# 6. Brain mechanisms of rhythm and the private synapse

* *What are brainwaves?*
* *How do we produce internal clocks and rhythm?*
* *How can periodic electrical activity arise in the nervous system?*

If we can sing and dance in rhythm, the nervous system must possess an internal clock. The clock needs to be able to adjust to the tempo and patterns we hear. For much music and dance, as in the previous chapter, we need to operate multiple clocks at once.

How could this happen? Spoiler alert: there are big gaps in our knowledge on these types of brain functions. We’ll discuss the basics here, and if civilization continues, we will know more later.

## Thinking about current

Our nervous system provides for our senses and controls our behaviors by activating or silencing a vast number of possible circuits. These are built from connections between neurons, named *synapses* by Charles Sherrington (1857-1952), that are activated or inhibited by chemical signals that trigger electrical signals. The neurons themselves are excited or depressed because they act like electrical batteries.

The Greeks called the note that doubles the fundamental to complete one octave and start the next the *synaphe,* which means *union*, while *synapse* is translated as “unite”. Did Sherrington know the ancient musical term?

The flow of water is useful for understanding electrical currents. Rivers run downhill, and the steeper the drop in elevation, the higher the downhill current of water molecules. A strong current, such as one that spills over a waterfall or dam, produces enough current to power a sawmill.

Batteries are similar. A flashlight or car battery has a positive and a negative “pole”, and when connected by a conductor such as a wire, electrons flow that provide current and power. Electrons are negatively charged with more on the negative pole of the battery and given the opportunity they will “flow downhill” to the positive pole. If we measure this potential difference by connecting both poles to a voltmeter, we read 9 volts for a battery used in guitar boxes and 12.6 volts when your car battery is fully charged.

Here’s a metaphor to intuit electric circuits and Ohm’s law (Georg Ohm, 1789-1854) that defines the relationship between current, voltage and resistance.

Imagine a full hot water tank placed a bit higher than an empty bathtub and a garden hose with a faucet that connects them. When the faucet is open, water current flows from the water tank to the tub. Eventually the water would reach equilibrium when it is the same level in the tank and tub, but we want to concern ourselves with events during the water flow.

The difference between the tank and tub water levels can be measured in centimeters (cm). The greater the difference in water level, the greater the difference in “hydrostatic” water pressure: this is why water towers are built at a high elevation (each 10.2 cm increase in the height of a water tower increases the pressure by 1 kilopascal: here what is important is that doubling the difference in water level doubles the water pressure).

The hose carrying water molecules between the tank and tub is a conductor or if you will, a “channel”. The flow rate of the water through the hose is in units of volume (1 milliliter = 1 cm3) per second. This flow rate of water molecules is called the “current” in rivers, and is equivalent to the flow rate of electrons or charged ions in electricity, also termed current.

Liquids like water cannot be compressed, and so for water flowing continuously through the hose, the flow through the intake must be the same as the efflux through the faucet. If the diameter of the hose is the same throughout, the velocity of the water moving through it (cm/second) is likewise the same (this velocity would change for liquids of different viscosity: you can imagine that molasses or tar have slower velocities).

Consider the water molecules flowing through the hose. A wider hose with twice the area (measured in cm2) doubles the number of flowing molecules, that is, increases the garden hose’s conductance. Doubling the length (cm) of the hose, however, makes the transit of a water molecule last twice as long, slowing the conductance from the water tank to the bath tub.

Since the flow of water molecules is proportional to velocity and hose area but inversely proportional to the length, we can define conductance as

hose conductance (cm2/second) = water molecule velocity (cm/second) \* hose area (cm2) / hose length (cm)

The movement of water downhill is proportional to the difference in water levels, and so the water flow rate (or current) from the tank to the tub is

current (cm3 /second) = difference in water level (cm) \* hose conductance (cm2/second)

Notice that if either the water level difference or the hose conductance is increased, the current becomes faster.

if we substitute the terms electrical engineers use for current (I), potential energy difference (V) and conductance (G), we have Ohm’s law

I = V \* G

Notice that as the voltage is lowered, the current decreases, as is intuitive from when a battery begins to lose its charge.

Engineers call the reciprocal of conductance (in units of seconds / cm2), resistance (R)

R = 1/G

Behold the standard version of Ohm’s law derived from a bathtub:

I = V/R or rearranged, V = IR

To make the calculations easier – this doggone bathtub model took me hours– engineers defined units of amps (amperes) for current, volts (naturally) for voltage, and ohms for resistance as

1 volt = 1 amp \* 1 ohm

Literally, one amp of current is when one “coulomb” of a ridiculously large number of electrons (6.241 \* 1018 electrons: remember that 1018 is a billion billions) flows per second. The flow of a coulomb of electrons may be more difficult to imagine than a milliliter of water, but in neurons we will be dealing with electrical currents measured in nanoamps (a billionth of an amp, and billions of ions) and picoamps (a trillionth of an amp and millions of ions).

## The nervous system produces electricity

If the fields of biology and electrical physics now seem unrelated, they did not appear separate to the pioneers.

Johann Georg Sulzer (1720-1779) published a study in 1752 reporting when his tongue touched two metals, lead and silver, he tasted something disagreeable not present when the metals were tasted separately. Sulzer’s phenomenon is still called the “battery tongue test”, and you can conduct it centuries later by touching your tongue to the two poles of a 9 volt battery. He conjectured that particles were being liberated from the metals that activated nerves in the tongue, which is true. I am happy to say that my namesake developed a way to measure electron flow by taste long before voltmeters.

A central question for these early electrical scientists was whether animals produced electricity.

A strong suspect for a dangerously electric animal was the torpedo, a cartilaginous fish closely related to the stingray and the namesake of the naval weapon. The torpedo fish was reported by the ancient Egyptians and Greeks to stun its prey and occasional swimmers. The torpedo is now also called the “electric fish”, which sort of gives away the answer.

The physicist and polymath Henry Cavendish (1731-1810) was convinced that the swimmer’s shock could be explained by the torpedo discharging electricity, and in a “stunning” paper published in 1776, described how to build a model of the fish at home. In a variation of Ben Franklin touching a wet kite string during a lightning storm, Dale tried to demonstrate that the torpedo could produce electricity by inviting visitors to touch points on the model to feel the shock.

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| Figure 6.1 Cavendish’s artificial torpedo Above, Henry Cavendish shows how he cut a piece of wood to the shape of a torpedo fish with a 40 inch handle covered in leather. A glass tube was placed between M and N. A wire at W was threaded through the tube and soldered to a strip of pewter meant to represent the electric organs. Below, the model was immersed in a bath of salt water, into which Cavendish discharged a current made from forty-nine Leyden jars, and the wire could be touched to feel a shock, and sparks were seen to fly from the handle.­  From in An Account of Some Attempts to Imitate the Effects of the Torpedo by Electricity. 1776, Philosophical Transactions of the Royal Society. |

The classic demonstration for a role for electricity in the nervous system was by Luigi Galvani (1737-1798) in Bologna, Italy in 1780. He wrote that when his student touched a nerve in a dissected frog leg with a scalpel that had accumulated an electrical charge, it discharged a spark and they saw the legs flex as if the frog were jumping. His 1791 publication for the Bologna Academy of Science, *De Viribus Electricitatis in Motu Musculari*, showed the frog leg jumping from a connection lightning rod during a storm, indicating that atmospheric electricity could drive motor function.

Galvani then found that if he attached a dissected frog spinal cord with a leg to two connected metal wires made of bronze and silver, the leg twitched. Galvani called these phenomena *animal electricity* and others later called it *galvanism* and *bioelectricity*. Whether triggered by lightning, by attaching two metals in Sulzer’s mouth, or from spark from a charged scalpel, Galvani believed that the energy that triggered the muscle constriction was made by the animal itself.

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| ../galvani%20experiment_2.jpg |
| Figure 6.2 Galvani’s description of animal electricity. Likely influenced by Benjamin Franklin’s kite experiment, and a precursor of Mary Shelley’s *Frankenstein*, Galvani used a lightning rod with a wire that caused the frog legs on the table to jump (1791). original figure is reproduced at <https://helix.northwestern.edu/article/experiment-shocked-world> see https://archive.org/details/historyoftheorie00whitrich/page/70 |

Galvani’s 1791 publication and its coverage in the newspapers -- *The Morning Post* wrote a grisly story on Londoners repeating the experiment on a recently decapitated dog in 1803 -- inspired Mary Shelley (1797-1851) to write *Frankenstein* (published 1818). She wrote:

*Many and long were the conversations between Lord Byron and Shelley, to which I was a devout but nearly silent listener. During one of these, various philosophical doctrines were discussed, and among others the nature of the principle of life, and whether there was any probability of its ever being discovered and communicated.*

*They talked of the experiments of Dr. Darwin (I speak not of what the doctor really did, or said that he did, but, as more to my purpose, of what was then spoken of as having been done by him), who preserved a piece of vermicelli in a glass case, till by some extraordinary means it began to move with voluntary motion. Not thus, after all, would life be given. Perhaps a corpse would be reanimated; galvanism had given token of such things; perhaps the component parts of a creature might be manufactured, brought together, and endued with vital warmth*.

In Pavia, Italy, Alessandro Volta (1745-1827) reproduced Galvani’s frog leg observation but claimed that frog legs were not required to produce the electrical current. To really prove his point, he connected disks made from different metals by cardboard soaked in salt water, he invented *Voltaic piles*, now known as the battery. To demonstrate that this contraption produced electrical current, he used the Sulzer / Cavendish / Galvani / Benjamin Franklin approach, reporting that one felt a shock when touching both ends. From these results, by 1793, Volta argued with Galvani by denying the existence of animal electricity.

Volta’s experiment was repeated in Britain by William Nicholson and Anthony Carlisle, who reported in 1800 that Volta’s battery formed the gases oxygen and hydrogen from the water. Volta and his colleagues thus also launched the field of electrochemistry that underpins virtually all contemporary electrical technology.

From our perspective over centuries, we can both appreciate Volta’s invention of our contemporary world, and also that Galvani was correct in claiming that animals produce electricity. Galvani even suggested that the oligodendrocyte cells in our nervous system insulate electrical fields, which jibes well with our current understanding, *and* he predicted the existence of ion channels to convey electrical charge by neurons, which underpins virtually all contemporary neurophysiology.

## The brain produces electricity

The classic demonstration that the human brain produces electricity was performed in 1924 by Hans Berger in Jena, Germany, who used as his experimental subjects his 15-year old son, Klaus and 14-year old daughter, Ilse. Hans inserted two electrodes under Klaus’ and Ilse’s scalps. The power of the signal was increased – i.e., the voltage between the electrodes was *amplified* - and used the electrical power to move a pencil across a paper chart recorder. Hans Berger’s approach to recording the brain’s electrical signals from the head is known as *electroencephalography* (EEGs), and the way the system works has barely changed over the next century.

Remarkably, the voltage on the children’s head was not constant, but displayed voltage waves depending on what he was thinking or sensed. In 1932, Hans recorded reported that when he asked Ilse to mentally divide the number 196 by 7 (she got the right answer), when she began to concentrate, she showed a large electrical peaks at 10 Hz, which are still called *alpha waves*: they also show up around the visual cortex at the back of the head when you close your eyes. We also still use Berger’s term, *beta waves*. Others uncovered additional frequencies in the cortex’s electrical activity, including delta (big slow waves when you sleep), theta, and gamma waves, each of which has a different tempo.

EEGs are now often recorded in the clinic with 16 or more electrodes on the outside of the scalp/ These electreodes are used to record activity of the cortex, the region of the brain closest to the skull. That EEGs effectively measure cortical activity is astonishing when one considers that there is skin, a skull, and additional cellular layers between the cortex and the electrodes outside the head. You might guess correctly that in order to see these waves, millions of neurons must be active simultaneously.

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| Figure 6.3 Alpha waves .  Three electrodes simultaneously recording a subject’s frontal (top) and occipital (rear of the head) cortex (lower two) electrical activity over 10 seconds. The time is shown on the horizontal (x) axis in seconds, and clear alpha waves are seen in the occipital traces around 4 and 5 seconds, while no alpha waves are seen from the frontal cortex.  *Recording by Joseph Isler (Columbia University), reproduced with permission.* |

The largest brain waves occur during sleep or anesthesia, when slow *delta* waves of about 2 Hz are prominent: it is as if the neurons are all holding hands, swaying together and singing *Kumbaya*. At the opposite extreme, when one is really concentrating, for instance on a math problem, brain activity is very complex and composed of a broad range of small brain waves. If you run a Fourier analysis as we did to measure the components of sounds in Chapter 4, you see a high representation of very rapid activity above 40 Hz, which are called *gamma* waves.

An important clinical use of EEGs is to detect epileptic seizures, which about 10% of people exhibit at some time during their lives. Contemporary clinical EEGs provide a means to tell where in the cortex a seizure begins and the pattern by which it spreads to other areas.

## Producing a heartbeat with batteries

For most of the neurons we are concerned with, the activity occurs when they “fire”, which is a large positive jump in their voltage, often 100 millivolts (mV) or more for about one thousandth of a second (a millisecond: ms), known as an *action potential*. Most brain cells do not spontaneously fire action potentials, and require activation from another neuron to drive their activity.

Some cells are however spontaneously active, fortunately including those that operate our heart: these are known as *tonically active* or *pacemaking* cells that incorporate an internal clock. This rhythmic activity is driven by the opening and closure of channels through which current flows across the membrane, the way that opening a faucet or channels in a dam allows water to flow from a higher to a lower level.

In biology, the electrical currents are carried by charged particles known as *ions*. Ions are produced in many situations. For example, when table salt, comprised of sodium and chloride atoms, is dissolved in water ot produces negatively charged chloride ions and positively charged sodium ions. For cells, the difference in ionic charges between the inside of the cell and the outside fluid are two poles of a battery.

For the heart to pump throughout our lives, we rely on pacemaking cells in the sinoatrial region of the right atrium to produce rhythmic action potentials. If you placed a tiny voltmeter between the inside of the cell and the surrounding fluid, you would measure a brief voltage jump from a *resting potential* of -70 mV to about +20 mV and back

The resting potential voltage is negative (“hyperpolarized”) due to the opening of channels for potassium ions, which are positively charged. As there are more potassium ions in the cells than in the outside fluid, they flow “downhill” or outward, making the interior more negative.

During the hyperpolarized phase, the low voltage activates the opening of another set of membrane channels, known as *hyperpolarization-activated cyclic nucleotide-gated* (HCN) channels that allow sodium, which is higher in the surrounding fluid, to enter and *depolarize* the cell as well as *T-type* (for *transient*) calcium channels that provide further entry of calcium, which is likewise higher in the surrounding fluid.

There is an additional depolarization during this phase from the action of an *exchanger* protein that trades the efflux of one calcium ion, which carries two positive charges, for the influx of three sodium ions, and so increases the depolarization by one ion for each exchange. Together, HCN channels and exchangers drive a progressively more positive voltage.

At close to -50 mV, the cell reaches a voltage *threshold* that activates the opening of a new group of calcium channels, known as *L-type* (for *long-lasting*) channels. As the concentration of calcium ions outside the cells is nearly 10,000 times higher than inside, there is an enormous potential to carry these ions inward through these channels, as if a water tank were many stories above the bathtub. This drives a sufficient increase of positive charge in the cell to drive the action potential to about +20 mV, the maximum voltage that these cells reach during their pacemaking cycle.

People with hypertension often take drugs (dihydropyridines) to lower blood pressure that partially inhibit these L-type calcium channels and so reduce the amount of blood moved by the heart.

As L-type calcium channels close, a set of potassium channels open again that hyperpolarize the cell, and the cycle repeats. The duration of the action potential in these heart cells is relatively long-lasting, about 200-400 msec, and as you know, the entire cycle lasts the period of a heartbeat, which at rest is about 50-85 beats per minutes, or about 0.8 to 1.4 Hz.

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| |  | | --- | | Figure 6.4 cycle of sinoatrial action potential, A sinoatrial action potential. At phase 4, there is a slow depolarization driven by what is still known as the “funny current” (i*f*), a type of HCN channel that provides a slow influx of sodium. As the depolarization drives the cell to reach the threshold voltage (at the dashed line), voltage sensitive “long-lasting” calcium (iCa(L) )and “transient” (iCa(T)) channels and a sodium/calcium exchanger (iNaCa) open, driving a much faster depolarization as these ions to diffuse inside (phase 0). At phase 3, a delayed potassium channel (iK) opens, causing this ion to diffuse outside, which returns the cell to a hyperpolarized potential where the cycle can begin again. *Figure by the author with advice from Michael Rosen (Columbia University).* | |

This opening and closing of ion channels to produce specific currents provides the ongoing rhythm of the heartbeat. It does not explain how the heartbeat is increased during exercise and slowed during rest: that is due to modulatory neurotransmission, a topic of the following chapter.

## Neurons are batteries

Moving to neurons in the brain, let’s ask why Klaus Berger’s head produce changes in voltage?

The concentration of sodium in the extracellular fluid is about 150 millimolar (mM), and at rest the concentration inside the neuron is about 15 mM. Neurons typically pump out positive sodium ions from the inside of the cell to the surrounding fluid, using an exchanger protein that expels sodium ions like water from a leaky boat, and so become hyperpolarized. If you placed our tiny voltmeter to measure the difference between the fluid and the inside of a resting neuron, the difference is typically about -70 millivolts.

Now let’s excite that neuron to make it “fire”. This is typically accomplished by release of a chemical signal from one neuron, known as a *neurotransmitter*, that binds transiently to a receptor protein on the membrane of a second neuron to trigger the temporary opening of a channel for specific ions.

While the action potential of the heart pacemaker cells above is driven by the entry of calcium ions through L- and T-type channels that are relatively slow to open, for most neurons the action potential is driven by the rapid opening of channels that provide for the fast entry of sodium ions. These particular *voltage gated* sodium channels are opened when the neuron depolarizes beyond *threshold*, often around -30 mV, and so the combination of neurotransmitters signals received by the neuron and its own state determine the decision to fire or remain silent. If a sufficient number of sodium ions enter through the open channels, they produce an action potential that typically lasts for 1 ms that depolarizes the neuron by roughly 100 mV. The action potential triggers events so that the neuron can in turn release its neurotransmitter and send signals to yet more neurons.

A Japanese puffer fish used to prepare *fugu* in restaurants has high concentrations of a toxin, tetrodotoxin, that blocks the voltage gated sodium neurons. The chef needs great skill, as ingesting too much of the toxin leads to asphyxiation and death.

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| Figure 6.5 of neuronal action potential. An action potential recorded from a acetylcholine-releasing neuron (sometimes known as the giant neuron) in the striatum of a mouse. The activity of these neurons helps to regulate the activity of all other striatal neurons including the responses involved in learning and reward as well as self-administered drugs such as nicotine, alcohol and cocaine. *Courtesy of Sejoon Cho, Sulzer laboratory (Columbia University).* |

These discoveries of neuronal function occurred during the era that home radios were developed. Radio uses a transmitter to broadcast a signal to home radios known as receivers, and so biologists adapted the term neurotransmitter for the chemical signal released, and receiver or receptor for the structure that was activated or “transduced”. The first receptor to be thoroughly characterized happened to be that of the torpedo electric fish, whose electric organ releases extremely high amounts of the neurotransmitter acetylcholine, and also contains very high levels of the acetylcholine receptor.

About the time the sodium channels close, another set of channels open so that the potassium ions flow from the inside of the cell to the outside, hyperpolarizing the voltage to return to its resting potential.

As ions have electrical charge, their combination contributes to the voltage. This relationship is modeled by the “Hodgkin-Huxley” equation (after Alan Hodgkin and Andrew Huxley who worked at Cambridge University), which adds together the conductances for each channel multiplied by the concentration difference (as voltage) of each ion across the membrane. The model is effective for determining how a neuron will respond by changing the rate of action potentials to changes in currents.

## Neuronal firing and private synapses

As a rule, neurotransmitters that activate sodium channels, allowing sodium ions to enter the cell, excite neurons: the most common of these *excitatory* neurotransmitters are glutamate and acetylcholine. The food additive monosodium glutamate activates glutamate receptors and leads to clinical issues from overexcitation in some, whereas many of the acetylcholine receptors are activated by nicotine, and play a central role in the effects of tobacco.

Neurotransmitters that open potassium channels that allow positive ions to flow from the neuron outwards, or chloride channels that allow negatively charged chloride ions at higher concentration outside to flow into the neuron, tend to decrease neuronal activity. In mammals, the most common *inhibitory* neurotransmitter is a glutamate metabolite known as GABA. Many commonly used drugs including sedatives, anti-anxiety drugs, and possibly alcohol work by altering GABA receptor function. If your perception of time or response seems slower with these drugs, their effects on your internal clocks may be the reason.

The mechanism by which neurotransmitters are released is chiefly by exocytosis. In this mechanism, small internal structures known as *synaptic vesicles* that contain high concentrations of neurotransmitters fuse with the neuronal membrane at synapses, thereby releasing the neurotransmitters into the synapses and close to receptors on adjacent neurons.

Fast acting synaptic connections that rely on ion channels are often called *ionotropic*, whereas the slower modulatory synaptic connections in our following channels are often called *metabotropic*. As the ionotropic synapses typically activate a very short acting local signal between a single presynaptic and postsynaptic neuron, I call them *private synapses*, and metabotropic synapses in which a single presynaptic site releases a long-lasting signal that diffuses to multiple neurons *social synapses*.

## Producing neuronal clocks in rhythm

Most neurons in the brain, including the cortical neurons in Klaus’s EEGs, are not pacemakers like heart cells but require excitation from synaptic inputs by other neurons. Many of these neurons form large networks that are generally active together. In the human cortex, these networks are even now still mostly measured by EEGs, including more invasive EEG like recordings in which electrodes are placed directly on the cortical surface during surgery for epilepsy.

EEG waves often are entrained to a regular beat a listener is hearing. The neuronal waves are very similar to the water, sound, air, light, string and other waves we have discussed, with the crest coinciding with the auditory beat and the troughs inbetween the beats, at the frequency and phase of the music.

The electrical rhythms of the brain are often used to produce sounds in the laboratory. The simplest approach is to amplify the voltage the electrodes measure and send them into a speaker. My lab uses this to tell when a neuron is active. The sounds aren’t “musical” as they are too slow (often 1-10 Hz) and too irregular, that is non–periodic, to be perceived as musical note, and they sound like a series of clicks.

Listening to the sounds of firing neurons is nonetheless important clinically. During surgery for deep brain stimulation, a treatment for Parkinson’s disease that has now been conducted in hundreds of thousands of patients, a neurophysiologist will listen to the patterns of sound, which change in different regions such as the border between the globus pallidus and the subthalamic nucleus deep in the brain to determine where the electrode should be implanted.

For people who study how the brain changes with rhythm, one approach is to play a simple rhythm multiple times until a steady pattern is clear to the listener, and then omit a beat, or delay it, or make the beat arrive too early. When the beat irregularity occurs, there is a short burst of high frequency “gamma” wave activity of 40 Hz and higher that appears to reset the cortical firing patterns to a different pattern. This gamma wave burst, called an event related potential (ERP), can be challenging to measure, and the experiment often needs to be repeated many times to confirm its presence.

ERPs code many sorts of unexpected stimuli. A classic way to invoke an ERP is unexpected syntax – “the moon jumped over the cow” – I just triggered an ERP in your cortex. The presence ERPs indicates that a series of expectations was violated. When an ERP occurs, we are recording the activity of massive numbers of both excitatory glutamate releasing and inhibitory GABA synapses neurons in the cortex, and the inhibitory neurons are likely changing the phase of waves.

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| Figure 6.6 of an event related potential. The blue trace shows a cortical response when a steady pulse of 1000 Hz tones at a steady volume. After the listener learns to expect the series, the green trace shows an ERP when an unexpected single louder pulse of 1050 Hz is substituted. |

Interestingly, Dale Purves and collaborators at Duke University showed these ERP occur even in infants as their mothers bounce them on their knees and change patterns by omitting a beat or adding a syncopation.

Sylvie Nozaradan and her colleagues in Belgium and Montreal had adult listeners tap specific rhythms, say two eighth notes followed by two quarter notes and two eighth notes, at different tempos. Where did the EEG and ERP activity occur when analyzed by the Fourier analysis? Why, right at the frequencies of the eighth and quarter notes. They concluded that beat and meter are both set by a series of ERPs.

When they sped up the rhythms, at some point (7 or 15 Hz), the tempo became too fast to perceive the beats, and the ERPs become much weaker and messier. This suggests that the ERPs are required for rhythmic perception and execution. It might also help explain why some tempos are too fast for much use in music – it might be interesting to test if drummers who perform the extraordinary fast snare rolls inspired by electronic drums have developed the ability to produce more accurate ERPs at rapid tempi.

The Nozaradan group also noticed that in some cases, an extra series of ERPs would show up at exactly twice the frequency of the rhythm they were hearing, i.e., at the first harmonic. This spontaneously occurring phenomenon might help to explain the appearance of binary rhythms, like clapping on the “off beat” in gospel church music. Perhaps the establishment of new ERPs in the brain due to the interplay of other ERPs underlies the ability to produce syncopations and polyrhythms.

# Listening

Examples of electronic drums performing seemingly impossibly fast drum patterns are by Aphex Twin (Richard James)’s *Flim* or Squarepusher’ (Tom Jenkinson)’s *ken ishii x-mix*, named for a DJ from Sapporo, and Venetian Snares (Aaron Funk)’s *Ketsarku Mozgalom*. A live drummer who has nonetheless learned to play these rhythms live is Mike Glozier, listen to his *Venetian Snares*.

Watch the 1931 film *Frankenstein* with Boris Karloff in which the good Baron reanimates his monster using Galvani’s lightning rod, and then follow it with the 1974 *Young Frankenstein* by Mel Brooks and Gene Wilder.

There have been multiple attempts to use brain rhythms to produce music. The composer Alvin Lucier, rather than amplifying the waves as in a neurophysiology lab, wired them to a device that struck a drum. He performed live concerts simply sitting on the stage triggering the drums by wearing an EEG in *Music for Solo Performer*.

