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Nonlinear Dynamics in the Life Sciences

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Chapter 1
From Ancient Math to Modern Science: The Fantastic Journey of the Exponential Function

Abstract For centuries, the exponential function has been a cornerstone of mathematics, and its influence has extended far beyond the confines of this discipline. This chapter will delve into the rich history of the exponential function, tracing its origins back to ancient civilizations and exploring its evolution over time. The chapter will also highlight some of the key mathematical breakthroughs that led to the exponential function. Finally, we will present a brief survey of how the exponential function is used in fields such as physics, and engineering.

A story goes that once God Krishna took the form of a wise man and went to the king's court. He challenged the king to a game of chess because he loved playing it. Before the game started, they had to decide what the prize would be if the sage won. The sage said that he only wanted a small amount of rice, but the amount had to be calculated using the chessboard. A grain of rice would be placed in the first square and the number of rice grains would double for each successive square on the board. The king lost the game and had to give the sage the rice. But as he started putting the rice grains on the board, the king realized that he wouldn't have enough rice to pay his debt. Krishna then showed himself in his true form and told the king that he didn't have to pay all the rice right away, but he could do it gradually. Every day, the king would serve free rice pudding to people who came to the temple until the debt was paid off.

This story has different versions. In some versions, God Krishna is replaced by a servant, the inventor of chess, or a craftsman who makes the best chessboards. In others, rice is substituted by wheat. The ending is also different. In some versions, the ruler has the person who should get the reward killed, while in others, the reward is given only if each grain is counted individually. But the message stays the same: the explosive increase in a pattern where each step is multiplied by the same number (geometric progression) instead of just being added by the same amount (arithmetic progression).

With a history dating back to the Greeks and possibly even the Sumerians, geometric progressions—a discrete form of the exponential function—boasts a rich legacy. Despite this, it wasn't until the 18th century, with the contribution of some of the world's most renowned mathematicians, that the exponential function was finally uncovered. Nevertheless, its influence has been tremendous and spans across numerous scientific domains. A key milestone in this history is the creation of logarithms, which was a seminal event.

Logarithms were independently developed by the mathematicians John Napier, from Scotland, and Jost Bürgi, from Switzerland, to simplify computations in spherical trigonometry, which is used in astronomy and celestial navigation. Despite Bürgi's probable creation of his system around 1600, Napier's discovery was published first in 1614 in the book *Mirifici Logarithmorum Canonis Descriptio* (*Description of the Wonderful Canon of Logarithms*), making him widely known as the inventor of logarithms and greatly influencing its subsequent evolution.

Logarithms establish a connection between the operation of multiplication on the positive real numbers and addition on the real number line. Napier, in particular, viewed logarithms as the relationship between two particles moving along a line—one at a constant speed, the other at a speed proportional to its distance from a fixed endpoint. In current terms, Napier's logarithm (NapLog) can be related to the natural logarithm (ln) in this way:

$$\mathrm{NapLog}(x) = -10^7 \ln(x/10^7).$$

English mathematician Henry Briggs made two visits to Edinburgh to collaborate with John Napier in 1616 and 1617. During their conversations, they reached an agreement on Briggs' proposed modification to Napier's logarithms. After his second trip, Briggs released the first table of his improved logarithms, now known as common or base 10 logarithms ($\log_{10}$), in 1617. The widespread use of common logarithms grew rapidly due to their ease in performing complex calculations during a time when calculators were not available. This was mainly due to the fact that our numbering system is built on powers of 10. Nevertheless, the natural logarithm holds a more prominent place in the history of mathematics because of its impact on the discipline's evolution.

In 1649, Alphonse Antonio de Sarasa, who was previously a student of Grégoire de Saint-Vincent, demonstrated that the area $A(t)$ of the region bounded by the hyperbola $xy = 1$ from $x = 1$ to $x = t$ obeys the following relation common to all logarithmic function:

$$A(t \times u) = A(t) + A(u).$$

It was soon realized that this characteristic could lead to the creation of a new type of logarithm. Mercator, in fact, published the first tables of what is now referred to as the natural logarithm in his book *Logaritmotechnia* in 1668.

In 1748, Leonhard Euler's classic book *Introductio in analysin infinitorum* (*Introduction to the Analysis of the Infinite*) marked the final step in the development of logarithms, exponential functions, and trigonometric functions. Prior to Euler, these mathematical concepts were usually defined using integral calculus. However, Euler changed this by introducing exponentiation a^x for constant a in the positive real numbers, leading to the creation of the logarithm to base a. He also named the natural logarithm, calling it the ”natural or hyperbolic logarithm” due to its connection to the quadrature of the hyperbola. Euler designated number e as the base for the natural logarithm, i.e. the number whose natural logarithm is equal to 1.

