Chapter 2
A World of Odors

Signals, Cues, and Information

The morning air has a slight bite to it, but despite this early morning chill, I decide to walk into my biology office. My young companion on this journey has a far more intimate knowledge about this world of odors than I do. I am just an interloper only vaguely aware of all of the smells around me. The traveler accompanying me on this particular trek is a 6-month-old Shiba Inu named Cedric. As any dog owner can tell you, smell is how dogs "see" the world. It is the sense that they use to greet each other, "know" where home territory is located, and when food is available. When I take Cedric to the dog park, the other dogs rush over to get a good sniff to see if they know him from a past encounter. As Cedric and I pass any standing object, be it tree, fire hydrant, or parked car, he wants to stop and take a good sample of the chemical milieu.

His behavior points to one of the unique properties of the chemical senses and their signals; odor molecules have a longevity beyond the mere presence of the organism that produced that signal. A common example of this phenomenon occurs when one enters an elevator after a person with a strong cologne or perfume has ridden the car. Those perfume molecules remain within that enclosed area for a considerably long time. Hotel rooms inhabited by smokers, even for a single night, have a distinct smell to them. Garlic lingers in the kitchen long after the last spaghetti noodle has been consumed.

For Cedric and myself, I can clearly define our two main chemical senses: smell and taste. To be simplistic, smell (olfaction) is done through our nose and taste (gustation) by our tongue. When Cedric sniffs a lamp post, he is using his olfactory abilities, whereas when he licks my hand, taste is being employed. These two processes are carried out by fundamentally different receptor types, they are sensitive to disparate classes of chemicals, serve very different behavioral roles for us, and have different active spaces. An active space is the area where a sense can receive information. In humans, our nose picks up distant sources of molecules: The pizza smell down the road, the smell of fresh cut grass across a lawn, the garlic of a spaghetti dinner. Whereas, our taste system has to be in direct contact with the stimulus: an ice tea with a hint of lemon or the sweetness of a crème brûlée. In many

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nonmammalian systems, this separation is quite murky. For the crayfish that I study (and other aquatic animals), the types of molecules that "olfactory" and "taste" sensory systems respond to are similar if not identical to each other. In addition, the types of neurons are also very similar in function and structure. Scientists often classify smell and taste in aquatic animals by their behavioral uses as both systems detect distant odor sources. (Finally, for ease of use, I will repeatedly use odor to indicate any type of molecule that activate the chemical senses.)

2.1 Stay for a While

The lingering of a signal (odor molecules) is conspicuously absent in visual and auditory signals. As I give the command "come" to Cedric, for he is lingering too long at an oak tree, the sound wave leaves my mouth and travels for a good distance. He hears the command and politely responds by ignoring me. The moment that I stop producing the sound "come," that signal is no longer present from the environment. (To be truthful, the sound is present as it moves away from me at roughly 1000 feet/second, but after a couple of seconds, that stimulus is gone from the environment). Although Cedric hears the command, he is intensely interested in the oak tree. The base of the oak tree has layer upon layer of the odor of previous dogs that have walked by and Cedric is reading this guest book with his nose. Each of those layers is a "name" that says "Hey, my name is Rover and this is my territory."

In Chap. 1, I described the red shouldered display of the blackbird as he is setting up his territory. With the full sun reflecting off of the red patches, his signal is quite conspicuous. As soon as the sun fades or the bird flies away, the signal vanishes. Given the tremendous speed of light, visual cues are generated and sent instantaneously. This characteristic is a tremendous advantageous when speed of transmission is a prime factor for evolutionary selection like when a hawk is bearing down on the blackbird. The problem with visual signals is that they disappear just as quickly as they appear. Any birder is keenly aware of this problem with visual signals as they attempt to catch a glimpse of their favorite woodpecker among the trees of a forest.

The ability of chemical signals to stay present in the environment even when the original source has moved on allows organisms to use these signals in ways that sight and sounds cannot be used. Scent marking, nest mate recognition, infant–mother connections, and odor memories are just a few unique examples found in chemical signals. Eventually, the odor molecules deposited by the previous dog will slowly diffuse away and the smell (Rover's name) will no longer be evident. That is unless Rover feels the need to lay down another signal at this particular tree. The long lasting characteristic of chemical signals is particularly evident for those odors we do not particularly like.

A previous four legged companion of mine, a playful black lab named Loki, had a particular habit of chasing and toying with neighborhood skunks. Unfortunately for me, Loki had a difficult time learning to avoid these animals. Time and time again, she would chase them down only to receive a dose of their "perfume." The dire consequences of her escapades would become quite evident as soon as we would let her in from our backyard. Immediately, our house would fill with the distinctive calling card of the skunk; the nasty little molecules (a class of compounds called thiols) would spread through our house. We would immediately dash into action, washing her down with special soap to remove the offending odor. Although the skunk was never in our house and had most likely departed our yard, its presence was certainly felt as the signature perfume permeated our house. Even weeks later, Loki would occasionally smell "skunky" as rain or humidity would release the skunk's second and more secretive weapon: a second class of chemicals, thioacetates, remain attached to Loki's fur until moisture converts them to the more pungent thiols. This reactivated calling card provides an evolutionary advantage of reminding the would-be predator of what happens when it attempts to attack a skunk.

2.2 Any Which Way the Wind Blows

One last tug on the harness and a little more forceful "come" alert Cedric that it is time to continue our walk. His ears pick up, tail curves over, and off we go down the sidewalk again. Although he does not stop his slow trot, Cedric is still connected to the world of odors around us. With a far less sensitive nose, I am admiring the colors of the flowers and trees on my short walk and listening intently for any song bird that may entertain me. In the meantime, Cedric is quickly sniffing to the left, to the right, up in the air, and along the sidewalk. We are all most likely familiar with this sniff as it is a characteristic of most if not all vertebrate animals. Whether we are sampling laundry to see if it is clean, checking the freshness of an unidentified food container in the refrigerator, smelling the intoxicating fragrance of a baby's head, or partaking of the wondrous odors of the fresh cup of morning coffee, we sniff in order to interact with our odorous world.