The electronic musician Brad Garton and I record the EEG brainwaves into a laptop and use software he wrote to assign its features to make sounds: for example, a higher frequency of EEGs might produce a higher note or louder volume. The signal can be separated by a Fourier analysis into component frequencies to produce harmonies or several lines of sounds simultaneously. We sometimes have multiple performers play together to see if their EEGs are in sync.

One use of our EEG system is for improvising musicians to perform live with their own brainwave-triggered sounds. A nice piece is *The Wheels* performed by drummer William Hooker on the *Brainwave Music Project*.

# 7. Neural mechanisms of emotion and the social synapse

* *How does art affect emotion?*

We face an enormous question, but the interactions between fast-acting *private* synapses and the slower, modulatory *social* synapses in this chapter are responsible for even more than effects of art on emotion: the interactions between the environment and our expectations form our personalities, our speech, our beliefs, who we are as individuals, and how we will act in the future.

We’ll start with hormones, travel to brain synapses, to an enormous variety of drugs that work by effects on these systems, and then approach how the interactions between private and social synapses determine how we experience the outside world.

## Adrenaline, the classic hormone

Hormones are defined as small signaling chemicals that are released from secretory organs: for example, insulin is released from the pancreas and regulates the level of blood sugar, while estrogen is secreted by the ovaries to regulate a variety of sexual characteristics.

Hormones circulate in blood and transmit signals by activating receptors on other organs. This concept is very close to that of neurotransmission, and some compounds are both classical hormones and neurotransmitters.

Let’s start with adrenaline, the first hormone identified, and like Hans Berger’s invention of EEGs, discovered by a scientist experimenting on his son.

The adrenal gland is a relatively small organ encased in gobs of fat near the top of the kidneys: hence, “ad-renal”, next to the renal gland. In 1894, the English physician George Oliver (1841-1915) discovered that an extract he prepared from dog adrenal gland increased blood pressure when he injected it into his son. He noted that the raise in blood pressure was associated with a contraction of his son’s artery.

After Oliver’s publication, a race was on to determine what component of the adrenal gland was responsible. Three different labs reported success in 1897. One called it *epinephrine*, which remains the most widely used term in the scientific literature. A competing drug company, Parke Davis, however, patented a preparation made from oxen or sheep adrenals under the reasonable name, *adrenaline*. There has been so much commercial interest in adrenaline -- for instance it is now used as the “EpiPen” to treat severe asthma and allergic attacks -- that it has been known by thirty-eight commercial names.

Consider what happens when you inject dog adrenaline into your son. The chemical moves through the bloodstream, and where it finds them, binds to two major classes of receptors, reasonably known as *adrenergic alpha* and *beta receptors*. In contrast to the receptors we discussed that rapidly open ion channels to drive electrical current in neurons, hormone receptors activate cascades of enzymatic changes inside cells that can drive a multitude of responses.

The modulatory receptors are now known as *G-protein coupled receptors* (GPCRs). There are an extraordinary number of them, but they are united in consisting of one member each from three protein families that can be mixed and matched. The term “G protein” is due to their activation by a small signaling chemical known as GTP, a derivative of guanosine, one of the four nucleotides that compose DNA.

The range of GPCRs is stunning. Humans have a total of about 23,000 genes, and eight hundred of them code GPCRs! Currently about 140 of these human GPCR genes are “orphans”, meaning that their activators are yet to be discovered.

The GPCRs are responsible for the effects of an enormous range of chemicals in biology, starting with insulin and adrenaline, as well as familiar compounds as dopamine, serotonin, histamine, melatonin, opioids, and cannabinoids (the active compounds of marijuana).

The receptors for sweet, sour, salty and umami tastes are GPCRs. Even light itself is sensed by GPCRs, the opsins and rhodopsin, which are the pigmented photoreceptor proteins in the retina that transform light into synaptic activity.

About 35% of used and abused drugs work by binding GCPRs. These include opium (and morphine, heroin and Oxycontin), cannabis, caffeine, antipsychotics, LSD and antihistamines. Still more drugs like cocaine, amphetamine, and the “SSRI” antidepressants don’t directly bind GPCRs, but release dopamine or serotonin and so act to increase the activity of GPCRs.

Gazing at this list of drugs, perhaps the claim that hormones and GPCRs are involved in emotion is starting to make sense…

The release of adrenaline in the bloodstream is mostly due to activation of the awkwardly named *splanchnic nerve* by pain, anxiety or trauma, which releases acetylcholine that stimulates receptors in the adrenal to release adrenaline and its derivative *noradrenaline* (a.k.a. *norepinephrine*) into the blood. Particularly by activating the alpha-adrenergic receptors on arteries, this leads to the artery constriction and increased blood pressure as in George Oliver’s son, increasing the delivery of glucose that supplies energy to muscles. This adrenaline-activated pathway is thought to underlie stories of amazing feats of strength during emergencies, such as unlikely people lifting up cars after accidents. It can also trigger tears (adrenaline and noradrenaline are found in teardrops), sweaty palms, trembling hands and “butterflies in the stomach”.

Remember that the regularity of heartbeat pacemaking is due to the currents conducted by the ion channels of the sinoatrial cells, but the changes in tempo are not? Adrenaline and noradrenaline are responsible for the change in heartbeat rate. Adrenaline and noradrenaline are released from the adrenal gland, while noradrenaline is released from sympathetic nerves that richly innervate the heart. The sinoatrial cells possess beta adrenergic receptors, and these control calcium ions by activating their release from organelles inside the cells that contribute to the calcium driven action potential. The initiating effect on pacemaker rates is due to these transmitter’s effects on the current known as Ih, and the effect on the speed of the heart provides an example of why these transmitters are called “modulatory”.

*Alpha-sdrenergic* *blockers* are used as drugs, including Trazodone, a widely prescribed antidepressant and sedative to assist in sleep. In addition to slowing heart rate, *beta-adrenergic* *blockers* are used to treat migraine headaches and stage fright. So you can see from these effects that the paradigmatic hormone, adrenaline, to some extent can affect emotion.

## Goosebumps

A challenge in studying emotions is how to measure them. How does one correlate brain activity with insights on beauty? This explains studies on goosebumps, known as *piloerection*, a phenomenon that we can identify when it occurs.

Goosebumps arise because tiny muscles known as *arrector pili* contract around hair shafts to form small depressions in the skin around the follicles that make the hair “stand on end”. While it might be nice to exercise your arrector pili in the gym, the medical literature reports that as of 2018 only three individuals have been found who can produce goosebumps at will.

I’ll give you a guess as to what triggers goosebumps … time’s up …. yes, it’s adrenaline! The hormone activates the arrector pili muscles. A psychoactive plant extract, yohimbine, is an alpha-adrenergic agonist and also causes goosebumps.

With so many effects of adrenaline, why do particular responses occur under different circumstances? We need to consider the interactions within the nervous system.

## Private and social synapses

The first physiological characterizations of synapses were at the connection of neurons from the spinal cord, known as *motor neurons*, that contact muscle fibers at the *neuromuscular junction* that contracts the muscle and is responsible for all of our movements. These neuromuscular synapses must be reproducible and rapid to provide fine motor control and are driven by the fast-acting nicotinic acetylcholine receptor, which opens sodium channels and drives an action potential in the muscle that lasts for about 1-4 ms.

The operation of the pitch receptive neurons of the ear (“hair” cells), as we will see, likewise send fast acting synaptic information through the auditory nerve, and a few rapid synaptic connections later, the signals triggered by hearing arrive at rapidly acting synapses in the auditory cortex, features required to perceive the fine and fleeting features of sound, all though fast-acting private synapses.

GPCR transmission in contrast exerts effects that are longer lasting, often from about 50 msec after release, and in some cases the effects of these events, although usually in the second range, can change circuits that last over a lifetime.

For example, the neurotransmitter *adenosine* binds to a GPCR to help you fall asleep, which obviously changes virtually everything you do. Caffeine is a blocker (*antagonist*) of adenosine receptors, and so helps to keep you awake. *Oxytocin* is a neurotransmitter in the brain and a hormone in the periphery that activates a GCPR enables states of closeness and social bonding, and to signal mothers to nurse infants.

For the control of emotion and mood, the most studied modulatory neurotransmitters are *serotonin*, as the most used antidepressant drugs*, selective serotonin reuptake inhibitors* (SSRIs), obviously work (indirectly) on serotonin (as well as dopamine and noradrenaline) receptors, and *dopamine*.

Serotonin binds to at least fourteen different GPCRs in humans. In addition to its modulation by SSRI antidepressants, these receptors are indirect targets for the “diet” drug fenfluramine, and direct targets for psychedelic drugs that can cause hallucinations including methylenedioxymethamphetamine (ecstasy), psilocybin and LSD.

Dopamine is a precursor to adrenaline and noradrenaline but is also a phylogenetically ancient compound found in many plants and animals: for example, bananas exposed to air become black due to oxidation of dopamine. Dopamine in the brain was initially thought to simply be a precursor for noradrenaline and adrenaline, although the Swedish neuroscientist Aarvid Carlsson (1923-2018) showed that an antipsychotic drug used to treat schizophrenic patients, chlorpromazine, was an antagonist of dopamine receptors.

A popular impression, right, wrong or in-between, is that dopamine is responsible for happiness, love and the appreciation of beauty. This notion originates in one of the most amazing experiments in neuroscience. In 1954, James Olds (1922-1976) at McGill’s Montreal Neurological Institute was attempting to study arousal behavior in a rat by stimulating the reticular formation in the brainstem, a region deep in the brain, with a stimulation electrode. The electrode, however, was not sufficiently deep when he tried applying the electrical stimulus.

In his words, “I applied a brief train of 60-cycle sine-wave electrical current whenever the animal entered one corner of the enclosure. The animal did not stay away from the corner, but rather came back quickly after a brief sortie which followed the first stimulation and came back even more quickly after a briefer sortie which followed the second stimulation. By the third time of the electrical stimulus had been applied the animal seemed indubitably to be "coming back for more" (Olds, 1973).

He rigged a lever that the rat could push to “self-stimulate” by triggering electrical current from the tip of an electrode implanted in their own brain. If the stimulation electrode were inserted into the region he had identified, rats would bar press 2000 times/hour for more than 24 hours straight. Indeed, their rate of pressing could progress from a starting exploratory rate of about 10 per hour up to 5000 presses per hour. Remarkably, he noted that this learned behavior was decreased by chlorpromazine, the antipsychotic drug that Carlsson was reporting contemporaneously to block dopamine receptors.

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| Figure 7.1 Olds’ reward pathway. After noting that the animal would return to the same section of the cage, apparently to receive the same electrical stimulus, Olds made a simple device so that the animal could administer its own stimulus by pressing a lever. He determined regions of the brain where an electrical stimulus was most “rewarding” or “reinforcing”, that is would establish self-stimulation, and other regions that animals would quickly learn avoid stimulating, that is, the stimulus was aversive. The region identified that caused the greatest increase in stimulation was a bundle of fibers that disinhibited the activity of the dopamine neurons. John Langley Howard, trying to find permission. | | |

Olds later altered the electrical stimulation lever so that animals could inject cocaine directly into local regions of the brain, which they would self-administer about ten times per hour.

For about a decade the neurotransmitter responsible for these behaviors was unclear. The initial research by Olds suggested that noradrenaline or a related transmitter was involved, and subsequent research from Roy Wise at the National Institute of Health, Gaetano DiChiara at the University of Cagliari in Sardinia, and others eventually settled on dopamine, the precursor to noradrenaline, as the major target. Indeed, all of the self-administered drugs that lead to addiction or dependence, including alcohol, opiates, nicotine, amphetamine and others, have been found to enhance dopamine neurotransmission.

## Dopamine transmission is implicated in the effects of listening to music

The evidence that dopamine neurotransmission underlies learned reward as in the self-stimulation experiments led to the widespread idea that dopamine causes pleasure, but this remains a difficult concept to test in the laboratory as it is challenging to measure pleasure. We can certainly measure increased dopamine release while animals have sex, drink alcohol, eat chocolate and peanut butter: it is suspected that the “pleasure” is due to the release of endogenous opiates rather than dopamine.

What we can observe is that increased dopamine release can lead to an increase in performing a particular task, a process known as reinforcement, and recordings of dopamine release during learning by Mark Wightman and Regina Carelli at the University of North Carolina have demonstrated this relationship at the level of changes that occur in seconds and even milliseconds. Experiments in monkeys during the performance of reinforcement tasks by Wolfram Schultz’s lab in Cambridge show that the pattern of action potential firing by dopamine neurons follows the sort of rules and changes over the course of seconds that psychologists conjecture are involved in reinforcement learning. Dopamine release is also implicated in the motivation of behavior, but this process remains poorly understood.

The tools for measuring dopamine release in people, where we can at least ask about emotions, are comparatively blunt. At present the field mostly relies on a brain imaging technique known as positron emission tomography (PET) in which a compound that binds to dopamine receptors is made radioactive and competes for binding with native dopamine release: the more dopamine release, the lower the binding of the PET ligand. This approach is used by Robert Zatorre and colleagues at the University of Montreal, who find that music that gives listeners “chills” is associated with greater dopamine release and increased blood flow in regions associated with dopamine release, and that there is less dopamine release and activity in these regions when people listen to “neutral” music or “unpleasant” sounds (realizing how subjective that is: consider our *Most Unwanted Music* project). While the popular image of more dopamine at least correlated with pleasure or emotional valence seems fair, this can’t be the whole story: why is it released, what is it doing, and how does it change brain circuits to reinforce future behaviors?

## Social and private synapses meet, win friends, and influence people

An action potential at a private synapse typically lasts a millisecond, whereas signaling by GPCR receptors responding to dopamine, noradrenaline and other modulators social synapses lasts for seconds and sometimes much longer. How can systems at such different time scales communicate? How can these allow us to choose what to do in response to the environment?

The striatum is a large brain region located under the cortex that integrates these signals, particularly from private synapses formed by cortical axons with dopaminergic social synapses. The role of these synaptic circuits is to integrate what we sense in our environment with our existing set of responses to choose from a set of competing possible behaviors. Some “loops” are chosen and others suppressed, and with a few more steps, the processed signals are sent back out to the cortex. The resulting decisions are sent to the spinal cord to activate the selected sequence of muscles one by one during voluntary actions. Even a simple behavior, like reaching and grabbing an object, requires many muscles to contract at the right sequence, and this system allows this to occur.

These synapses can also change themselves, allowing us to learn new skills. As befits the breadth of activities we can execute, there are perhaps billions of these cortical-dopamine-striatal synapses. While the midbrain dopamine neurons in human are a relatively small in number, about 300,000, they may each have about a million synaptic release sites, in which case we may be considering a bewildering 300 billion possible synapses.

But as in late night TV ads, “wait, there’s more”! When a release event occurs at a dopamine synapse, it overflows to interact with many other synapses. If we examine a single private synapse at immense magnification using an electron microscope, we observe a presynaptic input from the cortex making a private synapse with a “spine” of the striatal neuron, and a nearby input from the dopamine axon forming a social synapse. The striatal neuron itself releases the neurotransmitter GABA, and this also interacts with the other elements. There are additional nearby inputs from other striatal neurons and from other parts of the brain. We can call this a “synaptic microcircuit”.

At the microcircuit, each element has a receptor for the other transmitters, and also a receptor for its own neurotransmitter, which is called an “autoreceptor” that typically decreases the neuron’s activity. Even in this simplified version of a striatal microcircuit in the figure, that means there are 210 = 1024 receptor on/off combinations at any time. Add to these the numerous other receptors and transmitters and the different durations of effects and consider the many different inputs and synapses in this system, the idea that these interactions provide us with so many possible behaviors – how to speak and move, what to say, and what to not do – may begin to seem reasonable. I tell my graduate students not to worry too much about running out of research questions in their future career.

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| Figure 7.2 A striatal microcircuit. A highly simplified illustration of a striatal microcircuit by Nigel Bamford (Yale University) indicates D1 and D2 dopamine (DA) receptors (these are typically on different medium spiny neurons), AMPA-type receptors for glutamate (GLU), and M2, M4, and alpha7 nicotinic receptors for acetylcholine (ACh). Even with this vast simplification with only 10 receptors indicated, the circuit can have 210 = 1024 states. *Figure by Nigel Bamford, used with permission.* |

So how can the slow social dopamine synapse change the rapid private synapses? For the striatum, the prevailing theory is that the dopamine release occurs with unexpected “reward” from the environment, for instance, a performer realizing that the audience appreciates how she sang a particular note. The cortical signal that drove her to sing it in that fashion was recently active and sent a signal both to the spinal cord that activated the muscles that formed that note and a second *collateral* signal from an axonal branch to the striatum. In work by Nigel Bamford’s lab at Yale, it appears that the dopamine depresses the activity of those cortical axons that weren’t involved in producing that unexpectedly successful note, while leaving the neurons responsible for the success alone. The mechanism of inhibition, by the way, appears to require the release of a “cannabinoid”, a neurotransmitter that activates the same receptors as THC from marijuana, from a striatal neuron that feeds back to inhibit cannabinoid GPCR receptors on the presynaptic side of the cortical axon. The cannabinoid release appears to selectively occur when dopamine and glutamate activity are concurrent or nearly so.

You can imagine that if the new state of these circuits lasts long enough to favor new specific microcircuits, that the coincidence of a successful motor instruction and unexpected reward can teach us how to adapt to our environment, learn to speak a language, and change how we will sing the next time.

# Listening

This chapter might entail discussion on favorite songs about drugs that affect GPCR activity.

I skip the thousands of songs about alcohol because, embarrassingly enough, the neuroscience field still hasn’t clearly discovered its specific action or receptor in the brain.

*Spoonful* by Charlie Patton (dopamine receptors)

*Heroin* by the Velvet Underground (opiate receptors)

*Purple Haze* by Jimi Hendrix (serotonin receptors)

*Who put the benzedrine in Mrs. Murphy’s Ovaltine* by Henry the Hipster Gibson (dopamine receptors)

*If youse a viper* by Stuff Smith (cannabinoid receptors)

Hector Berlioz’s *Symphony Fantastique* is widely suspected to have been written under the influence of opium.

I collaborated with filmmaker Winsome Brown on *The Violinist*, a story of a Russian violin virtuoso in New York played by Rebecca Cherry who became addicted to opium when the drug was declared illegal by the Harrison Act in 1914: a piece intended to evoke drug effects is *The Unfolding Opium Poppy*.

# 8. Ear physiology: how air waves become sound

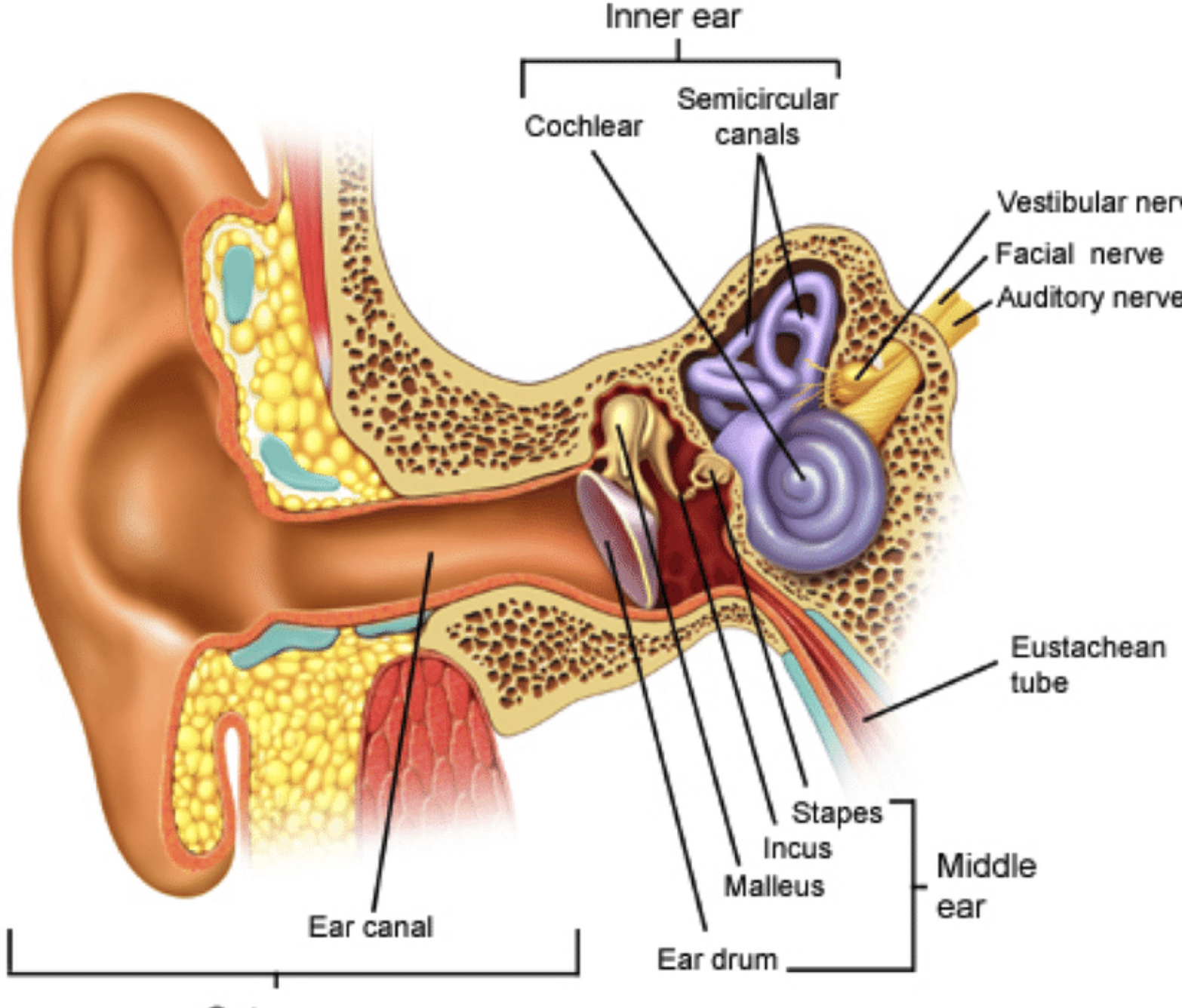
* *How does the ear transduce air waves into electricity and neuronal activity?*
* *Does the peculiar shape and structure of the ear change sound?*

Our Virgil for how the ear translates sound into electrical activity in order to transmit signals to the brain will be Elizabeth (Lisa) Olson, a professor of *Otolaryngology* (ear nose and throat) who studies hearing mechanisms in her lab at Columbia University. Some of her research examines the auditory system of the katydid, a.k.a. the bushcricket, a singing grasshopper-like insect, and while their ears are underneath their knees, they operate in ways similar to ours.

## Step 1: Why big ears?

Our massive external ear funnels a large volume of air into the smaller ear canal, thereby increasing the pressure of the signal. After the air waves enter the ear canal, there is still more amplification of air pressure as the canal narrows, so that sound wave amplitudes become much greater in the ear than in the outer air.

The folds of the ear, known as *pinna* or *auricle*, focus air waves towards the ear canal, and in the process slightly delay and defocus incoming sound. Like the body of a cello or guitar, the outer ear and canal resonate (!). The resonant frequencies are particularly powerful around 3 kHz, a bit above fundamental frequencies in music but important for hearing phonemes in speech.



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| Figure 8.1 The ear. *For Lisa Haney: we will use hammer anvil stirrup instead of stapes incus malleus, and pinna, and let’s more clearly label the ear drum, otherwise this is pretty good!* |

Our outer ear to ear canal ratio is not as impressive as that of house cats, who not only have a large area, but like mini-Linda Blairs in the *Exorcist*, can turn their ears 180 degrees to focus on sound coming from a specific direction.

## The ear drum, where air waves become mechanical waves

At the end of the ear canal, vibrations in the air encounter a small biological drumhead, the *eardrum* (a.k.a. the *tympanic membrane*). In an adult male, the area of the eardrum is about 60 mm2 (a dime is about 250 mm2). Its construction is reminiscent of vocal cords, with a thin layer of skin over a mucosal layer and a laminar layer.

The most influential scientist in this field, the Hungarian Georg von Békésy (1899-1972), examined dissected eardrums from cadavers to demonstrate that the vibrations were indeed similar to the stretched membrane on a drumhead.

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| Figure 8.2 Vibration of the eardrum. A contemporary version of von Békésy’s approach, this human ear drum was stimulated at three different sound frequencies, with the vibrations observed by high speed video. The rows represent three applied frequencies and the three columns show the vibration in each spatial dimension, with red indicating the greatest displacement and blue the least. The patterns show resonances that resemble a snare drumhead.  From Kaleghi et al., (2015) *Three-dimensional vibrometry of the human eardrum with stroboscopic lensless digital holography*, J. Biomed Opt., doi [10.1117/1.JBO.20.5.051028](https://dx.doi.org/10.1117%2F1.JBO.20.5.051028), Creative Commons. |

Until this point in the auditory pathway, sound has been transmitted as air waves, but the eardrum transduces these into a different form of energy, mechanical vibrations, the way that air waves are transduced to mechanical vibrations by the membrane in a microphone. After the eardrum, the vibrations remain in the form of mechanical energy for several more steps.

## Bones of the middle ear and how air waves are transformed to fluid waves

Interior to the eardrum is the **middle ear**, a region filled with air and separate from the next step within the fluid filled **inner ear**. At the border of the outer and middle ear, the eardrum passes its mechanical vibrations to the three smallest bones of the body, the *ossicles*. These are the hammer (malleus), *anvil* (incus) and *stirrup* (stapes, pronounced “staep-eez”): as you know if you make horseshoes, the hammer strikes the anvil. The ossicles vibrate with the mechanical version of the sound wave, and as the mechanical pressure at the ear drum increases and decreases, the ossicles move back and forth.

The final ossicle indeed resembles a stirrup, but rather than tapping the ribs of a horse, it raps on the entrance to the inner ear. The stirrup acts as a hammer or piston to transmit these vibrations to a membrane known as the *oval window* at the border with the **inner** ear, where the energy is transduced again, in this case from the vibrations of membrane and bones to vibrations of the fluid within the inner ear, known as *endolymph*.

Throughout this process of changing the mechanical means by which the energy of sound is conveyed, one might think that there would be a great deal of entropy and loss of the signal. Lisa Olson tells us, however, that while there is some reflection in the middle ear that dissipates sound energy, at the frequencies where hearing is most efficient about half of the sound energy that entered the ear canal is effectively transmitted by the middle ear to the inner ear.