Jacob Bernoulli’s groundbreaking work in compound interest paved the way for the discovery of the constant later named e by Euler. Bernoulli’s contribution can be succinctly described as follows: he examined the growth of capital when invested at an annual interest rate of 100% and is compounded at n intervals. At the end of the year, the capital would have multiplied by a factor of

$$\left(1+\frac{1}{n}\right)^n.$$

Bernoulli showed that as the number of compounding intervals increases, this factor approaches a constant value between 2 and 3.

Euler expanded upon Bernoulli’s work by defining the exponential and natural logarithmic functions as follows:

$$\begin{aligned}\exp(x) &= \lim_{n\to\infty}\left(1+\frac{x}{n}\right)^n\\ \ln(x) &= \lim_{n\to\infty} n(x^{1/n}-1).\end{aligned}$$

Additionally, Euler established that the exponential function is a exponentiation function with base e ($\exp(x) = e^x$) and that the exponential and logarithmic functions are inverse of each other.

Godfrey H. Hardy wrote in *A Mathematician’s Apology* that ”a mathematical idea is *significant* if it can be connected, in a natural and illuminating way, with a large complex of other mathematical ideas. Thus a serious mathematical theorem, a theorem which connects significant ideas, is likely to lead to important advances in mathematics itself and even in other sciences.” Hardy used Pythagoras’s proof of the irrationality of $\sqrt{2}$ as an example, highlighting how a simple and elegant theorem can open up new avenues for the development of mathematics.

The exponential function is a prime example of a mathematical idea that has left a lasting impact, not just in mathematics but in other fields as well. It is considered a cornerstone for the advancement of all modern areas of mathematics. Its applications are diverse and can be seen in fields such as physics, where it explains processes ranging from radioactive decay to population growth. In finance, it is employed in modeling interest rates and stock prices. The exponential function is also a critical component in engineering, contributing to the development of electrical circuits, control systems, and communication systems, just to mention a few examples.

In *Introductio in analysin infinitorum*, Euler introduced the equation named after him:

$$e^{ix} = \cos x + i\sin x.$$

Specifically, when $x = \pi$, this formula leads to the well-known Euler identity:

$$e^{i\pi} + 1 = 0.$$

which is considered by many to be one of the most beautiful equations in mathematics, as it combines the three basic mathematical operations (addition, multiplication, and exponentiation) and relates five fundamental mathematical constants (0, the additive identity; 1, the multiplicative identity; the unit of imaginary numbers, i; e and π). The Euler identity is a point of convergence of various mathematical disciplines, such as arithmetic, trigonometry, and complex number theory.

Euler formula has been a vital aspect in physics and engineering, particularly through Fourier analysis. This method allows the transformation of complex functions into sums of simple trigonometric functions. Some of the most significant uses include:

- Signal processing: Fourier analysis is used to analyze and manipulate signals such as audio, images, and voice.
- Image compression: Fourier analysis is used in image compression algorithms to reduce the amount of data needed to represent an image.
- Spectral analysis: Fourier analysis is applied to study the frequency components of signals, such as those produced by vibrating objects or electromagnetic waves.
- Filter design: Fourier analysis is used to create electronic filters that remove unwanted frequencies from signals.
- Heat transfer: Fourier analysis is applied to examine heat flow in solids and fluids.
- Quantum mechanics: Fourier analysis is used to analyze the behavior of particles in a quantum state.
- Seismology: Fourier analysis is employed to examine the propagation of seismic waves.
- Electromagnetic analysis: Fourier analysis is applied to study the behavior of electromagnetic fields.

In conclusion, the exponential function transcends the realm of mathematics theory and has become a vital tool across various fields. Its impact has been revolutionary in shaping our comprehension of both natural and social sciences and has been a driving force behind numerous technological advancements.

Further reading. For those seeking a deeper understanding of the history of logarithmic and exponential functions, the *History of the Exponential and Logarithmic Concepts* series of articles, published in 1913 in the American Mathematical Monthly, volume 20, numbers 1 through 7, may be of interest. These articles can be accessed for free on `Jstor` at the following URL: `https://www.jstor.org/`

Chapter 2
Exponential Decay

Abstract This chapter develops both deterministic and stochastic models to analyze how population size changes over time under the assumption of an age-independent death rate in closed populations. Beginning with a distribution function describing population age structure, a convection equation governs aging in the absence of deaths. Introducing constant mortality leads to exponential decay of total size. A stochastic approach models population size as a random variable and relates transition probabilities, recovering the deterministic solution when averaging expected size. Solving for individual lifetime distributions links dynamics across scales through averaging. Extensions to age-dependent but stationary mortality demonstrate self-organized exponential decay, connecting perspectives from random interactions to emergent collective behaviors. The established foundations connect stochastic and deterministic views on simple populations and lay the groundwork for further complexity.

Population dynamics is the study of how populations change over time and space due to various biological and environmental factors. Central topics in population dynamics include birth, death, immigration and emigration, density dependence, and biotic and abiotic interactions between individuals within a population or between species.

