Chapter 1: The Shape of Hands

Symmetry, Chirality, and Handedness

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In my series of Gresham Lectures this year, I will explore the Geometry of Nature and the Shape of Things. Our aim is to observe the forms that surround us, both in the natural world and in the objects we create, and to uncover the geometric principles that govern them. We begin with one of the most striking and universal observations: in a mirror, things appear the same, yet they are different. A hand, a shell, or a spiral seems perfectly reflected, but on closer inspection the mirror version cannot be superimposed onto the original. How can two shapes be at once so similar and yet fundamentally different? And how can we give a precise language to capture both their similarities and their differences?

1.1 Chirality

Look at my right hand and its mirror image shown in Figure 1.1. Whatever I do, I know that I cannot superimpose my right hand on its mirror image. Indeed, since the mirror image is almost indistinguishable from my left hand, I know that my left glove does not fit on my right hand better than my right shoe on my left foot. These two objects are fundamentally different. In the words of Immanuel Kant: “*What can more resemble my hand or my ear, and be more equal in all points, than its image in the mirror? And yet I cannot put such a hand as is seen in the mirror in the place of its original...*” [6]. This observation points to a limit of purely geometric description: mirror images may be perfectly congruent and in all description somewhat similar, yet not interchangeable in actual space. Kant uses this to discuss the relative and absolute notion of space.

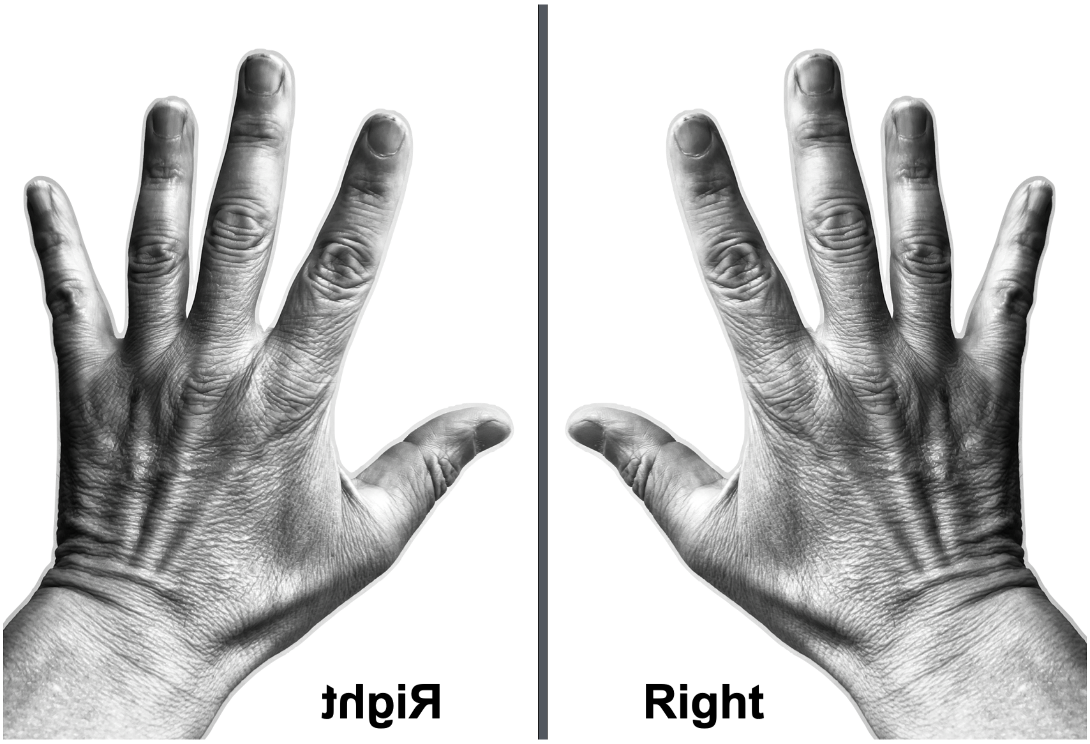

Figure 1.1: My right hand and its mirror image.

Mathematically, we can characterise the difference between left and right by introducing the notion of *chirality*. In 1893, William Thomson, freshly renamed Lord Kelvin, gave the first precise definition of chirality in the Robert Boyle Lecture delivered to the Oxford University Junior Scientific Club: *"I call any geometrical figure, or group of points, **chiral**, and say it has **chirality**, if its image in a plane mirror, ideally realised, cannot be brought to coincide with itself."* An object is *achiral* if it can be superimposed on its mirror image. Otherwise, it is said to be *chiral*. Chirality is therefore not a property of a body but the absence of a property. By *supreimposition*, we mean any combination of translation and rotation in space, the so-called *rigid-body transformations* that explicitly exclude mirror transformations. This group of transformations corresponds to our understanding of moving an object in space without deforming it (hence the *rigid* part): the relative position of any pair of points in that object does not change during the transformation.

The very word *chiral* comes from the Greek *kheir* ($\chi\epsilon\iota\rho$), meaning *hand*, the paradigm for chirality: the asymmetry of our own hands became the root metaphor and the name for chirality in geometry, chemistry, and physics. Looking around us, it is sometimes easy to figure out if an object is chiral or not. Typically, achirality is associated with a mirror symmetry (but not always). Hence any object that can be split into two parts that are the mirror image of each other is achiral. For instance, looking at the natural world *Bilateria* are the vast group of animals whose bodies can be divided into left and right halves by a single plane of symmetry during development. Humans, insects, worms, and many familiar animals belong here. To a first approximation, many adult bilaterians are also achiral (Figure 1.2): their body plan is symmetric under reflection through the sagittal plane, so the left half mirrors the right. This is why we can talk about a generic bilaterian body without worrying whether it is "left-handed" or "right-handed." The symmetry is of course not perfect: the heart and gut coil, and the brain is not perfectly symmetric. The tendency for certain functions or structures to be specialised to one side of a bilaterally symmetric organism is called *lateralisation* in biology. But at the structural level that defines the group, bilaterians are described as achiral organisms (at least initially), with chirality appearing as a secondary modification.