The behavior of sniffing is a requirement for the sense of smell and points to a second unique feature of the chemical senses. Chemicals need assistance to get from point A to point B, and that help involves movement of air or water. As Cedric and I continue our walk, we approach an intersection with a stop sign. The characteristic red of the sign needs no help from an outside agent to reach my eyes. Inherent to the color red, and to all light, are properties that move that signal through the world to my eye. For all practical purposes, the light leaves the sign and is instantaneously at the receptors in my retina. If the sign were to change colors, say blue for instance, the color would travel just as fast, but because of the shorter wavelength there is a greater potential for the light to be reflected off of small particles in the air. For visual signals, the color of the light not only conveys meaning (red equals stop/halt) it also impacts how the signal moves through the environment. The sky is blue because the shorter wavelength is scattered by particles in the atmosphere. In a similar fashion, sound has inherent properties that move that signal through the environment.

Fig. 2.1 Odor plume

This situation is very different for chemicals. We can perform a little thought experiment to demonstrate this difference. Let us say, I take a handful of those skunk's thiols, place them on a table, and remove any air movement from a room. Next I invite you into the room and ask if you can notice anything. You would not be able to smell the skunk odor at all even though those chemicals are present within the room. The moment I placed a small fan behind the chemicals, you would run from the room and probably not accept any more invitations from me. Whether those chemicals are the scent of a skunk, red roses, or cherry pies, you would be essentially blind to the odors without a little air movement to aid the delivery of those molecules to your nose. When Cedric sniffs, he performs the same trick as that small fan in the room. During the sniff, he draws those molecules from the environment and delivers them to his nasal passage in order to determine what he is smelling.

On a scale significantly larger than Cedric's nose or the room with the fan, the wind does the work of spreading, transporting, or dispersing odorants. The pleasant smells of fresh cut hay in the middle of August, a set of barbeque ribs on a grill, or the sweet fragrance of a blossoming lilac bush would be hidden from us without at least a gentle breeze blowing toward us. We call these wind delivered chemicals an odor plume (Fig. 2.1). The same phenomenon occurs within aquatic habitats. Water movement is necessary to deliver signals to their waiting recipients.

The interaction of odor molecules with the wind or water that moves them gives rise to the sensation we call olfaction. Unlike the red stop sign or my command "come," odors are almost always intermittent. The red from the stop sign is constant and as long as I produce a sound, the voice command is there. Imagine walking through an English Garden in full bloom. During your pleasant stroll among the vibrant colors, you would receive periodic whiffs of the various flowers even though the flowers are constantly emitting their calls to bees. If we could visualize the movement of odors through our imaginary garden, we would see a mixture of puffs shaped like little mini-clouds with fine tendrils of odor between those puffs. The scene would be similar to the white wisps of steam emanating from the chimney of a steam plant. In our garden, each flower, each stem, and blade of grass is a tiny

Fig. 2.2 English garden plumes

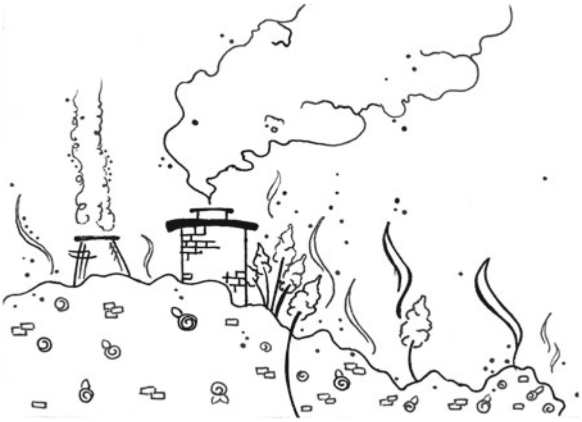

Fig. 2.3 Odor landscape

chimney churning out their unique blend of chemicals. As we walk along our path between the flowers, each of these odor plumes mix together to form the odor symphony that is the English Garden (Fig. 2.2). As bees, being quite smaller and faster than we are, fly through the garden; they are greeted with giant chimneys creating great puffs of odors.

We can scale this analogy to both larger and smaller sizes if need be. An entire farmer's field is a thousand chimneys of corn each producing their own odor plume. Next to the field could be a small wood lot and within the wood lot, every living thing (and some nonliving) is producing their own plumes. With each and every exhale, the squirrel high in the branches of the trees creates a signature plume. All of the leaves, as they respire, produce chemical upon chemical wafting through the woodlots wind. This image, writ large, is the world of odors and organisms great and small all have their unique set of odor plumes (Fig. 2.3).

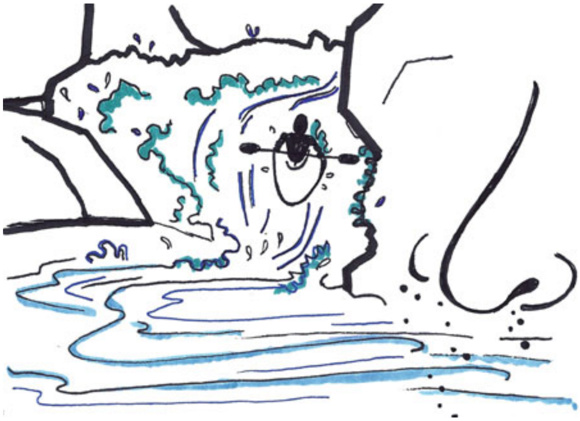

Fig. 2.4 Kayaker riding an odor plume

A third contrast can now be made between the chemical world and the visual and auditory worlds that we live in. That stop sign at the crossing is constantly on, as long as there is light shining on it. I do not have to 'locate' it because there is a direct path from the red light emanating from the sign to my eyes. My command to Cedric travels directly from my mouth to his ears and by comparing the difference in arrival time between his right and left ears, he looks directly at me knowing that I am the source of the sound. The odor world is directly impacted by the movement of air and water without which we would be odor blind.

