Included in this group are long-spurred orchids, wild gingers, moon flowers, evening primroses, jasmine, and a few others. Linalool is the "neon light" that serves to call the moths to the nectar. The powerful fragrance is lifted by night winds and is dispersed to the moths. Upon smelling the fragrance, the moths begin a characteristic upwind search pattern that eventually helps them locate the flower. Dr. Raguso has focused his studies on the hawk moth. This is a rather large-bodied moth and has been described as the "apache helicopters" of the moth world. Being a large moth means that there is a constant need to refuel and, as a consequence, the moth makes multiple flower stops throughout the night. Without the linalool odor, the flowers are ignored by the moths. Thus, this "open for business" sign is essential to ensure these flowers are visited and pollinated by moths.

Surprisingly, linalool appears to be a very common smell among flowers. This common chemical appears in a number of daytime blooming flowers that are pollinated by bees, butterflies, beetles, and hummingbirds. There are also bat pollinated flowers that produce linalool. Although common among floral fragrances, linalool appears to play a minor role in bee pollination and no role at all in bat pollination. Instead of using a multilingual sign communicating to the whole host of pollinators, these night blooming flowers are attuned to the "language" of the hawk moths.

This is similar to the old 1960s style American diner I passed on my way into my office (Fig. 3.3). The classic neon sign that claims "Hamburgers, Chili, and Fries" is bound to deter vegetarians and attract grease lovers. Certainly, the more refined palates in town may have more money to spend, but these advertising words are not aimed at them. Hamburgers and fries are targeted at a specific group of consumers: hungry students. This restaurant cannot supply everything for everyone, so they have tailored their wording and advertising to a specific group. This is similar to the case of the night-blooming flowers, who likewise have tailored their advertising (the flower's fragrance) to their most likely patrons, the nighttime pollinators.

Taking a different approach to communication with pollinators is the group of flowers known as Angelica. These herbs are often prized for their stems and roots.





The stems are used for making wonderful candies, and even the leaves impart odors to foods if used in the right way. The roots are used in medical treatments. Turning back to pollination and fragrances, Angelica prefers not to rely on a single group of pollinators. Instead of focusing on moths and developing a unique odor aimed at moths, these flowers have a complex group of chemicals that form a tantalizing bouquet for a number of different insects—a blend that reminds humans of something ranging from musk to a sweet odor. These flowers are the "all you can eat buffets" of the plant world. One of the appealing aspects of buffets is that there is a style of food for every palette: all different types of meats, vegetables, fruits, and desserts to satisfy even the finicky eaters. Angelica has a little bit of smell for every pollinator out there.

3.3 The Smell of Fear

Nearing the end of my walk to the office, I approach one of the single most defining features of Bowling Green. A north–south running railroad splits the town almost in half: both symbolically and culturally dividing the town into the eastern University section with its dormitories and student apartment buildings and the western residential and business section with Main Street and more permanent housing.

Typical of many American railroad crossings, there are numerous warning signals; the most prominent of which is the flashing red lights that signal an approaching train. This is quickly followed by a loud bell and the black and white crossing bars that prohibit cars from crossing the tracks. All of these signals are designed and placed here for the sole purpose of providing adequate warning to those that approach this crossing. Without really thinking about me personally, the people (or company) that placed these signs are essentially shouting directly to me "Watch out for the train" or "Be wary of trouble." Although the warning signals are not directed at any specific person, they are just as effective nonetheless. Nature has its own vibrant warning signals, just as common and necessary as they are in our world. One of the most dangerous situations that virtually all animals face at some point in their life is predation. The outcome of this situation is simple and intense. Avoid predation and live to see another day; fail to avoid it, and you and your genes are forever lost.