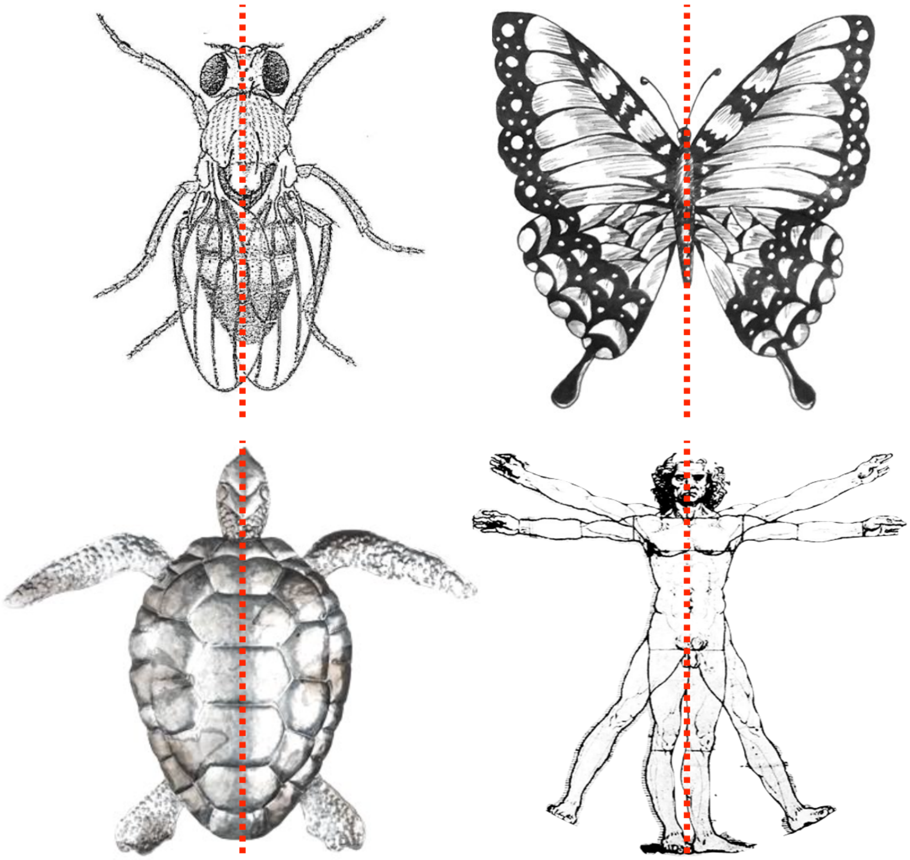

Figure 1.2: An example of achiral structures in nature: *Bilateria* are a clade of animals characterised by bilateral symmetry during embryonic development. Many of these animals preserve that symmetry while mature as shown here. Others lose that symmetry in the adult form. Note that the mirror symmetry is never perfect and all animals exhibit secondary chiral structures.

Because we ourselves are bilaterians and perceive the world through an approximately achiral body plan, we naturally design many of our tools and artefacts to share that bilateral symmetry. A chair, a table, a ladder, even a book: all of these are achiral in the same first approximation, since they can be mapped onto their mirror images without any change. Of course, details can introduce chirality, the driver position in a car, the buttons on a shirt, a chair with an armrest only on one side, or a spiral staircase that turns one way rather than the other. But the default tendency in many human-made objects is to respect bilateral achirality, mirroring the general body plan of their makers. It also explains why the world seen in a mirror is not shockingly different, until we start looking at the details.

While many animals and the objects they make are approximately achiral, many structures in nature are intrinsically chiral. Mollusks are also bilaterians but their chirality appears very early in development and leads to strong "handedness" (Figure 1.3). A seashell that coils to the right cannot be superimposed on its mirror image that would coil to the left. The same is true for instance for the twisted growth of a vine. At the molecular level chirality is even more fundamental: amino acids, sugars, and DNA helices all occur in specific handed forms that cannot be matched with their mirror images. Thus, although the large-scale body plans of many bilaterians or of chairs and tables are close to achiral, the fine structure of life and many natural forms is dominated by chirality. Since our left foot is definitely different from our right

Figure 1.3: Many objects are chiral with a very well defined left or right chirality, inherited from our own body handedness.

foot, a shoe, just like a glove is chiral.

It is easy to define left and right for seashells: hold the shell with the tip of the spiral, the apex, pointing upward and with the opening, the aperture, facing toward you. If in this position the aperture is in the right side of your field of vision (on the right), the shell is said to be *dextral* or right-handed. If instead the aperture lies on the left-hand side, the shell is *sinistral* or left-handed. Strangely, the majority of gastropods are dextral, but sinistral forms occur in some lineages and sometimes as rare variants within a normally dextral species.

Naturally, we would like to extend the definition of handedness (left or right) to mathematical objects. The simple canonical one being a helix, a clearly chiral structure. The scientific usage is to call the helix on the right of Figure 1.4, right-handed and the one on the left, left-handed. This is called the *right-hand rule*: take your right hand and curl the fingers in the direction in which the helix winds as it rises away from you. If the thumb, held straight, then points along the axis of advance, the helix is right-handed. If instead you must use your left hand to make the curl match, then the helix is left-handed. As Feynman, once said:"*We know that the 'right-hand' rule was merely a convention: it was a trick."* But what is this convention? and where does it come from?