In this chapter, we will begin exploring population dynamics by studying a simple death process in closed populations. Specifically, we will develop both deterministic and stochastic models to analyze how population size changes over time under the assumption of an exponentially distributed age-independent death rate. This forms the basis for understanding more complex population dynamics incorporating additional realistic features like age-structure, density dependence, and other stochastic birth and death mechanisms.

By establishing these foundations, we aim to connect individual-level stochasticity to emergent deterministic behaviors at the population scale.

Dynamics of aging

Let us analyze the dynamics of a closed population with no births or deaths over time. We define the function $\eta(\tau,t)d\tau$ as the fraction of individuals in the population with ages in the interval $[\tau, \tau + d\tau]$ at time t. This function fully describes the population state at any given time and how it evolves. Specifically, the total population at any time t is given by:

$$N(t) = \int_0^\infty \eta(\tau',t)d\tau'.$$

In the absence of births, deaths, and migration, individuals can only age over time. This means the plot of the function $\eta(\tau,t)$ shifts to the right as time passes. We can mathematically express this as:

$$\eta(\tau,t+\Delta t) = \eta(\tau - \Delta t, t).$$

Expanding the left-hand side (LHS) and right-hand side (RHS) terms in a Taylor series about t and τ, respectively, gives:

$$\eta(\tau,t) + \frac{\partial \eta}{\partial t}\Delta t + \cdots = \eta(\tau,t) - \frac{\partial \eta}{\partial \tau}\Delta t + \ldots.$$

Simplifying and taking the limit as $\Delta t \to 0$ yields the governing equation:

$$\frac{\partial \eta}{\partial t} = -\frac{\partial \eta}{\partial \tau}. \tag{2.1}$$

The RHS can be viewed as an age-related flux term. Therefore, this equation expresses conservation of population as the rate of change within an infinitesimal age interval equals the net outflux due to aging.

Since the total population $N(t)$ was assumed to remain constant over time due to no births, deaths, or migration, the last integral must satisfy:

$$\int_0^\infty \frac{\partial \eta}{\partial \tau'} d\tau' = 0.$$

This expresses the fact that aging redistributes individuals among age classes but does not change the total population size.

Age-independent death rate

We can modify Equation (2.1) to account for deaths by including an additional death rate term

$$\frac{\partial \eta}{\partial t} = -\frac{\partial \eta}{\partial \tau} - \mu(\tau)\eta, \tag{2.2}$$

where $\mu(\tau)$ is the death-rate constant for individuals of age τ. It represents the probability per unit time that an individual of age τ dies.

Integrating Equation (2.2) gives:

$$\frac{dN}{dt} = -\int_0^\infty \mu(\tau')\eta(\tau',t)d\tau'.$$

Now assume the death rate is independent of age. Then:

$$\frac{dN}{dt} = -\mu N. \tag{2.3}$$

This differential equation has the well-known solution of exponential decay:

$$N(t) = N_0 e^{-\mu t},$$

where N_0 is the initial population size. This demonstrates that under the assumption of a constant, age-independent death rate, the population will decrease exponentially over time.

An important parameter that arises from this solution is the population half-life ($t_{1/2}$), defined as the time required for the population to decrease to half its initial value. Specifically:

$$\frac{N_0}{2} = N_0 e^{-\mu t_{1/2}}$$

Solving this equation for $t_{1/2}$ gives:

$$t_{1/2} = \frac{\ln 2}{\mu} \tag{2.4}$$

Stochastic description

In the previous section, we modeled population dynamics deterministically and showed the population decays exponentially over time when death rates are independent of age. Here, we develop a stochastic framework to analyze this process more rigorously.

Let n be a random variable representing population size. Define $P(n=N;t)$ as the probability the population has a value of N individuals at time t:

$$P(n=N;t)$$

Additionally, let μ denote the probability per unit time that an individual dies independently of others. Considering these variables, the evolution of $P(n=N;t)$ is described by:

$$P(n=N;t+\Delta t) = P(n=N;t)(1-\mu N\Delta t) + P(n=N+1;t)\mu(N+1)\Delta t \tag{2.5}$$

This equation accounts for two possibilities that could result in a population of size N over a short time interval Δt. 1) the population was already size N at time t and no deaths occurred. 2) The population was size $N+1$ at time t and one death occurred. We assume that Δt is small enough that more than one death is highly unlikely.

We can rearrange Equation (2.5) to obtain:

$$\frac{P(n=N;t+\Delta t)-P(n=N;t)}{\Delta t}=P(n=N+1;t)\mu(N+1)-P(n=N;t)\mu N$$

Taking the limit as the time interval Δt approaches 0 yields the following differential equation governing the time evolution of the probability $P(n=N;t)$:

$$\frac{dP(n=N;t)}{dt}=P(n=N+1;t)\mu(N+1)-P(n=N;t)\mu N \tag{2.6}$$

Equation (2.6) describes the forward Kolmogorov equation for this stochastic death process. It relates the time derivative of the probability of being in state N individuals to the probabilities of transitions between states due to individual death events.