On our human size and time scale, air and water move through their respective environments in what is called turbulent motion. Within turbulence, streams of water or air crisscross in a chaotic fashion. Think of the last bumpy flight you might have taken or imagine pictures of kayakers racing down the Colorado River (Fig. 2.4). Traveling through this turbulence, the plane bounces up, down, left, and right in a way that is impossible to predict. The kayakers (as representatives of odor molecules) have little control compared to the power of the river over where they go. They are thrashed about as the river delivers them down stream. The seemingly random motions of the fluid (both air and water can be treated as fluids) causes the puffs and tendrils of odors to be torn and shredded as they move from the source of the odor to our nose. What we perceive when we detect a turbulent odor plume is an interesting mixture of odors that vary wildly in intensity. In one moment, the odors appear to be quite intense and close, whereas in the next moment, we sniff empty air with no odor. Locating the source of these odors is complex and challenging task because of the intermittent and varying nature of the signal as it moves through the environment. Imagine trying to find a rabbit dyed pink among a warren of rabbits. For odors, this simple task would be akin to attempting to locate that same pink rabbit let lose in a Las Vegas night club while someone was flashing the lights on and off.

Cedric is fully at home in this chaotic world of swirling odors. He can navigate these plumes and locate their sources with tremendous precision honed through natural selection. We, on the other hand, are lost in the whirls and whirls of odor parcels moving somewhat randomly around our nose. As we sniff, these odors seem to randomly appear and vanish as we move through our environment. As I glance around and take in the visual landscape during our walk, I can easily reconstruct the visual image in my mind. Without too much difficultly, I could recall the spatial relationship of the previous stop sign, the side walk, and all of the houses we are passing. I can create a map of these different locations and even with my eyes closed, I could point, in a rough direction, to anything queried about. I can do this because the visual landscape is relatively static and what that means is the images within the landscape (the houses, stop signs, and sidewalks) have a set location that is constant through space and time. This is not necessarily true if the visual sources themselves are moving such as birds, cars, or clouds.

The odor landscape is dynamic regardless of whether the chemical sources are still or moving. Quick shifts in the wind (or water) cause the odor plumes to shift dramatically in both space and time. A sudden gust of wind and odors can disappear completely. Another shift and the plume work its way back to your nose. This dynamic landscape is a fundamental aspect of the world of odors. The sensory landscape of odors is a constant shift in mixtures and intensities that for the most part we are blithely unaware of. This landscape can be quite frustrating to us as we try to find the source of a sour smell inside of our house or some other offending odor.

Despite this unstable stimulus environment, many animals have evolved mechanisms that allow them to thrive by using chemical signals. In subsequent chapters, I will cover some of the more interesting ways in which a wide variety of organisms use chemical signals to locate their sources and ways in which this dynamic landscape influences our own behavior.

2.3 By Any Other Name Would Smell as Sweet

After entering the University campus, we turn left, head down a small slope in the sidewalk, and approach my office in the biology building. I get a sense that Cedric knows we are close to my office because he picks up his pace ever so slightly. A very stoic dog, I still perceive a subtle shift in his body posture which, to me, signals an increase in his excitement. This shift is probably caused by two things that await him when we enter the building. First, and probably far more important, is a box of dog treats. This is his first reward for making the trek into work with me and for not sampling the flowers too often on our walk. The second treat is the host of individuals that want to pet, hold, or say hello to him as we make our way to my office door. This is jokingly known as puppy therapy as Cedric is more than obliging in letting people hold him or pet him. Timid as well as stoic, Cedric is cautious even with people that have known him since the day we brought him home.

Because of his timid nature, everyone walks up to him with their hand in front of them to allow him to smell them in order to recognize them. Each of my students has a unique smell which would identify them as Sara, Thom, Maryam, or Ana. In nature, this signature mixture of chemicals would be a combination of chemicals derived from their diet and a set derived from their daily experiences. For example of these unique odors, a beef loving farmer would have a distinct odor from a pork eating botanist. Today, we tend to mask these odors with scented hand soap, shampoo, perfume, and cologne. Even if we forgo the daily cleansing and covering ritual, we would have a singular signature smell that would allow a blindfolded Cedric to determine your identity.

In this sniffing and greeting behavior, we can find the fourth distinction that chemical signals have when compared to visual or auditory stimuli. When we scientists consider sensory stimuli, we often categorize the stimuli based on important features. These features are considered important because they carry information that allows the receiver to make sense of what the signal is conveying. With visual signals, color is an important feature. The stop sign we passed on our walk is red. If we were to change that color to yellow or green, we would be conveying very different meanings. My command of "come" has a certain frequency (or suite of frequencies) that is characteristic of my voice and the command issued. Interestingly, both of these signal features (color for light and frequency for sound) reside along a linear scale, and their position on that scale influences, in part, how those signals move through the environment. By linear, I mean a systematic organization that moves in one dimension. Looking at a rainbow or the cover of the Pink Floyd album Dark Side of the Moon, one can name the colors in descending order of wavelength size by remembering the mnemonic device Roy G. Biv (red, orange, yellow, green, blue, indigo, violet). Sounds, too, have a linear relationship that influences their movement through the environment. Comparing the differences between the signals in these three sensory channels, light, sound, and chemical, helps to illuminate how humans use information from these senses in various ways.

We perceive rainbows because different colors of light have different wavelengths, and these wavelengths influence how these colors move through the environment. Blue color has a much shorter wavelength than red light. If we wanted to extend the spectrum of light more fully, ultraviolet light, often invisible to us, has even shorter wavelengths than blue light. At the other end of the spectrum, there is heat which has very long wavelengths that are detectable with special cameras and special sensory structures such as pit organs in snakes. Taken in totality, the electromagnetic spectrum stretches from ultrashort gamma rays to the exceedingly long wavelength radio waves. The morning sky and large bodies of water often appear blue because the short wavelength of this light gets scattered easily. What this means is as this light travels from the sun to our eyes, tiny particles in the atmosphere redirect the blue light to scatter it throughout the sky. At the other end of the spectrum sits red light. Red light, with its long wavelengths, does not get scattered as easily as blue light, but does get absorbed rather quickly. The point of this little detour into light and sound is to explain that these patterns of absorbance and scattering are perfectly predictable based on physical theories. Within the world of odors, there is no simple relationship between signal (the color of a red stop sign or the sound of a tenor aria) and its movement through the environment. Thus, any kind of organization of signals is quite messy.