Some animals have developed fairly sophisticated means of communicating to each other the presence of a potentially lethal predator, largely by using auditory signals. For example, some species of primates have different warning calls depending on whether the threat is terrestrial (as in a cheetah), arboreal (as in a python), or aerial (as in a large raptor). Each of these calls has separate pieces of information (look up or look down) and results in predator-specific behavior (climb up or crouch down). Crayfish have also developed a predatory warning system, but instead of using vocal calls, they use chemical signals. In the scientific literature, these signals have been called alarm signals, which in the crayfish world take two different forms. Before we get into these signals, a little background on crayfish biology is necessary. Crayfish, and most crustaceans in general, have the remarkable ability to regrow body parts, legs, claws, and other appendages. The ability to drop a claw has evolved into an effective anti-predatory behavior. When attacked by a predator, a crayfish will voluntarily drop one of its claws. The predator will smell the claw and begin to consume the claw while the crayfish scuttles away.

This process, called excising, is a fairly expensive behavior in terms of the physiological costs. Claws are not cheap and the crayfish may take up to a year or 2 to regrow a new one. Given this extended time without a weapon, excising a claw is really a last ditch effort to escape predation. When a claw is excised, internal body fluids are released into the environment, and if the claw is eaten, more tissue and chemical signals are released. Since crayfish do not drop claws unless the situation calls for an ultimate sacrifice, the presence of these body fluids, tissues, and chemical signals could potentially provide valuable information to other crayfish in the area. Basically, if a crayfish were to smell these body fluids, the chemical cues in those alarm signals would almost certainly inform other crayfish that at the very least a claw has been excised somewhere but, more drastically, maybe a whole crayfish is being eaten by a predator. Here we have a very specific signal that is being released at a very specific time just as the railroad lights, and sounds only occur during the approach of a train.

Dr. Brian Hazlett at the University of Michigan has worked on this crayfish alarm system for years. He has shown that crayfish have developed the excised claw, not only as an effective anti-predatory behavior but also as an early warning system for a potential predation event. Other crayfish, in the presence of this alarm signal, will respond with the appropriate anti-predatory behaviors. If they are near a shelter, they will quickly run and hide in the safety of their home. If out and away from the shelter, the crayfish will freeze presumably hoping to go unnoticed by a passing predator. This is a very effective system of communicating immediate danger but the production of the signals is very costly, especially from the point of view of the animal that is losing the claw. If this alarm system were to be considered a form of language, then losing a claw in order to send a message limits your vocabulary to two sentences: the right claw and the left claw. At first glance, this system appears to be rather limited in the flexibility and long-term use. There is more to this story of alarm signals and crayfish.

Crustaceans, including crayfish, have another unique feature in addition to the ability to regrow limbs. They have a bladder in which they store "urine." (I have used quotes around the word urine to differentiate between what we think of as urine [waster products, ammonia, etc.] and that liquid substance that is stored in the crustacean's bladder. More appropriately, this chemical mixture should be called bladder water or some other bland term.) While a common feature among terrestrial animals, most aquatic animals do not have a bladder, as they do not need a highly developed kidney/bladder system to store and excrete urine. Most have a fairly porous skin or gills which allow them to slowly release metabolic waste products across these porous areas, as opposed to terrestrial animals with their water tight skin which have evolved other means of ridding their bodies of waste products. Crayfish excrete some of their waste products across their gills, so why would they need a bladder? They also seem to have a number of glands situated around the bladder which may release specific chemical products into the urine.

Work on lobsters and crayfish has shown that they "urinate" only when they are in a social situation as in fighting another lobster or crayfish (see Chap. 6), or when they are scared. Through the use of a simple catheter system, collecting urine while the crayfish or lobster performs different types of behaviors is possible, and thus, context specific urine can lead to insight into how these crustaceans use these chemical signals in different situations. If you place a crayfish in a tank with a large mouth bass, and the two animals are physically separated from each other by a transparent and porous screen, the crayfish will release 20 times the "urine" in 10 minutes that they do when sitting quietly alone in the tank for 2 days.