1.2 A convention

The struggle of scientists to come up with a formal definition of what is left and right demonstrates the difficulty of the concept. Indeed, the question of left and right was not just a curiosity: it troubled some of the greatest minds of the nineteenth century. James Clerk Maxwell, as he was in the last steps of shaping the theory of electromagnetism, found himself caught in the puzzle. In a letter to his friend Peter Guthrie Tait on 8 May 1871 he poured out his frustration: "*I am desolated! I am like the Ninevites! Which is my right hand? Am I perverted? a mere man in a mirror, walking in a vain show?*" [2]. He ended the letter with a more practical thought: "*I must get hold of the Math. Society and get a consensus on the craft*" [12]. He meant the London Mathematical Society, and true to his word, just three days later he raised the issue at one of its meetings. Around the room sat towering figures such as William Thomson (not yet Lord Kelvin) and the mathematician Arthur Cayley. The discussion was considered important

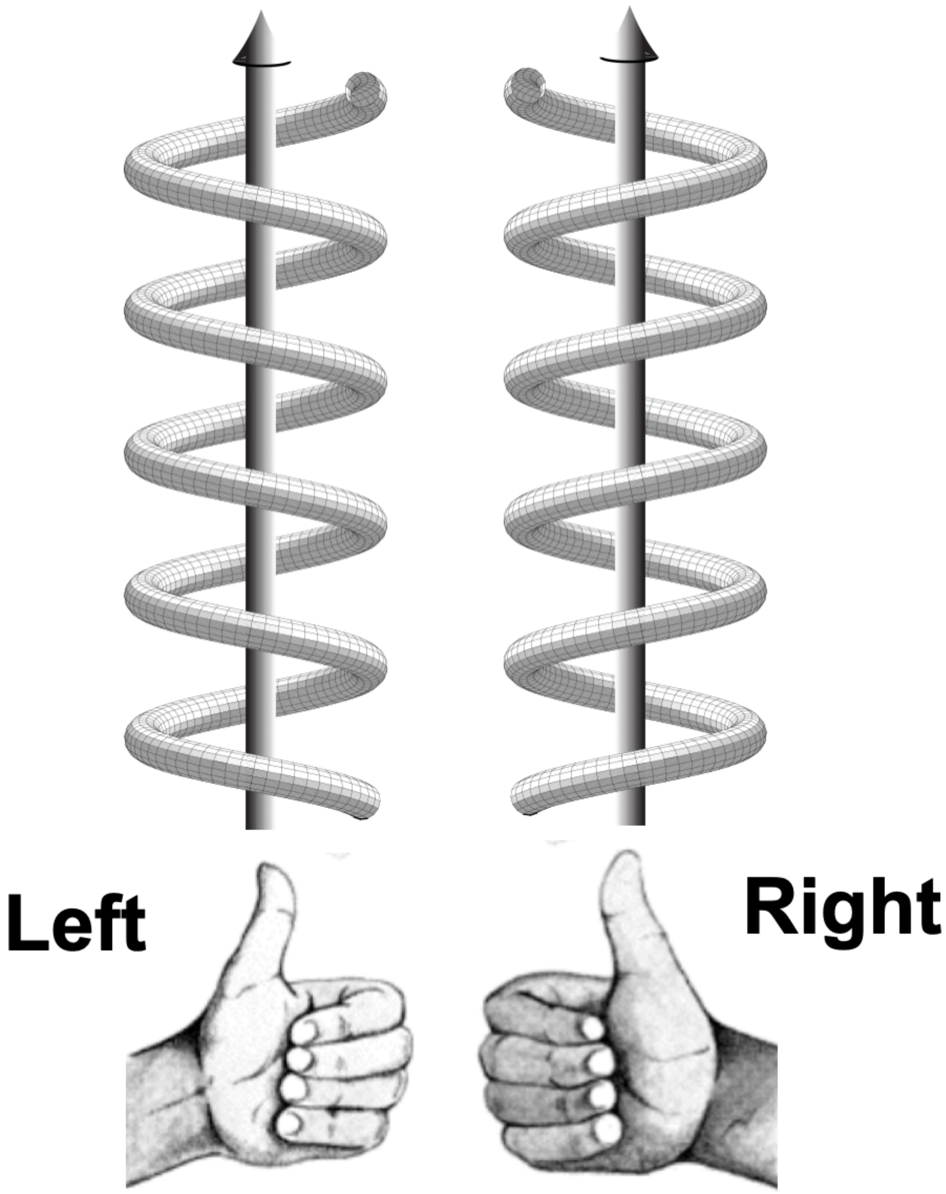

Figure 1.4: A left and right-handed helix, following the right-hand rule.

enough to appear in Nature on 25 May 1871 (issue 82). There Maxwell put the problem plainly: "*In pure mathematics little inconvenience is felt from this want of uniformity, but in astronomy, electromagnetics, and all physical sciences, it is of the greatest importance that one or the other system should be specified and persevered in.*" Maxwell had realised that if you want to define operations like the curl of a vector in three dimensions, you must first settle on whether space is organised around a left-handed or a right-handed frame. But which choice should science adopt? After weighing the options, the Society agreed on a convention: "*the right-handed system, symbolized by a corkscrew, or the tendril of the vine, was adopted by the society.*"

The same issue resurfaced two years later in Maxwell's Treatise on Electricity and Magnetism [7, p.24], where he quoted a suggestion by the crystallographer William Hallowes Miller:

> *"Professor W. H. Miller has suggested to me that as the tendrils of the vine are right-handed screws and those of the hop left-handed, the two systems of relations in space might be called those of the vine and the hop respectively. The system of*

the vine, which we adopt, is that of Linnaeus, and of screw-makers in all civilized countries except Japan."

Let me unpack Maxwell's multiple comments.

First, Maxwell's comment about screws in Japan is enigmatic. We have not found evidence that left-handed screws were in use there in the nineteenth century. Intriguingly, though, ethnographers have documented the use of left-handed screws among Inuit peoples [11].