This messiness is readily apparent when there is any attempt to classify the psychology of odors. Naming and classifying the world of odors is called determining odor qualities. The concept of odor quality is quite different than measuring the wavelength of red light (620–750 nm) or the frequency of my command to “come” (somewhere between 85 and 155 Hz for my baritone voice). Both of these measures are independent of any receiver psychology which includes the neural architecture that underlies the reception of sensory signals as well as the ability to discriminate and remember signals. Scientists have instruments that will measure these values and these measurements should be identical whether one is 15 or 80, French or German, or male or female. Odor quality is a very different concept.

The field of psychophysics is a branch of study designed to elucidate the relationship between stimuli and human perception and sensation of those stimuli. Psychophysics has developed a number of terms to describe odor qualities such as earthy, floral, minty, spicy, and fishy. As standard as these terms have become within the psychophysics literature, fishy or spicy is still quite subjective compared to 120 Hz or 710 nm for auditory and visual signals and is very dependent upon the person being asked to identify the smell.

Having spent 4 years on Cape Cod during my graduate school time, my wife and I absolutely fell in love with fresh seafood. Some 25 years later, the sweet smell of a freshly cooked lobster or the aroma of mussels simmering away on the stove is joy for us, and in many ways, the odors evoke powerful memories of a scientific youth spent walking the hall of the Marine Biological Laboratory. Thus, the odor quality of seafood has an additional element of pleasantness added into that fishy or lobster smell. Unfortunately, our children do not feel the same about these odors and are often eager to leave the house when a seafood dinner is planned. This is the subjective nature of aromas and many researchers have spent years attempting to tie together the perceptual quality of an odor to something about the structure of the molecule that evokes that quality.

Chemical compounds that stimulate our nose come in a large variety of shapes and sizes. Organic compounds, by definition, have a carbon atom as the backbone of the compound. The backbone consists of a series of carbon atoms hooked together with either a single or double bond. The backbone can be as short as in a single carbon atom in methanol or methane to extremely long chains of carbon atoms found in some of the toxins in marine Dinoflagettes which have over 300,000 carbon atom chains.

In addition to this backbone, carbon chains can have different configurations of atoms somewhere along that backbone which gives the compound its unique smell. This part of the molecule is defined as its functional group and are important from a chemical point of view because the exact structure determines the majority of the molecules’ chemical properties (volatility, boiling point, freezing point, etc.) and more importantly for this book, the functional group provides the unique odor quality to the molecule. Any change in the molecular configuration or shape of the chemical compound has the potential to change our perception. The functional group and length of the carbon backbone are the two main elements that determine the odor quality of any particular chemical compound (Fig. 2.5).

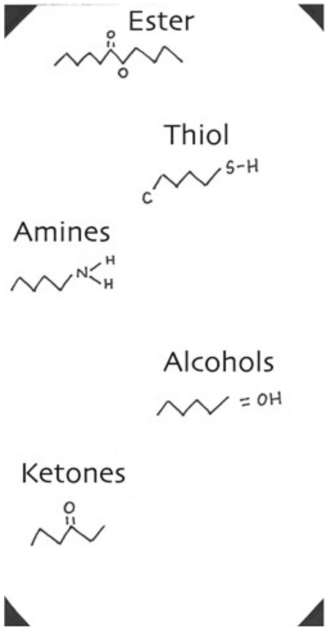

Fig. 2.5 Functional groups of chemicals

Amines (nitrogen connected to two hydrogen atoms) tend to be some of the more offensive odors. If we were to construct a backbone of four carbons and add the amine functional group to both ends, we should have produced the aptly named putrescine which smells like rotting flesh. Add another carbon to the backbone? We have the sister compound named cadaverine which too smells like rotting flesh. As an odor group, amines are relatively easy to categorize. They are somewhat offensive to our nose and can be described as fishy or repulsive. Different functional groups will have wildly varying odor qualities and to explore the totality of human odor perception is really beyond the scope of this book. Yet, we can take a mental stroll through the department store of nature. Instead of an annoying sales assistant ready to ambush you with unannounced spritzes of the latest perfume, Mother Nature herself is here to simply point to different bottles for our nasal pleasure. After quickly passing by the amine counter (which really smelled like a fish market), the wonderful makers of the alcohol odors are ahead on the left. Alcohols are organic compounds with an oxygen and hydrogen as their functional groups. As with other chemicals, alcohols vary greatly in their odor quality. Simple alcohols, such as methanol (one carbon) and ethanol (two carbons), are probably quite familiar to us as fuel smells. Adding carbons to these molecules does something amazing to the odors. Instead of smelling like fuel or drinking alcohol, the odor becomes fruity and light when the number of carbon atoms in the backbone hits six and seven (hexanol and heptanol, respectively). Adding even more carbon atoms changes the perception of the odor and the chemical smells floral or sweet. At the far end of the alcohol counter is a small little bottle with a hexagonal shape on the label. (In addition to the branching of carbon atoms above, some organic compounds have rings of carbon atoms attached to the functional group.) Upon lifting the glass stopper on the bottle and bringing our nose carefully to the end of the stopper, a cool sensation passes over us and goose bumps appear on our arms. This bottle contains menthol which not only activates our sense of smell but also triggers that little known third chemical sense called the trigeminal sense. (More on this sense later in the chapters). This odor is often described as refreshing and stimulating. Having sniffed enough of the enormous variety of alcohol-based fragrances, the next perfume counter awaits our arrival.

If we close our eyes as we approach this set of fragrances, we could imagine that we are at a fruit stand rather than nature's department store. This counter contains a number of different esters from around the world. Esters are characterized by the presence of two oxygen atoms often in the middle of the carbon backbone. One of the oxygen atoms has a double bond attached to the carbon and the other oxygen is sandwiched between two carbon chains. These chemicals are often found within fruits and flowers and provide that sweet smell often associated with the ripening of fruit. This perfume counter full of color-coded bottles is just waiting to pleasure our nose. The closest bottle is a bright yellow with a few speckled dots that appear randomly sprinkled across the label. Lifting the stopper, our nose is greeted with the very familiar smell of bananas. The chemical stimulating our senses is called isoamyl acetate and is often used as banana flavoring in many foods. A large and diverse family of chemicals, these esters are found in apples (butyl acetate), cherries (geranyl butyrate), and even honey (methyl phenyl acetate). As we sample bottle after bottle, the subtly different chemical compounds all bring to mind fresh fruit ready to be eaten. Our noses are in a veritable heaven when we notice two separate bottles at the end of the counter. The first bottle is plain and white, while the second bottle has no label and is simply clear. Intrigued by the mysterious colors, we carefully sniff the white bottle and our minds are flooded with images of elementary school craft days. The chemical (methyl acetate) is the main fragrance in white glue. After clearing our noses of this odor, the clear bottle draws our attention. Upon uncapping this bottle, the pungent odor of nail polish remover is released into the air. This compound is yet another form of an ester (ethyl acetate) and is distinctly different than the fruity odors sampled previously.