Maybe this urine release serves another purpose for a crayfish under attack. There is an old myth that when animals are frightened, they will often either urinate or defecate before fleeing from danger. The idea is that this sudden release of bodily fluids serves two purposes: one is to lighten the fleeing animal so that they extradite themselves from the dangerous situation more quickly and the other is to leave behind a chemical signal to crayfish in the vicinity that something dangerous is near. Testing the second possibility (that the crayfish are actively signaling to fellow crayfish) is incredibly difficult, although evacuating the bladder before fleeing has been well documented in other animals. The most common example of relieving the body of weight before (literally) taking flight occurs with birds.

The "urine" collected during the bass attacks is appropriately called "stress urine," and some very interesting things occur if this "urine" is released into tanks with other crayfish. If different crayfish smell this stress urine, they immediately begin to move away from the odor source. The closer they are to the source, the faster they move in the opposite direction. They have a heightened sense of awareness and they often get their claws ready to defend themselves. The urine sends warning signals. "Run away, danger is here," just as surely as the red flashing lights at the railroad crossing warn of potential danger.

3.4 A Bitter Pill to Swallow

Down the street from my bakery is a new bar that has a Celtic theme. The inside has two beautifully designed bars in separate ends of the building. In the side of the building that is more of a restaurant, the bar is topped with a large piece of copper that has been purposefully etched with acid droppings to give the appearance a distinctive look. All around the area, the walls have horizontally placed stones that give an earthen feel to the room. At one end of the bar is an inviting fireplace where a good meal and an excellent lager can be enjoyed.

The other bar is quite different. This room is designed to be a classic sit and chat style bar. At one end of the room, there is a small stage for local acoustical groups to play to the small intimate crowds. The centerpiece of the bar is a rather large mirror that reflects the patrons moods back to them. The bar itself and the shelves surrounding the mirror are all made from a lightly stained wood. On one side of the mirror is a long list of Irish and Scottish whiskeys and single malts and on the other side a list of the beers on tap for this week. The owner does an excellent job of rotating the beers from week to week to provide a bit of variety for those daring enough to explore something other than traditional beers.

I look forward to a late afternoon hour pint or an evening sit for a couple of reasons. The Celtic atmosphere probably draws on my Scottish heritage and makes the ancestral blood in me feel at home. This is also a nice quiet bar where I can sit and chat with my graduate students without having to speak loudly over the usual din of a college town bar. Finally, I enjoy a good beer from time to time, and the diverse choices let me explore a different world of chemical signals every week. Since I enjoy brewing my own beer at home, exploring lagers and ales from professionals occasionally gives me an idea for new home creations.

The Reinheitsgebot (the Bavarian beer purity law) originally stated that beer could contain only three ingredients: water, barley, and hops. Yeast and the mechanics of fermentation were unknown when the law was put into place in 1487. The barley provides the sugars that allow yeast to produce the alcohol of the beer and the hops give the beer the characteristic bitter taste that tends to divide people into hopheads (those that love highly hopped beer which tend to be quite strongly bitter) and those that prefer smoother tasting brews. For those that are interested, beers can be quickly and effectively categorized on three different scales. The beer color can be measured on a European Brewery Convention (EBC) scale that varies from pale lagers and witbiers that are yellow in color (EBC=4) to the deep rich black color of stouts (EBC=79). The colors result from the roasting of the barley and other grains used to produce the malt. The second scale measures the alcoholic content of the beer and really measures the density of the beer. One of the scales used to measure the density and alcohol content of the beer is called the specific gravity. Since the alcohol in beer (ethanol) is less dense than water, beers with higher specific gravities have higher alcohol content. Finally, and most important for this book, is the measurement of the amount of bitterness imparted to the beer from the use of hops. The scale most commonly used is called the International Bittering Units (IBU) and can range from 0 to 100.