The *stapedius reflex* (also known as the *acoustic*, *middle-ear muscle*, *attenuation*, or *auditory* reflex) occurs in response to loud sound and when one speaks. The stapedius, at 1 mm in length the smallest skeletal muscle in the body, stabilizes the stirrup. When the muscle contracts in response to loud sound, it pulls the stirrup back a bit from the oval window and decreases the transmission of vibration to the inner ear. When the stapedius doesn’t operate properly, for example in cases of Bell’s palsy, this causes *hyperacusis*, in which normal sounds are perceived as being very loud.

## The cochlea, a snail with seawater

The inner ear consists of a coiled bony tube known as the *cochlea*, the Greek word for snail, and as mentioned, is filled with fluid. The length of the spiral stretched end to end from the outermost (*basal*) spiral to the innermost (*apical*) coil is about 30 mm. The basal end eventually broadens and develops into large striking lobed M.C. Escher-esque *semicircular canals* of the *vestibular labyrinth* that are responsible for other the major function of the ear, the sense of balance.

The tissue within the cochlea’s spiraled tube is divided into three chambers. The uppermost is the *scala vestibuli* (or *vestibular duct*: *scala* means ladder and *scale* means stairs in Italian), the middle is the *scala media* (or *cochlear duct*), and the lower is the *scala tympani*.

These three chambers are separated by two membranes. The separation between the *scala vestibuli* and *scala media* is the thin t(wo-to-three cell layer thick) *Reisner’s membrane*. The *scala media* and *scala tympani* are separated from the lower chamber (*scala tympani*) by the elastic *basilar membrane*, which is our primary focus.

The scala media is filled with endolymph, which has a density similar to seawater. Unlike the other fluids of the body such as blood or cerebral spinal fluid, or for that matter genuine sea water, all of which are high in sodium, endolymph is composed of high levels of potassium. In this special case, opening potassium channels carries potassium into instead of out from cells and causes a depolarization. The other two chambers of the cochlea are filled with the fluid *perilymph,* which is a usual biological fluid high in sodium*.*

Running above and along the length of the basilar membrane is a layer of epithelial cells known as the *organ of Corti* after the Italian anatomist, the Marchese Alfonso Corti (1822-1876), who described it in 1851. Corti’s organ is made from a variety of epithelial cells, including *hair cells* that are responsible for sending sound information to the auditory nerve and from there to the brain: these important cells will be discussed shortly. The organ also features an interior liquid filled “tunnel” filled with perilymph. Yet another membrane, the gelatinous *tectorial* membrane, sits atop the organ of Corti within the endolymph of scala media, and is important for the operation of the outer hair cells.

The organ of Corti and its associated basilar membrane provides the essential step for our hearing of separating the sounds arriving from the outside world into their component frequencies.

Lisa Olson explains the steps by which sound energy transfers from the tapping bones of the middle ear to the inner ear structures as follows:

*When the movement of the stirrup pushes the oval window in and out, this distends the basilar membrane. This distension moves the organ of Corti close to the stirrup in an up and down direction. That motion in turn launches a fluid and tissue wave of transverse motion down the length of the cochlea. At very low frequencies below our range of hearing, the fluid may be pushed longitudinally all of the way to the apex of the cochlea. At audible frequencies, however, the fluid moves only part of the distance.*

So we have an organ of only about 30 mm in length that allows us to hear our entire frequency range. But this is far too short!

Recall from our ancient pre-Pythagorean text, Chapter 1, that the wavelength of the note A4 above middle C (440 Hz) in air is 3.5 meters, about the height of two adults. Now remember that the speed of sound in seawater is nearly 5-fold faster than air at sea level (1500 m/sec vs. 340 m/sec), which means that the note A4 in endolymph has a wavelength of about the height of a five story building. The A0 at the bottom note of the piano in the ear would have a wavelength of 54 = 625 stories tall!

Our (or Whomever’s / Whatever’s) design problem: how can an organ only 30 mm long provide all of the frequency information that runs the range of our hearing, from about 20 to 20,000 Hz?

As you will now see, the term “organ” of Corti is appropriate not only as a body part but in analogy to the keyboard instrument.

Imagine the basilar membrane as a rubber band that becomes wider and thicker along its length: you remember that thicker piano strings vibrate at a lower frequency than thin strings, and so the skinny base of the membrane resonates at higher frequencies than the thicker apex.

(I know for musicians this is confusing, remember that the “base” of the organ of Corti is actually responsible for transmitting the more treble notes.)

Now picture the band crossed diagonally with railroad tracks of tough collagen fibers, the protein that stiffens skin, with thicker and stiffer fibers at the base, yielding to floppier fibers at apex and recall that lower tension strings vibrate at a lower frequency. The outcome of this design is that the higher frequency components resonate at the stiff, thin basal end, and the lower frequencies resonate at the larger, floppier apex.

You can imagine the isolation of resonant frequencies along the basilar membrane like the slats on a marimba, where larger slats vibrate at lower frequencies and each slat is isolated from the next, so that striking a B natural transfers virtually no audible vibration to the neighboring A or C natural slats. The stiffness of the basilar membrane makes the vibration fall off quickly that the neighbors don’t wake up. This design allows the component frequencies of a sound, like the components of sound observed in a Fourier transform, to be distributed like the notes of a chord along the organ (or marimba) of Corti.

So far, the auditory pathway has transduced air vibrations into mechanical vibrations in tissue and fluid and now to a separation of the component frequency waves of the original sound at specific resonant regions of the basal membrane. To send this signal to the brain, we need two other forms of transduction, from mechanical to electrical waves and then to chemical signaling at synapses. These processes are the topic of most of the rest of this book.

Amazingly, this design of the basilar membrane was introduced during the American Civil War by the German polymath Hermann von Helmholtz (1821-1894) in *The Sensation of Tone* (first edition, 1863). This book has inspired me since high school, and kindled Harry Partch’s exploration of tuning.

*It is probably the breadth of the basilar membrane in the cochlea that determines tuning. At its commencement opposite the oval window, it is comparatively narrow, and continually increases in width as it approaches the apex of the cochlea … the radial fibers of the basilar membrane may be approximately regarded as forming a system of stretched strings, and the membranous connection as only serving to give a fulcrum to the pressure of fluid against these strings. In that case, the laws of their motion would be the same as if every individual string moved independently of all the others [like a piano] …. Under these circumstances the parts of the membrane in unison with higher tones must be looked for near the round window, and those with the deeper, near the vertex of the cochlea.*

OK, he wrote what I did, only a century and a half earlier and more elegantly (I hate him!). What’s more, he determined from the number of fibers he could observe in the human cochlea that we should be able to distinguish about 4200 different musical pitches, extremely close to the estimates we report now: it would seem that Phill Niblock’s 500 pitch composition could be expanded upon.

## Hair cells transform mechanical sound waves to electrical sound waves

The transformation of mechanical energy to electrical energy is known as m*echanotransduction* and accomplished within the hair cells within the organ of Corti. “Hair” is a confusing name for a cell type, but they appeared to possess “very peculiar, stiff, elastic hairs”, now known as *stereocilia,* to their discoverer, the German microscopic anatomist Max Schultze (1825-1874). Hair cells are used not only for hearing, but in semicircular canals for the sense of balance. The human cochlea contains about 12,000 *outer* and 3,500 *inner* hair cells.

The stereocilia arranged in *hair bundles* atop each of these cells consist of 20-300 individual hairs with the rows sloping so that each successive hair is taller than the last, suggesting a Mohawk haircut. Each hair in a row attaches itself to the next taller by a tether near the cell’s top, providing a means to make all of the hairs in a row move together.

Hair cells have synapses at their basal end, but in other ways are unusual for neurons. They do not fire action potentials and lack both axons and dendrites, but are sausage shaped with the characteristic tuft of hair at the top. They are typically classified as “epithelial” cells, a class that includes cells of the skin and tissue linings.

The base of the hair cells is within the organ of Corti, and the body of the cell extends upward, and in the case of the longer stereocilia of the outer hair cells reach to and strongly attach to the tectorial membrane. The upper part of hair cells are exposed to endolymph, while the base is surrounded by supporting cells and bathed in the perilymph of the lower chamber.

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| Figure 8.3 of the cochlea showing the layers and hair cells.  We don’t need the Deiters cells or stria vascularis shown. The stereo clila (hair tufts) should be more clear and show the tethers. We can label endolymph and perilymph. |

An essential job for the hair cell is to respond to the mechanical movements of the inner ear and transduce to electrical energy by opening ion channels. For the hair cell to accurately transduce sound information, the lack of the requirement of an action potential to activate their synapses to the auditory nerve is important. Consider that typical neurons require an action potential depolarization of 100 mV or so to trigger the release of neurotransmitter, and so small changes in excitation don’t activate these cells: their firing can be described as “all or nothing”.

In contrast, for sensory systems, including seeing and hearing, there is an activation by small changes in light or sound: for vision, a rod cell in the retina can under the right conditions see a single photon, the lowest possible light! The human eye can respond to about a billion-fold differences in light intensity.

For hearing, the sound wave amplitude range we perceive can also vary by about a 10,000,000-fold, as detailed in our discussion of loudness in Chapter 1. Therefore, these systems need to be “graded”, meaning a response can react to a broad range of inputs and the typical all-or-none synapse is ineffective. Indeed, increased synaptic transmission at the inner hair cell to auditory nerve neuron can occur with only about a thousandth of the voltage change of an action potential.

When the hair tufts are pushed and pulled by the sound-evoked movements of the basilar membrane, a mechanical force is produced that opens an unusual cation channel that is activated by motion rather than a chemical signal. As the endolymph is high in potassium, the channels provided a potassium current that depolarizes the hair cell (remember that in most other biological fluid, potassium hyperpolarizes neurons), as well as calcium. This is the step where sound is transduced from waves of mechanical vibration into waves of electricity.

The depolarizing currents from the hairs at the tip of the hair cell open our old friends from two chapters ago, voltage sensitive calcium channels, at the base of the hair cell. Depending on the graded size of this calcium current, there is a wide range of numbers of synaptic vesicle that fuse and release glutamate as a neurotransmitter. The synapses, mostly of the inner hair cells, activates the first bona fide neuron in our auditory pathway, the cells of the auditory nerve. About 95% of the inputs to the auditory nerve are from inner hair cells, and only 5% from the outer hair cells. Thus, the inner hair cells are mostly responsible for transducing vibrational energy to synaptic signals and electrical activity conveyed by the series of neurons in the nervous system.

While hair cells are found throughout the animal kingdom, but outer hair cells are only in mammals. Outer hair cells have fewer synapses on the auditory nerve neurons than inner hair cells but play an important role as mechanical amplifiers that increase the basilar membrane’s sound response. When outer hair cells move, they produce tension because the taller hairs are fastened tightly to the tectorial membrane above and the upper and lower membranes can move in opposite directions. As with inner hair cells, the push and pull of the hair tufts produces a mechanical force that opens cation channels that drive depolarization by entry of positively charged calcium as well as the from the high potassium of the endolymph.

The important job of the outer hair cells is to amplify the movement of the basilar membrane to further stimulate inner cells. This amplification by outer hair cells occurs because their membrane contains millions of molecules of a protein known as *prestin*. Prestin is a transporter protein that is considered to act as a piezoelectric mechanism, as it transduces mechanical and electrical signals by changing shape, in this case by very rapidly changing the length of the hair cell in response to changes in membrane potential, a sort of reverse mechanotransduction.

The prestin molecules are on the sides of the outer hair cells, embedded in the membrane. When the outer hair cell is depolarized, the prestin molecules are physically compressed in the plane of the membrane, effectively making their area and the area of the membrane smaller so that the cell shortens. Hyperpolarization makes prestin’s area larger, perhaps by about 3 nm2 per molecule, and the so the outer hair cell membrane grows and the cell becomes longer. This mechanical vibration of hair cell length is large enough to be viewed in a microscope video camera,and amplifies the vibrations at its resonant location on the basilar membrane. This local extra vibration of the correct region on the basilar membrane acts to enhance the sharpness of the frequency response and so the accuracy of the frequency response of the local inner hair cell. The importance of outer hair cell amplification is seen in that mutations of prestin that cause deafness.

Piezo electricity was discovered by the brothers Jacques and Pierre Curie in 1880 while studying the electrical properties of crystals including table salt and sugar. Piezo microphones are used to amplify musical instruments in live performance, as they don’t respond to vibrations in the air and are less prone to feedback and transmitting unwanted sounds that microphones that pick up from air waves. For string instruments, piezo mics are often mounted on the bridge and so pick up little of the sound from the body. Piezo pickups are made of hard material, often ceramic, and some biological materials like bone, some proteins and even DNA can be used as piezo microphones as they accumulate and discharge current as they change shape with applied vibration.

## Cochlear otoacoustic emissions

The cochlea can produce sounds itself, sometimes loud enough to be heard by others, known as *otoacoustic emissions*. These occur spontaneously in at least half of the population, although most of us are unaware of them when they occur. They are not illusions and can be recorded by microphones, but as their production requires an intact inner ear structure, they are used as a noninvasive test for hearing, particularly in newborn babies.

They can be evoked by playing clicks or tones into the ear, which are thought to activate outer hair cells to produce sufficient energy to move the basilar membrane. One approach, known as a *distortion product otoacoustic emission*, is to play to two frequencies, typically between 800 and 8000 Hz, with one usually about 20% higher than the other. If the inner ear is functioning normally, it responds by emitting the difference frequency.

Other studies, however, indicate that difference tones can also be heard when the two played frequencies are separated into the left and right ear, suggesting that the difference tone might arise at a later stage of the auditory pathway where inputs from the two ears are integrated. Of course, both the ear and brain might be found to play roles.

# Listening

James Hudspeth at Rockefeller University produced an animation of how the cochlea would respond to the fundamental frequencies of Bach’s *Toccata and Fugue* in D minor.

Maryanne Amacher’s piece *Chorale* is intended to produce otoacousgic emiissia as well as combination tones within the ear.

# 9. Deep brain physiology of sound

* *How do we tell the direction that a sound comes from?*
* *We only have two ears: how can we separate a conversation in a party and identify a single instrument in a band?*
* *Why are we usually unaware of the loud sounds from our own breathing and chewing and other background sounds?*
* *How do we associate music with times, places, and dreams?*

Let’s retrace the steps of sound’s voyage into the brain:

1) the mechanical vibrations of *air waves* are amplified by the aerodynamics of the outer ear

2) the amplified air waves are transduced to *mechanical waves* of vibrating tissue, initially at the ear drum which acts like a microphone membrane, and then to vibrating bones of the ossicles

3) the final ossicle, the stirrup, drives the oval membrane to stimulate liquid filled chambers in the cochlea, producing *fluid waves* that drive the basilar membrane to vibrate

4) due to the increased size and decreased stiffness along the length of the basilar membrane in the cochlea, the constituent frequencies that comprise the sound produce resonant waves at specific locations, running from the highest pitches at the membrane’s base to the lowest pitches at the apex

5) the local waves on the basilar membrane create shearing forces at stereocilia at the tip of local outer hair cells: this produces effects like a piezo microphone, driving compression and lengthening of the cells, to amplify the local waves

6) the local waves on the basilar membrane activate mechanosensitive ion channels on inner hair cells, driving calcium influx into the cells

7) the calcium influx triggers synaptic vesicle fusion and release of glutamate from inner hair cell onto the postsynaptic neurons in the cochlea that bundle together to form the auditory nerve that enters the brain.

For the rest of the pathway of sound perception, we will remain in the brain. Here, the synaptic / electrical version of sound is sent to many regions: indeed, neuroscientists often call the synaptic pathways from the cerebral cortex throughout the rest of brain *corticofugual* in homage to the complexity of the fugue in music. The more the field looks for synaptic connections, the more we find.

## The auditory nerve broadcasts on 30,000 channels

We last left the auditory pathway at the synaptic inputs from the inner cells to the peripheral axon of neurons that form the auditory nerve. In humans, there are about 30,000 auditory nerve neurons per ear.

The neurons of the auditory nerve have an unusual anatomy. The cell bodies are in the *spiral ganglion* inside the cochlea, and they are considered to have two axons, a short *peripheral* axon that receives inputs from the hair cells, and a much longer *central* axon that bundles with the central axons of other spiral ganglia cells to form the *auditory nerve*. These take the signals from the ear to the brain, where things get pretty complicated… allowing us to listen to, create, and imagine sound and music.

Amazingly, recordings with electrodes similar to those used for EEGs auditory nerve firing can essentially be played back through a speaker and still be recognizable as the sound that drove it.

This occurs in part because dozens of the peripheral axons of the auditory nerve neurons can receive inputs from a single hair cell, and so many of the neurons can transmit the sound of a given frequency: this redundancy is important when we consider how the nervous system transmits frequencies of electrical activity that are higher than individual neurons can fire. Recall that we hear frequencies as high as 20,000 Hz, but even very fast neurons rarely fire faster than 200 Hz: while the neurons of the auditory system have the fastest firing rates of any in the body, but they still tend to peter out at around 300 Hz. This problem is solved because some of the 30,000 neurons that have axons in the auditory nerve fire at some point during the wave peaks so that a sound wave can be reconstructed.

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| Figure 9.1 of auditory nerve response to musical intervals. Mark Tramo’s lab played harmonic intervals built on a just intonation scale into the ear of a cat while recording action potentials from individual axons in its auditory nerve. The root of the interval was always A4 (frequency = 440 Hz, period = 1/440 = about 2.3 ms). The plots show the temporal activity of 50 axons. The x axis shows the time between action potentials, known as the *interspike interval* (ISI); the y axis shows the number of times each ISI occurred. In each plot, the peaks are at multiples of the root and interval and their subharmonics. When the periods of the two pitches coincide at an ISI, the height of the peaks at that ISI is larger. The arrows point to the peaks at the fundamental period of the harmonic interval that corresponds to the fundamental, f1. The “consonant” perfect 4ths and 5ths have more regular intervals than the relatively “dissonant” minor 2nd and tritone, not only in air (Chapter 4) but also in the temporal discharge patterns of axons in the auditory nerve. (Permission from Mark Tramo.) |

You can consider wave sampling by the auditory nerve as similar to the data in a digital sound file. The CD format used 41,000 Hz per mono track to sample sound waves. If the 30,000 neurons of an auditory nerve fire at 200 Hz, we could sample at 600,000 Hz, much faster than a CD. But our nervous system is better still, as a CD file samples at the same rate no matter what, whereas only the appropriate axons for a specific frequency are activated in the auditory nerve. Score one for biology as an engineer!

## Sound reaches its first synapse within the brain

The region of the brain that receives the auditory nerve axons is known as the *cochlear nucleus*, an unfortunate name as it is actually in the brainstem. The output axons from the auditory neuron map onto this nucleus in a high to low frequency gradient, so that the pattern of the genuine cochlea’s frequency distribution is preserved in the deep brain. Some of the auditory nerve axons produce enormous synapses known as the *endbulb of Held* (after the German anatomist Hans Held, 1866-1942) that transmit signals to cochlear nucleus neurons known as *globular bushy cells*.

The axons of globular bushy cells cross the midline of the brain to innervate a region on the other side associated with the opposite ear, the *trapezoid* body. This synapse is the most rapidly responding synapse in the nervous system, and is known as the *Calyx of Held,* due to Hans’ impression that its appearance resembled a flower calyx. In contrast to a typical synapse of about 1 µm (micron), the Calyx of Held is 20 µm across, the size of an entire cell body. This is so large that the presynaptic side can be recorded by a recording electrode similar to a tiny electrical wire, and so the Calyx of Held has been valuable for the study of fundamental properties of synaptic communication.

## Marching to the midbrain

Eventually, whether through a direct path or indirect path like the Calyx of Held and through the exotically named *superior olive nucleus*, the outputs of the auditory pathway mostly converge into a bundle of axons known as the *lateral lemniscus* that extends from the brainstem into the midbrain. These axons synapse on neurons in the *inferior colliculus*, often referred to as the midbrain “sound center”.

Nina Kraus’s lab at Northwestern University has shown that if they place an electrode into the inferior colliculus of a guinea pig, the original sound can *still* be fairly well recreated by playing the electrical activity through an amplifier and speakers. This means that even at this advanced stage, the frequencies of the original sounds are transduced to similar frequencies of electrical activity in the deep brain.

An important function of the inferior colliculus is to determine the direction of a sound in the environment. The way that small differences between the time that a sound reaches each ear work to localize sound were characterized by Eric Knudsen at Stanford and Masakazu Konishi at Caltech in the barn owl, a bird that requires an ability to map the source of sound to find food.

As mentioned, the Calyx of Held synapse can transmit information at a very fast rate, with the smallest (*quantal*) units of glutamate release due to the fusion of a single synaptic vesicle, as rapid as 1000 Hz. Sound traveling from one side of a room takes nearly a millisecond to travel around your head, and so the more distant ear hears it a millisecond later. Because the Calyx of Held synapses are so rapid, time differences between the arrival of sound to each ear (known as *interaural delay*) can be compared when they arrive the inferior colliculus, and the ability to detect these tiny delays serves to triangulate the direction from which the sound must have arrived.

## Onward to the thalamus

With the exception of smell, the pathways from each sense, including vision, touch, and perception of hot and cold, converge into a large inner brain region known as the *thalamus*. For example, vision related axons project to the *lateral geniculate* nucleus in the thalamus. The thalamus is often called a “relay station” for sensory inputs on the way to the cortex.

For sound, the output axons from the inferior colliculus run major axonal output projections on both sides of the brain into a region of the thalamus known as the *medial geniculate nucleus* (MGN). Even at this advanced stage, the MGN maintains a frequency map, with the edges more responsive to low frequency sounds and the center portions to high frequencies. The neuronal activity in the MGN is also controlled by the volume and duration of sound.

Daniel Polley’s lab at Harvard shows that inputs to the MGN also arrive from the auditory cortex, a region that we haven’t yet arrived to. This backward projection from a later stage in the auditory pathway produce what engineers call a *feedback* system, in which the cortical feedback can enhance or depress sensitivity to volume and frequency depending on the rhythm and timing of the cortical inputs. This feedback loop appears important for deciding which sounds we notice or ignore. For example, in a noisy environment, the cortical feedback to the MGN may instruct us to ignore the high background sounds by inhibiting the neurons that would otherwise transmit the “background noise” that we ignore, allowing us to focus on the important aspects of the sound signal that continue to pass.

Victoria Bajo’s lab at Oxford demonstrated that the feedback of the cortex to the MGN is important for determining if particular frequencies present in a sound are absent from the normal harmonic series. This ability should help in separating sounds into specific sources, for example which sounds are coming from a particular person speaking in a crowded room (the cocktail party problem) or distinguishing the instruments in a band.

A striking realization is that we are mostly unaware of the sounds of our own chewing and breathing, although their sounds are loud in our ears. (Refer also to the stapedius reflex which occurs when we speak or sing back in the previous chapter).

Eric Bowman’s lab at St. Andrew’s University suggests this is due to feedback from the cortex that inhibits the activity of another region in the thalamus, the *reticular nucleus*. It appears that feedback from the cortex and other brain regions to the reticular nucleus, perhaps by inhibition of appropriate MGN neurons, also confers the ability to ignore particular sounds, allowing us to concentrate on those that are more important. It is even suspected that the auditory hallucinations experienced by people with schizophrenia may result from an abnormal connectivity of these synapses, and also could contribute to the sensory overload experienced by some individuals with autism.

## The auditory thalamus projects into the striatum

One of the MGN’s major projections is to the *auditory striatum*. You will remember from Chapter 7 that activities in the striatum are linked to emotion, learning and choice. The auditory striatum receives dense input both from the MGN and the auditory cortex. How can the striatum integrate these signals?

A recent study from Qiaojie Xiong at Stonybrook University suggests that thalamic inputs from the MGN to the striatum act as an amplifier, whereas the cortical inputs to the striatum determine the frequency response. The coincidence of both inputs determines which will be effective and which will be ignored.

Another recent study from Mitsuko Watabe-Uchida at Harvard indicates that sounds can activate dopamine axons in the auditory striatum, which could enable learning. For example, the sound of a train whistle might release striatal dopamine and encode a new synaptic circuit that associates that sound with a learned response to “get off the track”.

A clinical manifestation of the thalamostriatal auditory projections may occur in Parkinson’s disease patients, who have trouble initiating movements but can still respond rapidly to a sudden sound like a car horn. This could be due to thalamic activation of the striatal circuits that initiate a motor response, even in the absence of normal cortical synaptic inputs. The circuit might also explain why Parkinson’s patients often to continue to dance well to music.

## The auditory thalamus projects to the cortex

The MGN’s auditory information also travels by massive axonal outputs to multiple cortical regions, particularly the *auditory cortex*. This region was discovered in the 1940’s by the neurosurgeon, Wilder Penfield (1891-1976), who left the Columbia University Department of Neurology in 1928 due to academic power battles – some things never change – to cofound the Montreal Neurological Institute where he conducted his most influential research.

Together with his colleague Herbert Jasper (1906-1999), Penfield introduced the idea that EEGs could determine where epileptic seizures were initiated prior to surgery, and developed the *Montreal Procedure*, a surgical approach to treat of epilepsy. The Montreal Procedure and its offspring are still used to treat epilepsy when drug-based approaches are unsuccessful.

After locating the general cortical region in which the seizure begins with the EEG, these operations locate the specific region source by applying a small amount of current to the electrode at different locations. The patient is awake during the surgery and can report their response. Once the correct spot is located, because it triggers the characteristic seizure, the surgeon applies a bit more current to damage a small number of neurons in that part of the cortex. In most cases, the patient returns weeks later to the clinic with normal function and no further seizures.

Penfield’s scientific writing is a rare pleasure to read, and he could have been an excellent mystery novelist – indeed, he wrote novels after retirement. His famous drawing of the “homunculus” illustrates the regions of the cortex that controlled muscle activity, which he naturally enough named the *motor cortex*. Just across the central sulcus from the motor cortex are regions where stimulation produced sensation in specific regions of the body, which he called the *sensory cortex*.