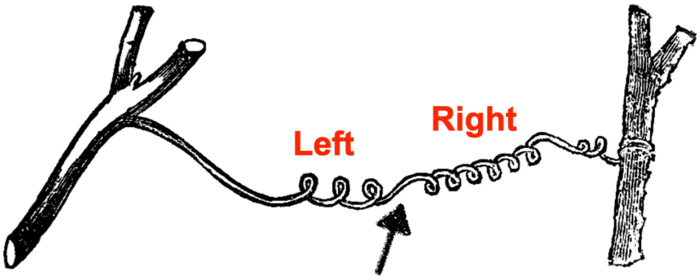

Figure 1.5: A tendril is a modified leaf, used by some climbing plants to attach themselves to support. They always appear as a mixture of left- and right-handed helical filaments.

Maxwell's attempt at a definition is rather puzzling on many fronts. Miller was a giant in crystallography but certainly not a botanist, and the biology here is shaky. In Britain the word "vine" meant grapevine, *Vitis vinifera*. But the tendrils of the grapevine are not consistently right- or left-handed: they always switch their handedness along their length (see Figure 1.5), a behaviour that Darwin had already described and that I coined *tendril perversion* in my early work [9]. What Maxwell seems to have in mind is not the tendrils at all, but the way a vine stem twines around a support. Yet the grapevine is not a twiner; it climbs with tendrils, which are modified leaves, not stems. By contrast, the hop plant really is a twiner, but it does not produce tendrils.

Maxwell's second problematic statement lies in his appeal to Linnaeus. In the first edition of *Philosophia Botanica* (1751) [13], Linnaeus does indeed classify handedness: the hop (*Humulus*) is left-handed (sinistrorsum) while the bindweed (*Convolvulus*) is right-handed (dextrorsum), as shown in Figure 1.6. Indeed, the bindweed stem winds around a pole in a right-handed helix, just like a regular corkscrew. However, in the third edition Linnaeus inserted an erratum, saying that "left" should be changed to "right" on page 103, without correcting the parallel passage on page 39. This inconsistency created a lasting confusion. Nineteenth-century botanists split into two camps: Gray, Eichler, Duchartre, and Darwin sided with the first version, while de Candolle, Mohl, Bischoff, and Sachs followed the correction.

The mystery of a proper physical definition of left and right lingered well into the twentieth century. For physics, the decisive moment came with the discovery of beta decay, the process in which a neutron turns into a proton, an electron, and a neutrino. For decades, it was assumed that the laws of nature made no distinction between left and right, a principle known as *parity conservation*. But in 1956 Chien-Shiung Wu and her collaborators performed a now-famous experiment on cobalt-60 nuclei, showing that in beta decay electrons were emitted preferentially in one direction relative to the nuclear spin. Hence proving that nature itself, at the deepest level of particle physics, is asymmetric [15, 14]. In 1957 this breakthrough finally gave physics a physical definition of left and right, not just a matter of convention but built into the weak interaction itself. Yet one of the most notorious omissions in the history of the Nobel Prizes, the prize went to Tsung-Dao Lee and Chen-Ning Yang, who had proposed the idea, while Wu, who carried out the difficult and conclusive experiment, was left out.

Figure 1.6: Climbing plants can be left-handed or right-handed. But are they suitable for a definition of handedness?

Here we will follow Maxwell's convention. If in doubt, simply go home, pick up an ordinary screw or a corkscrew, and trace the path of its thread. Unless by chance you have stumbled on one of the rare left-handed utensils, the curve you follow will wind in a right-handed helix, just as shown in Figure 1.4.

1.3 Chirality everywhere

It's not just physics where chirality plays a crucial role. Biology is full of left- and right-handed structures, and life itself depends on this asymmetry. The molecules that make up living organisms are almost always chiral, and nature has chosen one hand over the other with astonishing consistency. Amino acids, the building blocks of proteins, are found almost exclusively in their left-handed form, while sugars in DNA and RNA are right-handed. This strict molecular handedness is essential: if the opposite form were substituted, proteins would not fold correctly and genetic information could not be read. This asymmetry cascades up the scales and it is the reason why even larger biological structures carry chirality, from the spiral twist of a snail's shell, the helical arrangement of collagen fibres to the position of our heart. In this sense, life on Earth is fundamentally one-handed.

The importance of chirality in chemistry was first revealed in the middle of the nineteenth century by Louis Pasteur. While studying crystals of tartaric acid salts, he noticed that some crystals came in mirror-image forms. By carefully separating them with tweezers, Pasteur showed that solutions of one form rotated the plane of polarised light to the left, while the other rotated it to the right. When the two forms were mixed in equal amounts, they cancelled each other out and produced a so-called "racemic" mixture. This was the birth of stereochemistry, and it revealed that most *enantiomers* (left or right version of a molecule) behave differently.

It is striking how clearly Pasteur grasped the essence of chirality. His description, written decades before Lord Kelvin introduced the term, is virtually identical in spirit:

"If one considers material objects, whatever they may be, in terms of their shapes and the repetition of their identical parts, one quickly recognizes that they can be divided into two broad categories characterized as follows: one group placed before a mirror gives an image that is its superimposable counterpart; the image of the other could never be superimposed such that it faithfully reproduces all its details. A straight staircase, a stem with distinct leaves, a cube, the human body... are objects of the first category. A spiral staircase, a vine, a hand, an irregular tetrahedron... are forms of the second group. The latter lack a plane of symmetry." [10]

A striking everyday example of the difference between enantiomers is provided by carvone, a molecule found in essential oils. One enantiomer of carvone gives the smell of spearmint, while its mirror image gives the smell of caraway seeds. Chemically they are almost indistinguishable: the same atoms in the same sequence of bonds. We cannot always see the difference between left and right, yet our noses can. Since, they rely on chiral receptors, they detect the two enantiomers as completely different.