In Chap. 2, I discussed one of the problems with the scientific investigation of chemical signals in both animals and humans and that was the measurement of the

exact nature of the chemical stimulus. I used terms like earthy, fishy, or woody to describe the quality of odors, and this same problem arises when we think about quantifying bitterness units in beer. Measuring the color or alcoholic content of beer can be quite precise when using a spectrophotometer (an instrument to measure color) and a simple weight and scale to measure the density of the beer. Bitterness of a beer is dependent upon the type and amount of hops used as well as the amount of malt (fermentable sugars) used in the recipe. Even though the IBU scale runs from 0 to 100, not all IBU 40 beers evoke the same quality for the same person. Added to this lack of precision, different people are more or less sensitive to the bitter taste. Some people are referred to as "supertasters" and have a heightened sensitivity to the bitter sense. (More on the genetics of this interesting taste phenomenon below). Still, despite the wide variation in the perception of bitterness, there is a scale for beers that contain very smooth or low hopped beers near zero and India Pale Ales (a very highly hopped beer style) near 100. I am not a supertaster, but the highly hopped beers aren't an enjoyable experience for me. So, I am not a hophead and actually prefer smoother, high gravity beers.

From an evolutionary point of view, our and other mammal's ability to perceive bitter compounds is linked to the need to parse out food that would provide nutritious and good meals from those potential food items that contain harmful or poisonous compounds. The bitter taste stands as a sentry point for the ingestion of potentially dangerous and deadly compounds. Our history is rife with examples of illicit use of these chemicals to change the course of history. Perhaps the most famous was Socrates being sentenced to death by drinking hemlock. Hemlock contains the bitter alkaloid coniine that causes respiratory failure in both animals and humans. Some plants are so dangerous that whole generations of myths and legends have arisen from potential poisoning: Wolfsbane, Oleander, and Cerbera odollam which is aptly named the suicide tree. A 2004 study by a French team of forensic toxicologists found that more suicides are caused by the ingestion of this plant than any other method. A large number of these poisons are alkaloid in nature and unlike some of the other chemicals mentioned in Chap. 2, alkaloids have a large range of structural diversity making these compounds hard to classify like esters or alcohols. Despite the large diversity of compounds included in the alkaloid group, almost all of the compounds produce a bitter taste.

Plants produce these harmful and bitter compounds mostly as a protection against grazing herbivores. Termed secondary metabolites (and allelochemicals) because the alkaloids do not serve a primary role in the growth and reproduction of the plant, these compounds are critical in the plants' survival against the army of herbivores that would like to consume all of the plants' leaves. The alkaloid compounds that can be produced continuously and sequestered in the edible parts of the plant or some plants (like the oak trees in Chap. 1) can specifically upregulate their production when they are attacked by herbivores. The continuously produced chemicals are called a constitutive defense because the chemicals constitute a basic element in the edible material of the plant.

Other chemical defenses are termed "induced" because a specific act of herbivory sends the plant into action where the biochemical machinery switches on those pathways that produce the toxic defense. This is akin to a biochemical version of a

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siren horn used to call troops to battle, although here the troops are individual alkaloids called to the front line attack by a caterpillar. This active analogy is specifically chosen because plants are not necessarily a passive organism in this game of survival. Some plants are actually quite clever about their chemical defenses, if one can attach the word clever to plants (Fig. 3.4).

The common flower Geranium has over 400 species of flowers and is found among the temperate climates across the globe. A small and pretty little flower that has quite a dark side to its protection against herbivory. The Japanese beetle is an invasive and voracious herbivore that is relentlessly attacking gardens where the beetle has been introduced. The flowers of the Geranium produce an anacardic acid that is located within the petals of the flowers. Upon consumption of the petals, the Japanese beetle flips over to its back and becomes paralyzed. The legs and the antennae of the beetle will twitch slightly during the time that the beetle is on its back. This simple act of paralysis is enough to stop the beetle from consuming more of the plant and seems an adequate defense. The particularly dark side of this story comes after the paralysis. If left alone, the beetle will fully recover in 24 hours and go about its way consuming more plants. Thus, the paralyzing chemical doesn't actually kill the beetle outright. What does happen during the paralysis stage is that predators of the beetle are attracted to the easy prey. Additionally, the twitching appendages serve as an attraction to birds such as starlings. The Geranium uses the beetles' own predators against them by providing the predators with an easy to consume meal of paralyzed beetle. The chemical used to paralyze the beetle does nothing to the starling or other predators.