The cortex in some mammals, including human, is highly folded, increasing the surface area. An inward valley is called a *sulcus* or a *fissure*, and the large one that runs sideways across the temporal cortex on the sides of your head and contains the auditory cortex is called either the *sylvian fissure*, after the Dutch scientist Fraciscus Sylvius (1614-1672), or *lateral sulcus*. The hills that jut out from *sulci* (the plural) are called *gyri* (singular is *gyrus*) and the one that inhabits the auditory cortex is *Heschel’s gyrus* after the Austrian anatomist Richard Heschl (1824-1881).

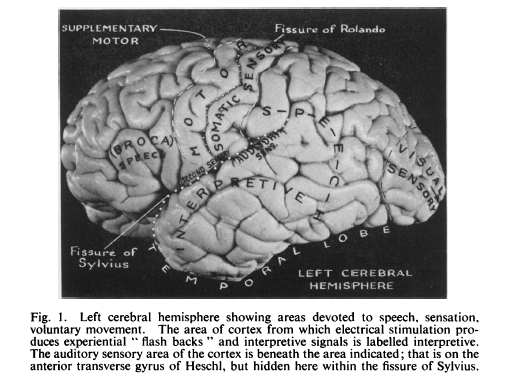
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| Figure 9.2 Penfield’s cortical homunculus. The central sulcus runs vertically to separate the sensory and motor cortex. The large invaginations on either side below the faces are the lateral sulci, which run horizontally and separates the frontal and parietal lobes above from the temporal cortices below. The cortical region around the lateral sulcus contains much of the primary auditory cortex (a.k.a. Brodmann areas 41 and 42: after the German neurologist Korbinian Brodmann, 1868-1918): the hill within the valley of the lateral sulcus is *Heschel’s gyrus* and contains the primary auditory cortex. The region where the lower temporal cortex juts out at the bottom of the drawing contains the “interpretive cortex” of the temporal lobe (a.k.a. Brodmann area 22) as well as “*Wernicke’s area*”, required for speech comprehension. |

While neurons in virtually all lobes of the cortex contain neurons that respond to sound,

Penfield and Jasper, by stimulating regions of the cortex during the Montreal Procedure, found that a region of the cortex was most responsive to the *perception* of sound from the verbal reports by the patients. Penfield and Phanor Perot (1928-2011) reviewed these results in a 1963 review, *The Brains’ Record of Auditory and Visual Experience*. They relate that stimulation with their electrode deep in a difficult to access section of the cortex within the lateral sulcus, the *buried anterior transverse temporal gyrus* “results in crude auditory sensation” and patients would say that they heard a tone, a buzz, or a knocking sound.

This *primary auditory cortex* is fairly difficult to reach with an electrode, as it is deep within a large cortical fold known as the *lateral sulcus* (a.k.a., the *sylvian fissure* or *Fissure of Sylvius*) that separates the frontal and parietal lobes of the cortex from the temporal lobe below. Anatomists divide the primary auditory cortex on the basis of neurons with specific peptides and wiring into regions known as *core, belt* and *parabelt* regions that may differ between individuals.

If the primary auditory cortex is damaged, even if the rest of the auditory pathway function is intact, individuals can lose the ability to be aware of sound.



### Figure 9.3 the regions of the temporal cortex

## Maps of the aspects of sound in the auditory cortex

The classic research on how the range of features of a sensory input are interpreted in the cortex is on *primary visual* cortex. This region uses a set of rules revealed by Torsten Wiesel and David Hubel, who recorded from the cortex of cats while they watched flashing bars or spots. As you might suspect from playing with a cat and laser pointer, the firing of neurons in their visual cortex is highly stimulated by light movement. Hubel and Weisel found that the visual cortex is organized like a three dimensional chess set, with some vectors (rows) of neurons firing in response to the different angles of the light bars, and others to movements of spots or bars in a specific direction.

The situation appears similar in the auditory cortex, where recordings in humans, macaque monkeys and mice indicate that vectors of neurons respond to particular frequencies. Studies by K. V. Nourski at the University of Iowa suggest that specific neurons in Heschel’s gyrus respond to specific sound frequencies and location. Likely, additional vectors are associated with “periodic” sound information, for example beats when pitches move to each other, or to the repetition of a specific sound.

Some neurons in the core region of the auditory cortex appear to map to specific consonants and syllables. Daniel Abrams and Vinod Menon report that the core region of the auditory complex and striatum form a network by which infants recognize the sound of their own mother’s voice rather than voices belonging to other women.

## Sounds can be reconstructed from the activity of the auditory cortex

You’ll remember that even after sound waves are transduced to synaptic activity and electrical waves at the hair cell synapse to travel as far as the inferior colliculus, the sound can be reconstructed by playing the neuronal firing patterns through a speaker. By the time the auditory pathway reaches the primary auditory cortex, however, the features are too abstract, and playing back the firing through a speaker only produces only clicks and buzzes. How does the abstract information in the vectors of the auditory cortex allow us to tell what we are listening to?

One clue is from Nima Mesgarani’s lab at Columbia University, who defined small regions in the ferret auditory cortex that respond to specific phonemes, the distinct units of sound in spoken language. This is amazing given that ferrets didn’t evolve to comprehend human speech!

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| Figure 9.4 Neuronal response to human spoken phonemes Response of a ferret’s primary auditory cortex to human-spoken words. The letters show the positions of neurons that best respond to the phoneme, or characteristic sound of each letter. The *plosive* sounds of d, b, t, k, p, and g are separated from the *fricative* sounds of f and they each overlap somewhat with z*. Image courtesy Nima Mesgarani.* |

This research, even on ferrets, may provide clinical benefits for patients with speech and language disorders.

In a contemporary version of the Montreal Procedure, an array of electrodes, rather than Wilder Penfield’s single electrode, is placed on the surface of the temporal cortex. This provides a means to determine which small regions of the cortex are activated by particular sounds. Nima’s lab played recorded conversations to patients while they undergo the procedure while recording the response by the cortical neurons in the upper region of the temporal gyrus under the Sylvan fissure. They then analyzed the recordings at each electrode and use an algorithm to analyze the response to each component sound (*phoneme*) in English speech, and eventually can use that information to reconstruct what the patient heard!

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| Figure 9.5 cortical response to human speech in the temporal cortex Human cortical in the temporal gyrus selectivity to sounds in speech. (A) An MRI reconstruction of one participant’s brain. The placement of electrodes during epilepsy surgery are shown in red. (B) An example spoken phrase, *and what eyes they were*, its sound waveform, spectrogram, and phonetic transcription. (C) Neural responses evoked by the different sounds within the spoken phrase at selected electrodes, with red color showing the greatest response to that sound: anterior is towards the front of the brain and posterior to the rear. (D) Average responses for five example electrodes, labelled e1 to e5, to all English phonemes used in English*. Image courtesy of Nima Mesgarani.* |

This may allow those with damage to the auditory system to regain language comprehension, and perhaps eventually more understanding of music and sound. Both Nima’s lab and Edward Chang’s group at UCSF have been able to reconstruct speech from human brain waves, albeit recorded by quite invasive techniques with the electrodes touching the surface of the auditory or near the auditory cortex. At this point, the rules that provide the interpretation of specific sounds by the auditory cortical regions is far less advanced than those of the visual cortex from Hubel and Weisel’s research, but the Mesgarani lab’s findings show that they exist to be revealed.

The research on perception these regions has mostly been conducted with speech rather than music, reflecting an assumption that the pathways developed for speech during evolution: but given the roles for music in culture and biology, including in other species, perhaps research to come might hint at how responses to language and music co-evolved?

## The interpretive cortex, the stuff that dreams are made of

Each cortical region projects to all of the others, most notably through *the corpus callosum*, a multilane highway of millions of bundled axons. The cortical axons further projects to the striatum, the cerebellum, and many other regions of the nervous system, including the spinal cord to activate voluntary movements. These myriad loops are involved in the pathways that underlie emotion, logic, intuition, deduction, and all of the other experiences in music and sound. Well, if we weren’t so complex, we probably wouldn’t examine why we have experience and thought.

Another striking example is again from Penfield and collaborators. They discovered a connection between the primary auditory cortex and a region just to the south in the upper temporal lobe they called the *interpretive cortex*. Penfield was so fascinated by the responses triggered in this region that he wrote an entire book on it.

The patients reported not only sounds, as if the primary auditory cortex were stimulated, but entire pieces of music or specific sounds and smells and associated scenes. Often these were experiences that seemed to be re-experienced – the patients would often insist on this – but after the operation it became clear that they had never actually occurred. The perception of the scene would end abruptly once the surgeon stopped stimulating or moved the electrode.

The patients said that these experiences occurred while they were aware that they were in the operating room, so that they experienced “two simultaneous situations” at once, and that both appeared real.

For example, for one patient (D.F: at that time, initials of the patient names were used in publications), a point on the surface of the right temporal lobe was stimulated an, the patient heard a specific popular song being played by an orchestra. Repeated stimulations reproduced the same music. While the electrode was kept in place, she hummed the verse and chorus, and verse, accompanying the music she heard*.* The points that produced these and other illusions were a region next to the auditory cortext that he called the “interpretive cortex”.

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One of Penfield’s collaborators on memory’s localization in the brain during the 1950s was Brenda Milner, known as the founder of the field of neuropsychology. As of this writing in 2019, she is at the age of 100 still conducting outstanding research in her lab at McGill University in Montreal. Her husband Peter, who worked with James Olds in the 1950s on the discovery of the reward pathway (see Chapter 7), died in 2018 at the age 99. In the 1950s, the faculty at McGill and its Montreal Neurological Institute featured a large share of the personalities in this book, including Brenda Milner, Wilder Penfield, Herbert Jasper, James Olds, Peter Milner and Donald Hebb. An extensive interview of Brenda by Heidi Roth and Barbara Summer is entertaining and very informative about that period, including her perspectives as a woman scientist during the mid 20th century.

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# Listening

Regarding the cocktail party problem in musical compositions, my vote for the ability to provide complexity of many lines while retaining the ability to discern disparate sounds within the mass is Maurice Ravel’s orchestration of *Une Barque Sur l’Ocean*. At least to me, all of the instruments seem transparent, even when there is a massive amount of action.

Musicians have long used sound coming from different directions as a compositional feature, particularly with organ and choral music in churches, and in musical theater with sound arriving from offstage or in the audience. In film scores with surround sound, what started as a revolution is now a common place.

Henry Brant explored sound arriving from multiple directions in multiple orchestra works. You might try *Ice Field* played in a binaural recording, a technique intended to recreate the sensation of sound arriving from different directions by careful calibration of timing to emulate the small differences between the time sounds arrive at the two ears.

Dream-like states are meant to be evoked in many traditions. Maybe all music is intended to activate your interpretive cortex and produce something of a dream.

Music played by the Gnawa in Morocco, the Master Musicians of Jojouka in the Atalas mountains and indeed many groups in that region, the ecstatic dance music for Sufis including the whirling dervishes, and some Hasidic dances, are meant to evoke a sort of trance like state, as is some electronic club music.

Some pieces like Berlioz’s *Symphony Fantastique*, Karlheinz Stockhausen’s *Gesang der Junglinge* with its abnormal manipulation of a child’s voice and Pauline Oliveros’s *Bye Bye Butterfly*, with its disturbing setting of Giacomo Puccini arias, wear this intention on their sleeves.

The most awe-inspiring dream like states I have experienced with music and dance were in Cuban rumba ceremonies in Havana, where musicians, dancers and audience seem entranced by a single rhythmic pattern for hours. There is no substitute for attending the ceremony, but you might listen to Celia Cruz’ recordings of prayers to the orishas to hear it from one aspect, and anything by Orlando Puntillia Rios or Daniel Ponce, who moved to New York City and recorded prolifically, for another. I was told that Puntillia maintained a good Yoruba vocabulary hundreds of years after his ancestors had been kidnapped to be brought to the new world.

Since we filter out listening to our own breathing and swallowing, can we focus on them as a form of music? Alan Watts recorded a lecture, *Listen and breathe*, that provides advice on listening to breath as a form of mediation, and perhaps it can work and alter a circuit in your nervous system.

# 10. Sound disorders, illusions and hallucinations

* How does brain damage alter sound and music perception?
* Can epileptic seizure be triggered by music?
* What produces the auditory hallucinations associated with schizophrenia?
* What causes ringing in the ear?

In medicine and biology, insights into normal function are often made by studying disease, the apparent errors made by nature. Here we examine examples of disorders, illusions and hallucinations that lend insight into how we perceive sound.

## Common and benign illusions

**The telephone illusion**

An universal illusion, first described by the German physicist August Seebeck (1805-1849) using mechanical sirens, occurs whenever we listen to speech on the telephone. Telephones reproduce sound in a frequency range from 300 Hz (about a D above middle C) to 4000 Hz. Indeed, applying a cutoff filter at those frequencies to a recording provides a pretty good impersonation of speech through a telephone.

The fundamental frequencies used in speech range in adult women from 165 to 255 Hz (middle C) and in adult males from 85 to 180 Hz, all below the low-end cutoff. Yet we “hear” the absent fundamentals clearly over the telephone.

This illusion depends on the presence of the harmonics we discussed in Chapter 3. When we hear the higher harmonics of a fundamental, say starting at the f2, f3… our cortex apparently fills in the fundamental f1. For men with low voices, we only require the harmonics starting an octave or octave and a fifth above to regenerate the presence of the fundamental frequency.

This illusion may seem too spooky to believe, so record your voice into a frequency analyzer –a free download program is Spear, written by Michael Klingbeil for his PhD thesis at Columbia – and simply erase the fundamental frequency. It’s surprising how much erasure of component frequencies one can do on a natural sound before it becomes unrecognizable.

This telephone illusion is not the only example of the brain filling in missing information. Normal vision includes a “blind spot”, the *fovea*, in each eye that corresponds to a region in the retina that lacks photoreceptors. Objects in the blind spot disappear in our vision, but the region is filled in by a calculation by the brain based on the surrounding visual input. These auditory and visual illusions that fill in missing information assist us in navigating our world.

**The McGurk effect**

This auditory illusion was described by British psychologist Harry McGurk (1936-1998) and John MacDonald in their 1976 study, *Hearing Lips and Seeing Voices*. It occurs when there is a mismatch between an expected and genuine sound and is often demonstrated with a video of someone pronouncing a “p” sound but overdubbed with a a “b”. When one watches the video, the sound associated with the movement of the lips and face is perceived: but when the observer choses their eyes, the genuine overdubbed sound is perceived.

The McGurk effect depends on a learned expectation of a sound. There are disorders, including some injuries to the cortex and learning disabilities, that decrease the McGurk effect, and so in this case, the *absence* of an illusion may indicate a disorder.

**The ticktock illusion**

Also known as “subjective accenting”, this illusion was reported by the American psychologist Thaddeus Bolton (1865-1948) in 1894, and you can perceive it listening to a watch or a turn signal in your car.

In his 1894 article *Rhythm*, Bolton built a device to produce controlled clicking sounds through a telephone in the next room. When subjects listened to a series of identical clicks, they would initially hear them, accurately, as all alike. With further listening, however, they grouped the clicks in sets of two, three or four, with one beat perceived as more prominent than others.

In 2003, Renaud Brochard and colleagues from the University of Burgundy returned to analysis of the the ticktock illusion using EEG recordings. They found that if clicks were identical, listeners would impose differences in ERP activity on perceived strong and weak beats (for a reminder about ERPs and expectation, refer to Chapter 6). When Renaud disrupted the perceived patterns by genuinely making particular clicks louder, listeners who were musicians tended to display larger ERPs, perhaps because they had stronger expectations of repeated rhythmic patterns.

**Difference tones**

The violinist and composer Giuseppe Tartini (1692-1770) introduced the idea that two frequencies played simultaneously can produce a third tone that is the difference between the two. Called the *third sound* by Tartini, and a *difference tone* since Helmholtz, this is an illusion when the third tone is not present in the air waves. (This type of difference tone contrasts with another type of difference tone produced by instruments including distorted electric guitars and saxophone virtuosos who sing into their instruments while playing, as these are present in the sound signal.)

The perception of the difference tone illusion varies among individuals, and I tend to not perceive them unless the volume is quite loud and I really concentrate on distinguishing them. You might explore your own perception by using a sound program to play a 1000 Hz and 1250 Hz wave and listen for a 250 Hz third frequency: for many, an effective approach is to hold one constant frequency and sweep the second.

The biological origins of this hallucination remain in debate, but Fernan Jaramillio and James Hudspeth at Southwestern Medical Center in Dallas recorded from hair cells of the bullfrog and reported that difference frequencies arose within the hair cell itself. If these difference vibrations were then conveyed to the to the basilar membrane, they would excite hair cells at that resonant frequency. Other labs, in contrast, have reported difference tones even if one frequency is played into one ear and another into the other, indicating that the difference tone must be perceived at a later stage of the auditory pathway. Perhaps there are multiple ways to produce this illusion.

Can these kinds of auditory illusions be used to create new music from the inside of one’s own head? The virtuoso of this sort of composition is Maryanne Amacher (1938-2009), who wrote music with high pitched closely packed waves intended to activate difference tones and distortion products, including the otoacoustic sounds produced in the cochlea we discussed in Chapter 8.

## Hearing voices

It is surprisingly common to hear imaginary voices, and some estimate that vocal hallucinations are perceived by a quarter of the general population, and these hallucinations are especially common in children. While many who report hearing voices are otherwise normal, it is by far the most common hallucination for people with schizophrenia and disorders associated with psychosis.

A possibly related phenomenon, including one experienced often by your author, is to hear specific musical pieces in the mind. I have grown up thinking this was universal but am told that it is not!

A synaptic pathway regulated by the neurotransmitter dopamine is seemingly involved in hearing voices because drugs that block the D2 dopamine receptor act as “antipsychotic” drugs in patients with schizophrenia, decreasing auditory and other hallucinations. While these drugs have been so used since the 1950s, the reason that they are effective is poorly understood.

Another clue is that auditory hallucinations appear to occur in tandem with a higher activity in the auditory and experiential cortex and thalamus, pathways that send sensory information to the cortex and striatum, suggesting that during hallucinations there are abnormally low levels of synaptic inhibition.

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An explanation has­ been suggested by Stanislav (Stas) Zakharenko from St. Jude Children’s Research Hospital in Memphis. Stas studied a mouse that was mutated to express a genetic mutation found in a fraction of patients with schizophrenia and observed that the mutant mice had higher than normal levels of D2 dopamine receptors on neurons that project from the thalamus to the auditory cortex. As the activation of these receptors decreases synaptic activity, antipsychotic drugs inhibited the cortex only in the mutants. Since antipsychotic drugs in most of the population cause sedation but have no obvious change in sound perception, it is possible people with auditory hallucinations are undergoing dopamine-modulated thalamic overexcitation of the auditory cortex.

## Seizures driven by music

A related process may occur in rare patients with *musicogenic seizures*. In contrast to the widespread triggering of “goosebumps” by specific music, musical triggering of seizures occur in perhaps one in a million people. EEG recordings show the presence of a typical seizure that begins in one cortical region and spreads through much of the rest of the cortex. These are triggered by different music for different people, sometimes by a particular song or sometimes by a style or sound such as “church music”. One woman has seizures triggered only by the hearing songs by the band, Alabama. These are often effectively treated with anti-epileptic drugs and in some cases by surgery including the surgical Montreal Procedure.

Some studies report that Gordon Shaw’s “Mozart effect”, in which he theorized that children would be smarter if they listened and learned to play Mozart, can be used in the treatment of childhood epilepsy. In some studies, the decrease in seizures lasts beyond the duration of the music, suggesting that it may be therapeutic. While the evidence is unclear, we have traced how sound and music follows a quite direct input to the cortex to modulate its synaptic activity, and in that way sound is analogous to a stimulation electrode.

Scientists studying these cortical responses generally choose to play Mozart’s Sonata for Two Pianos in D major, K448. Gordon and his wife Lorna told me that this piece was first used as the boyfriend of Frances Rauscher, the first author of the original paper, had it in his record collection.

## Tone deafness and amusia

A small fraction of people, generally from musical families with lots of early exposure to music, develop “perfect pitch” that allows them to report the note name of a sound without a reference pitch. These people can be asked to sing for example an Eb and nail it.

While early experience is clearly important, the reason that only some people have perfect pitch is not understood. One possibility is that the skill is more common than realized, as people will often sing a piece they learned in the same key in which that they learned it without a reference pitch, but not be aware of the name of the key.

This possibility is consistent with a study by Robert Zatorre and colleagues from the Montreal Neurological Institute who examined synaptic connectivity in people with absolute pitch. They concluded that these subjects have an improved ability to retrieve the name of the pitch due to enhanced synaptic connections between the right auditory cortex, which appears to be more specialized for hearing pitch, and areas in the left temporal cortex more devoted to speech, enabling them to name the pitch.

A majority of people have “relative pitch”, meaning that they can learn to recognize intervals, and with practice and training determine a note from its relation with a reference pitch. These people can for example sing a triad or scale correctly.

A small fraction of the population cannot learn to do this. The label *amusia* was introduced by the neurologist August Knoblauch (1863-1919) for those who are colloquially known as “tone deaf” and cannot recognize musical pitch or sing a melody in tune. Some tone deafness is “congenital” and present throughout life, but the loss of the ability to distinguish frequency also occurs following brain damage, particularly in the auditory cortex.

People with congenital amusia maintain a normal understanding of speech and can recognize speakers by the sound of their voices but cannot tell if singing is out of tune or remember short melodies, and they learn to identify songs from the words. For some congenital cases, listening to music is unpleasant, but many others are passionate music lovers.

While the cause of lack of relative pitch is not clear, work by Isabelle Peretz and others using EEG recordings report that there are reduced connections between the right auditory cortex and frontal cortex, the latter of which is involved in active “working” memory. This suggests that even if the auditory system works well until the perception of pitch in the auditory cortex, there could be less conscious awareness of the sound information. This condition may resemble a decrease in connectivity between the two sides of the brain as implicated in dyslexia, and amusia and dyslexia present somewhat analogous impediments in processing music or language.

Those with acute amusia usually have undergone brain damage to the auditory cortex, typically on the right side of the brain. The damage can occur through epilepsy, accidents, or from brain surgery. An extensive study was conducted of a patient known as GL who had an aneurysm on his right middle cerebral artery, and after two surgeries was found to have two lesions, one in the left temporal lobe and one in the right frontal cortex. He previously enjoyed music and concerts, but after his operations at age 51, while his life continued normally and successfully otherwise, he noticed that he could no longer identify or enjoy previously familiar music. By testing for a range of discriminations of different musical parameters, Isabelle Peretz found that he continued to discriminate pitches normally but lost the ability to follow the contours of melodies and could not sing back pitches were played to him. Since he no longer enjoyed listening to music, these results may provide a clue exactly what is rewarding in in music.

## Tinnitus and ringing in the ears

The most common hearing disorder is tinnitus, defined as the perception of “phantom” sounds in the absence of a corresponding external acoustic stimulus. This is usually perceived as a buzz or hiss, and often presents as a ringing sound at a specific frequency, most commonly at around 4000 Hz.

While some estimates of prevalence report that 10-15% of people have tinnitus with severe impairment in 1-2%, Lisa Olson finds that virtually everyone over age 50 has this, in that they hear sound that is not present in a quiet room. If the tinnitus is noticeable, this is particularly debilitating for musicians, some of whom must contend with a constant frequency while playing or listening.

As for deafness, there are many causes of tinnitus, and a specific diagnosis can be very difficult. The causes of tinnitus further overlap with those of profound deafness including noise, older age, tumors, and exposure to some drugs. It is associated with exposure to loud sound, and so is unfortunately common among musicians, and very common among those who are exposed to the noise of warfare. Often the region of the ringing matches the frequency where hearing is lost.

The most common treatments for tinnitus are counseling and cognitive behavioral therapy. Some patients are helped by cochlear implants, hearing aids, and other experimental therapies including brain stimulation. For many, the condition changes with stress and emotional factors and some treatments appear to work by placebo effects.

Some investigators state that the most common form of tinnitus is *somatosenory* that is associated with head and neck trauma that alters nerve input. This type often changes in volume, frequency or localization of the ringing tone with altered head or neck position and can be altered by clenching teeth, turning the head, or applying pressure to the head or neck. Somatosenroy tinnitus may occur due to changes in synaptic inputs to the cochlear nucleus that affect its output. For some, the cause may be altered inputs from nerve fibers, or jaw or neck injuries that may change sound conduction. Experimental treatments for this form include subcutaneous stimulation of these regions or even controlled botox injections (the incredibly poisonous bacterial botulinum toxin), which decreases muscle activity by severing proteins involved in synaptic vesicle exocytosis.

One musician friend had very debilitating ringing in the ear that was destroying his career and was treated poorly by doctors but improved significantly after he stopped smoking marijuana.

Some less common forms of tinnitus are produced in the body and can be audible to the examiner, and so are called *objective tinnitus*. This can be caused by altered blood flow in blood vessels near the ear or contractions of the ear drum. The most common occurs in synchrony with the heartbeat and is due to an impediment in transporting blood through veins and arteries. Other forms are related to spontaneous otoacoustic emissions.

Even if the initial cause stemmed from a problem in the ear, for many the tinnitus continues even when the auditory nerve is sectioned, indicating a deep brain pathology. Some reports hint that tinnitus may be associated with auditory remapping anywhere along the synaptic auditory pathway, including synapses from inner hair cells to the auditory nerve or the cochlear nucleus to the cortex. Another cause is a decrease in inhibition of firing in the cortical tonotopic map of a region corresponding to the specific ringing frequency.

## Mechanisms that produce deafness and the effects of loud sound

People who do not hear well can find themselves cut off from music and are challenged in social situations. We have discussed the many physiological steps required for hearing, and so it may not be surprising that over 300 syndromes are associated with hearing impairment or loss.

While there are a host of causes of deafness that cannot be avoided, one is simply from loud noise, and noise-induced hearing loss is estimated to account for 40% of total occupational disease. Cumulative sound above 85 dB, which is quieter than the sound in some restaurants, seems to cause gradual damage, and obviously this is a major problem for active musicians, particularly those who play loud instruments. Other preventable causes are due to chronic exposure to heavy metals or benzene.

The disorders of hearing loss are bundled into four major categories, defined by where the problems occur in the sound pathway.