The consequences can also be far more serious, as the story of thalidomide makes clear. Marketed in the late 1950s as a treatment for morning sickness, thalidomide was sold as a mixture of two enantiomers. One had the intended therapeutic effect, while the other caused severe birth defects and death in thousands of children worldwide. Even worse, once inside the body the two forms could interconvert, making separation ineffective. Thalidomide remains a tragic textbook case of what can happen when chirality is ignored in drug development, and it taught chemistry and medicine that the handedness of molecules is not a minor detail but a matter of life and death. It also illustrates why strict scientific regulation of medicines is essential. When this principle is weakened or sacrificed for political expediency as we are sadly seeing these days, the result is measured in human lives.

1.4 Chirality and Dimension

The relation between chirality and dimension is subtle. In one dimension, the situation is very simple. Take a connected domain, for example an interval on a line as shown in Figure 1.7. Such an object is always achiral, because a translation maps the mirror image of the interval onto itself. However, if we consider a disconnected set, such as two distinct intervals, chirality can appear. Imagine two segments placed asymmetrically on a line: their mirror image cannot be mapped back onto the original configuration without swapping the order of the pieces, which is not allowed. Thus, disconnected one-dimensional sets can be chiral, while connected ones cannot.

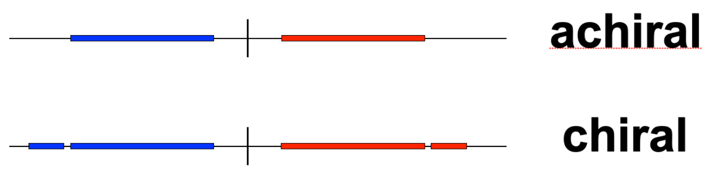

Figure 1.7: A 1D connected set in 1D is always achiral, whereas some disconnected sets may be chiral. However, in 2D, the 1D set is always achiral.

However, there is a subtlety: A set that is chiral in one dimension becomes achiral in higher dimensions. Consider again two intervals on a line, arranged asymmetrically so that their mirror image cannot be superimposed in one dimension. If we now place the same set in the plane, the apparent chirality disappears. After reflecting the figure in two dimensions, we can rotate it in the plane to bring the image back to the original. In other words, any one-dimensional set is achiral when embedded in two dimensions.

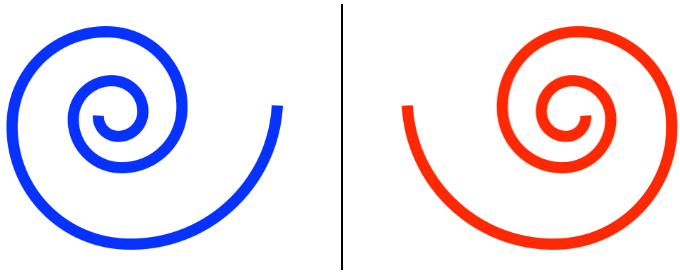

Figure 1.8: A spiral in 2D is always chiral since it is either clockwise or counter-clockwise. However, the same shape is achiral in 3D.

In two dimensions, the story becomes richer. Simple shapes like a circle or a square are achiral because a reflection across a line brings them back to themselves (see Figure 1.8). But many planar figures, such as spirals are chiral, since no reflection can superimpose them onto their mirror image without changing the direction of rotation. However, again any 2D objects is achiral in 3D as we can just flip them in the third dimension to recover the initial one.

This dependence of chirality on dimension was already noticed in the nineteenth century by August Ferdinand M´obius. He proved a general result: any figure in n dimensions is achiral if it is allowed to be moved in $n+1$ dimensions. The reason is that the extra dimension gives enough freedom to "flip" the object into its mirror image. Thus, a one-dimensional set that is chiral on a line becomes achiral in the plane, a two-dimensional figure that is chiral in the plane becomes achiral in three dimensions, and so on. Chirality is therefore always relative to the space in which the object is embedded. The philosophical weight of this idea was not lost on later thinkers. Almost a century later, Wittgenstein put it in his characteristically sharp way: "*A right-hand glove could be put on the left hand, if it could be turned round in four-dimensional space.*" Chirality depends not only on the object itself but also on the space in which it is considered

The astute reader will know that in modern physics, theories such as string theory or grand unification often invoke spaces with more than three spatial dimensions. In those contexts, the question of chirality becomes crucial once again. For example, the particles of the Standard Model, like electrons and neutrinos, display chiral behaviour in our three-dimensional world: they distinguish left from right in weak interactions. If we imagine these particles embedded in higher dimensions, M´obius's result warns us that their chirality might vanish. Yet, many such theories in higher dimensions also require chirality.

1.5 Chirality measures

When dealing with 3D objects, it is often useful to go beyond a simple "yes or no" answer to the question of chirality and ask how chiral an object is. There are two questions really. First, can we find numerical quantities that assign a degree of chirality to a structure? The measure should be zero for an achiral object and positive for a chiral object and should increase when the object is further from an achiral one. The second question is how do we differentiate between a left- and right-handed structure? If I decide that a handed helix is indeed right-handed according to Maxwell's convention, can I decide whether a potato (which is generically chiral) is right or left?