3.5 It's an Acquired Taste

Summer field work at a biological station is a real treat for me. One of the most pleasurable aspects at my main field station is the communal meals. Cafeteria style meals eaten at a leisurely pace lead to intellectually stimulating conversations over

the day's field course, experimental frustrations, future research, or even less scientific topics. One of the frequent topics of conversations that I have had over the last 18 years of field work is the meal at hand. Appreciation of the day's dessert (say a raspberry cheesecake brownie) or critique of the selection of spices for the main dish (beef or tofu stroganoff) leads us down paths to personal preferences. Occasionally, a simple yet challenging question is thrown out for discussion. Since we are eating, a question could take the form of "What would be your choice if you had one last meal?" Being scientists, we aren't just satisfied with an answer "Steak," "Fried chicken," "Raspberry cheesecake brownie," we demand in a gentle and intellectual way, an explanation of why that meal would be chosen.

We recently went down this path while sitting at a table with some friends, graduate students, and colleagues. My answer changes slightly day to day or year to year because I truly enjoy the sensory experience of eating. (My enjoyment of good food probably results in the plodding runs described in Chap. 1.) A good meal is a combination of a multitude of senses. Certainly, the sight of food plays a role in the total experience. We have been culturally raised to expect certain appearances of our food, and if the image presented before us doesn't match our expectations, then this dampens our appreciation of the taste and smell of the food. For example, while making lunches in preparation of heading out for a full day of field work, one of my students walked over to my table with two slices of bread covered in what appeared to be a mound of bright purple birthday cake frosting. After inquiring about her sandwich, I was informed that the mound was beet hummus and not birthday cake frosting. Unfortunately, my mind was so focused on the frosting appearance that I could not get myself to attempt a sample of the hummus. On top of the visual appearance, texture of food is important as indicated by a continual debate between the qualities of lumpy mashed potato versus smooth mashed potatoes. I know of several people, including my wife, that say that texture of the food is almost more important that the smell and taste. Their selection of the last meal may be completely based on their sense of touch.

Of course, the main sensory component for most meals, and especially if this was our last meal, is our sense of smell and taste. (Forgive me if I do not include the trigeminal sense which is most important for Buffalo wings, jalapenos, and carbonate beverages). In answering the question about the last meal, I would start to think about what odors I would want to inhale to maximize my enjoyment and what combination of sweet, bitter, salt, sour, and umami I would want to envelop my taste buds. Personally, I love cheese, so any meal that involved some level of cheese or cheese mixture would have to be the choice. So, after a long pause, I settle on lobster macaroni and cheese. For me the cheese would be a combination of a good smoky Gouda, a touch of goat cheese, followed by a very sharp cheddar. Mixed with elbow macaroni and the meat from a lobster claw broiled with butter and a hint of cayenne pepper. The combination of smoky odors, the sweet meat of the lobster contrasted with the bite of the cheddar and cayenne would be such a delight that I would be ready to move on from this world.

If any of the descriptions above seemed attractive as you read them, you might have found yourself salivating slightly as you imagined this meal or maybe your own meal. I was almost like Pavlov's dog thinking and writing about my last ideal meal. The concept of an unconditioned response, Pavlov's dog salivating at the ringing of a bell signifying dinner, should indicate the hidden or unconscious importance of odors (and tastes) for the singular act of eating. For most of us, we take these smells as a common place occurrence and can't imagine what our meals would be like without these senses. Thankfully for science, there are ways that one can begin to understand what our meals would be like without these odors.