There are several approaches to analyze Equation (2.6). One method is to take the time derivative of the expected population size, represented by:

$$E_n=\sum_{N=0}^{\infty} NP(n=N;t)$$

By multiplying both sides of Equation (2.6) by N and taking the sum from 0 to infinity, we obtain:

$$\frac{d}{dt}\sum_{N=0}^{\infty} NP(n=N;t)=\mu\sum_{N=0}^{\infty} N(N+1)P(n=N+1;t)-\mu\sum_{N=0}^{\infty} N^2P(n=N;t)$$

Through some algebraic steps, this equation can be shown to reduce to:

$$\frac{dE_n}{dt}=-\mu E_n \tag{2.7}$$

Notice that Equation (2.7) is identical to the deterministic Equation (2.3). This implies the deterministic solution corresponds to the average behavior of repeated stochastic experiments, rather than describing any single experiment. It predicts exponential decay when considering expected population sizes over numerous trials.

Another approach is to find an exact solution to Equation (2.6). It can be verified through substitution that:

$$P(n=N;t)=\frac{E_n^N(t)e^{-E_n(t)}}{N!},$$

where $E_n(t)$, satisfies Equation (2.7). This has the form of a Poisson distribution, with mean E_n and standard deviation $\sqrt{E_n}$.

For large values of E_n, the standard deviation becomes negligible compared to the mean. Therefore, even though the deterministic model in Equation (2.3) does not describe individual stochastic trajectories, its predictions are expected to closely match the behavior of single realizations when population sizes are sufficiently large.

While stochastic fluctuations are prominent for small populations, the deterministic exponential decay approximation becomes increasingly accurate as the number of individuals grows. This solution helps connect the statistical properties of the underlying stochastic process to the emergent deterministic behavior predicted by the differential equation model.

Here is one way to rewrite the section on the individual lifetime distribution:

2.1 Individual Lifetime Distribution

As individual death is a stochastic process, the survival time of each individual, denoted by the random variable τ, is also random. Let $P(\tau = T)dT$ represent the probability that an individual survives up to age T and dies between ages T and $T + dT$. We can write an equation for this probability as:

$$P(\tau = T)dT = \left(1 - \int_0^T P(\tau = T')dT'\right)\mu dT$$

The term in parentheses is the probability of surviving until age T, while μdT is the probability of dying between T and $T + dT$.

Differentiating this expression gives the differential equation:

$$\frac{dP(\tau = T)}{dT} = -\mu P(\tau = T)$$

Subject to the normalization condition, the solution is:

$$P(\tau = T) = \mu e^{-\mu T}$$

Therefore, individual lifetimes follow an exponential distribution. The mean lifetime is thus:

$$E_\tau = \frac{1}{\mu}$$

Discussion

So far, we have analyzed a simple decaying population model considering both deterministic and stochastic frameworks. The key deterministic result was that when death rates are constant over time, the total population size decays exponentially according to Equation 2.3. By developing a stochastic description, we were able to account for randomness at the individual level. Interestingly, when considering expected population sizes, the deterministic and stochastic descriptions coincide as shown by Equation 2.7.

This emergence of deterministic behavior from underlying stochastic processes is an important phenomenon. While survival of individuals is inherently random, averaging over many trials washes out variability, resulting in smooth exponential decay. This demonstrates how populations self-organize simpler collective dynamics from complex interactions between constituents.

The death rate parameter μ takes on different meanings depending on the description. Deterministically, it characterized the system's exponential decay profile. Stochastically, it represented the probability of individual mortality. Such multiscale modeling allows μ to provide insight across descriptive levels.

In summary, even simple population models like exponential decay showcase the interplay between stochastic and deterministic perspectives. Randomness at the individual scale shapes probabilistic population fluctuations, yet deterministic laws emerge at larger scales where variation averages out. This theory establishes foundations for more realistic extensions incorporating additional biological complexities.

Epilogue

Let us reexamine the population distribution function $\eta(\tau,t)$. We can define the normalized function:

$$\rho(\tau,t) = \frac{\eta(\tau,t)}{N(t)},$$

where $N(t) = \int_0^\infty \eta(\tau',t)d\tau'$. Function $\rho(\tau,t)$ describes the probability density that a randomly selected individual from the population has age τ at time t.

Rewriting Equation (2.2) in terms of ρ:

$$\frac{\partial \eta}{\partial t} = -\frac{\partial \eta}{\partial \tau} - N(t)\mu(\tau)\rho(\tau,t).$$

Upon integration, this leads to:

$$\frac{dN(t)}{dt} = -\widetilde{\mu}(t)N(t), \tag{2.8}$$

where $\widetilde{\mu}(t) = \int_0^\infty \mu(\tau')\rho(\tau',t)d\tau'$ is the average death rate.