Therefore, a good chirality measure should vanish exactly for achiral objects, increase in absolute value smoothly as the object becomes more asymmetric, and ideally have a sign that

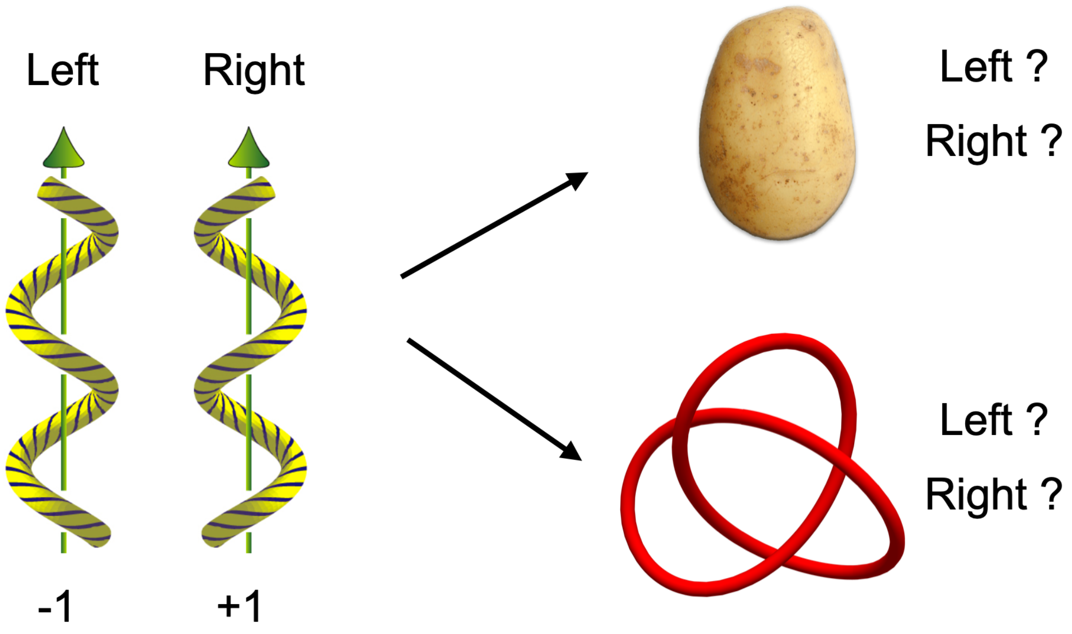

Figure 1.9: A trefoil knot or a potato are classical examples of chiral objects. But are they left- or right-handed? How do we go from the definition of handedness for a hand, a shoe, or a helix, to the definition of handedness for an arbitrary curve in space?

indicates whether it is left- or right-handed.

We will consider the simple case of smooth curves in three-dimensional space (lines, circles, helices, and smooth knots are part of that set).

The first step in quantifying chirality is simply to detect whether an object is achiral. This can, in principle, be done with a measure that does not distinguish between left and right. Suppose we have a three-dimensional body $\mathcal{S}$ of volume $\mathrm{vol}(\mathcal{S})$. We can reflect it in a mirror, obtaining $\tilde{\mathcal{S}}$, and then look at how much volume overlaps between $\mathcal{S}$ and any rigid motion $\mathfrak{R}(\tilde{\mathcal{S}})$ of its mirror copy [4]. If the object has zero volume, as in the case of a curve or a surface, we replace volume with the corresponding measure of length or area. Minimising over all possible rotations and translations, one arrives at

$$\chi_{\mathrm{vol}}(\mathcal{S}) = 1 - \max_{\mathfrak{R}} \frac{\mathrm{vol}\left(\mathfrak{R}(\tilde{\mathcal{S}}) \cap \mathcal{S}\right)}{\mathrm{vol}(\mathcal{S})}. \tag{1.1}$$

This quantity vanishes exactly when $\mathcal{S}$ is achiral, and otherwise takes values between 0 and 1, which allows it to be interpreted as a measure of “how chiral” the object is.

The drawback is that such measures depend heavily on the underlying choice of metric. For example, one can define a distance in which any chiral triangle in the plane lies arbitrarily far from an achiral one [1]. Moreover, the minimisation over all rigid motions is computationally difficult, and the result does not distinguish handedness, since by construction $\chi_{\mathrm{vol}}(\mathcal{S}) = \chi_{\mathrm{vol}}(\tilde{\mathcal{S}})$ [4]. Therefore, χ_{vol} provides a way of quantifying how far a body is from perfect mirror symmetry. However, this definition, while correct is not easy to compute and would typically require numerical integration, which is not satisfactory.

The second step, assigning a chiral sign to an object, is more difficult. Let me give you an example. In the Frenet–Serret description of a space curve $\mathbf{r}(s)$, the torsion $\tau(s)$ measures by what amount a curve does not remain in a plane at any given point. A helix has constant torsion (positive for right-handed helices, negative for left-handed ones). However, in general, torsion changes from point to point, so a single local value cannot capture the global handedness of the shape.

A possible chirality measure is the *integrated torsion*

$$\chi = \frac{1}{L}\int_0^L \frac{\tau(s)}{|\tau(s)|}\,\mathrm{d}s, \tag{1.2}$$

which averages the sign of the torsion over the full arc length L. At each point, the ratio $\tau(s)/|\tau(s)|$ extracts only the sign, equal to $+1$ for right-handed torsion and -1 for left-handed torsion. The integral therefore records how much of the curve prefers right- or left-handed torsion.

If the curve has perfectly balanced regions of opposite torsion, the average vanishes and $\chi = 0$, consistent with an achiral or perverted structure such as a grapevine tendril that switches handedness along its length. If the curve is a perfect right-handed helix, then $\tau(s)$ keeps a constant positive sign and the integral gives $\chi = +1$. Similarly, a perfect left-handed helix yields $\chi = -1$.

However, there is a possible problem, known as the problem of *chiral connectedness.* Suppose we have two shapes, $\mathcal{S}_-$ and deform it continuously to a shape $\mathcal{S}_+$, both of which are chiral but with opposite handedness (see Figure 1.10). One can find a path between the two so that each curve on that path is chiral. Since chirality should be continuous and takes positive and negative values along the path, it must go through a point where it is zero. Hence, for any chiral measure, we can find a chiral object for which that measure would vanish, a false positive!