We could very well continue through the mental construct of the store's perfume section, but we would be there for quite some time. In addition, to the amines, alcohols, and esters, there are thousands of other compounds like ketones, acids, phenols, and other aromatic organic chemicals. None of these fit into a neat and tidy organizational structure like sound or sight. In some ways, the qualitative nature of chemical signals (i.e., our reliance on a person's perception of an odor quality) has hampered the scientific progress in understanding the human nature of this sense. In other ways, the exciting unknown nature of new aromas has been a boon to those interested in developing the latest new taste or odor. In particular, a lot of research (both scientific and not so scientific) has gone into the search for pheromones.

2.4 The Scent of Love

Probably the word most associated with the sense of smell and the most misunderstood is the word pheromone. In many of my conversations with people on this topic, the word pheromone conjures up many different images often revolving around sex or reproduction. The most common description given to me during these conversations center around an aroma that is so powerful and overwhelming that a mere sniff turns the receiver into a behavioral zombie unable to think of anything but sex. Pheromones are thought to be nature's aphrodisiacs on steroids. A mere drop of the compound will draw in males (of the same species) in from miles around in a frenzied state. Like most common interpretations of scientific concepts, there is only a kernel of truth to this description. The most common use of the term pheromone, particular in early instances, was associated within mating in animals. In reality, the definition of pheromone is simply a chemical signal released into the environment that evokes a behavioral response in organisms of the same species. The first instance of the identification of a sex pheromone comes from the silk moth.

Female moths, of the species Bombyx mori, produce a compound with the explosive moniker bombykol (taken from the Bombyx genus name). Discovered by Adolf Butenandt in 1959; Butenandt was a German biochemist who won a Nobel Prize at age 36 for his work on sex hormones. Given the economic importance of the silk industry at the time, Butenandt and others had ample access to both the males and the females of this species. Upon smelling the pheromones, male moths initiate a series of behavioral patterns that appear to be unstoppable. They begin to fan their wings as if warming up for an intense flight. Once ready, they launch themselves into the air and by a mixture of cross wind search and upwind flight for intense spots of aerial sex pheromone, the males make their way to distant "calling" females. Interestingly, we use the auditory term "calling" to describe the female's act of pumping out pheromones to draw the males in. Typically, the females will climb some relatively tall structure (tall for them) and initiate their pheromone release. Once the males are within vicinity of the female (same tree or branch), they will land and begin a local search for their prospective mate. At a glance, the behavioral acts of the male silk moths do appear to be "involuntary" as if the female's pheromone has put the male into a sex-starved zombie state. It doesn't do this to males, but to understand why there is this belief, a brief history of the word pheromone is necessary.

A quick search on the internet or through any number of magazines will quickly show how the concept of pheromone has been stretched beyond recognition and into the realm of magic love potions. The first broad categories of searches will produce a laundry list of sites where one can purchase small amounts of special chemicals that will give the wearer unstoppable sexuality, power, and control. Sold only in very small quantities, these ultrapowerful scents are guaranteed to give the wearer what they desire. Obviously, the concept behind these scams is that the recipient of the pheromone scent can't help fall in love or be awed by the power of the wearer. Some sites even claim that the pheromone is odorless and yet still functions to elicit the appropriate behavior. Another product (aimed at men) will give the wearer trust and respect. As the site claims, both men and women will "give you their attention and respect, and will want to take your lead. You'll find more people than ever 'bending over backwards'". Finally, a new trend within the dating circles is something called pheromone parties. Days before the actual party, attendees wear identical shirts (blue for boys and pink for girls) for 3 days. The idea is that the essential smell of the individual will be trapped in the t-shirt. Party goers arrive at the host's house with t-shirt in a plastic bag with a number attached to the bag. Over drinks and snacks, participants walk around and sniff shirts in hopes of finding their one and only soul mate. Of course, that soul mate has to be completely compatible as determined by the nose. The "science" behind this concept is that the personal pheromones will quickly trigger a set of biochemical pathways associated with love. So, instead of love at first sight, it is love at first sniff.

The term pheromone originated around 1959 and was constructed from two separate words. The first part, phero, is derived from the Greek word, pherein, which means to transport and the second part, mone, comes from a shortening of the word hormone, which means to stimulate. Several researchers at that time, including another Nobel winning scientist Karl von Frisch, developed the terms to describe a set of chemical signals transported outside of the body in order to elicit a behavioral reaction in the receiving organism. During this scientific period, the concept of innate behaviors was quite prevalent. Innate behaviors, at this time, were thought to be a set of behaviors that animals were born with and that were identical every time the behavior was enacted. Thus, the concept of pheromone, releasing a behavioral reaction, and innate behavior, something not learned or altered, were unfortunately brought together to produce the concept of pheromones presented above.

In reality, the sex-starved, love struck, soul mate zombie producing pheromone doesn't exist, but numerous pheromones that produce different behavioral reactions in the receiver do indeed exist. Pheromones are a sub-class of chemical signals, and the term is reserved for those chemical signals that have evolved to produce reactions with conspecifics (same species). Pheromones, then, are released by one organism in order to produce an expected behavior in another one of the same species. To differentiate between the terms chemical signal and pheromone, we can return to the story of my black lab and skunk. The skunk produces the wonderfully odorous set of chemicals evolved to ward off or deter predators. These cues are interspecific signals or signals where the intended recipient is a different species: my black lab. Antipredator cues or compounds within plants that deter herbivory are just such types of compounds. Conversely, pheromones are those chemicals that are intended to send information to organisms of the same species. There is a host of chemicals that fall within this category.