*Conductive hearing loss* is a mechanical disturbance of the conductance for sound from the pinna through the ossicles. If the problem is in the external ear canal, sound is perceived as being quiet, whereas if it is with the ossicle or ear drum, there is generally a problem with frequency response so that high or low frequencies are perceived as louder of softer than normal.

The causes of conductive hearing loss range from simple blockage by earwax, which is particularly common in children as the canals are smaller and they are more prone to infection, to eardrum perforation, or a growth known as a *cholesteatoma* behind the ear drum.

As we will discuss for hearing by whales, for whom sound is conducted through the head to their ears, some of our sound perception is conducted by bone, as you can experience by striking a tuning fork and touching a bony area of your head. For this reason, damage to jaws and other regions also leads to conductive hearing loss.

*Sensory hearing loss* is due to dysfunction of hair cells or their synaptic connections to the cochlear nerve. This is particularly common with loss of outer hair cells and thus their amplification. This type of loss can be identified by a decreased response in evoked otoacoustic emission tests that report outer hair cell function.

Sensory hearing loss is responsible for the common loss of perception of quiet sounds in older age (known as *prebycusis*) and for distorted perception. It is very commonly due to noise, including the use of guns, explosions, and sadly, very loud music heard in concerts or through headphones and earbuds.

Hearing loss from the sound levels at loud concerts appears to be due less to direct injury to the hair cells than to oxidative stress caused by a metabolic reaction to the sound, possibly following to inflammation. This sort of hearing loss appears to be greatest in frequency ranges of 4000 Hz and higher. The best protection is obviously to avoid the concert or use earplugs, but if one is exposed, there are controversial claims that dietary antioxidants including n-acetylcysteine may be helpful, perhaps by decreasing the levels of an inflammatory protein known as tumor necrosis factor. Several other disorders are now treated by tumor necrosis factor inhibitors, and it will be interesting to see if over time this leads to the protection for age and noise-dependent sensory hearing loss.

The loss due to age may further be due in part to loss of microvascular blood supply for the hair cells or other cells associated with the middle ear. It can also be caused by infections of the ear including mumps, measles, and ironically, by some antibiotics including streptomycin and gentamicin. For some, sensory hearing loss has been attributed to the use of tobacco, cocaine, heroin or alcohol. Finally, a quarter of cases of sensory hearing loss are thought to be due to a large set of mostly recessive genetic mutations.

*Neural hearing loss* is chiefly due to cochlear nerve dysfunction. This often causes a problem in perceiving speech rather than frequency perception. It is often due to an abnormal growth or a tumor. The most common such tumor is an *acoustic neuroma* or *vestibular schwannoma*. If you notice a loss in of sound acuity in one ear, speak to a doctor immediately about whether an MRI scan is called for. Fortunately, these are often treated successfully with surgery.

Finally, *central hearing loss* occurs with damage to the cortex and can be due to a host of reasons including infarcts, bleeding, a tumor, or inflammatory problems that are consequences of other disorders including multiple sclerosis.

Treatments for severe hearing loss vary with the diagnosis, but the technology for cochlear implants has advanced impressively. For small children whose hearing is impaired by more than 90 dB, cochlear implants are credited with vastly increasing the ability to acquire speech. Nevertheless, the implants have not yet proven successful for regaining the ability to perceive music.

The American composer Richard Einhorn was struck with sudden severe hearing loss, perhaps from an allergy that damaged the vestibulocochlear nerve. He reports that he can perceive music well again by the use of a hearing loop or “t-coil”, a copper wire that radiates radio signals that can be picked up by hearing aids and cochlear implants.

Far more research on profound deafness and hearing loss is needed, but the improved understanding of sound perception in the cortex as discussed in Chapter 9 provides an optimistic outlook for new approaches and devices for prevention and treatment.

# Listening

The classic telephone frequency cutoff in popular song must be Paul McCartney’s *Uncle Albert*.

A nice video demonstration of the McGurk effect – this one has to be seen and heard – is made by the magician Mark Mitton, who has a deep interest in science. He produces only one sound, *ba*, and by dubbing it onto his mouth apparently speaks a different sound. If you watch and listen together, you might hear *tha*, *va*, *fa*, but if you shut your eyes, you will perceive different syllables.

Provocative attempts to produce / receive inspiration from musical illusions can be heard in Maryanne Amacher’s *Head Rhythm 1 and Plaything 2*. These pieces use different patterns on two stereo speakers and seem to produce music that is very different than you might expect when listening to the tracks separately.

The *Sonata for Two Pianos in D major K288* by Mozart is the usual work used to observe the “Mozart effect” as performed by Murray Perahia and Radu Lupu. Gordon Shaw, who was a personal friend, disliked contemporary composed music. I’m afraid he felt that minimalist music destroyed the ability to concentrate. I will not mention the pieces he played to test that, as it is pretty unfair!

There are multiple instances of great composers who somehow to create continue wonderful work despite experiencing severe hearing loss. The most well-known by far is Ludwig von Beethoven, who composed his last five piano sonatas, last five string quarters, the mass *Missa Solemnis*, and the *Ninth Symphony* while he is thought to have been completely deaf or nearly so. Reports of the premiere of the *Ninth* state that he did not realize the audience was cheering until one of the singers turned him around to face them.

Bedrich Smetana was deaf when he wrote his best-known orchestral work, the symphonic poem *Vltava* or *The Moldau*. Gabriel Faure wrote his piano trio and only string quartet after being struck deaf. Vaughn Williams, who lost his hearing due to noise exposure in France while fighting in World War I, also wrote his *Ninth Symphony in E minor* after he became deaf.

Composer Richard Einhorn has partial deafness that arose suddenly and continues to create marvelous music. He has written about various hearing aids and other approaches that helped him maintain his abilities, including the “t-coil” mentioned.

Evelyn Glennie is a composer and master of percussion with dozens of great recordings in a range of styles who has been profoundly deaf, that is with hearing impairment, since childhood. Her *Hearing Essay* discusses this issue in detail. One of the excellent pieces written for her is John McLeod’s *Percussion Concerto*.

# 11. Animal sound, song and music

* Is music limited to our species?
* Can other animals play musical instruments?

It seems important for our species to define ourselves as unique. This task shouldn’t be too overwhelming: name another species whose set contains Groucho Marx (OK, Bugs Bunny). Our attempts to define a rule for our unique nature, such as “only humans use tools” or “a sense of ethics” or “maintain bank accounts”, exist to be violated.

Most mammals, birds, and amphibians and some insects, reptiles and fish produce short calls, such as roars, chirps, and barks. These vocalizations occur on land, and in the air and sea in great choruses at dawn and dusk and during migrations. It is a challenge to perceive them as anything other than a fugue of many voices.

Bernie Krause, a musician and ecologist who records the sound of natural environments, introduced the idea that animals alter their frequency and timing of vocal production so that they are heard and not masked by others in the vicinity. He suggests that the health of a wild environment can be measured by examining its “soundscape” for the distribution of sound frequencies, and that a healthy frequency distribution becomes damaged with broad gaps in the spectrum after our species damages it.

Beyond the collective choir of natural environments, individual songbirds, baleen whales, bats, and gibbons produce songs so rich and complex that no one hazards labeling them as anything else. If we insist on being special because we make or appreciate music, we must explain away bird song as ”not music” and I haven’t heard a cogent argument for that.

To appreciate some animal music, we need to overcome barriers particular to our species. For example, recordings of brain activity in frogs and some birds indicate that their neural activity responds to songs by their own species far more than other sounds, so that they may live in a hyperaware state of their cousins amidst a cacophony of other less interesting sounds.

As another example, we only recently realized that mice produce songbird-like songs, as their vocal frequencies were above our range of hearing.

It has only become recently known that there is a “dawn chorus” of fish making calls in some regions of the sea.

We simply aren’t around in the caves when bat species sing bird-like songs to each other or while millions of bird flocks produce complex and interlocking, likely interacting, night migration calls.

The biologist and naturalist Roger Payne calculates that prior to the noise of turbine-driven commercial shipping and mechanical drilling, whales produced songs at frequencies and volumes that could be received by other whales over the span of an entire ocean, in which case whales were surrounded by an orchestra of calls and song throughout their lives.

Species besides our own sing to be attractive to mates, proclaim their individuality, location, and territory, to practice their skill, for social bonding, to decide who belongs or is excluded from a community, and because they find solo or group singing rewarding. Are these familiar reasons?

## How birds sing

The bird’s vocal apparatus doubles our own, in that the *syrinx*, named for the double pipe instrument played by the god Pan, produces two frequencies. This organ, found in all birds except vultures, is located further down the throat than our larynx, in the chest, where the trachea branches into the two lungs, with two sets of muscles that control *labia* (from lips) on either side. This anatomy allows birds including the brown thrasher, catbird and vireo to sing two notes at once, or to move very rapidly between pitches.

For an example of how the double pipes of the syrinx can be used, Roderick Suthers from Indiana University reports that the two octave sweep in song of the cardinal, begins the right branch of the syrinx at 9 kHz, and then switches seamlessly around 3.5 kHz to the left branch to finish the phrase at around 2 kHz.

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| Figure 11.1 American songbird sonograms.  Bird songs are usually analyzed as a sonogram in which time in seconds is on the horizontal (x) axis and frequency in hertz on the vertical (y) axis.  The upper trace shows two downward sweeps during the song of a northern cardinal that each last about one half of a second. The fundamental frequency *f1* of these segments of this song starts at about 9.5 kHz (near D9) and over about 200 msec falls by nearly two octaves to about 2.5 kHz (about Eb7), followed by a more gentle swoop and a short hump. The natural harmonic series is quite strong up through roughly *f5* or *f6*. Playing these songs back at a lower speed suitable to our nervous system can help us ponderous slow thinking humans appreciate their beauty.  The lower trace shows a song by a wood thrush with two notes sung at once. After one note at about 3.5 kHz is held for about half a second, with prominent f2 and f3 harmonics, the other branch of the syrinx is simultaneously sounded along with the sustained note. The peaks that run between about 5 and 8 kHz combine with the held notes produce a gorgeous trill like song |

Songbirds principally vocalize and hear mostly in the range of 500 Hz to 12 kHz, although hummingbirds produce sound at up to 16 kHz.

One of the most celebrated singers is the European common starling: Mozart is said to have taught a theme from his *Piano Concerto 19* to his pet startling. Stewart Hulse and collaborators on perception found that starlings can distinguish rhythmic patterns by training them to respond by pecking specific associated computer keys for a food reward. (As we will discuss, zebra finches will even operate tiny musical instruments to trigger specific sounds they want to hear, including songs of other birds and music by humans.)

The ability of birds to distinguish rhythm was famously demonstrated by Irene Pepperberg’s grey parrot Alex, who moved to a beat, as well as the domesticated cockatoo Snowflake, as analyzed by Aniruddh Patel of Tufts University, who moves to the rhythms of human dance music.

Carl ten Cate from the University of Leiden has studied the ability of parrots and songbirds to learn rhythm and other musical features, and they appear to have a broad range of different abilities, even between individuals in the same species.

## Why birds sing

Our Virgil for understanding why birds sing will be Ofer Tchernichovski, a professor at New York’s Hunter College, who wrote the classic article *How a Zebrafinch Learns its Song*.

Ofer says that bird song not only serves to attract a mate and keeps competitors away, but promotes social bonds: indeed, he says that “at the population level, bird song is a culture”.

The culture can be observed in duets between mates. In couples of black-faced rufous warbler, the males sing a “see”, the female an “ooo” and the males an “eee”, producing a “see-oooo-ee” song that sounds as it is sung by a single bird. Similarly, Karla Rivera-Caceres of the University of Miami, found that canebrake wren couples in Costa Rica spend considerable practice time to perfectly coordinate their duo into a seamless single song.

The classic studies of song culture by large flocks of wild birds are of white crowned sparrows, who range from northern Alaska to Mexico City. The ornithologists Luis Baptista, Peter Marler, and Barbara De Wolfe found that white crowned sparrows sing in local dialects, with songs of birds in a region similar to each other. Both sexes of white crowned sparrows sing, with the female quieter but with a larger variety of repertoire. During their first 100 days of life, the males learn a song by imitating songs of other local other male birds, and they will sing that song throughout their life, which can last more than 13 years. In this way, white crowned sparrows use song to identify their own regional flock, as if they hang specifically with fans of surf music or gangster rap or tango.

For domesticated songbirds, the most studied species are canaries, who have been selectively bred for centuries for color and singing abilities, and zebra finches, social birds who live in large flocks in Australia, and in contrast to domesticated canaries, remain essentially identical to the wild birds.

Canary song learning has been explored in detail by Fernando Nottebohm and colleagues at Rockefeller University. The male sings during the breeding season, stops when the season is over, and then relearns the ability to sing each year. Fernando’s lab made the discovery that this occurs due to the annual death of old neurons and birth of new neurons to replace them in a brain region corresponding to a region of the avian cortex, the higher vocal center (HVC). The birth and survival of the new neurons is highest during the fall after the breeding season when adult males begin to learn a new song for the year. The birth of the new HVC neurons is triggered in part by testosterone and injecting female canaries with testosterone can increase the size of these nuclei and induce them to sing more.

“People think that zebra finches have ugly songs, but they are wrong”, says Ofer. One reason our species has such bad taste is that birds perceive, act and presumably think faster than we can, experiencing humans as slow moving bores. If we slow the finch song by 60%, which you might try, we begin to appreciate their melodies, and how the individual bird’s songs differ from each other.

It is suspected that zebra finch singing provides social bonds. Although they live in large flocks, zebra finches form monogamous pair bonds. The male learns his own song over the first three months of life by accurately imitating the complex songs of another zebra finches, typically his father, and learning to reproduce the original, in Ofer’s words, “as fast as a brain can do: people cannot do it.”

Female zebra finches perform unlearned innate calls of shorter duration. Ofer’s lab find that females have more precise rhythm than males and learn more rapidly to alternate short calls between individuals to produce a “hocket” (see Chapter 5).

Zebra finches will “work”, that is undergo an unpleasant experience, in order to hear songs sung by other zebra finches. A study by the late Kirill Tokarev from Hunter College reports that this likely occurs because dopamine neurotransmission is increased in males when they hear song, and that male birds will “pay” to watch videos of other zebra finches sing by undergoing a mild punishment – a puff of air on their face. The study found that females will undergo mild punishment as well, but only to hear their own mate.

Bird song is thought to define membership in a group, something that Ofer calls a “stable polymorphic culture” as some groups remaining stable and others change the patterns of their song. The personality of each group can achieve a particular style by magnifying unique features of the songs. Perhaps this is like the way we identify the sound and performance of an individual musician, say Miles Davis’s trumpet from his trademark Harmon mute.

From these studies, we might guess that the purposes of song are for practice, to declare territory and announce “I am here”, to form bonds with a mate, and to form bonds and define membership in a group.

### Birds who imitate other species

In contrast to the songbirds who specifically learn a song from members of their own species, parrots and parakeets can imitate human speech, as do members of the crow family, including ravens and even occasional blue jays.

In the wild, the African grey parrot imitates other species, whereas Amazonian parrots of the western hemisphere imitate only their own species and learn local dialects in the wild. The best-known individual parrot was the Africa grey Alex, belonging to Irene Pepperberg at Brandeis University, who learned to call objects by name.

Among the songbirds, the starlings, which include common starlings and myna birds, sing their own songs and imitate other bird species and other sounds.

In North America, our champion songbird imitator is the northern mockingbird. Both sexes sing their own songs and also mimic the sounds of frogs and other birds, including blackbirds, orioles, and aggressive species like jays and hawks. Mockingbirds continue to learn new sounds throughout their lives.

A champion songbird imitator is the African red-capped robin-chat, who has been heard singing the songs of at least forty other species, including roosters and eagles that they hear far above in the air. Thomas Struhsaker, affiliated with Duke University, reports from the Kibale Forest in Uganda that a single robin-chat can imitate the combined male / female duet of the black-faced rufous warbler AND that two robin-chats can also sing the warbler duet together, one having learned the male and the other the female part.

The world grand master vocal imitator in the wild is the lyrebird of Australia and Tasmania, the tail of which indeed resembles Greek lyres, although lyrebird fossils have been dated to 15 million years ago, just a bit before Pythagoras. These large birds, nearly a meter long, live as long as thirty years, and sing and dance throughout the year, mostly in the winter (that is June to August) during the mating season.

Both sexes sing their own song. Young lyrebirds learn the song of local adult males, and once the song is learned, it remains mostly unchanged. About 70% of their vocalizations, however, are calls, songs, and beak snaps by other bird species, and even flocks of birds, as well as calls of wild mammals including koalas and dingoes.

David Attenborough’s documentary *The Life of Birds* shows two lyrebirds who imitate a camera shutter, drills, hammers and saws. These two are captive birds in a zoo and wildlife sanctuary, and wild lyrebirds have not yet been recorded who imitate mechanical sound.

The single verified and deservedly renowned example of wild lyrebirds imitating human-produced sounds are a population of “flute lyrebirds”. A century ago, a family of potato farmers in the town of Allan’s Water in the New England Tablelands of New South Wales are said to have raised a lyrebird as a pet in a house with a flute player. Whether the original bird was domesticated or wild, he taught other lyrebirds, and now generations of wild lyrebirds in the region sing a flute-sounding call include bits of melody from the Irish dance *The Keel Row*, and a DO RE MI practice scale. Vicki Powys and collaborators wrote a detective-like study, *A Little Flute Music*, to determine the veracity of this story, and as with all good scientific investigations, come up with additional questions, but do listen, as recordings of the flute lyrebirds are astonishing.

### Night flight calls

During the spring and fall, and usually hidden from us, a massive vocal choir of millions occurs during night flight migrations. These enormous flocks are composed of species ranging from tiny sparrows to enormous herons, and some migrate thousands of miles. For example, the small virtuoso, the white crowned sparrow, can fly over 300 miles in a single night during their annual 2600 mile trips between Alaska to Southern California. Some black poll warblers, a tiny bird, migrate from Canada and Alaska to the Amazon, with the longest leg of the journey an average distance of 1580 miles. This part of their migration takes only three days during which they fly without pause at 25 miles per hour.

These migrations occur at night so that the birds escape predators like hawks and cats, because cooler nocturnal temperatures keep them from overheating or dehydrating, as the lack of daytime air thermals minimizes the turbulence they create and make it easier to maintain a steady course, and because the moon and stars aid in navigation.

In contrast to complex songs, night flight calls are short chirps or buzzes, typically a tenth of a second or less, and relatively quiet. The distinctive calls by a species or group of individuals probably help maintain a “flock” to stay together while flying in the dark and may help them to avoid mid-air crashes. Intense bouts of flight calling probably indicate severe instances of disorientation

The classic study of the night flight calls was by a historian and ornithologist, Orin Libby (1864-1952) in 1899. Libby listened from a quiet hill near Madison, Wisconsin on a chilly September night with no cloud cover as the flocks flew south. He could identify many of the species from their flight calls. He counted 3,800 calls from the sky before he stopped at 3 AM. He estimated the number of birds migrating by counting those who crossed the face of the moon and multiplied that by the fraction of the sky occupied by the moon. As he counted 358 crossings in a single night, he estimated that a minimum of 9,000 birds flew that night.

The ornithologist Andrew Farnsworth from the Cornell Lab of Ornithology and his colleagues analyze the patterns of night flight calls using contemporary means to record and process these signals. One of their approaches is to place directional microphones on skyscrapers pointing skyward and compare the recordings with live radar reports of the migrations from the National Oceanic and Atmospheric Administration. Current reports of bird migration, using methods to exclude meteorological phenomena routine in radar data, can be viewed on Cornell’s BirdCast website. An outcome of their research has been to provide new information about the effects of exposure to light pollution on migrating birds, assessments of aircraft hazards that can occur from bird collisions, and the large-scale characterizations of bird migration.

The National 911 Memorial & Museums’ Tribute in Light memorial commemorates

the lives lost during the destruction of the World Trade Centers in New York City by shining two intense beams of light skyward where the towers stood. This occurs around September 11, a busy time for migrations. Andrew and his colleagues found that this significantly disoriented bird migration behaviors, causing them to gather and circle and fly more slowly, and to vocalize much more intensively. As a result of these findings and the work of many volunteers from the New York City Audubon Society, the lights are shut off periodically when birds are in danger or gathering in large numbers, allowing them to proceed on their migration.

## Insect music

There are something like 900,000 species of insects, but only a minority are thought to hear or sing. For example, of the 350,000 beetle species, only a small group of scarab and tiger beetles are known to have developed ears or respond to sound.

How insects hear

Insects use sound and hearing for familiar reasons: to attract mates, as a feature of aggressive behavior between males, and escape predators, but also for some particular insect behaviors.

For example, parasitic flies known as *tachinids* have ears placed on their necks that are sensitive to male crickets mating calls, allowing them to deposit their maggots on the crickets.

Or, some moths have ears near the base of the wings that detect very high frequencies in order to detect ultrasonic echolocation used by the bats who hunt them: when the moths hear the bats, they stop producing their own sounds that they otherwise use to attract mates.

The first insects about 400 million years ago are thought to have been deaf, but all insects possess *chordotonal* *organs* that detect vibration and the relative movement between insect body segments. For example, the chordotonal *subgenual* (meaning *below the knee*) *organ* detects surface vibrations, as from a leaf on which an insect might perch. This organ is also used to detect vibrations insects use to communicate with each other. Another type of chordotonal organ known as *Johnston’s* *organ* is at the base of antennae and detects movements driven by wind or gravity.

Chordotonal organs are composed of multicellular units known as *scolopidia* that are typically found just under the exoskeleton. The scolopidia are in turn composed of sensory neurons and supporting cells. The sensory neurons are bipolar with a single dendrite and axon. They perform a function analogous to the inner hair cells of the cochlea, with the dendrite possessing a primary cilium reminiscent of the mammalian hair cell stereocilium. As with hair cells, these neurons are stiff and movement activates mechanosensitive ion channels that open very rapidly.

As observed in katydid (a.k.a. bushcricket) fossils from 165 million years ago, some chordotonal organs eventually evolved to detect sound. By tracing evolutionary pathways, Martin Göpfert from the University of Göttingen, a neuroscientist who specializes in insect hearing, estimates that chordotonal ears in insects evolved more than twenty separate times.

The chordotonal organs that detect sound are of two major types, a *tympanal organ* that is similar to the eardrum, and the aforementioned *Johnston’s organ*.

Tympanal ears can be found in many parts of insect bodies, including a single *cyclopean ear* with two eardrums on the middle of the chest of the praying mantis. Some moths have ears within their mouths. Grasshoppers often possess tympanal organs on the first abdominal segment, but the bladder grasshopper *Bullacris membraciodes* possesses twelve ears on its abdomen.

The sugenual tympanal ears of katydids, crickets, and grasshoppers feature a hearing organ known as the *crista acustica* or *Siebold’s organ*~~.~~ In katydids, air waves enter tubes on the leg known as *trachea* to vibrate an eardrum (*tympanum*) from both the interior and exterior sides. The crista acustica has a graded frequency response with larger scolopidia at one end sensitive to low frequencies that progress to smaller scolopidia at the other end that vibrate at higher frequencies, in some cases as high as 300 kHz. It is striking that these distant relatives evolved to parallel the mammalian inner ear with features analogous to the tonotopic organization of inner hair cells on the basilar membrane.

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| Figure 11.2 A katydid ear  The katydid’s hearing organ, the *crista acustica*, is in the middle region of all six legs. Sound waves enter the trachea to vibrate eardrums from both the interior and exterior sides. Located alongside the trachea, the *crista acustica* detects sound-induced air motion that trigger motion mechanosensitive ion channels in sensory neurons. These channels are opened in the stiffer end of the organ by high frequencies and in the more flexible end in response to low frequencies, a tonotopic mapping similar to the mammalian ear. *Figure from Manuela Nowotny (University of Jena) used with permission.* |

In contrast to tympanal ears, Johnston’s organ in the antenna is used to perceive sound by *Hymenoptera,* including bees and ants, and by mosquitoes and fruit flies. The antennal eas responds to air particle movement that drive the antenna’s outermost segment, known as the flagellum, to vibrate. In contrast to the ability of tympanal ears to sense very high frequencies, the scolopidia of Johnston’s organ are usually excited by frequencies below 1 kHz.

The fruit fly *Drosophila melanogaster* is by far the most studied insect, mostly because they are useful for genetics due to their short reproduction time, producing the next generation of offspring in as little as twelve days. Not to mention that they are virtually free to grow, requiring only a jelly jar with a change of food every two weeks. Early genetic studies, about a century ago, were facilitated by enormous ‘polytene’ chromosomes in the salivary (spit) glands of these flies, enabling gene mapping within the chromosomes.

In Drosophila, Johnston’s organ contains about 480 scolopidia and is used to sense gravity, movement and sound. The ability of fruit flies to detect sound is required for detecting courtship songs and the wing beating frequency of mates as well as for aggressive behaviors between males.

In honeybees, Johnston’s organ is used to detect sound from the buzzing of the wings around the range of middle C (C4) during the *waggle dance* that communicates the location of flower nectars to other bees. Their ear further appears to sense changes in electric fields caused by the dancing bee, a form of communication using a sense that is challenging for us to imagine.

The number of auditory neurons that run from insect ears to other regions of the nervous system is extremely variable, from only a single neuron in moth tympanal ears specialized to hear bats, to 2,200 neurons in cicada,s and about 15,000 in the Johnston’s organ in male mosquitoes, a number close to that in the human cochlea. The frequency of incoming sound appears to “phase lock” with neuronal firing, so that higher frequencies produce higher auditory nerve firing rates. The full auditory neuronal circuit can be very large in some flies, consisting of as many as 20,000 neurons, with the Johnston’s organ nearly half of the diameter of the entire head.

The detection of sound by insects can be extremely rapid, as might be expected if one must constantly avoid bats to survive, much less a swat by a human. This is in part due to a very short auditory circuit that projects directly from the first synapse. This rapid listening can also be useful for mating, and during katydid mating calls, females can respond to the male within 25 msec.

## How insects sing

The singing insects that we typically notice are male cicadas, katydids, grasshoppers, locusts, and crickets. Some other species, including moths, produce sounds that are too quiet or too high frequency for our hearing.