Notably, if the age distribution $\rho(\tau,t)$ remains stationary (independent of t), then the average death rate $\widetilde{\mu}$ is constant. In this case, Equation (2.8) again predicts exponential decay of $N(t)$, even with age-dependent mortality $\mu(\tau)$.

In conclusion, a stationary age structure is another way of producing exponential population decay through a constant average death rate. Therefore, observing exponential decay alone does not fully characterize the underlying stochastic process.

Additional information, such as the lifetime distribution of individuals, is needed to distinguish the underlying stochastic process.

Chapter 3
The interdisciplinary journey of oscillators: from transatlantic navigation to neurophysiology

Abstract Oscillators have proven profoundly versatile, weaving through numerous disciplines to unlock innovations. In this chapter, we explore how oscillators have had a significant impact on the advancement of science and technology throughout history. Both mechanical and electromagnetic oscillators, along with the mathematical models that describe them, have played a crucial role in various fields such as navigation, communications, and the study of neurophysiology. Key contributions in the science of oscillators that have left a lasting influence on other areas are highlighted, and the influence of figures like John Harrison, James C. Maxwell, Heinrich Hertz, Balthasar van der Pol, Alan Hodgkin, and Andrew Huxley is emphasized. We analyze how oscillators have bridged disciplines as diverse as telecommunications and neurophysiology, and discuss how they continue to be essential in current research and the development of advanced interdisciplinary approaches.

Physics encompasses a number of notable concepts that have shaped the course of scientific and technological progress. The ideal gas and the black-body radiator, for example, have had a significant impact on various branches of physics and inspired the development of novel technologies. However, the harmonic oscillator is arguably the most profound and versatile concept of all.

The study of oscillators has a long and rich history, weaving together ideas and discoveries from diverse disciplines including physics, mathematics, engineering, biology, and medicine. Research on oscillators has unlocked fundamental insights about the natural world while also enabling transformative technologies.

This chapter will trace the winding journey of oscillator research over centuries, highlighting interdisciplinary collaborations that produced groundbreaking innovations. We will explore how the quest for accurate timekeeping at sea drove innovations in clock engineering, and how this converged with discoveries in electromagnetism to enable radio technology. Electrical oscillator models would come full circle, providing key insights into biological oscillators underlying heart rhythms and nerve impulses. By tracing this vivid narrative, we will reveal how the incessant human drive to understand and manipulate oscillatory systems has profoundly reshaped civilization.

3.1 The Longitude Problem and the Development of Clocks

In the 2nd century BCE, the Silk Road was established as a network of trade routes linking China with the Mediterranean region, fostering the exchange of goods, ideas, and technologies between Asia and Europe. However, after the fall of Constantinople in 1453, the Silk Road was disrupted, making trade routes to Asia and the Middle East more cumbersome and expensive for Europeans. To circumvent this challenge, explorers set out to discover direct sea routes to Asia, leading to seminal voyages such as Christopher Columbus' discovery of the Americas in 1492, Vasco da Gama's expedition that reached India by sailing around Africa in 1498, and the voyage of circumnavigation initially commanded by Ferdinand Magellan and completed in 1522 (Parry, 1992). These journeys were soon followed by others from various European powers, marking the beginning of the Age of Exploration, which spanned from the 15th to the 18th century and produced significant changes in global trade, culture, and politics.

The contributions of Islamic scholars during the Islamic Golden Age, which spanned from the 8th to the 14th century, in the fields of mathematics, astronomy, medicine, and geography are partly responsible for the accomplishments of the Age of Exploration (Hodgson, 1977). They contributed significantly to the translation and preservation of works from the Greek and Roman eras, which had a major impact on philosophers of the European Renaissance. Since navigation relied heavily on the observation of celestial bodies prior to the 18th century, the contributions in astronomy and mathematics were particularly notable. However, astronomical methods only allowed sailors to determine their latitude, or their north-south position, while determining longitude was a more challenging task. This challenge came to be known as the longitude problem.

Accurate determination of longitude was vital for ensuring safe navigation, particularly during lengthy voyages. Vessels capable of precisely calculating their position faced reduced risks of grounding, collision, or becoming lost at sea. This not only protected the lives of sailors but also safeguarded valuable cargo, minimizing losses for ship owners and merchants. Additionally, efficient navigation reduced travel time, enabling ships to undertake more voyages and enhance profitability. To promote advancements in this crucial area, the British government introduced the Longitude Prize, also referred to as the Longitude Act, in 1714. This competition aimed to encourage the creation of a dependable and feasible method for determining longitude at sea (Sobel, 2007).