Another potential misconception with regard to pheromones is that these are a single chemical. One can think of an ancient search for the holy grail of chemicals. Among the popular concepts of pheromones is there is a single chemical (or grail) that will produce the desired behavior. One drop of the sacred compound and the "victim" is hopelessly under control of the wearer. Pheromones can be mixtures of compounds, although that mixture is tightly controlled by the biochemical production in the perfume factory of the body. Often there is a predominant chemical within a pheromone mixture, but the mixture is needed to really call the signal a pheromone. A fuller discussion of pheromones, in particular regarding sex pheromones, awaits in Chaps. 8 and 9.

So if pheromones are used for things beyond reproduction, what ranges of behavioral situations are pheromones found? Pheromones can be grouped in regard to their behavioral function (almost similar to the chapter headings of this book). First and foremost are the commonly recognized sex pheromones. This class of compounds are used to send information about the sex of the sender, the age of the sender (is the sender of reproductive age?), and the sexual state of the sender (is the sender in a reproductively receptive status?). Many primates, other mammals, and invertebrates use pheromones within all of these contexts. Surprisingly, birds are a major grouping of animals where chemical signals, in general, and pheromones, in particular, are relatively unknown. Pheromones are also used to send warning signals associated with predatory events or invasions from rival neighbors. These pheromones are called alarm signals. Aquatic crustaceans produce alarm signals when attacked by predatory fish that causes other crustaceans in the area to quickly find shelter. Aphids produce a chemical substance when attacked that causes other aphids to quickly disperse. Trail pheromones are used by a number of ant species to find their way to and from food resources. Finally, a subset of pheromones are called primer pheromones. Primer pheromones aren't necessarily "smelled" as other pheromones (more on this in Chap. 8), but cause significant changes in the hormones of the receiver. These pheromones "prime" the receiver's physiology for certain behaviors such as copulation. One of the best examples of priming pheromones is found in mice where female rats grow to sexual maturity faster in the presence of adult male odor. The male odor primes the female rat's physiology for sexual maturity and potential mating.

2.5 Feeling with Our Nose

During my adolescent years, my whole family was involved in our church choir. The church's music director was also the band director in middle school band where I played the baritone. Because of these overlaps in musical interests and the close relationship that the music director had with me, our two families became close friends. In fact, my parents still use one of her sons as their dentist. Through this deep musical friendship, my family was invited to visit the choir director and her family at their summer cabin in northern Minnesota.

As evidenced by my ultimate career decision as something of an aquatic field ecologist, I love nature and spending time at a cabin surrounded by woods, lakes, and streams seemed like heaven to me. Thinking back to those couple of summers visiting their cabin, I can picture the cabin in my mind's eye as if it were yesterday. It was a typical wooden cabin sitting about 30 yards from the shores of Shagawa Lake in Ely, Minnesota. The cabin consisted of a large open room that functioned as both a dining room and living room. There was the obligate and for most nights necessary fireplace with a stone mantel. The main floor had a couple of bedrooms and I believe a loft bedroom upstairs. The wooden beams which were evident everywhere on the inside were all varnished a maple color. Outside the main house located halfway between the cabin and the lake was a small wood fueled sauna. Although we visited during the height of summer heat, the lake was deep and spring-fed and would remain icy cold throughout the summertime which made swimming excursions short.

These were glorious times for me, as a young teen. The surrounding woods were a joy to explore and their big blonde shaggy dog (presumably a bushy golden retriever) would often come with me. They owned a small two person handmade speedboat and we would buzz around the lake at breakneck speeds. Fish were abundant in the lake, but fishing would require me to sit still far longer than I was capable of doing. After a day of strenuous activities that included water skiing, chopping wood, and hiking, I would often walk to the pine sauna for a short relaxing and sweaty spell. After sitting and releasing any tiredness from my muscles, I would sprint down the hill, on to the dock and plunge myself headfirst into the icy cold water. Being young, naïve, and foolish, I would repeat this heating and cooling until I got called in for a substantial supper. What made supper particularly enjoyable for me was the presence of handmade, just out of the oven bread that usually accompanied a stew. The smell of this simple, yet hearty white bread that overwhelmed us when we entered the cabin was intoxicating. I believe that most of my meals consisted solely of large slices of that bread covered in either honey or butter. It was perfect for soaking up the beefy soups and stews that made up our lunches and dinners.

The summers of my teen years, as with most people, were impressionable times, and there was an abundance of opportunities at the cabin on the lake or frequent camping trips that would influence me. The long hikes through the woods to distant streams would certainly reinforce the young biologist in me. Running through the woods, playing in the lake, the big shaggy dog, and the sounds of a forest alive with wildlife are just some of the memories that remain with me today. Yet, the two most potent stimuli for evoking memories of those summers are the smells of the pine sauna and that of fresh-baked bread.

Even now, more than two decades later, these odors have immense power over me. One of my favorite rituals after a hard workout at the university gym is a 15 minute sit in the sauna. Upon entering the sauna, the smells of hot air, steam, and heated pine wood immediately envelope my nose. This mixture of scents is hard to describe as are most complex mixtures of odors. For me, the moist heated air of a pine or oak sauna is a unique odor. Being exhausted from my taxing workout and if the sauna is not crowded, I will lay down, close my eyes (just like my sushi ritual from Chap. 1), and breathe deeply. The influence and control of odors in our lives is quite evident during that deep breath. As soon as those first molecules of heated pine reach the olfactory cells in my nose, I am immediately transported back in time to my teens and that sauna by the lake. This is not a conscious act on my part. I am not actively searching for this memory and recalling it. The odor molecules have effectively reached inside of my memory bank and activated those long bygone days. Just as if viewing a virtual reality movie of my life, I am surrounded by my past. I can hear the gentle breeze passing through the tall pines of northern Minnesota. I am glancing out the imaginary window of that sauna and can see the lake right there at the bottom of the hill. If I didn't know any better, I feel as if I could bolt out of the door and sprint down to an icy cold refreshing lake. These visual images of that distant summer flood my mind uncontrollably.