The cicadas are the superstar insect vocalists, as only they are known to have developed a specific organ for singing. Cicadas possess two curved plates known as *tymbals* in their abdomen. The abdominal muscles contract and relax the tymbals and the abdominal chamber resonates like the body of a cello to amplify specific frequencies.

Most cicada species sing in a buzz saw-like whine – one species is known as the *scissor-grinder cicada* for a reason. Listening to the *dusk-singing cicada* will be a pleasure for fans of noise music. The song of *Linnaeus’s 17-year cicada*, who indeed spend 17 years as nymphs underground to emerge on one night in May and die in July, is genuinely disturbing, and the species ought to receive royalties for their use in horror movie soundtracks.

Cricket singing is far more popular with our species and tend to be around 4 kHz frequencies, not far from our own musical preference.

Nathaniel Hawthorne wrote in the *Canterbury Pilgrims*:

*He listened to that most ethereal of all sounds, the song of crickets, coming in full choir upon the wind and fancied that, if moonlight could be heard, it would sound just like that.*

Crickets, along with grasshoppers and katydids, produce songs by rubbing the inside edges of their forewings with one wing, the *scraper*, to scrape the *file* wing, a process known as *stridulation*, This generally produces high trilling sounds, although *mole crickets* produce frequencies so low that they sound like frogs. *Tree crickets* have evocative and simple trilled songs, and some, like the *snow tree cricket,* sing in synchrony with other males in outdoor cricket choirs. Cricket stridulation is faster when the air is warmer, and the pulses speed of the cricket songs can be used to estimate the temperature.

The *common true katydid* in the eastern United States has a pleasant song with three syllables that provides its name. Groups of katydids possess different regional dialects and for example the *southwestern katydid* drawls in a lower pitch, as seems appropriate.

Locusts produce their sound differently: they are essentially violinists, rubbing the femur of their hind legs against the edge of their forewings like a bow on a string.

While as mentioned, most beetles are deaf, some create sound by rubbing a surface against an external surface with ridges, which could be described as stridulation with another object.

Female fruit flies require a highly discriminating auditory system as there are 1500 species, each with a unique song, and they are most receptive to the courtship songs of their own species. Male Drosophila produce a courtship song by vibrating one or both wings, to produce 100-400 Hz vibrations. We can hear this song by placing a tiny microphone into the jar. The female hears the song with Johnston’s organ. The singing, together with dancing, licking, and males tapping (tasting) the female with their forelegs, can lead to successful mating. The female chooses the male with which to mate, primarily by assessing his song quality: if she doesn’t want to mate, she kicks the male in the face until he leaves.

The neurotransmitter dopamine stimulates not only courtship song by Drosophila, but as noted by Aike Guo and colleagues at the Chinese Academy of Sciences, also drives male-male courtship. These behaviors have been observed in both mutant flies with altered dopamine and after dosing flies with drugs that stimulate dopamine transmission, including aerosolized free base cocaine and methamphetamine.

Some male moths sing by rubbing scales on their wings. Ryo Nakano from the University of Tokyo showed that the female Asian corn borer moth stops moving when she hears the male’s courtship song. She also halts if she hears ultrasonic bat calls, suggesting that this species has adapted a behavior that may have originally been in response to predators – playing dead – to sex and mating.

In contrast, the Japanese lichen moth reacts to bat calls by emitting ultrasonic clicks to jam the bat’s sonar. In contrast to Asian core borers, female lichen moths react differently to their male mates and their bat predators.

## Singing by other primates

My vote for the most astonishing song by a land animal is by the gibbon. These are highly endangered apes with nineteen species in southeast Asia. Their song bouts last from 10 minutes to a half hour in the morning and are loud enough to be more than a mile away. Some of their singing sounds startlingly like whales.

Both sexes sing, with females producing a “great call” that lasts about 20 seconds. They are monogamous species and the pairs sing in duets to advertise or reinforce their bond, while single gibbons sing to attract mates.

Esther Clarke and collaborators at the University of St. Andrews analyzed gibbon songs at Khao Yai National Park in Thailand, and built full size models of leopards, tigers, pythons and eagles, using catapults to hang them over branches of trees in the forest. They concluded that gibbons also use their songs are used to repel intruders. These songs used the same notes as their other repertoire but were assembled differently.

Lemurs, also our fellow primates, are native only to the island of Madagascar in the Indian Ocean east of Africa. Of 100 or so species, all under threat of extinction, the indri is the largest and known for “contagious” calling, when one starts a loud call and the rest of the community who are two years and older in age join in. Both female and male indri sing, including in duet like the gibbons, with glissandos that resemble humpback whales.

Marco Gamba from the University of Turin in his paper *The Indris Have Got Rhythm!* analyzed singing in indri social groups, which are dominated by females who typically have a monogamous relationship with a male. The dominant female and male in a group seem to sing together more than the non-dominant, non-paired members. The authors suggest that the non-overlapping phrases might “advertise” individuality and potential availability.

Howler monkeys, the largest of New World monkeys, live in southern Mexico and through much of South America. Their calls, generally at dawn and dusk, can be heard three miles away. The songs can be individual solo or in groups. Both sexes call, and the females are quieter and overlap more. Margarita Briseño Jaramillo and colleagues from the National Autonomous University of Mexico studied calls of black howlers in Palenque National Park. She identified twelve different calls including roars, barks, moos, and metallic cackling: you can hear singing that will provide inspiration for heavy metal bands. The moo was only used when monkeys were reunited after separation. The grunt is used during play. The bark is used during conflicts with northern brown howler monkeys.

## Sound under water

The French oceanographer Jacques Cousteau produced a film called *Le Monde du Silence* (the silent world), but the whale song pioneer, American biologist Roger Payne, calls the ocean “a very loud place.” This is in large part due to propeller ships, oil drilling, and sonar. For example, the ambient noise at 30-50 Hz frequencies measured west of San Nicolas Island in California was 10-12 dB higher in 2004 than 1964, a period that saw a 4-fold increase in shipping.

In Chapter 1, we discussed how decibels (dB) report volume relative to a constant value of “excellent hearing” set at an air pressure of 20 µPa. We also said that liquids like water are “virtually incompressible”, which is virtually valid (at 200 times normal air pressure, water volume is decreased by 1%), but sound produced in water forms pressure waves within the water.

The volume of sound in water is also reported in dB, but by convention is relative to a water pressure standard of 1 µPa: this is a tiny amount of pressure, as water pressure at sea level is already at about 101 kPa, and climbs another 10 kPa with each 10 m of depth. The change in reference pressures in water and air works out to an equivalent sound pressure reported as 26 dB higher in water than air.

An extremely loud humpback whale has been reported as 176 dB “loud”, which corresponds to

176 dB – 26 dB = 150 dB in air.

To find the increase in water pressure by this very loud humpback we can rearrange the equation for dB in air in Chapter 1 for water as

176 dB = 20 \* log10 (X µPa)

176 dB/20 = 8.8 dB = log10 (X µPa)

To solve for log10 X, raise both sides of the equation by an exponential of 10

X µPa = 108.8 dB = 630,957,344 µPa = 0.631 kPa

So even a sound that is immensely loud changes water pressure by a tiny amount: this extremely loud 176 dB song at a 100 m depth (201 kPa) increases the pressure by only

0.631 kPa / 201 kPa = 0.3%

Ocean sound has effects on animals that can’t “hear”, at least by means we understand. For example, coral larvae settle in areas with relatively high levels (10 dB) of low to mid frequency (24 – 1000 Hz) sound that likely reflect a healthy reef. While most fish are deaf, their larvae similarly appear to use sound to find suitable habitats.

Of the sea invertebrates who can hear, squid, crab, and some others use organs known as *statocysts* that also sense balance and acceleration. These are two fluid-filled sac-like organs near the base of the brain lined with hair cells, and so resemble ears. They also contain a few grains of sand or a small mass of calcium carbonate known as a *statolith*. In response to sound, the hair cells activate the statolith (rather than the organ of Corti) to generate signals sent to the nervous system.

The range of frequency perception by sea invertebrate hearing varies. Hearing has been detected in crayfish from 20 to 2350 Hz and by prawns between 100 and 3000 Hz. According to T. Aran Mooney from the Woods Hole Oceanographic Institute, longfin squid can hear frequencies between 30 and 500 Hz, a range well adapted to perceive waves and wind, but not useful for detecting the echolocation signals emitted by their major predators, the toothed whales including dolphins.

Sea invertebrates respond to changes in sound volume. Mooney reports that when he played sufficiently loud sounds, squid release ink, propel themselves (*jet*), and translocate pigment within specialized cells known as chromatophores, which changes the color of the cells and alters their body pattern, a response typically used for camouflage. Loud human-made noises such as sonar are reported to damage the statocysts and to thus kill squid.

Fish hearing is surprisingly little studied, and while most species are thought to be deaf, the sand lance hears between 50 and 400 Hz and responds to the sounds of their major predator, the humpback whale.

But some fish produce calls and so presumably must also hear. These include freshwater and seawater drums and ocean clownfish, toadfish (the most studied vocal fish, who hums at night) and “grunters” and tiger perch. Similar to songbirds, many of these species tend to call together in a “dawn chorus”, and at times related to lunar phases.

## Singing amphibians and reptiles

The calls of male frogs and toads are one hopes familiar to the reader, and involved in mating and chorusing with regional dialects, with a nervous system attuned to potential mates, including some species in which the female taps onto surfaces to advertise her readiness.

For some of the most impressive vocalizations, the singing occurs underwater. The biological underpinnings of these vocalizations have been extensively studied by Darcy Kelley and colleagues at Columbia in African clawed frogs – *Xenopus*- who sing under water during the breeding season. Using hydrophones, they found that the male’s song sounds are two note chords with harmonic intervals are shared by related species. These pulses are created by the larynx, which can be induced to sing even when removed from the frog provided that vocal nerves are stimulated in the species-specific pattern.

Each *Xenopus* species’ larynx is tuned to produce different sound pulse chords. Females are specifically attuned to the pitches and harmonic chords of their own species’ males, suggesting that the production and perception of songs evolved together. A species’ specific song can be evoked directly from the brain after it is removed and exposed to the neurotransmitter serotonin, allowing *Xenopus*researchers to uncover the neurons responsible for the evolution of different song patterns.

In 1923, D. H. Lawrence composed the poem *Tortoise Shout* on vocalizations during tortoise sex.

*And giving that fragile yell, that scream,*

*Super-audible,*

*From his pink, cleft, old-man's mouth,*

*Giving up the ghost,*

*Or screaming in Pentecost, receiving the ghost.*

In spite of Lawrence’s familiarity with their voice, a lesson for our species is that we did not realize until very recently that turtles vocalize and hear. Camila Ferrara, Richard Vogt and Renata Sousa-Lima from the National Institute of Amazonian Research reported in 2013 that not only do female giant Amazon River turtles produce eleven types of sound, mostly but not only in the river, but that hatchlings also produce sound even while inside the egg.

These vocalizations are involved in gathering adults and hatchlings together in mass migrations and provide the signal by which hundreds of turtles emerge from the sand of a beach in the Amazon within a span of minutes to lie in the sun. The authors suspect that all turtle species vocalize. Why was this previously missed? In part because the sounds are mostly under water, and because as you might guess, turtle songs are slow, infrequent and of low frequency, so that one needs to record far from human noise pollution. A sadder additional reason is that once in captivity or in zoos, they simply stop singing.

Above the water, the reptile that has been most studied for call production is the tokay gecko, but multiple lizards hiss and growl. Carl Gans and Paul Maderson of the University of Michigan and Brooklyn College classified three overall types of sound production in modern reptiles including the hisses and the tail rattles of snakes and the calls of crocodiles.

## Whale song and hearing

The discovery of whale song seems similar to Columbus’s discovery of the new world, where people had been living for at least 15,000 years.

Traditionally, the discovery of whale song is attributed to a whaler, Captain William H. Kelly, who in 1881 heard a struck whale groaning when he put his ear to a harpoon line in the Japan Sea. According to Kelly’s colleague, Captain Herbert Lincoln Aldrich, writing in 1889:

*It has been known for a long time that humpback-whales, blackfish* [the pilot whale], *devil-fish* [the gray whale] *and other species of whales sing, and that walruses and seals bark under water, and it is believed that all animals having lungs and living in the water, as these do, have their own peculiar cry, or as whalemen express it “sing”…*

*With bowhead-whales the cry is something like the hoo-oo-oo of the hoot-owl, although longer drawn out, and more of a huing sound than a hoot. Beginning on F, the tone may rise to G, A, B, and sometimes to C before slanting back to F again. With the humpbacked-whale, the tone is much finer, often sounding like the E string of a violin.*

Captain Aldrich was right, as all eighty-six of the currently designated species of whales, which include dolphins and porpoises, vocalize, ranging from grinding clicks produced by narwhals to the well-known squeal of the porpoise and the long and extremely complex songs of humpbacks.

There are two major divisions of whales and they vocalize differently. The majority of whale species are toothed predators (*odontocetes*), including dolphins, narwhals and killer whales, who use echolocation to image their environment with ultrasonic signals in addition to other calls.

Fourteen whale species are baleen whales (*mysticetes*), named for their baleen plate that sifts seawater while swallowing large amounts of prey. These include humpbacks, bowhead, blue, fin, and minke whales. The baleens are the master singers of complex repertoire.

Whales are the only mammals who have evolved ears adapted for underwater hearing, and they perceive the broadest frequency range of any animal known. During their long evolution from land mammals, the ears of whales lost the pinnae and outer ear and migrated away from the skull to behind the base of the jaw. While an ear canal still exists, it is not directly connected to the eardrum and is thought to not conduct sound. Instead, whales hear by picking up the vibrations from the water that travel through the head, including through blubber, to the jaw and mandibles, which conduct the signal to the ear. Their middle ears are protected from the large pressure changes between breathing air and deep dives due to dense bony ossicles and eardrums.

A comparative anatomical study by Darlene Ketten from Harvard Medical School reports that toothed whale ears are adapted to sensing frequencies above 150 kHz, that is into the high range of bats, while baleen whales appear to have more acute low frequency hearing. The whale ear’s basilar membranes have larger pitch gradients than those of terrestrial mammals and are associated with a far greater density of nerve cells, especially for toothed whales, providing them an outstanding ability to distinguish frequency, an important feature for echolocation.

It is not straightforward to assess the sensitivity of whale hearing for long distance communication. Beluga whales in Bristol Bay, Alaska can hear at volumes as low as 35 dB in water (corresponding to the pressure of 9 dB in air: for comparison, audiologists rate hearing sensitivity of 20 dB to be normal for us). They also hear a far greater range of frequencies than us, on average from 22 to 110 kHz with some individual belugas found to hear frequencies as low as 4 Hz and as high as 150 kHz: two octaves lower and three octaves higher than we do! This provides a sophistication and detail for perceiving the sound of their environment we can only imagine.

## Songs of the baleen whales

Baleen whales evolved not only ears for underwater hearing under but also an extraordinarily expressive voice for singing. Joy Reidenberg from the Mount Sinai School of Medicine and colleagues find that the baleen whales contract muscles in the throat and chest that drive air flow between the lungs and an inflatable sac in the larynx next to structures similar to the vocal cords, the *u-fold*s, causing them to vibrate and produce sound. This vibration propagates through the surrounding tissue into the water. The change in frequency and volume of the voice can be controlled by the shape of the sac in the larynx. This mechanism of singing doesn’t expel air, allowing the whales to produce very loud sounds without coming up to the surface to breathe.

One of the singing whales heard by Captain Kelly, the bowhead, spends its life entirely in Arctic waters, and can grow to 59 feet in length and 100 tons with the largest mouth of any animal. While formerly driven close to extinction by whaling, the population has recovered in Alaska since commercial harvesting has been halted. Bowheads are named for an arch on their head that can break through breathing holes in ice sheets. They sing with an immense variety of different sounds. Kate Stafford from the University of Washington and colleagues recently recorded 184 different songs from bowheads, over three years off the coast of Greenland during the winters under nearly complete ice cover and total darkness.

The humpback whale, at up to 52 feet long and 30 tons, lives in all of the oceans and is by far the most studied and appreciated singer. When the world population decreased to 5,000 animals in 1966, the brink of extinction, the International Whaling Commission banned commercial humpback hunting, and the current worldwide population is now estimated at 80,000.

In striking contrast to bowheads who sing under ice in the Arctic, humpbacks migrate between summer months near the poles where food is plentiful to tropical oceans to breed and sing in winter. Some travel over 5000 miles from Antarctica to Costa Rica. Humpbacks who spend the warmer months near Iceland and Norway arrive at breeding grounds off the Dominican Republic and Puerto Rico at the end of February, to be joined a bit later by whales migrating from the east coast of North America. One highly recorded population spends most of the year off the coast of Alaska to return each year to breeding grounds in Hawaii. Louis Herman from the University of Hawaii has recorded individual males singing for over twenty years, a span that allows them the opportunity to change their songs over a lifetime of singing.

The contemporary understanding of whale song is due to the efforts of the American biologist Roger Payne and the poet explorer Scott McVay, who heard recordings made with a hydrophone (a microphone used to record sound underwater) made by Frank Watlington, a Navy engineer, who accidentally recorded whales off Bermuda while listening for Russian submarines. Reminiscent of Captain Kelley a century before, on one exceptionally quiet evening off Bermuda, Payne heard a humpback singing through the bottom of the boat.

Payne and McVay wrote in 1971 that the humpbacks produced songs that lasted for 7 to 30 minutes and repeated the songs precisely, with each individual whale adhering to its own song. The songs are complex and mostly use frequencies we hear (mostly 8 Hz to 10 kHz) and are very loud (from 151 to 173 dB underwater). They wrote

*The principal differences between bird and humpback songs are that bird songs usually last for a few seconds, while humpback songs last for minutes; and one song of a bird is usually separated from the next by a period of silence, whereas humpback songs are repeated without a significant pause or break in the rhythm of singing.*

Roger released the record album *Songs of the Humpback Whale* in 1970, a bestseller that popularized whale conservation and the environmental movement, and helped to bring about the moratorium on commercial whaling by the International Whaling Commission in 1982. The album features solo and group songs and contains three recordings attributed to Frank and two by Roger and Katie Payne, whose work on subsonic sounds by elephants we will come to. They and others have also produced commercial recordings of blue and right whale songs,

I think that to some extent, the recent recordings of whale music have helped to save them from extinction due to our species.

## Humpback whale conservatori

Only male humpbacks sing entire songs, both alone and in groups, while females make occasional vocals and produce percussive sounds from flipper or tail slaps. For the males, singing is very common in the warm water breeding grounds during the winter, in the northern hemisphere increasing between mid-February and mid-March, coinciding with ovulation. Singing has also been recording during migration and is occasionally recorded in the subpolar feeding grounds in late spring and late autumn, possibly from younger males practicing.

During the winter, in addition to solo songs, a chorus of males can be heard singing simultaneously at different sections of the song, like a canon. This chorus is speculated to be from whales in a *lek* that females without calves visit for mating. Leks are formed during mating season not only by whales but by sea lions, harbor seals, walrus and dugongs, each of whom also vocalize throughout the breeding season. It seems that females don’t visit the lone singers, but often leave the lek pregnant.

Male humpbacks learn songs both from their father and from other unrelated males, and individuals have their own song but can modulate the song or can change to a new one. A population within a shared ocean basin usually conforms to a dialect or song type.

The humpback songs change within the population, sometimes over the years, but occasionally in a “revolution” when a complete complex song takes over for a whole population in about a year.

Roger Payne suggested that the new songs arrive from individuals moving from one breeding population to another or during a shared feeding ground or migration. Similar new songs have been recorded in both the Caribbean and Cape Verde Islands off the West African coast, in both Mexico and Hawaii, in both eastern Australia and French Polynesia, in both northeastern Brazil and Gabon in west Africa, and even across the African continent between the Atlantic and Indian Ocean coasts. This suggests that new songs are learned in summer grounds and that by winter, most singers have converged on the new style.

## Long distance calls of the fin whale and of elephants

Toothed whales produce calls for other reasons, including to notify others of their presence. The most studied long distance call is from fin whales, who are found in deep water on all sides of pack ice fields that often extend for hundreds of miles, particularly in the Antarctic during spring. Hearing another fin may help them find their way among the ice packs.

Like elephants, fin whales use low frequency sounds, around 20 Hz, apparently to trigger their location as the herd moves. These “blips” of sound are very loud trains of near sine wave pulse train, or can be pairs of pulses that last about one second and are repeated at regular intervals about 5 times per minute for about 15 minutes. They are followed by a period of silence of about two and a half minutes, suggesting that they are interrupted by the breathing cycle.

Roger Payne with Douglas Webb from the Woods Hole Oceanographic Institute, estimated the distance that fin whale vocals would travel based on the background noise of the sea, which is far louder now than before propeller ships and sonar. As with the bass frequencies entering your apartment from your neighbor’s party, low frequencies, particularly around 20 Hz, travel well in the water under ice, as shorter wavelengths are reflected by the rough surfaces of the ice. They estimated that before steamships, fins might detect another fin from 450 miles away over an area of 610,000 square miles. If their hearing were somewhat better still, they may be able to hear another fin from across the Arctic ocean.

Toothed whales have a different means of control of the voice from baleens. The beluga or white whale vocalizes by forcing pressure through its nasal cavities, which have a set of lips. They possess the ability to lower their pitch into the human range. Sam Ridgway from the National Marine Mammal Foundation and colleagues recorded a beluga whale named Noc (*no see*) who was trained for operations with the US Navy, mimicking human speech, including ordering a diver, Miles Bragget “out” of the water: listen to their recording of Noc imitating the sound and cadence of human speech, something he did not do with other belugas….

Keepers at the Vancouver Aquarium report that one would speak his own name, “Lagosi”. Beluga whales are reported to make human-like sounds in the wild. Elena Panova and Alexandr Agafonov from the Russian Academy of Sciences report that a captive beluga whale in an aquarium in Crimea who was housed with bottlenose dolphins learned to imitate the signature whistle calls of the dolphins.

Elephants also use low frequency for long distance communication. Elephants are highly vocal and use a very wide vocabulary of sound for communication, including snorts, grunts squeals (usually for delight in my experience) and the well-known trumpet. Part of the diversity is due to the use of the trunk to produce some sounds and the mouth for others.

The production by elephants of the very low frequencies has been described in part by anatomical studies of the larynx by Christian Herbst and colleagues from the University of Vienna. As you would suspect, it is the largest mammalian larynx yet studied and is thought to make calls down to 10 Hz. Herbst concludes that some of the sounds are made by vibrations of the vestibular folds, which our species uses in some Tuvan “throat singing” and death metal growls.

These infrasonic sounds were discovered by the biologist Katie Payne, who at the Portland zoo felt the elephants produce a very low frequency rumble, under 20 Hz and so inaudible to us. To demonstrate their existence as sound, she simply sped up the tape recorder playback speed.

The rumbles shake the dense molecules of the ground and propagate long distances. Katie Payne and colleagues estimate that low frequency rumbles are probably heard in East Africa for about 50 square kilometers around the elephant, and in some atmospheric conditions perhaps even to 300 square kilometers. Elephants eat a tremendous amount of vegetation (in Asia about 400 pounds per day) and need to spread around a large area. The low frequency sounds are used during their travels to keep the pack together. They are now used by scientists to track and study elephant herds in Africa in the Elephant Listening Project.

Other animals who produce infrasound include rhinoceros and giraffes. Elizabeth von Muggenthaler and colleagues from the Fauna Communications Institute in North Carolina have described low frequency singing by the rare Sumatran rhinoceros in the Cincinnati Zoo, which sounds similar to whale song.

Surprisingly, the far smaller koala possesses a vocal organ that allow them to produce bellows as low as 9 Hz.

Alligators produce underwater infrasound, using rumbles to produce waves in the water.

## Echolocation by bats and toothed whales

One might not imagine two groups of mammals more different than bats and whales, and yet both sing – singing by male bats has been relatively little studied but can sound very much like birdsong.

Bats and toothed whales both tend to hunt in the dark, and so also developed a very different sense of sound, *echolocation*, in which they emit high pitched clicking sounds which bounce back from prey: the shorter the time for the return, the closer the object. Due moreover to the Doppler effect discussed back in Chapter 1, as the echo frequency increases, they are getting closer.

Echolocation was discovered and named by Donald Griffin, an undergraduate at Harvard while working with the physicist G.W. Pierce who developed a means to detect ultrasonic sound. Griffin and a fellow student, Robert Galambos, proved the existence of echolocation to skeptical observers by showing first how bats avoid flying into wires suspended from a ceiling, but collided with the wires when their mouths were tied shut or ears plugged.

Bats mostly generate the clicks in the larynx. These calls are short, from 0.2 to 100 milliseconds, and range in frequency from 11,000 Hz, within our hearing range, to over 200,000 Hz, more than three octaves above pitches we perceive. The volume ranges between 60 and an ear shattering 140 db, particularly in open skies. Bats exhale and produce clicks during the upstroke of their wing. Some species decrease the volume as they near reflective surfaces to prevent damaging their own ears.

When searching, bats typically click about 20 times per second, but increase the rate when they hone in on an insect, increasing the pulse rate, sometimes to as high as 200 clicks a second. In addition to distance and movement, bats can estimate the elevation of targets from the echoes reflecting from the *tragus*, a flap of skin within the ear. The inner ear is also specially constructed, with the cochlea longer in regions corresponding to the frequencies of the call.

The auditory cortex of the bat has been studied by Nobuo Suga and colleagues at Washington University at St Louis. A region they call the *FM-FM area* responds to the call and echo, with neurons responding to a specific time delay, thus reporting the distance of the bat to the target. Another known as the *CF-CF* detects Doppler shifts, and thus the change in distance to the target.

It appears that all toothed whales use echolocation, including dolphins, porpoises, beluga, killer and sperm whales. Their clicks are of a wide variety, including the very low 20 Hz long distance calls of the fin whale discussed above. For echolocation, dolphins use very short clicks of about 50 microseconds at frequencies as high as 150 kHz. The clicks are emitted as a beam in the direction that their head points toward plus a small incline upward. Different click frequencies produce the well-known barks and squeals of the bottlenose dolphin.