John Harrison, a British clockmaker, successfully tackled the problem of determining longitude. Harrison recognized the importance of accurate timekeeping in solving this problem. Rather than relying on celestial observations, Harrison proposed that a meticulously crafted timepiece could allow sailors to keep track of the time at a reference location and compare it to the local time. By comparing the local and reference times, it was possible to convert the difference in hours, minutes, and seconds into a reliable indicator of longitude.

John Harrison was born in 1693 in Yorkshire, England. From a young age, he displayed exceptional skill as a carpenter and clockmaker. In the 1720s, Harrison moved to London and began designing innovative clocks, including longcase clocks with novel mechanisms. Interested in the Longitude Prize, he set out to design a marine chronometer that could maintain accuracy under the harsh conditions encountered on transoceanic voyages.

Following on the steps of scientists and clock-makers like Christiaan Huygens, Harrison crafted a series of marine chronometers. The first, known as H1, was finished in 1735. It pioneered innovations such as the use of 'grasshopper escapement' and temperature compensation through a bimetallic strip. However, issues with operation at sea meant further refinements were needed.

Over the next few decades, Harrison went on to develop the H2, H3 and finally the H4 models, incrementally improving the timekeeping accuracy and durability. The H4 chronometer, completed in 1759, was a compact, high-performance device that fully met the demands of marine navigation. In rigorous sea trials, it kept time to within a few seconds per day, allowing longitude to be calculated to within half a degree.

The Board of Longitude was reluctant to fully award Harrison the prize money, leading to a prolonged dispute. However, his chronometers were widely recognized as a monumental achievement. Their unprecedented accuracy revolutionized navigation and enabled the great voyages of exploration that expanded global knowledge.

At its core, Harrison's ingenious solution to the longitude problem required developing a sustained mechanical oscillator that could remain perpetual and constant for months under the harsh conditions of ocean voyages. The marine chronometer's clockwork mechanism is precisely an oscillator in which energy dissipated through friction is continually replenished. This allows the periodic motion to be maintained indefinitely, enabling accurate timekeeping over long periods.

The marine chronometer was a keystone technology that helped inaugurate the modern scientific era. By solving the centuries-old quest for accurate timekeeping, Harrison's ingenious clocks allowed great leaps forward in astronomy, surveying, navigation and mapping. His contributions epitomize the enlightenment values of rationality, progress and the mastery of nature through science and technology.

3.2 Harnessing Oscillators for Wireless Communication

The chronometer's sustained mechanical oscillations enabled transformative advances in global navigation and mapping. However, the nineteenth century ushered in a new paradigm as scientists sought to harness the power of electromagnetic waves. Just as the perpetual motion of Harrison's clocks arose from carefully sustaining a harmonic system, steady electrical oscillations would prove vital for powering modern wireless communication.

The pioneering experiments on electricity and magnetism conducted in the eighteenth and early nineteenth centuries laid the foundation for understanding oscillatory electrical phenomena (Baigrie, 2006). Notable contributions came from Hans Christian Ørsted's discovery of the connection between electricity and magnetism in 1820, demonstrating that an electric current produces a magnetic field, and the efforts of Michael Faraday to quantitatively relate electric and magnetic forces. However, it was James Clerk Maxwell who, through his seminal treatise published in 1873, unified the previously fragmented theories into a comprehensive framework (Maxwell, 2011a,b).

Maxwell synthesized prior knowledge within a system of equations describing the interrelation between electric and magnetic fields. A key insight was that these fields could propagate through space as waves, spreading energy outward from a source. One remarkable conclusion was that light itself was simply a high-frequency electromagnetic wave. Although controversial at the time, this revelation that light was electromagnetic rippled across physics and enabled huge leaps in scientific progress.

Maxwell's equations predicted that, in principle, electromagnetic waves of any frequency could propagate through empty space. However, generating such waves to study their properties proved challenging. It was not until 1887 that Heinrich Hertz conclusively demonstrated the existence of electromagnetic waves in a pioneering experiment (Shamos, 1987).

In his laboratory, Hertz sought to generate and detect the elusive electromagnetic waves predicted by Maxwell's equations. To achieve this, he devised an electrical oscillator circuit connected to a dipole antenna. When operated at high voltages, oscillations in the circuit induced corresponding oscillations in the antenna, launching electromagnetic radiation. To detect the waves, Hertz used a separate loop antenna connected to another resonant circuit. When placed in the path of the radiation, oscillations were induced in this receiver loop, providing experimental evidence of propagating electromagnetic waves.

The apparatus engineered by Hertz definitively confirmed Maxwell's theories and opened up a new paradigm in physics. Additionally, Hertz measured properties of the waves including polarization, reflection, refraction and interference, verifying they obeyed the same rules as visible light. This cemented light's electromagnetic basis.