Similarly, the smell of fresh-baked white bread also transports me through space and time to my youth and to dinnertime at the cabin in northern Minnesota. These joyful memories are uniquely tied to odors that were present during those youthful summers. The phenomenon of odor memory is very powerful and the instant transportation through space and time that odors evoke does not occur with other senses. Within the fantasy world of Harry Potter, wizards and witches instantly travel to distant places through a process called "Apparition." When one apparates, the body is pulled toward the destination. Odor memories apparate our mind in that the smell of bread or a pine sauna pulls the mind back to that place in time. We all have formative odor memories that are the most vivid memories that our mind can produce. Sometimes, these memories are not necessarily pleasant (as in cases of food poisoning).

I often see big shaggy dogs during my runs or walk through town, yet none of these beautiful beasts transport me to my youth. My current summers are spent in northern Michigan performing research in the abundant streams of that area. During my treks to distant field locations, I often pass by cabins that look remarkably similar to that one in northern Minnesota. As I view these places, I am reminded of those distant summers, but my mind and body are still located in northern Michigan in the present time. As strange as it may seem, the sights and sounds of a big shaggy golden retriever, entering a log cabin, or walking through large pine forests evoke wistful thoughts of my youth, but these wistful thoughts are mere shadows when compared to the memories induced by the specific smells.

2.6 I Think, Therefore I Am

Throughout this book, I have and will repeatedly mention that humans are acutely unaware of the prevalence of chemical signals in nature. I have alluded to the idea that humans are essentially blind to the use of chemical signals in nature, and yet, we have these powerful odor memories. These two ideas are seemingly incongruent, being blind on one hand and powerfully moved on the other, and require some explanation. That explanation comes from an understanding of how odors and other senses are encoded, processed, and perceived by our minds.

Visual and auditory stimuli can be grouped together as highly processed senses. This means that, in common terms, we consciously think about the majority of these stimuli before we react to them. Imagine that part of your morning ritual involves turning on the morning news while you get ready for the day. Even if the stories about the latest world crisis are in the background, the sound waves travel from your ear through the cochlea on to the auditory cortex. Here, in the cortex, is where the brain processes the information in order for you to identify words, sentences, and extract information. If you turn the TV on to watch the morning weather, the visual signals are sent through the retina through the optic nerve to the visual cortex. In the visual cortex, the images are processed in a similar fashion as the sound waves and your mind thinks about what the eyes are seeing.

Interestingly, olfactory signals, within the mammalian brain, are handled very differently. Behavioral and mental responses to chemical signals have more of an emotional response than the highly thought-out response visual and auditory responses. The basis for this difference can be seen in how our senses send information to our brain. The mammalian brain is a very complex and intricate structure. There are numerous structures and substructures that are designed to deal with very specific types of tasks. There is an area for processing sounds, an area for processing sights, an area for movement, and so on for the many different tasks that our brain performs. In a general and simplistic view and for the purposes of this book, the brain can be divided into three broad sections: the spinal cord, the brain stem, and cerebrum (Fig. 2.6). For the purpose of this discussion, we can focus in on the middle of the cerebrum onto the areas called the amygdala, the thalamus, and the hypothalamus. The hypothalamus and thalamus, often called the limbic system, which tightly control the release of hormones into our body and the amygdala is often called the emotion seat of the brain. So, this seat of the emotions and the visceral responses that our body produces to intense stimuli is directly stimulated by the olfactory bulb. The cerebral hemisphere, and in particular the outer layer called the cortex, is the upper and outer areas of the brain that make us who we are. It is believed, with good evidence, that the cerebral hemisphere of our brain is that area that makes us aware of our surroundings and ourselves. It is where we think, where we construct abstract ideas, and it is this area of the brain that makes us conscious. The visual and auditory stimuli of our world are shipped off to the thinking areas of the brain, and the olfactory stimuli pass through the emotional centers first.

I can provide an illustrated example of how our brain processes information by taking a short trip to my garden. My gardening thumb is more brown than green, but I do make the effort to have some roses in my garden. One of my favorite roses is a lavender rose called “Angel Face.” This rose is a light purple in color, but has an excellent and powerful fragrance associated with the blooms. Now, when I see a blooming angel face, the visual image is detected by the retina in my eye. This information is then passed along after a single stop to the visual cortex of the brain. Initially by passing the emotional centers of our brain, the visual images are sent to the “thinking” centers of our brain for digestion. Among other things, I see the edges of each petal. I can recognize the lavender color as different from the deep green leaves and the blazing red rose bush next to it. There is a small metal tag that labels this rose and I see letters, and recognize the words “Angel Face.” Only after the “cognitive” recognition of these signals is this information passed on to other areas of the brain. After a few seconds, a pesky Japanese beetle lights upon the rose. In a similar fashion as the visual signals, I recognize the slight buzz of the beetle’s wings as it flies in. The sound waves from the beetle’s wings stimulate the hair cells

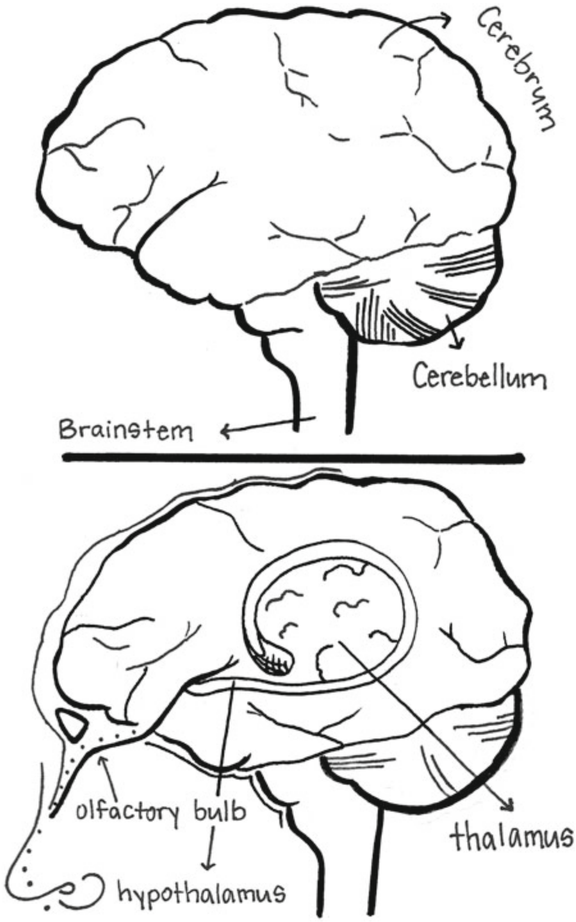

Fig. 2.6 Mammalian brain structures

in my inner ear. Once there, the information is filtered according to its frequency and is quickly passed onto my auditory cortex. Again, this information is digested and filtered so that I can recognize the sound of a flying beetle from the sound of a flying bee or bird. From this processing, I can estimate the location of the flying beetle and can distinguish this singular sound from the other springtime sounds present in my little garden. Once the buzzing is recognized and filtered, the information is passed on to the other parts of my brain.