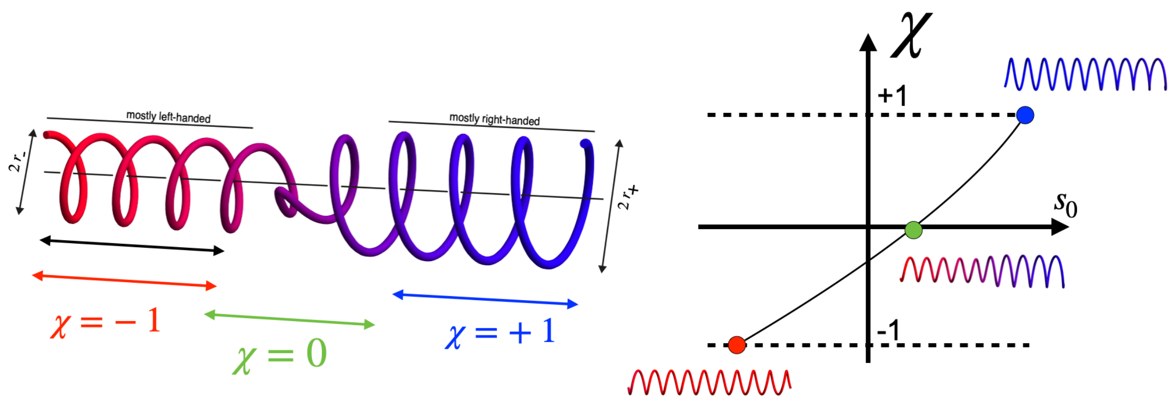

Figure 1.10: Here is a family of curve, obtained by sampling this curve with a window in arclength. On one side, the curve is almost a perfect righ-handed helix (with chirality +1) an on the other, the curve is almost a perfect left-handed helix (with chirality -1). Since chirality χ is continuous by assumption, there must be a curve with $\chi = 0$, despite the fact that this curve is chiral (which is ensured by choosing the two helical radii to be different)

A more refined way to capture chirality is through the idea of a *chirality matrix*. The inspiration comes from physics: when an asymmetric body is placed in a uniform external field, such as a molecule in a liquid crystal, or a filament in a viscous flow, the field does not simply push it along, but also tends to twist it. This twist can be described by a linear relation between the field vector and the induced rotation vector, and the object that maps a vector to another one is a matrix. Because the sense of rotation reverses under a mirror reflection, this matrix is a pseudo-matrix: it changes sign in a mirror transformation, just as angular momentum does in mechanics. When defined carefully for a curve or filament, by integrating the local forces and

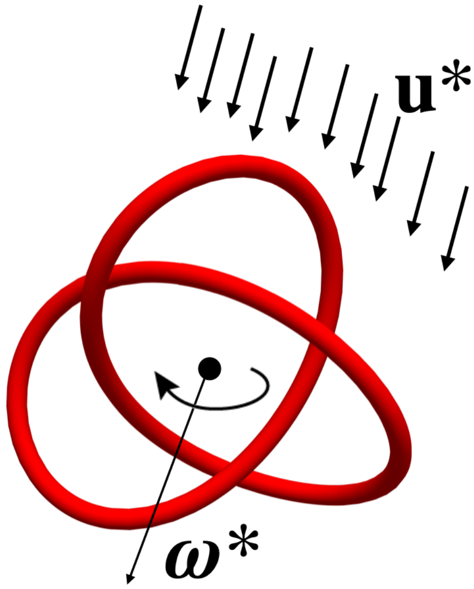

Figure 1.11: Under a wind or flow $\mathbf{u}$, the torque applied to the object induces a rotation $\boldsymbol{\omega}$. When they are aligned, the amplitude of the rotation vector $\boldsymbol{\omega}$ is the eigenvalue, whose sign can be used to assign chirality.

torques along its length, one obtains a global chirality matrix $\mathcal{Q}$. Its mathematical properties are striking: it is symmetric and traceless, and its eigenvalues provide a diagnostic of handedness. If all three eigenvalues are nonzero, the curve is chiral, with the sign pattern indicating whether it is left- or right-handed. If one eigenvalue vanishes, the situation is ambiguous, reflecting the deeper problem of chiral connectedness. Thus, the chirality matrix offers a powerful but subtle way to connect the geometry of a shape with the physical notion of how it twists when pushed.

The chirality matrix $\mathcal{Q}$ provides a compact algebraic way of diagnosing handedness. Because it is a symmetric pseudo-matrix, it can always be diagonalised with three real eigenvalues $(\gamma_1, \gamma_2, \gamma_3)$ that satisfy the condition $\gamma_1 + \gamma_2 + \gamma_3 = 0$. Under a mirror reflection $\mathfrak{M}$, the matrix changes sign, $\mathfrak{M}(\mathcal{Q}) = -\mathcal{Q}$. If the underlying object is achiral, its chirality matrix must remain invariant under reflection, and the only way this can happen is if the spectrum takes the form $(\gamma, -\gamma, 0)$. In such a case one eigenvalue vanishes, while the other two are equal in magnitude and opposite in sign. For a genuinely chiral object all three eigenvalues are typically nonzero. The sign pattern then determines handedness: if two eigenvalues are positive and one negative the object is called right-handed, while if two are negative and one positive it is left-handed. This convention matches the familiar definition of helices. In this way the eigenvalues of $\mathcal{Q}$ give a purely mathematical fingerprint of chirality, linking geometry and handedness through linear algebra.