Hertz's experiments proved that coordinated electrical oscillations could be harnessed to generate and receive wireless signals. However, the capabilities of Hertz's apparatus were limited. While suitable for laboratory studies, more powerful and efficient oscillators would be needed to enable practical applications like radio communication.

Early radio transmitters used crude ore detectors and inefficient spark gap generators to produce electromagnetic radiation. Generating steady, high-frequency electrical oscillations was key to enabling continuous wave radio broadcasts. This relied on certain analogies with mechanical oscillators like those used in chronometers. A resonant LC circuit can exhibit oscillations, but losses due to resistance will dampen the oscillations over time. To sustain continuous oscillations, energy must be continually fed into the system, analogous to rewinding the chronometer's drive spring. In an electronic oscillator, amplifying elements like vacuum tubes are used to replenish the energy dissipated in the resonant tank circuit. This negative resistance precisely counteracts losses, allowing persistent high-frequency oscillations. By maintaining energy balance in an electrical harmonic system, electronic oscillators enabled modern wireless communication.

The parallels between mechanical and electrical oscillators highlight the continuity in physics concepts across disciplines. Whether weighing a clock's escapement or balancing amplifiers and dissipation in a radio transmitter, the goal of sustaining an oscillator despite losses united these efforts. Powered by electronic oscillators, radio technology would fundamentally reshape society in the 20th century (Clarke, 2011).

3.3 Modelling Neural Excitation with Oscillators

The transmission of signals in nerves and muscles relies on the propagation of electrical impulses known as action potentials. Understanding the nonlinear dynamics underlying excitation in neurons and cardiac cells would require integrating concepts from physics, mathematics and biology. Once again, oscillator models would provide vital insights, this time by mimicking the spikes and rhythms produced by biological cells.

The Dutch physicist Balthasar van der Pol joined Philips Research Laboratories after receiving his doctorate in 1913. During his time there, he made significant contributions to the field of electronics, especially in radio technology. Van der Pol was a key figure in the development of the Philips radio receiver, which was a huge success at the time. According to one of his biographers, "Radio might have remained a field of haphazard empiricism along with wild commercial ventures, but for the influence of men like Van der Pol who stressed the need for a more scientific approach" (Bremmer et al., 1960, Introduction).

In 1926, van der Pol derived a nonlinear differential equation to describe the behavior of vacuum tube circuits used in early radios. While analyzing his model equations, van der Pol made an intriguing discovery. When the value of a parameter known as the damping coefficient was small, the system exhibited the familiar traits of a harmonic oscillator. However, as the damping coefficient increased to larger values, the model solutions diverged from the conventional behavior of harmonic oscillators. Instead of following smooth periodic sinusoidal oscillations, the model solutions displayed alternating periods of rapid and slow changes. Van der Pol coined the term "relaxation oscillations" to describe this behavior (van der Pol, 1926).

The spiking behavior of Van der Pol oscilator was analogous to the action potentials transmitted along neurons and the cells of the heart pacemaker. Building on this, van der Por created a circuit with three oscillators to reproduce the electrical behavior of the heart. Using this method, he successfully replicated specific cardiac arrhythmias, demonstrating the model's ability to capture the complex dynamics of cardiac electrical activity (van der Pol and van der Mark, 1928).

In parallel to the oscillator modeling work, new technologies enabled direct measurements of neural electrical signals. The development of operational amplifiers (op-amps) in the early 1940s was a key advance. Op-amps can perform high-gain voltage amplification and mathematical operations like addition, subtraction, integration and differentiation. This made signal processing and analysis much more feasible. In 1949, Kenneth Cole and Howard Curtis invented the voltage clamp technique using an op-amp based feedback circuit to control the voltage across a cell membrane (Brown, 2020). This allowed the underlying ionic currents to be precisely measured for the first time. The voltage clamp provided pivotal insights into the ionic basis of neural electrical signaling.

Fundamental discoveries in thermodynamics and physical chemistry by pioneers like Max Planck and Walther Nernst also contributed to understanding the electrical behavior of cell membranes. Nernst's work led to his eponymous equation in 1889, relating an ion's equilibrium potential to its concentration gradient. The Nernst-Planck equations described the motion of charged particles, extending diffusion to include electrostatic effects.

Another significant milestone was Cole's adoption of the squid giant axon as a model for studying membrane electrical properties in 1936, following J. Z. Young's suggestion. The size and spacious lumen of the squid axon made it more amenable to experimental techniques such as intracellular recording, which were previously impractical with smaller axons.

While collaborating with Cole in the 1930s, Hodgkin realized the potential of using the squid giant axon to record intracellular action potentials. Returning to Cambridge in 1938, he recruited the undergraduate Andrew Huxley. Huxley's outstanding physics and mathematics background paired with Hodgkin's neurophysiology expertise. Their collaborative project resulted in a series of papers providing quantitative insights into the biophysical basis of the action potential (Brown, 2020).