As I wrote in Chap. 1, two simple demonstrations about the influence of chemicals during eating can be performed at home with common household items or done in schools to help kids understand the difference between smell, taste, and even trigeminal. This is the jellybean example with a cherry, raspberry, and cinnamon jellybean. To quickly review, with the nose blocked, the cherry and apple jelly bean "taste" indistinguishable because the sugars in the two beans are identical. The only sense that is activated is the taste buds and they signal to the brain that sugar is present. The cinnamon jellybean is different from the cherry and apple because the cinnamon actually activates the trigeminal sense. Anosmic people (either those with their nose plugged, or colds, or permanently anosmic through disease or trauma) can determine the difference between spicy and non-spicy foods. In this demonstration, taste alerts our brain to the presence of sugar, and the trigeminal sense sends information on the level of spiciness. The nose is not needed to discriminate cinnamon from apple or cherry jelly beans, without it, the apple and cherry are indistinguishable. If the nose is unplugged halfway through consuming the cherry jelly bean, the odors flood our receptors and the cherry is instantly recognizable. The second demonstration is quite similar, but somewhat more shocking in regard to how we enjoy our food. If a participant is blindfolded and their nose is blocked, they can be fed slices of apples, potatoes, and even onions, and the ability to distinguish these three distinct foods is almost eliminated. Given the powerful and pungent smell of sliced onions and the sweetness of apples, this demonstration is difficult to believe, but the nose (not the tongue) is the sense that allows us to enjoy a good tart apple or the sharp flavor of raw onion. This difference in taste and olfaction is why meals and food don't seem quite as delightful when we have colds that inhibit our ability to smell.

Instead of having a cold block their sense of smell, some people are permanently anosmic. Anosmia can happen through a number of possible mechanisms. Some people are born with a defective sense of smell and, thus, never will have known any of the aromas associated with foods. Other people lose their sense of smell by head traumas or through severe allergy issues. The olfactory receptors in the nose could vanish through cell death, or trauma to the brain may damage the olfactory nerve that leads to the inner workings of the brain. There are a host of diseases where one of the possible consequences is either a reduced or eliminated sense of smell. Despite all of the surveys that indicate that the sense of smell is the first sense that we would prefer to lose if we had a choice, for those that lose this sense, the world becomes a dull but dangerous place. Almost akin to the reverse of the famous black and white to color transition that Dorothy Gale makes when landing in Oz during the 1939 classic movie. Each meal becomes an adventure in the black and

white world of texture and temperature rather than the sensuous colors of taste and aromas. The dark and deep rich aroma of the morning coffee has no effect on your state of awareness. The morning bacon is loudly sizzling in the skillet, but the only thing that can be sensed is the sight and sound. A bite into a pumpkin muffin from the bakery would provide me no symphony of flavors; just a solo note of mush as I would dejectedly chew my breakfast.

The hidden power of chemicals turns our consumption of food from a necessary task into an endless choice of sensory adventures. Eating is, quite obviously, essential to our well-being. However, our choices of how to cook food and what to eat is decided more by our sense of smell than by logical (and healthy) choices on what our bodies need. A mere sniff of the plumes of food odors reveals to the chef whether more cayenne pepper is needed for the jambalaya. A taste of the soup is used to apprise the need for more oregano or garlic to enhance the stew. For the patron of the meal, a wave of the hand over the dish delivers the meal's concoction of flavors and starts the emotional reaction to the potential first bite. For the liquid refreshments, we talk about the bouquet of a fine wine or the nose of a single malt scotch as a measure of their quality. These odors are the first, and in some cases, the most powerful engagement we have with the liquor. I would hate to imagine attempting to taste a good single malt scotch without a sense of smell.

Although these examples above might seem somewhat trivial compared to navigating our modern world without our eyes or ears, the matter is not trivial for those that lose their sense of smell. Severe depression and a state of anxiety are often one of the consequences for anosmic individuals. Some medical studies estimate that up to 50 % of individuals suffering from anosmia also suffer from depression, and many of those individuals go through significant weight loss as a result of a lack of appeal in most foods.