Recall that sound travels over 4 times faster in water than air. As with bat echolocation, the rate of the toothed whale clicks can be shortened as the target is closer so that the estimate of distance is not confused due to overlapping echoes. The echo is received similarly to the baleen whales, in the lower jaw and conducted to the middle ear. The whales can deduce the type of object from the echo.

Toothed whale clicks can be immensely loud, up to 230 dB underwater for the Atlantic spotted dolphin. The distance that echolocation can be used to detect a small object in experimental settings is about 100 meters. Sadly, the entrapment of scarred whales and dolphins in fishing nets, and toothed whale deaths from boating accidents, indicates that this echolocation can be confused by our technology.

## Animals improvising on musical instruments

Here’s a syntactically simple sentence fraught with semantic complexity:

Can animals play musical instruments? I think that, to paraphrase President Bill Clinton, it depends on what you mean by the words “can”, “other” “animals”, “play”, “musical” and “instruments”.

Circuses have long trained seals and walruses to use their snouts to play tuned car horns in a sequence, and street performers traditionally trained monkeys to use sticks to play drums. But will non-human animals create their own music on instruments?

## Chimpanzees and bonobos

The primatologists Jane Goodall and Adam Arcadi of Hofstra University studied drumming by apes in the wild. In the forest, chimpanzees use their hands and feet to hit trees and play low frequency drumming sounds heard by humans a kilometer away. Some naturalists, including Peter Marler, suspect that chimpanzee drumming is very similar to the well-known chest beating by mountain gorillas.

In the Tai National Park of the Ivory Coast, the chimpanzees usually drum while they are calling in “pant hoots”, whereas in Kibale National Park in Uganda, they tend to drum on trees without calling. Chimpanzee drumming is used to communicate between individuals far from each other who are not in visual contact. The Tai chimpanzees drummed in distinct styles, while those in Kibale are reported to drum in a collective style.

Valérie Dufour from the University of Strasbourg and colleagues studied spontaneous music making on human made drums by captive chimpanzees living in a research center in the Netherlands. The longest duration performance they observed was by Barney, who in January, 2005 spontaneously performed on an upturned bucket in a style reminiscent of a bongo drum in a solo for over 4 minutes.

Together with the late Gordon Shaw, I explored whether the close relatives of chimpanzees, bonobos, would play on human designed instruments. Gordon was a physicist at the University of California at Irvine, who developed the notion of the “Mozart effect”, in which he theorized that children were smarter if they listened and learned to play Mozart.

We brought tuned musical bells to the bonobo colony at the San Diego zoo. They immediately played the bells, but after a few minutes realized it was better to throw and smash them against the walls: bonobos are far stronger than any human and that smashing the bells required no appreciable effort.

Bonobo colonies, both wild and in the zoo, have a matriarchal culture, and when I played a marimba that we designed for them, they ignored it at first, until Lena, the matriarch, cuddled up to my leg for perhaps an hour, and then the others began to pay attention. They would listen and react, but I didn’t observe them trying to play the marimba during the few sessions we had with them.

Far more impressive results were from the singer and keyboard player Peter Gabriel, who spent many hours singing and playing electronic keyboards with two bonobos, Kanzi and Panbanisha, as well as from the efforts of the primatologist Itai Roffman from Yezreel Valley College in Israel who has been working with Kanzi.

The psychologist and primatologist Susan Savage-Rumbaugh has lived and worked with bonobos for decades, beginning with Matata, who was imported to the Yerkes primate center in Georgia at puberty, after having learned the culture of wild bonobos. Matala’s son, Kanzi, grew up with his sister Panbanisha and Matata in a language laboratory with a 200 acre forest in Georgia in the 1990s, alongside Susan’s own son. Kanzi understood spoken English, and with coaching learned to make stone tools, start fire, and paint. He also learned to speak both Matata’s language and to humans by manipulating geometric symbols to communicate wishes and feelings.

In Susan’s words:

*The bonobo language is quite musical and often at night bonobos sing together before going to sleep. One of many “bonobo rules,” set by their matriarch, is that no one should go to sleep until everyone is happy with everyone else, which they express by singing with considerable jubilation each night.*

*Reading about Kanzi and his sister, Panbanisha, the musician Peter Gabriel wondered if they might be musically inclined and requested a visit. Peter brought his electronic keyboard and played to them and they were offered a similar keyboard and urged to play along. They were polite and pressed a few notes, but mostly listened to Peter. He continued to play for over a week, several hours per day and they continued to listen but not “play music.”*

*One afternoon when they were again listening to Peter but not playing, I noticed that they were also listening to Matata who was about 500 yards away. I decided that since they were paying attention to her and sending sounds her way, that I could request that “they play a song” to their mother. They immediately brightened, and I said to Peter, why don’t you all play a “Matata song.”  Peter began, and this time they played keyboards with him and also sang to Matata.*

*It seemed that we found a key. Music needed a functional purpose, a topic. To co-create with Peter, they needed to make music together. They played songs about apples, bananas, grooming, and other bonobos. Peter immediately emulated their rhythms, chords, and melodies and they took note. Prior to this, human musicians had always expected them to do what they did, but while bonobos could follow it, they did not find it interesting. Here was a human playing the kind of music they played with them that had a purpose. They tuned in. Peter felt that they had a “sense” of music already available to them.*

*About 15 hours of video data were created by Peter Gabriel and the bonobos. Kanzi was more interested in rhythm and Panbanisha more in melody. It was clear that their songs have a beginning, middle and end, as does a conversation. Watching the videos reveals that while Kanzi and Panbanisha are not remotely as skilled as Peter, they are making music with him of their own free will, not for a grape, and that they enjoy it.*

*It might be thought that the Peter was simply “making the bonobos sound good” rather than co-creating songs with them, but our analysis reveals that this is not what took place.  In Panbanisha’s* Grooming Song*, in which she played 226 notes, they go back and forth with each taking turns as the leader or the follower, thereby co-creating the song. At one point, she wanted to alternate between the highest and lowest notes of an octave and signaled this to Peter with her fingers before she does so.  He saw her intent, and they both alternated the octaves. To do this requires a sense of what an octave is, a knowledge of the location of the notes on the keyboard, an understanding that the lead can alternate between partners, all while continuing the song and maintaining the rhythm. None of these things were taught to Panbanisha and prior to Peter’s visit no one had ever co-played or co-created music with her. She had been allowed to explore the keyboard and any knowledge she accrued of the location of various keys and notes, she taught herself.*

Altogether, studies, both by Jane Goodall and others in the wild, and of apes in captivity demonstrate that that chimpanzees and bonobos have behaviors that we generally claim for ourselves.

Reminiscent of the way that Roger Payne and Scott McVay’s humpback recordings helped the protection of whales, Itai, Susan and other students of ape behavior wrote a manifesto in 2019 calling for chimpanzees and bonobos, our closest relatives by genetic analysis, to be classified as homonids with the official and legal status as our species. One can only ask that this well-reasoned legal reclassification will help preserve and protect the chimpanzee and bonobo societies and cultures in the wild.

## Songbird instrumentalists

While one might guess that performing on musical instruments would be particularly successful for vocal imitators like mockingbirds, only limited efforts have been made for developing ergonomic songbird musical instruments,

An artist in France, Céleste Boursier-Mougenot, has developed a means for zebra finches to make music in art galleries, for example by allowing them to alight on and thus trigger active electric guitars.

An approach was introduced by Ofer Tchernichovski for his zebra finch colony, in which he rigged a lever that they could peck to hear the singing of another zebra finch, which in some cases they will do hundreds of times a day and even hundreds of times an hour.

Linda Wilbrecht from Rockefeller University, Douglas Repetto from Columbia University, and I extended that approach using a set of multiple levers to offer a means for zebra finches to trigger songs by other birds or other sounds. We were amazed to find that for some human music, including from trumpets that sound a bit similar to zebra finch calls, they would press the levers hundreds of times a day, although there was no reward other than hearing the sound. Very often, they would vocalize at the same time that they triggered the instruments.

The zebra finches had a musical “taste” as some sounds, like punk rock guitars, would be played only once and not returned to. In addition to human-made sounds, they would also press for some bird calls from other species: once they triggered a canary call, which can attack the smaller zebra finches, and as apparent from their loud squawks in response, the canary call frightened them, and they would not trigger that lever again.

No one has yet tried this kind of bird instrument in the wild, although Ofer suspects that they would also play the instrument if it were ergonomically designed and placed. Until this is attempted, we won’t know, to paraphrase Maya Angelou, why the caged bird plays.

I would take Ofer’s side of the bet for some species: consider that the cedar waxwing has two common calls but is considered to have no full song, while a male brown thrasher can have a repertoire of over 1000 songs. I would guess that an ergonomically designed instrument in the wild might be played at times by a male brown thrasher, and also by his intended audience, the female brown thrasher.

## The Thai Elephant Orchestra

Of all species that ours has learned to domesticate, the Asian elephant is the one for which future survival is in doubt. With rapidly falling numbers of both wild and domesticated animals due to loss of habitat and their traditional work roles with humans, their best long-range hope is now in the establishment of sufficiently large breeding populations in managed semi-wild habitats. For the foreseeable future, these will have to be funded by a mixture of tourism, government and private support.

Domesticated for thousands of years, but genetically no different from the wild populations from which they were captured, the Asian elephant has been trained in skills that in breadth, variety, and complexity certainly surpass any other animal. Formerly used in war as conveyors like horses and as effective weapons, and later as loggers and commercial transport, their most recently developed employments are in traditional human arts, including painting, musical performance, and soccer. These new roles have been invented over the past three decades, and they at least begin a new chapter in the long history of elephant training that we hope will be safer and more pleasant.

By far the largest attempt at instrumental composition by other animals was the Thai Elephant Orchestra at the Thai Elephant Conservation Center (TECC) that is run by a branch of the Thai government, the Forest Industry Organization (FIO), between Chiang Mai and Lampang in northern Thailand. The TECC is a government owned center that was the first devoted to the care and conservation of out of work domesticated elephants: following the TECC there are at present about one hundred privately owned centers.

The TECC was initially a home for logging elephants that belonged to FIO but were no longer employed due to a nationwide logging ban following the country’s deforestation. The Center’s elephant population, which typically hovers around sixty, is supplemented by other working elephants whom owners can no longer maintain, donations from zoos, and “white elephants” that belong to the royal family. As befits social animals, they live in a large well-maintained group with extensive time each afternoon and night in the jungle. Due to the requirement for revenue via tourism, nearly all of the elephants must engage in some relatively light work in the morning, such as demonstrations of logging techniques or giving rides through the forest.

The idea for the orchestra was planted in 1999 in New York, when I met Richard Lair, an American who has lived in Southeast Asia for about fifty years. Richard, known as “Professor Elephant” in the region, is the author of *Going Astray*, the primary reference on the Asian domesticated elephant, as well as the standard elephant veterinary manual, and at the time hadn’t visited the USA in over nineteen years.

Richard had recently inaugurated a painting project for elephants with the aid of the Russian émigré New York artists Vitaly Komar and Alex Melamid, who had painted with Renee, an elephant in the Toledo, Ohio zoo in 1995, with help from Don Red Fox. The artists proposed to establish “Elephant Art Academies” for out-of-work elephants to raise money for the animals and their mahouts. At the TECC, the team and the elephant’s mahouts (trainers and caretakers of domesticated Asian elephants) quickly taught the elephants to paint abstract designs. The paintings raise significant support for the Center, and more importantly, raised awareness of conservation efforts, particularly for the most important audience, the Thai public. Numerous other centers have followed suit and elephant paintings are at present widely sold by public and private centers.

Komar and Melamid’s Thai speaking guide, Linzy Emery, arranged for Richard to stay in my apartment. We both enjoy listening to music, and one evening after hours of listening to Junior Kimbrough, Aretha, Maurice Ravel, and an unaccustomed dram from Scotland’s fair shores, we naturally wondered whether elephants would learn to play music. Richard told me that the elephant’s mahouts know that elephants like to listen to music; they often sing to or play an instrument for the elephants as they walk together through the jungle, and the elephants are calmed. Elephants, moreover, are social animals and might enjoy an activity like playing music together.

While there was good reason to suppose that this idea could work, there were also lots of questions to consider. Do elephants have any comprehension of music? We read that they did. Rickye and Henry Heffner at the University of Kansas used a simple food reward experiment to elicit an Indian elephant’s ability to distinguish simple two note melodies. They could distinguish microtonal pitch gradations, smaller than the half-steps on the piano.

A study by Karen McComb from the University of Sussex even showed that wild elephants in Kenya could distinguish ethnicity (the Maasai tribe, who herd cattle and chase elephants away in contrast to the Kamba tribe, farmers who do not) age, and the gender of humans from the sound of their voice.

What sort of instruments should we make for elephants? The instruments should be suitable to the elephant’s anatomy, which means large and operated by the trunk. They should also sound Thai, because the regular daily audience is from Thailand (although at present most of the audience is from China), the mahouts would enjoy the music more, and the elephants have heard Thai music all their lives. Thai tourists who stumbled on the practice and recording sessions told me that the elephants sounded as if they were performing a style of music that can be heard in the Thai Buddhist temples, which I took to be a good sign.

We constructed and adapted many instruments, some of which never worked, often because they weren’t easy for the elephants to play.

The mahouts told us the elephants especially enjoyed playing the large marimba-like Thai *renaats*. To make the large metal instruments, including the elephant version of the renaat, I mostly worked with Sahkorn, a talented metalworker in Lampang, about 30 km from the Center. I chose a pentatonic musical scale that would suggest traditional northern Thai music (such as D E G A C), and in some cases added two American blues notes (for example Eb and Bb).

Designing elephant xylophones.

The classic Thai renaat is a marimba in that its sound is made by vibrating wooden slats. The standard instrument is too delicate to withstand elephants or being left outside during monsoon season. Sakhorn and I constructed the elephant renaat with the stainless steel tubes used to protect fuel and heat lines.

The relationship of the length of a hollow tube and the frequency of sound is different that a string, in which dividing the length by two produces the next higher frequency (remember Chapter 2): for a tube, the pitch changes with the square root of the length. For example, if the fundamental *f1* is a two-meter tube that sounds middle C (C4), and you want a tube the next octave higher (C5), the length would be

2 m \* 0.707 = 1.414 m

The most common scale I heard in northern (Lanna) Thailand near Lampang is a pentatonic scale consisting of a fundamental, minor third, fourth, fifth, seventh and octave that we adopted (e.g., E G A B D). I chose a just intonation (also Chapter 2) and the square root relationship to make relative tube lengths of

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| --- | --- | --- |
| *scale name* | *frequency ratio* | *tube length* |
| fundamental | 1/1 | 1 |
| minor third | 6/5 | 0.913 |
| perfect fourth | 4/3 | 0.866 |
| perfect fifth | 3/2 | 0.816 |
| minor seventh | 9/5 | 0.745 |
| octave | 2/1 | 0.707 |

We then need to attach the tubes to the body of the instrument, and (remember from Chapter 3), it would be best to do that at the motion nodes, where a string vibrates the least, so that the rest of the tube can vibrate to it maximum extent and produce a good ring.

In a string, the nodes are at the nut and bridge at the ends, or where you depress the string with a finger, and the largest movement is in the middle. In a bar or tube, the greatest motions are not only in the middle but also near the two edges, and so the holes should be drilled where the nodes are between the three spots. This turns out to generally occur about 2/9 (22.2%) of the distance from the ends. For hanging elephant tubular bells, one hole can be placed at this distance and threaded with rope to suspend them. For the renaats, we drill two holes and tie them with rope at those points.

Most remarkably, the elephants learn on their own to beat the tubes of renaats at the antinode, that is the ‘sweet spot”, where the tone sounds clearest, and they avoid hitting the nodes.

Richard, the mahouts and I constructed giant tuned slit drums. We made a gong from a circular saw blade confiscated from an illegal logging operation. The harmonica maker Lee Oskar donated harmonicas and we adopted a mouth organ (*kaen*) played in the neighboring region, Issan in Northeast Thailand: I cut the lengths of the reeds of the kaen to match the orchestra’s tuning. Together with Neepagong, director of the woodworkers at the Conservation Center (Northern Thais generally use only a single name), we constructed giant slit drums, and an enormous string instrument that sounds like an electric bass, the *diddley bow*, which inspired the name for Bo Diddley, and our instrument was in turn named after him.

In addition to the specially made instruments, on my first visit, the instrument builder Ken Butler and I chose harmonicas and pre-made instruments that would mesh with that scale, while an artist, Don Ritter, produced a synthesizer. The elephants took easily to the harmonica, which sparked the first elephant music fad: one morning I arrived to hear the sound of harmonicas from all around, from the hills and from the river. The elephants were in from the forest playing harmonicas, which they hold easily in the tip of their trunk and sometimes blew them into their own ears.

The gong and thundersheet initially scared some elephants, but they soon adapted. The kaens worked well for sound production, but the elephants couldn’t hold it and needed to use the mahouts as instrument stands. The elephants didn’t seem interested in the bells, theremin, or synthesizer keyboard, but would play when asked. They disliked playing the wind instruments with a large mouthpiece (i.e., trunkpiece). A mahout told me they were afraid that a snake might jump through the wind holes into their trunks!

On our first trip, Mei Kot, then an 8,000 pound seventeen-year-old girl, was first frightened by the gong, but around the third afternoon of her performance, we couldn’t get her to stop playing it. Her mahout would take the mallet out of her trunk, but she would pick it up and continue playing. This music can be heard in the delayed ending of some of the pieces.

Rory Young, a recording engineer, constructed a studio in a clearing in the jungle and on subsequent trips, a team of recording engineers drove up from Bangkok. Over the course of six visits, we have tried out about forty instruments, and another instrument that worked well were angalungs, tuned rattles that northern Thai children learn to play in grade school.

One of the successes in incorporating the local culture was to record school children from a nearby village performing a nursery rhyme about elephants, *Chang Chang Chang*, and then arranging it into a big orchestrated piece on our second CD. In each public show at the Center, that piece is blasted over the PA system as the elephants pass through the viewing stands built in the teak forest.

It was gratifying to see the mahouts become more and more interested in the Orchestra, teaching their elephants, inventing new instruments, and expanding the size of the band from the original six to perhaps eighteen players in total. Indeed, the group by weight is the largest orchestra in the world, at several times the combined weight of the Berlin Philharmonic.

The Orchestra indeed raised public awareness for the Center, particularly where it counts most, in Thailand. Sometimes the orchestra plays with human musicians, leading to an infamous incident where I arranged the first movement of Beethoven’s *Pastorale Symphony* for the elephants and a sixty piece school marching band from the Galyani middle school in Lampang, conducted by the band teacher, Rakhorn. We were proud that a BBC simulcast of the concert was picked up by the American TV show, *Jon Stewart’s Daily Show*, as their “moment of zen.”

The local Thai newspaper article wrote:

*The Thai Elephant Orchestra, conducted by Richard Lair, had a command performance for HM Queen Sirikit of Thailand. The concert was a collaboration with the 60-strong concert band of Galayani School. The warmly received performance started with the elephants on their own; subsequently, the children’s orchestra came in, selected elephants jammed along with it to then segue into elephants only. Most of the music was Thai but there were two western songs,* I Did It My Way *(a favorite of Her Majesty) and* Oh Danny Boy*.*

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| ORCH21.jpg |

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| ORCH10.jpg Figure 11.3 The Thai Elephant Orchestra Members of the Thai Elephant Orchestra on renaats in a recording and on the standing percussion section with a Thai temple gong, a gong made from an illegal confiscated logging saw blade, and a set of tuned tubular bells. Photos courtesy Millie Young, Mahidol University International College. |

I don’t think it’s interesting to teach elephants to play prewritten human melodies. It’s much more interesting to hear how they “choose to play”. After teaching the elephants to play the instruments and giving some indication of how the instrument should be played for that piece, Richard or I would cue the elephant and mahout to start and stop. The mahout would encourage his animal by moving his arms in a mime of the elephant’s trunk.

Except for *Chang Chang Chang*, a thirty-two note melody that the mahouts on their own taught the elephants to perform on the angalung, the notes and rhythms of the pieces are chosen completely by the elephants. One surprise is that they play variously in duple meter (straight eighth notes), triple meter (alternating quarter and eighth notes), and a dotted rhythm (dotted eighth and sixteenth). Sometimes they found motifs for a particular piece and repeated them. I cannot say why they made these choices.

On returning to the USA, many people asked me: is this music? I propose an answer based on the Turing test, which was designed to determine if a computer possesses intelligence. Play the recording for people who don’t know the identity of the performers and ask them if it’s music. They may love it or beg you to stop, but I think they will say “of course it’s music.” I tried this once with a music critic from the New York Times, who eventually guessed “it’s an Asian group.” He was initially upset when I told him who the performers were, but by the next day asked to write about the Orchestra.

I’m also confident that the elephants understand the connection between many of their actions and the sounds they produce. They don’t operate the instruments randomly but aim for where the sound is best. You can watch this process occur over time on the renaats. The elephants can easily keep a fairly steady beat on numerous instruments, and in the case of Luk Kop (“Tadpole”) can alternate between several drums. Long before, Richard had trained Luk Kop to be the elephant in a Disney movie, *Operation Dumbo Drop*. He can be a very sweet elephant who loves to be fed candy and have his tongue petted, but over the past few years as an enormous adult, he is sometimes very dangerous – but only to humans, never to other elephants and never to his chief mahout. He has, however, chased other people through the forest. So Luk Kop has been retired from the orchestra and all other forms of activity where he might encounter tourists. Still, he was our most avid and talented drummer.

I suspect that at least some of the elephants enjoy playing instruments that are well tuned and have a pleasant resonance. As mentioned, elephants learn on their own to hit renaat bars on their sweet spot, where a more resonant tone is produced, rather than near the nodes, which produces a sharp percussive clank. On a renaat, I planted a dissonant note to see what would happen, and the filmmaker Kurt Ossenfort recorded Pratidah playing on videotape. For the first several minutes, she avoided the note, but later would not stop playing it. Perhaps like a punk rocker or early 20th century composer, Pratidah had discovered a pleasant dissonance. At any rate, she certainly outsmarted my test design.

On one trip, I was accompanied by Aniruddah Patel, a neuroscientist at Tufts who specializes in animal musicality. Aniruddah felt that while the elephants can actually keep a steadier beat than most humans on the drums, they may not play in synchrony at all. I am not convinced, however, as it appears that the elephants often play in off-beat and triplet rhythms with each other, which would be counted as “out of synch”. As with Pratidah’s dissonance, we may simply not have designed the right test or analysis for such smart animals.

I have seen a few instances when an elephant will walk over to an instrument spontaneously and play it for a few seconds, and Richard and the mahouts tell me this is fairly common. I suspect that this is when the elephants are bored. I have not seen two elephants spontaneously perform together. The urging by the mahouts can range from a single word to ongoing ear tugs for every movement. Some elephants, primarily Poong and Pratidah, can walk over to a renaat and play a solo with no urging during the appropriate time during the daily logging show and with no mahout near them, and know when to begin and end a solo.

Prattidah was originally the outstanding renaat player, coming up with beautiful phrases and melodies. Sometimes she would refuse to stop playing her renaat. As with Mei Kot, it is very hard to get her to stop if she doesn’t want to!

An outstanding example of one of such solo, played without any instruction during the performance albeit with a single edit in the recording studio, is from Poong on the Orchestra’s second CD, *Elephonic Rhapsodies*. The sole instruction by humans was to give Poong a stick to initiate the solo, and Poong himself decided when to end the music. When he finished, he simply dropped the stick and walked away. It was on a cadence where it sounds to us like the song should end. The solo has a repeated theme and rhythm, but the extent to which this is random, ergonomic, or intended is guesswork. There is still the remarkable situation where a non-human animal is creating its own beautiful music intentionally on an instrument, whatever the underlying mental processes and extent of understanding.

This brings us to parting troubling thoughts. Some say that it is wrong that non-human animals be trained to perform human-like activities. One should certainly question the notion of teaching elephants to perform human tasks, whether in warfare, logging, riding, babysitting (!), or art and sport, all of them obviously not a part of their wild behavior. I agree with this belief at least for those animals that we have not selectively bred – I think domestic horses can love being ridden once they are trained, etc. - but only if a healthy wild behavior is a genuine alternative. The Asian elephant has been domesticated and trained for human-like activities for thousands of years, and light work performing for tourists in activities that are enjoyable, like playing in the Orchestra, is preferable to using the elephants as war machines, trucks, and loggers.

I believe, as does Richard Lair, that the optimal situation would be to have large wild spaces for the elephants to live in herds, with a means for us to view them without interfering with them except for situations such as medical intervention – perhaps similar to how Kenya provides well run game parks such as the Masai Mara. But we are certain that this will not occur to any reasonable extent in our lifetimes, and steps must be taken now to help the long-term survival of the species, as well as to support out-of-work elephants and their mahouts who cannot otherwise support themselves. I think it likely that the long-term survival of the Center and like-minded camps for elephants may become extremely important for maintaining genetic diversity to avoid diseases that would possibly lead to extinction as both domestic and wild populations dwindle. For far more detail on the sad facts behind this situation, I recommend Richard’s book, *Gone Astray* (published by the Food and Agriculture Organization, a division of the United Nations). And to learn about and enjoy the wonderful elephants and their old relationship with our species, consider a visit to the Center and any of the other well-run conservation centers in Southeast Asia.

A further troubling concern from this type of animal training is the temptation to make spurious claims for human-like behavior. For instance, after Komar and Melamid and Richard Lair introduced elephant painting, some mahouts trained elephants to make figurative paintings, such as trees and flowers, with the implication by some that the elephants know what they are painting. The tourists usually don’t realize that this is a “trick” in that the mahout is surreptitiously telling the elephant how to move the brush, often by pressure on a tusk: I have heard, but not yet observed, that some animals have been trained to do this without the mahout touching them. The animal has no notion that it is painting a representative figure. We should guard against these kinds of misunderstandings is it will lead to people suspecting and dismissing the amazing things that Asian elephants are truly capable of.

Whatever fantastic abilities humans presume that Asian elephants may have will be less amazing than the genuine abilities we learn from careful observation. Due to the complexity of the music production, I think that a great deal of experimentation would be required to discern how elephants experience the music.