1.6 Controlling chirality

Elephant trunks provide a most impressive example of handedness in nature. Trunks can go up and down and curl to grab objects. But to do so, they have to curl. If you present an elephant with a vertical log, it will have to decide to take it from the left side or the right side. Surprisingly, elephants show a distinct preference for how they grasp objects. Careful observation revealed that individual elephants consistently coil their trunk either clockwise or counter-clockwise, much as humans favour one hand over the other. This behavioural asymmetry has been termed "*trunkedness*," and it mirrors the more familiar concept of handedness in people (but unlike handedness, trunkedness is about 50/50 in a population). What makes this so fascinating is that chirality here is not imposed from outside, as in the case of a screw thread, but must be actively controlled. The elephant's brain sends signals that bias the trunk into one helical direction rather than the other, and over time this preference becomes consistent. The challenge is similar to that faced in engineering soft robotic arms or tentacle-like manipulators: how to impose a global handed motion on a structure that is, in principle, equally capable of bending either way.

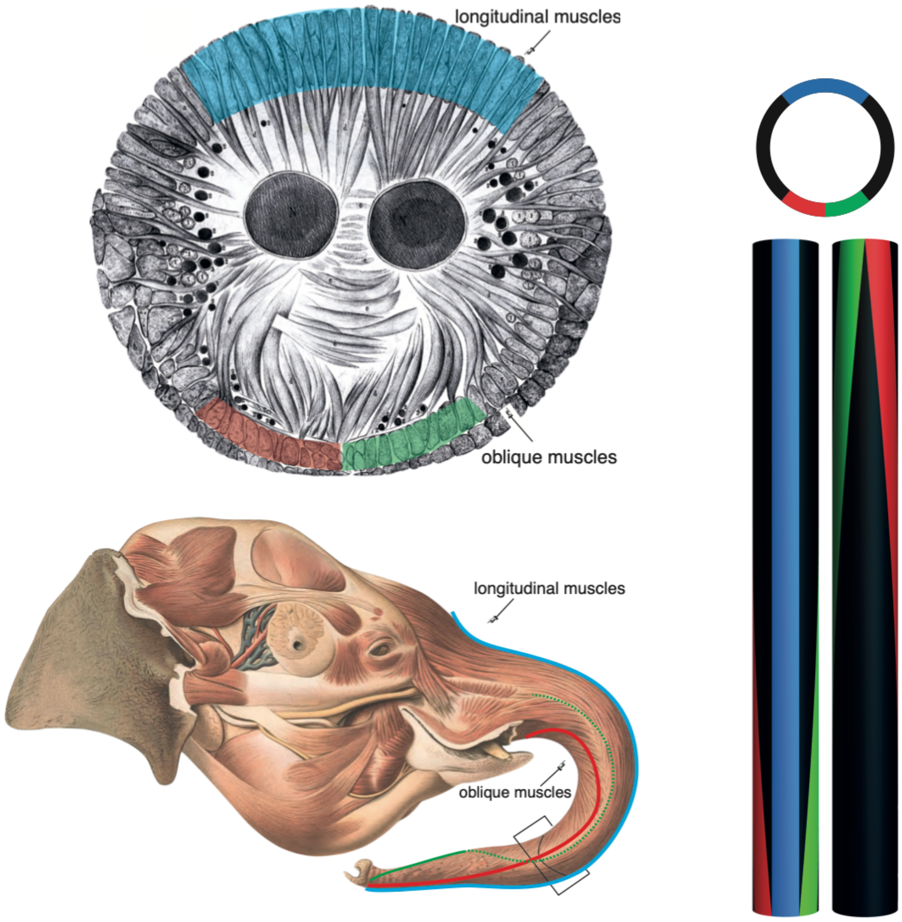

Figure 1.12: An elephant trunk is a highly complicated muscular hydrostat with longitudinal, radial, and helical (oblique) muscle group. It can be simplified into a minimal design with three actuators.

The elephant trunk is a muscular hydrostat with no bone, but inside it are more than 90,000 individual fascicles organised into 17 major muscle groups. These include longitudinal, radial, and helical bundles. The most important ones for complex motion are the oblique or helical muscles that wrap around the trunk in spirals. When they contract, they bend the trunk but also develop torsion, which is essential for curling, grasping, and rotating objects. This oblique organisation, combined with longitudinal fibres running along the length, gives the trunk its extraordinary versatility, strength, and fine control.

To capture the essence of this design in a minimal model, with my collaborators in Stanford, we decided to reduce the design to only three actuators: one longitudinal bundle and two helically arranged bundles of opposite handedness [5]. The longitudinal element provides simple bending, while the pair of helical actuators introduces twist and torsion. With these three components working together, the model reproduces a large part of the trunk's motion repertoire, even though it is vastly simpler than the biological original.

Controlling torsion in such a system comes from balancing the activation of the helical bundles. Activating them equally but in opposite directions cancels the torsional effect and produces pure bending. Activating only one helical bundle creates twisting, while asymmetrically combining them produces mixed states of bending and torsion. In this way, torsion is t a controllable mode of deformation, one that can be dialled up or down depending on the relative strength of muscle (or actuator) activation. Elephants achieve this with thousands of coordinated muscle fascicles; but we can understand it with just a pair of helically placed actuator.

1.7 Epilogue

With our right or left hands, we have only scratched the surface of chirality. There are many fundamental problems that have yet to be solved: How come the human population has a majority of 90% of right-handers? Why are 90% of seashell species also right-handed? How was biomolecular chirality selected so that only one form of DNA and amino acids are found and not their mirror image? How is body achirality controlled so that our hands are almost perfect mirror images of each other? How is chirality transferred from the smallest molecular scale to the organ scale? Why do we so easily confuse left and right? And does the water in your bathtub really swirl counterclockwise when you empty it? I invite you to think about all these problems as you walk in the forest, on the beach, or relax in your bath!

1.8 Further Reading

A classic popular-science exploration of symmetry and parity violation, including the landmark discussion of the 1956 Wu experiment is *The Ambidextrous Universe* by Martin Gardner (1964) [3].

A wonderful and comprehensive look at asymmetry across brains, bodies, atoms, and culture, blending neuroscience, biology, and the broader theme of chirality is *Right Hand, Left Hand* by Chris McManus (2002) [8].

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