At the other end of a theoretical spectrum from anosmia are the supertasters. Given the discussion above about the depressive nature of the loss of smell, super tasting might be thought of as a true joy, but this would not be so. Supertasters are like having taste buds on steroids. These individuals have enhanced experiences while tasting their food and drinks. The underlying mechanism is related to the presence of a single gene (the TAS2R38 gene) that is absent in regular tasters. Although all of the impacts of this gene are not quite known, the supertaster sensation is due to, in part, an increase in the number of fungiform papillae which contain taste buds. Estimates on the total number of human supertasters are around 25 %, and a simple test can be performed to determine a supertaster. Dr. Linda Bartoshuk has been at the forefront of this phenomenon in humans since the start of the 1990s. The compound PTC (Phenylthiocarbamide) or PROP (propylthiouracil) is placed onto a small piece of dissolvable paper and subsequently placed on the tongue of the testee. If this person is a supertaster, the reaction is immediate and obvious. These compounds will taste exceptionally bitter and will produce a reaction of disgust once the PTC square is placed on the tongue.

Although this group of supertasters is found by a bitter taste test, the enhanced sensory experience of the tongue has implications beyond just this one of the five tastes. Through Dr. Bartoshuk's lifelong work on the psychology and behavioral

consequences of taste, supertasters have been found to have different preferences for those foods that contain bitter compounds. One of the most hated vegetables in the world, the Brussel Sprout, may be hated because of the large contingent of supertasters that are disgusted by the bitterness of these green vegetables. Supertasters will also avoid other green vegetables, grapefruit juice, and soy beans. They may have a more intense burn from alcohol and the chemical compound most commonly found in spicy foods (capsaicin). On the end of the taste "spectrum," these same individuals have an enhanced sensation to sweets. Cakes, ice cream, and candy have an enhanced flavor to them and for many supertasters, these treats are too sweet. Supertasters are perpetually stuck in food equivalent of the Goldilocks' fable. Instead of the porridge being too hot or too cold, foods and drinks are often too bitter and too sweet. They are constantly on the hunt for baby bear's food that is just right.

3.6 And Finally, Monsieur, a Wafer Thin Mint

Throughout this chapter, I have attempted to explain a wide variety of examples that show how an animal's behavior is influenced and controlled by the odorous world around them. From crayfish detecting the fear of predation from other's urine to flowers tuning their chemical advertising to the specific wants and needs of their pollinating customers, animals and plants have evolved elaborate uses for chemical signals in their quest for food. In our own world, the smell of a marshmallow toasted just right over a roaring fire or the odor of grilled onions placed on top of a broiled streak triggers both overt behaviors (grabbing a graham cracker and chocolate) and hidden physiological responses (the enzymes in our digestive system). Given the wide range of food related odors that influence our lives, I can leave you one last tasty morsel of a chemical story or as Monty Python would say, "a wafer thin mint."

One of the most common and powerful odors that influences our physiology and mental state is that of mint. Derived from plants in the Lamiaceae family, mint essential oil and menthol are used as flavors and fragrances throughout the human household. Mint is found as flavoring for candy, but also can be used for medicinal purposes (treating stomachaches) and as natural insecticides. Peppermint has also been used in hospitals to reduce some of the nausea that occurs after coming out of anesthesia for a surgery. These uses are fairly well known and are not that surprising. Yet, the impact of mint (and its odors) upon both our psychology and physiology is a great example of the hidden power of the chemical senses.

Peppermint, either the flavor or the scent, has the ability to improve mental acuity when performing tedious tasks. Dr. Bryan Raudenbush and his students have performed an interesting series of studies demonstrating that different cognitive abilities are enhanced following exposure to peppermint odors. When challenged with computer tasks that required counting, puzzle solving, and memory skills, those participants that inhaled peppermint improved on their ability to focus and performed these tasks much more quickly. In similar studies, the odor of peppermint decreased the perceived workload or frustration when participants ran on treadmills. These studies show that food odors (even at very small concentrations) can control our moods and focus. Far beyond just the necessity of nutrition and health, the smells and tastes of foods are entryways for odors to influence everyday tasks and everyday moods.