## Other musical species and us

With the exception of the Cretaceous-Paleogene extinction 66 million years ago, apparently due an asteroid that struck Mexico, the period of extinction of other species driven by us, known as the Holocene or Anthropocene extinction, is the highest since life began. There has been some recent population increase of several whale species for which appreciation of their singing played a role, but still a devastating ongoing loss as of this writing, particularly for the right whale.

The whales, the most exceptional and inspiriting singers on earth, elephants, who rank among the advanced vocal communicators and improvise entire orchestral works, the chimpanzees and bonobos with skills and cultures we are only starting to comprehend, along with other exceptional and inspiring of singers and species, are now on a rapid path to extinction, and will never be replaced in the entire future of the universe.

If other species produce music the way that we do, does that mean that we must guarantee their future survival rather than destroy them due to our wish for more money and thoughtlessness? Why, yes it does.

Art for all Species!

- New York City, 2019

# Listening

Bernie Krause has recorded “soundscapes” in environments throughout the world.

There are few commercial recordings of animal sounds, and most are presently on individual’s or foundation websites.

The monumental website for animal sound is the Macauley Library Archive at the Cornell Lab of Ornithology. It is said to have over 7000 hours of recordings from over 9000 species.

The lyrebird should be listened to and viewed, or you will not believe it… the David Attenborough films are classic. The birds that produce the mechanical noises from humans are in captivity, but the songs of the birds after human flute music are by wild birds.

Of all written musical compositions influenced by birdsong, a large body of work by Olivier Messiaen truly stand out. He would take walks into the woods and transcribe the songs and calls as best he could before the ability to simply make sonograms and write them out as best as possible for the musical instruments available to him. Some pieces are “soundscapes” with birds that would alternate singing in the wild. Try *Catalogue d’oiseaux* as recorded on piano by his wife, Yvonne Loriod.

Songsofinsects.com has a great collection of North American cicada, katydid, and cricket songs.

Some have slowed the songs of crickets to be more appealing to our species, including at the Department of Entomology by Thomas Walker University of Florida web site.

My webpage on Animal Music has recordings of zebra finches triggering musical samples, and recordings from Jay Hirsch of the University of Virginia of fruit fly courtship song and fruit flies exposed to cocaine aerated in their jar.

Mirjam Knoernschild from the Museum of Natural History in Berlin has recorded an excellent collection of singing and calls by the greater sac-winged bat, which chirps like a songbird in addition to using the voice for echolocation.

A classic commercial album is *Songs of the Humpback Whale*, featuring the classic recordings by Frank Watlington, Scott McVay and Roger and Katie Payne.

Recordings of several whale species can be heard from the Monterey Bay Aquarium Research Institute. The blue whale song sped up by 5-fold is quite gorgeous for us.

Bowhead whale songs recorded by the Norwegian Polar Institute can be heard in a 2013 recording in the Fram Strait between Greenland and Norway, available from the Washington Post. Among their many voices is a dead-on cat meow.

The Cornell website, also has a page on elephants with sine waves at 10, 20, and 30 Hz to explain the long range communication. Still most of the sounds made by elephants are in our audible range, and a large vocabulary can be heard from recordings by Richard Lair and myself as *Elephant Field Recordings*.

*The Thai Elephant Orchestra* recorded three commercial albums. A good solo piece is *Phuong’s solo* on the renaat, and a nice piece with five elephants is *Thung Kwian Sunrise*, which is the name of the village where the local mahouts live between Chang Mai and Lampang. I arranged these elephant compositions for human musicians, the first for solo piano, as performed by Steven Beck and Jai Jeffryes, and the second for full orchestra, as performed by the Composer’s Concordance Orchestra.

There are several recordings of the Thai Elephant Orchestra playing along with human musicians, including the local high school brass orchestra on Beethoven’s *Pastorale Symphony*, pieces with the cellist Jamie Seiber, traditional Thai musicians including a lovely jam between the mahout string band and the orchestra on *Floating Down the Pin River*, and yours truly playing violin on *Little Elephant Saddle*.

The simplest and most elegant of the human with elephant pieces in my opinion is when Luk Kob’s mahout, Boonyang Boonthiam, who is also a priest of the Lanna Thai religion, sings a traditional elephant prayer with the full orchestra of 14 elephants on *Invocation*.

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Andrew Farnsworth (Cornell University) for discussion of bird night flight calls,

Brad Garton (Columbia University) for critique on the entire volume,

Wulf Hein (Archaeotechnik, Germany) for insights on ancient bird bone flutes,

Jay Hirsh (University of Viriginia) for discussion of Drosophila song,

Ben Holtzman (Columbia University) for discussion of soundwave propagation,

Nima Mesgarani (Columbia University) for discussion of cortical processing of speech,

Manuela Nowotny (University of Jena, Germany) for insect hearing

Michael Rosen (Columbia University) for cardiac action potentials and comments on the entire book,

Giancarlo Ruocco (Italian Institute of Technology, Rome) for very through critiques on the entire volume, especially on physics,

Susan Savage-Rumbaugh (University of Iowa) for deep discussions on animal music and communication,

Ofer Tchernichovski (Hunter College, CUNY) for insights on birdsong,

Mark Wightman (University of North Carolina) for comments on the bathtub Ohm’s law analogy and general advice throughout the book,

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Thanks to students in the Music Math and Mind class who proofed the text, particularly Shashaank Narayanan.

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and my collaborator, conservationist Richard Lair and his colleagues at the Thai Elephant Conservation Center and the Forest Industry Organization of Thailand for our work on the Thai Elephant Orchestra.

Thanks to artists Lisa Haney and Jai Jeffreys, both of whom are also outstanding musicians and friends, for their marvelous original artwork.

# Appendix 1

## Musical pitch to frequency table

The pitch names of 12 tone equal temperament for conventional A440 tuning are at left and the octave at top, with the corresponding frequency in Hz in the table.

Middle C (named from the four octave organ keyboard) is C4, with A0 the lowest note and C8 the highest note of a conventional 88 key piano keyboard.

The fundamental frequency f*­1* of C0 is below the keyboard and below our range to hear it as a musical note, and we perceive only the harmonics. The lowest pitch on a conventional string or electric bass is E1 or 41 Hz, and with a fifth low B string, 31 Hz. The highest note f*­1* on a piccolo is C8 and pretty disturbing, but higher frequencies up to about Eb10 contribute perceptibly to speech and the sound of human music.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| octave | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|  |  |  |  |  |  |  |  |  |  |  |
| C | 16 | 33 | 65 | 131 | 262 | 523 | 1047 | 2093 | 4186 | 8372 |
| C# | 17 | 35 | 69 | 139 | 277 | 554 | 1109 | 2217 | 4435 | 8870 |
| D | 18 | 37 | 73 | 147 | 294 | 587 | 1175 | 2349 | 4699 | 9397 |
| Eb | 19 | 39 | 78 | 156 | 311 | 622 | 1245 | 2489 | 4978 | 9956 |
| E | 21 | 41 | 82 | 165 | 330 | 659 | 1319 | 2637 | 5274 | 10548 |
| F | 22 | 44 | 87 | 175 | 349 | 698 | 1397 | 2794 | 5588 | 11175 |
| F# | 23 | 46 | 92 | 185 | 370 | 740 | 1480 | 2960 | 5920 | 11840 |
| G | 24 | 49 | 98 | 196 | 392 | 784 | 1568 | 3136 | 6272 | 12544 |
| Ab | 26 | 52 | 104 | 208 | 415 | 831 | 1661 | 3322 | 6645 | 13290 |
| A | 28 | 55 | 110 | 220 | 440 | 880 | 1760 | 3520 | 7040 | 14080 |
| Bb | 29 | 58 | 117 | 233 | 466 | 932 | 1865 | 3729 | 7459 | 14917 |
| B | 31 | 62 | 123 | 247 | 494 | 988 | 1976 | 3951 | 7902 | 15804 |

# Appendix 2: Further reading

The Egyptologist Rita Lucarell, my collaborator on the opera *The Eighth Hour of Amduat,* took me on a walk through the Egyptian wing of the Metropolitan Museum of Art in New York where she read the hieroglyphs from 5000 year old papyri on the walls.

I however cannot read computer drives from 8 years ago. Websites simply disappear, sometimes over the course of the year when I have written this volume.

During the past decade, multiple libraries at my university have closed, the books destroyed. I hope that you can find whatever the media in whichever resources survive when you pursue this study.

Due to their transience, I limit mention of websites as much as possible, although some like the Cornell McCauley lab birdsong website, are so irreplaceable that I will take the chance.

For those interested in pursuing scientific topics, I try to mention the names of the scientists who published specific findings throughout. The most convenient way to find the primary articles is currently to enter their names on PubMed, an enormous website maintained by National Institutes of Health. While some journals require exorbitant fees to read their old literature, many articles are open access. Often there are review articles that cover the field well.

The classic book on these topics is Herman von Helmholtz’s *Sensations of Tone*, first published in 1863. I have returned to it for about 35 years, and always find an insight I missed. My highest recommendation.

Bart Hopkin has written many books on homemade instrument building.

Nicolas Collins has a cool book, *Handmade Electronic Music*, on analog circuits that can be used to make sound.

Harry Partch’s *Genesis of a Music* is idiosyncratic, inspirational and brilliant, with an introduction by the intrepid Otto Luening.

On microtones and blues, explore in Alan Lomax’s *The Land Where the Blues Began*, and for how experts disagree on any topic, Robert Palmer’s *Deep Blues.* When American culture disappears from the face of the earth, it can be reconstructed from these two books.

For the study of the syncopated drum patterns, I think the classic are the collections of West African transcriptions and analysis by Revered A.M Jones.

*Nature's Music: The Science of* *Birdsong* by Peter R. Marler, Hans Slabbekoorn.

*Going Astray: The Care and Management of the Asian Elephant* by Richard Lair published by the Food and Agricultural Organization of the United Nations.

# The author

Dave Sulzer is a Professor of Psychiatry, Neurology, and Pharmacology. His laboratory investigates the synapses of the cortex and basal ganglia including the dopamine system, and their roles in habit formation, planning, and decision making. They have made contributions to understanding the action of addictive drugs and causes of diseases including Parkinson's, Huntington's and autism and have made important contributions to neuroimmunology and chemistry. They developed the first method to directly measure the fundamental unit of neurotransmission (quantal neurotransmitter release) and the first optical method to visualize neurotransmission at the synaptic level in the brain (fluorescent false neurotransmitters).

He played violin and the guitar while growing up in Minnesota, Illinois, and Connecticut, and as a teen toured in country, rock and rhythm, western swing and blues bands. He attended Michigan State where he studied plant genetics while studying composition privately with Roscoe Mitchell. He studied plant breeding at the University of Florida and played guitar in rhythm and blues groups including with Bo Diddley prior to moving to New York where he performed in salsa, experimental and classical groups and received a scholarship to attend Columbia University for a Ph.D. in biology. While there he studied composition privately with Otto Luening and at night school at Juilliard.

As his group, the Soldier String Quartet, became better known, he changed his musical name to Dave Soldier to avoid being thrown out of graduate school. The quartet, pioneered the fusion of classical, punk rock and hip hop styles in multiple albums of Soldier’s compositions, performing at venues ranging from the punk rock club CBGBs to Carnegie Hall and Lincoln Center, and from 1984-2004 group premiered over 100 compositions including major works by Teo Macero, Leroy Jenkins, Phill Nibolck, Zeena Parkins, Fred Frith, Elliott Sharp, and Ivan Wyschnegrasky. The group provided a training ground for performers including violinists Regina Carter and Todd Reynolds. The Quartet also recorded with many rock, pop and jazz acts including Guided by Voices, Jessie Harris, Butch Morris, Tony Williams (Miles Davis), Lambchop, Bob Neuwirth, John Cale (with whom they toured from 1992-1998), Bill Laswell, Lee Ranaldo (Sonic Youth), Amina Claudine Myers, the Plastic People of the Universe, Joanne Brackeen, Myra Melford, Sussan Deyhim, and Lenny Picket.

Dave further worked as a violinist, guitarist, producer and arranger in a broad variety of pop, jazz, experimental, world music and classical styles including John Cale (Velvet Underground), David Byrne (Talking Heads), Ric Ocasek (the Cars), Richard Hell (the Voidoids) Van Dyke Parks (the Beach Boys), Robert Dick, Bob Neuwirth, Lee Renaldo (Sonic Youth), Henry Threadgill, William Hooker, Billy Bang, Marshall Allen, Pedro Cortes, Pete Seeger and Eliza Carthy. He founded the cult Memphis/New York punk band, the Kropotkins with singer Lorette Velvette, a group that recorded four albums and included Mo Tucker (Velvet Underground). He performs in SoldierKane with drummer Jonathan Kane (Swans, LaMonte Young).

Dave arranged the scores for film including *Eat* and *Kiss* (Andy Warhol) *I Shot Andy Warhol* (Mary Harron) and *Basquiat* (Julian Schnabel). He wrote soundtracks for Sesame Street and the black and white silent film *The Violinist* (Winsome Brown) is based on his compositions for violin and piano.

As a composer for classical musicians, his work includes the operas *Naked Revolution* with the Russian painters Komar and Melamid, and *The Eighth Hour of Amduat* which features Marshall Allen, head of the Sun Ra Arkestra. He composed two oratorios (*Ice-9 Ballads* and *A Soldier’s Story*) with author Kurt Vonnegut, who performs on the recordings. His album *Chamber Music* was named by the New York Times as a top classical recording of the year. His compositions are recorded by the Manhattan Chamber Orchestra, the Absolut Ensemble, the PubliQuartet, violinists Miranda Cuckson, Regina Carter and Rebecca Cherry, cellist Erik Friedlander, accordionist William Schimmel, pianist Steven Beck and flutist Robert Dick.

Many of his projects are unusual collaborations, including the Thai Elephant Orchestra with conservationist Richard Lair, an orchestra consisting of 14 elephants at the Thai Elephant Conservation Center, who recorded three CDs: The People’s Choice Music: the most wanted and unwanted songs, following poll results of likes and dislikes of the American population, a collaboration with artists Komar & Melamid; coaching musically naïve children to compose their own music in Harlem (*Da Hiphop Raskalz*), Brooklyn (the *Tangerine Awkestra*), Washington Heights, and northern Guatemala (*Yol Ku: Mayan Mountain Music*); music performed by electroencephalography of brain activity in the *Brainwave Music Project* with computer musician Brad Garton which has been featured on PBS and BBC TV with Stewart Copeland (the Police); and music played on specially created instruments by songbirds and pygmy chimpanzees.

## Selected compositions with classical notation

**opera:**

**Naked Revolution**, an opera in the socialist realist style (1997) with Komar & Melamid and Maita di Niscemi, libretto

**A Soldier's Story** (2002) radio opera with book by Kurt Vonnegut

**The Eighth Hour of Amduat (**2015) opera with libretto adapted from The Book of the Amduat, about 3000 BC, featuring Marshall Allen of the Sun Ra Arkestra

**oratorio and song cycle:**

**The Apotheosis of John Brown** (1990) text adapted from Frederick Douglass

**Smut, a.k.a., Chorea Lascivia**,  (1991) Latin homoerotic medieval lyrics

**Mark Twain's War Praye**r (1993) for gospel choir and orchestra or organ

**Ice-9 Ballads** (1995) lyrics by Kurt Vonnegut

**Dean Swift's Satyrs for the Very Very Youn**g (2011) Twelve pieces for singer flute, viola, and harp with lyrics from Jonathan Swift

**orchestra:**

**Ultraviolet Railroad** (1991) Double concerto for violin and cello or piano trio

**Thung Kwian Sunrise** (2012) arranged from an improvisation by the Thai Elephant Orchestra

**SamulNori (**2013)

**Bambaataa Variations** (2013) concerto grosso for string quartet and orchestra

**Stuff Smith's Unfinished Concerto** (2017) violin, piano, string orchestra, transcription and arrangement for Stuff Smith's working concerto from 1963

**Jaelo** (2019) rhapsody for piano and strings or piano solo

**West Memphis, 1949** (2019) big band

***string quartet:***

**Sequence Girls** (1985) string quartet and trap set drums

**Three Delta Blues** (1986) string quartet from songs by Robert Johnson, Skip James, and Charlie Patton  
**String Quartet #1 The Impossible** (1987) string quartet and trap set drums

**String** **Quartet #2, Bambaataa Variations** (1992) for prepared string quartet (bobby pins hair brushes, combs)

**String Quartet #3, The Essential** (2011) for string and EEG headband software) after Schoenberg's Second string quartet, second movement

**for chamber ensembles:**

**Duo Sonata** (1988) for violin and cello

**To Spike Jones in Heaven** (1989) for accordion and tape (or CD)

**Utah Dances** (1990) dance suite for solo saxophone, clarinet or flute

**Sontag in Sarajevo** (1994) for accordion, violin (or clarinet), cello (or bass), guitar

**The People's Choice Music** with Komar & Melamid) lyrics Nina Mankin

The Most Wanted Song (1997) for soprano, baritone, electric piano, synth, piano, 3 guitars, e bass, trap set, bass drum, vln, cello, double on sop and tenor sax

The Most Unwanted Song (1997) for soprano, children's choir, accordion, bagpipe, banjo, flute/piccolo, harmonica, organ/ synth/ tuba, harp, 2 bass drums

**East St. Louis, 1968** (1999) for solo viola or string quartet with recording

**Clever Hans** (2005) ballet for violin, cello, and harpsichord

**The Complete Victrola Sessions** (2010) twelve pieces for violin and piano

**Lewitt Etudes** (2015) Fifty architectural designs for musicians

**Vienna Over the Hills / Six Violins** (1986/2017) six or more violins

**solo piano**

**Five Little Monsters** (1985)

**Nocturnes** (2010)

**Variations on Chopin's Minute Waltz** (2010) some playable and some not

**Fractals on the Names of Bach & Haydn** (2011)

**Letter to Gil Evans** (2012)

**Girl with a hat in a car** (2012)

**Letter to Skip James** (1987/2012)

**Phong's Solo** (2012) arranged from an improvisation by a member of the Thai Elephant Orchestra

**solo organ**

**Hockets & Inventions** (1990) 12 pieces for solo organ or piano

**Organum, Book I** (2011) Five pieces for solo organ

**solo violin**

**Al-Andaluz** (2018) Six flamenco etudes for solo violin

## **Selected Discography**

**As leader / co-leader**

**Zajal** (lyrics from medieval Andalusian poetry in Hebrew and Arabic) (2019) **Naked Revolution** (opera with Komar and Melamid) (2018)  
**The Eighth Hour of Amduat** (opera with libretto from ancient Egypt, with Marshall Allen, 2016)  
**Dean Swift's Satyrs for the Very Very Young** (lyrics from Jonathan Swift, with Eliza Carthy, 2016)  
**Soldier Kane** (with Jonathan Kane, 2016)  
**In Black & White** (music for piano, 2015) **In Four Color** (music for string quartet, 2015) **Smash Hits by the Thai Elephant Orchestra** (2015) **With Kurt Vonnegut** (operas and song cycles, 2015) ***The Kropotkins* Portents of Love** (2015)  **Organum** (organ music, 2012)  
**The Complete Victrola Sessions / The Violinist** (2011)   
**Water Music,** Thai Elephant Orchestra (2011) ***The Kropotkins*** **Paradise Square** (2010) **Yol Ku', Inside the Sun: Mayan Mountain Music** (children in San Mateo Ixtatan, Guatemala, 2008) **Chamber Music** (2007) **Da Hiphop Raskalz** (children in East Harlem, 2006)   
**Soldier Stories** (2005) with Kurt Vonnegut  
**Elephonic Rhapsodies** (with the Thai Elephant Orchestra, 2004)  
**Soldier String Quartet Inspect for Damaged Gods** (2004)  
**Thai Elephant Orchestra** (2001)   
**Ice-9 Ballads** (2001) with Kurt Vonnegut  
***The Kropotkins*** **Five Points Crawl** (2000)  
**The People's Choice: Music**  (with Komar & Melamid, 1997)  
**the Tangerine Awkestra Aliens Took My Mom** (children in Brooklyn, 2000)  
**Jazz Standards on Mars** (1997) Soldier String Quartet with Robert Dick  
***The Kropotkins*** (1996)  
**Soldier String Quartet She's Lightning When She Smiles** (1996)  
**Smut** (lyrics of homoerotic poetry in medieval Latin) (1994)  
**War Prayer** (libretto from Mark Twain, 1994) **The Apotheosis of John Brown** (libretto from Frederick Douglass, 1993) **Soldier String Quartet Sojourner Truth** (1991)  
**Soldier String Quartet Sequence Girls** (1988)

**Arranger, performer, composer, conductor, producer**

**Vince Bell**,Ojos (co-produced with Bob Neuwirth, 2018*)*   
**John Cale**

Fragments of a Rainy Season (1992): Paris S'Eveille (1993); Antartida (1995); Walking on Locusts (1996); Eat and Kiss (1997); Dance Music (1998); I Shot Andy Warhol (1997)

**John Clark** Sonus Innerabalis (2016)

**Nicolas Collins** A Dark & Stormy Night (1992)

**Pedro Cortes** Los Viejos No Mueron (2013)   
**Sussan Deyhim** Madman of God (1999)

**Robert Dick** Third Stone from the Sun (1993)

**Grupo Wara** Malombo (1990)   
**Guided by Voices**

Do the Collapse (1999); Hold on Hope (2000); Isolation Drills (2001)

**Jason Kao Hwang** Symphony of Souls (2011)  
**Jessie Harris** While the Music Lasts, (2004)   
**Jonas Hellborg and Tony Williams** The Word (1992) **William Hooker**

Yearn for Certainty (2010) (trio with Sabir Mateen); Heart of the Sun (2013) (trio with Roy Campbell); Aria (2016)   
**Leroy Jenkins** Themes & Variations on the Blues (1994)

**Sylvain Leroux & L'Ecole Fula Flute** Les enfants de Tyabla (2014), Tyabla (2019) (children in Conakry, Guinea composing and performing on the Fula flute)  
**Mandeng Eletrik** (2004) **Bob Neuwirth and John Cale**, Last Day on Earth (1994)

**Phill Niblock** / Soldier String Quartet Early Winter (1994)

**Le Nouvelles Polyponies Corses (Corsican Polyphony)** Le Praiduisu (1999)

**The Ordinaires** The Ordinaires (1987)

**Christina Rosenvinge** Foreign Land (2002) **Sequitur** To Have and to Hold (2007)   
**Elliott Sharp / Soldier String Quartet**

Tessalation Row (1987): Hammer, Anvil, Stirrup (1989); Twistmap (1991); Cryptoid Fragments (1993); Rheo/Umbra (1998); Xeno-Codex (1996); String Quartets 1986-1996 (2003); Larynx (1987); Syndakit, (1999)

**Lorette Velvette** Lost Part of Me (1998)

**film scores   
Basquiat** (directed Julian Schnabel) (1998)  
**Eat** (directed Andy Warhol) (1995)  
**I Shot Andy Warhol** (for music by John Cale, directed Mary Herron) (1997)   
**In Bed with Ulysses** (directed Alan Adelson & Kate Taverna)   
**Kiss** (directed Andy Warhol) (1995)   
**Mekong Delta** (directed by Vanessa Ly) (2003), **winner** Hong Kong Film Festival   
**Serenade** (animation by Nadia Roden) **winner** New York Film Festival (2003)**Special Friends** (with **Teo Macero**) (1988)   
**Sesame Street** (6 cartoons for the TV show, directed by Nadia Roden) (1999)  
**The Violinist**, directed by Winsome Brown (2011)

**"pop" arrangements   
David Byrne**, **John Cale**, **Guided by Voices**, **Jonathan Richman**, **Christina Rosenvinge**, **Sesame Street, Ric Ocasek, Van Dyke Park**s, Jesse Harris, Alana Amram, Richard Hell, Rufus Wainwright, Syd Straw

# Back Cover

**Dave Sulzer** is a Professor of Neurology, Psychiatry, and Pharmacology at Columbia University and the New York State Psychiatric Institute. His laboratory has made important contributions to the study of brain mechanisms involved in autism, Parkinson’s disease, drug addiction and learning and memory, authoring over 200 scientific papers that have been cited more than 40,000 times.

In his alter ego, **Dave Soldier**, he is a composer, performer and producer, who worked with scores of major figures in the classical, jazz, and pop worlds and has recorded over 100 record albums. Some of his projects combine both interests, including the Thai Elephant Orchestra, an orchestra of 14 elephants in northern Thailand, and the Brainwave Music Project, which uses EEGs of brain activity to spontaneously create compositions.

**Music Math and Mind** grew out of a course Dr. Sulzer teaches at Columbia University that explores the mathematics, physics and neuroscience that underlie music. The book is written for musicians and music lovers and requires no knowledge of biology, physics or math beyond multiplication.

Topics include the *math* by which musical scales, rhythms, tuning and harmonies are derived, a topic that spans the ancient approaches of Pythagoras to manipulating sound waves. The *perception* of music encompasses the physics of sound, the functions of the ear and deep brain auditory pathways, and the physiology of emotion, and *animal music* by songbirds, cetaceans, and insects.

**Endorsements for back cover**

*It is rare that one finds a book where on opening any page, one is drawn to read on and… to read back. Every page has a story, every page a fascinating connection between the universal joy we find in music and some biological or mathematical fact. Here is the place to find out about the way crickets make music, and the McGurk effect! The science comes along gently, never intimidating. Only a neurobiologist who is a master composer and musician could have written this wonderful book!*  
- Roald Hoffmann, chemist and writer, Nobel prize in Chemistry

*This is an amazing book. Readers will come back to it again and again for its clear explanations, breadth of content and “listening” advice. It includes a chapter on nonhumans, acknowledging that the sophisticated production and perception of music is not limited to humans. It is accessible to all readers, but does not shy away from the direct presentation of science – it gives the reader things that anyone interested in this topic needs to begin to think about. It raises important philosophical questions while allowing the readers to gain the skills to explore these questions for and stops there – giving the reader the chance to pursue or ignore.*

-Susan Savage-Rumbaugh, primatologist and psychologist, specialist in communication by bonobos

*John Cale, David Byrne, Richard Lair, Meredith Monk, Eric Kandel, Bob Neuwirth, Van Dyke Parks, Henry Threadgill, Jaron Lanier, Peter Gabriel, Roscoe Mitchell*