In stark contrast to the highly cognitive processing of sights and sounds stands the wonderful fragrance that is emanating from the rose. Molecules of the rose's perfume are lifted off of the petals and are brought into my nose through a deep sniff. Once these molecules contact the receptors in my nose, neural information is generated and sent along the pathway to my brain. The first stop, the piriform complex, is a branching way station for the information. Here, the initial information about the rose's fragrance is split into two. Half of it is sent first through the thalamus and then onto the cortex. Here, like the sight of the rose and the sound of the beetle, the information is processed and "recognized" as a rose, beetle, or fragrance. The other half of the information is sent to the hypothalamus and to the limbic system. This is the noncognitive or "emotional" part of our brain. This is where aggression, serenity, love, and all range of emotions are created. Awareness, recognition, and all other "higher" brain functions are alien to this place.

What this rose example illustrates is that sights and sounds are highly "processed" pieces of information. These are sent to those areas of the brain that give us our cognitive abilities. Whereas, half of the olfactory information is sent for processing, but the other half is sent directly to the emotional centers of the brain. From the emotional center of our brain, the intense odor memories are being released and those memories flood our cognitive mind. These memoires and emotions are triggered at the same time or even before we begin to "recognize" what the smell is. Even the words commonly used to describe the impact that odor memories have upon us illustrate these differences. Words like flood and envelop are used to describe the action that odor memories enact on our mental state. Words like recall and remember are used for auditory and visual memories.

2.7 An Alien World

Cedric and I have finally made our way into my office. The usual routine at this point starts with me removing his harness and setting it down on my bookshelf. Cedric is pretty patient about letting me set my bag down and remove his harness because he knows that a delicious treat awaits his good behavior. I reach for the box and the rattling sound, which I enhance by raking my fingers through numerous treats, alerts him that his reward is at hand. Once he consumes his treat, he pads his way over to a small bed that sits to the left of my chair and computer desk. The bed is located under a section of my desk and is surrounded by a small two drawer filing cabinet on one side and the desk leg on the other side. Shiba Inus have a strong resemblance to foxes or dingos, so I can imagine that this is Cedric's version of his own den. After surveying his chew toys, he finds a spot to lay down and curls up in the shape of a gibbous moon. For the next few hours, I can get some work done and the only movement I can detect from Cedric is a couple of perked up ears tracking various sounds from around my office and the outside hallway.

At this point, Cedric is keenly aware of three different "scapes" that surround him. Those triangularly pointed ears that are roving back and forth like mini-radars are sampling the soundscape of my office. The dynamic soundscape is composed of students periodically walking in to have conversations with me, my choice of music for the day, and anyone passing my office talking on their phones, moving carts of equipment, or otherwise engaged outside of my office. Periodically, when an unexpected loud sound erupts, as when a student drops a textbook, his head will pop up and both ears instantly focus on the door of the office. If no further distressing sound arises, he lowers his head to a comfortable position on his bed, but those ears are still scanning the environment. The soundscape can be thought of as the sum total of all of the sounds, their spatial location, and the temporal dynamics of the appearance and disappearance of each of the sounds. If we were to visualize this soundscape, it would consist of waves of sound emanating from my speakers, peoples' steps, and from the mouths of students during meetings. One could think of the outward moving ripples of waves as a rock is dropped into a puddle.

The second "scape" that Cedric is aware of is the visual landscape. The visual landscape encompasses me, my desk, and the mini-fridge that stores my caffeine needs, my bookshelf, and any students or faculty that happen to walk into the office. Each of these objects creates a unique visual image that Cedric combines into a coherent and singular image. Similar to the soundscape, the landscape is dynamic in time and space. As people enter my office and move to the available chairs, the visual field is changing which is tracked by Cedric's mind. His cognitive analysis of these images determines whether he needs to walk forward because there is a treat in my hand or to stay in his "den" because someone unfamiliar is approaching.

The third and final "scape" has been described repeatedly in this chapter, and I shall call this "scape" the aromascape. Like the soundscape and landscape discussed above, each of the living beings as well as some inanimate objects produce each of their own individual aroma, and as Cedric "scans" the aromascape with his sniffs, he'll construct a mental "map" of the odors within his sensory range. I put the word map in quotes because science has yet to really understand how the spatial and temporal distribution of odors in nature are portrayed within our brain. Our understanding of the chemical senses is roughly 50 years behind our understanding of vision and hearing in part due to the difficult nature of controlling and producing aromascapes in experimental settings and in part due to our reliance on vision and hearing. Still we know that animals use odors to navigate in the world, so there has to be some type of spatial representation in their brain (and ours) of the aromascape around them. As with the soundscape, it is possible to construct a visual image of the aromascape that Cedric is sensing. Each odor source, be it student or my lunchtime sandwich, is a tiny volcano of odor that blows downwind of any air movement in my office. So, his nose "sees" 20–30 little and not so little puffs and clouds of aromas spewing forth from everything in the room. One for my can of soda, one for me, one from my trash bin, a couple from the two students who walk in, some small distant ones from people in the hallway, and so on.

This last scape, the aromascape, is the alien world that humans hardly pay attention to. The aromascape is the world that many different animals are aware of as they move deftly and respond behaviorally as easily as a mountain goat climbing the side of a steep hill. In contrast, we are bumbling our way through this world as we douse extra perfume on our bodies and walk through crowded plazas with food carts all around. In subsequent chapters, we will mentally stroll along side some of the best examples of animals using aromascapes to their advantage for specific behavioral tasks and then we will compare how the human animal is guided, controlled, and influenced to perform some of those same behaviors.