The culminating paper in the Hodgkin and Huxley series established the field of quantitative membrane biophysics, integrating mathematical modeling with empirical measurements. Hodgkin and Huxley developed a model of interconnected differential equations and performed painstaking calculations to match the model output to their voltage clamp data. Lacking access to early computers, Huxley relied on a desktop calculator, achieving remarkable precision through rigor. This yielded fundamental insights into the ionic mechanisms mediating the initiation and conduction of the action potential.

The Hodgkin-Huxley model marked a pivotal breakthrough in neuroscience, offering the first quantitative, mechanistic picture of neural excitability. Their integrative approach combining math and biology yielded insights into ion channel function while spurring new fields like computational neuroscience. This achievement emerged from interdisciplinary collaboration, as experts in physics, mathematics and physiology united around the common goal of demystifying the action potential. The Hodgkin-Huxley collaboration highlights the power of bridging disciplinary divides to propel discovery. Their synthesis of diverse perspectives unveiled fundamental insights previously out of reach.

Though groundbreaking, the complexity of the Hodgkin-Huxley model posed challenges for broader usage in an era before digital computers. In the 1960s, Richard FitzHugh at the NIH sought to investigate the model's mathematical properties using nonlinear dynamics techniques. To solve the equations across parameters, FitzHugh collaborated with John Moore to build an analog computer from op-amps, multipliers and plotters (Izhikevich and FitzHugh, 2006). This allowed them to graphically visualize solutions, though operating the intricate analog simulator required sophisticated engineering and math skills. The model complexity and lack of digital computing motivated efforts to derive simplified models of neural excitation.

Guided by Cole's insights, FitzHugh modified van der Pol's relaxation oscillator equations to distinguish key features of the Hodgkin-Huxley model. The aim was to separate the dynamics of sodium and potassium ion flow across the membrane from the regenerative excitation process. Originally called the Bonhoeffer-van der Pol equations, these were later renamed the FitzHugh-Nagumo equations because, around the same time, Japanese engineer Jin-Ichi Nagumo invented an electronic circuit using tunnel diodes that reproduced the key cubic nonlinearity. The simplified FitzHugh-Nagumo model provided an accessible approximation to the complex Hodgkin-Huxley system. Reconfiguring the analog computer to solve these reduced equations enabled more extensive mathematical analyses of neural excitation dynamics.

The quest to understand the electrical basis of neural signaling exemplifies the potency of cross-disciplinary pollination. Integrating oscillator models from physics and engineering with emerging techniques to probe nerve impulses yielded pivotal insights into the mechanisms of neural excitation. Constructing fruitful analogies between biological and man-made oscillators led to accessible mathematical representations that captured the essence of spiking dynamics. By breaking down barriers between physics, mathematics and physiology, pioneers transformed understanding of the fundamental processes underlying thought itself. The intertwined narrative of biological and technological oscillators underscores how synthesizing diverse perspectives propels discovery.

3.4 Conclusion

The history of oscillators unveils the intricate relationship between science and technology. Driven by practical needs, advancements in timekeeping brought about significant changes in navigation. Not only this pursuit had profound political and economical effects but also led to fundamental scientific discoveries.

Likewise, electronic oscillators played a crucial role in powering wireless communication systems that transformed society. Yet, when examined through mathematical models, they also shed light on the electrical rhythms of the nervous system. Time and again, the manipulation of oscillatory systems for engineering purposes unintentionally deepened our scientific understanding, crossing disciplinary boundaries.

The enduring significance of oscillators lies in their versatility as model systems. The concept of the harmonic oscillator provides an approximate description for a wide range of systems, including physical, biological, and engineering domains. This commonality across different areas facilitates analogies that enhance the process of discovery.

Whether it's adjusting escapement mechanisms, optimizing amplifiers, or simulating action potentials, researchers have consistently identified common patterns that can be expressed mathematically. The science of oscillators has thrived through the integration of ideas from various fields. Pioneers from diverse backgrounds collaborated to convey concepts between disciplines, building bridges that connected unexpected yet fertile intellectual territories.

By tracing the history of oscillations through the centuries, we gain insight into the very evolution of science itself. While curiosity guides exploration in specialized fields, it's the process of synthesis that breathes life into the deepest ideas. The journey of oscillators highlights how collaborative human effort, aimed at understanding natural rhythms, regardless of their origin, propels us toward a deeper understanding of nature and contributes to the shaping of our civilization.

Finally, oscillators still play a crucial part in today's science and technology. High-frequency electronic oscillators act like the heartbeat of modern computers, making sure that different parts work together and share information at the right time. In computer science, they facilitate complex calculations and data processing by synchronizing clock cycles and enabling high-speed data transfer within computer systems. In the internet, they play a central role in precise data transmission, ensuring the uninterrupted flow of information during digital interactions. These unsung heroes quietly contribute to the seamless operation of computer technology and the interconnected world we rely on daily.

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