CHAPTER 1

RHYTHMIC PHENOMENA, MECHANICAL PHILOSOPHY, AND VITALISM IN ENLIGHTENMENT BIOLOGICAL SCIENCE

THE modern scientific study of plant and animal rhythms in the nineteenth and twentieth centuries arose initially from consideration of plant movements during the Enlightenment, when the causes of what appeared to be autonomous movements in nature were a point of contention in natural philosophy. The mechanical philosophy that developed in the new science of the late seventeenth century had already challenged traditional Aristotelian explanations for such movements in animals, and the observation that certain plants also appear to move spontaneously broadened the scope of debate between those who viewed all matter as fundamentally inert and those who postulated a vital property to differentiate living and dead matter.

The idea that organisms possess some sort of internal agency that directs and carries out growth and development and coordinates the actions of the parts of complex organisms was already implicit in the Renaissance Aristotelian concept of nature, but in the late seventeenth century this was challenged by the development of Cartesian dualism and mechanical philosophy. Cartesian mechanics reduced organic actions to the motions and collisions of inertial matter and explained organisms as parts of the greater cosmic machine, ultimately moved by causes external to them. In this respect, mechanical philosophy pushed the ancient Greek cosmic system to its limits, ascribing the operation of its parts to inertia and removing from organisms the Aristotelian concept of *enteleche*, an inborn agency that Aristotle introduced to explain organic development.

Some phenomena, however, eluded convincing reduction to the simple principles of mechanical physics. Experimental demonstration of peristalsis in chemically stimulated intestines and the continual beating of the heart of a cold-blooded animal after it was excised from the host body were glaring examples that seemed to demand some kind of internal agency. This agency was attributed to a property of organic tissues called *irritability*, an innate capacity for tissues to act and react.

When in the eighteenth century naturalists observed cyclical movements of certain plants that seemed to be autonomous from external causal stimuli, and it was seen that these were rhythmic in nature, the concept of irritability came into play as an explanation. This stimulated discussion of biological rhythms in the context of ongoing philosophical debate about the materialist and vitalist nature of biological systems. Study of rhythmic plant movements bore on consideration of how organic and inorganic structures differed. In the late eighteenth and early nineteenth century, autonomous rhythmic movement of plants fed into debates over materialist and vitalist agency in nature and, in particular, interpretations of the similarities and differences between plant and animal life. The example of J. C. Bose's study of sensitive plants illustrates how this physicochemical reductionist philosophical framework guided experimental research on plant and animal behaviors into the early twentieth century.

The idea of internal agency, which in Aristotelian natural philosophy directs the development of things from what they are potentially to what they become actually, was embedded in a general cosmology that assigned ultimate causality to the outermost reaches of the cosmos. The medieval heritage of ancient natural philosophy supposed that activity in the terrestrial world was empowered and directed by activity in the celestial world, with the consequence that the timings exhibited by terrestrial phenomena, the beginnings, growth, decay, and other changes, were regarded as reflections of the timings of their celestial causes—namely, the movements of the planets and stars. In modern terms, the supposition was therefore that the causes of biological timing (and all other timing) were exogenous to organisms. A chief debate among biological rhythms researchers in the twentieth century centered around whether characteristic daily, tidal, and seasonal rhythms that are evident in plants and animals were in fact rhythmic responses to rhythmic cosmic stimuli or, rather, were produced by internal, heritable, endogenous organs or mechanisms, which were likened to clocks. Therefore, consideration that timings of organic changes and behaviors might be internal characteristics of bodies and imagining how these could be results of causal timing mechanisms of some sort are of central importance to the history of chronobiology. Debate about whether there is internal agency—and, if so, how this can be explained—formed the intellectual context in which plant movements were interpreted in the Enlightenment.

One manifestation of the dialectic between mechanical philosophers and vitalists concerning the fundamental nature of the material world in which we live was discussion of the role left for autonomous agency (in moral terms, free will) in a materialist, mechanical worldview. Christian doctrine traditionally assigned the human soul a divine origin and attributed free will to it, which was necessary for Christian salvation. Understandably, this was a concern for traditional theologians, for whom the materialism of mechanical philosophy and denial of Aristotelian substantial forms threatened the concord between natural philosophy and Christian theology that had been achieved in medieval Europe. The seventeenth-century nonconformist English theologian Richard Baxter, for example, rejected the mechanical philosophy of Descartes and Pierre Gassendi in terms that speak directly to the adoption of the clock as metaphor for mechanism, asserting about the materialists that "they differ as much from true Philosophers, as a Carkass or a Clock from a living man."[1]

But the existence of free will also slipped into biological discussions in light of modern scientific developments, which began to efface the boundary between mind and matter. This was partly encouraged by the mixing of religious and scientific ideas in natural theology in the period, which sanctioned the exploration of nature as a means of religious contemplation. The exchange between Thomas Cooper, an English lawyer and science educator who accompanied the chemist and dissenting religious figure Joseph Priestley when he emigrated to the new United States, and an unnamed respondent, J.R.W., reveals at the end of this chapter how explanation of the phenomena of autonomous plant movements and with them biological rhythms bore on this basic philosophical debate. Although overt worries over the moral consequences of materialist philosophy receded with the advancement of science in the later nineteenth and twentieth centuries, the dialectic between materialist and vitalist explanations for biological agency persisted in the background of explanations of biological rhythmicity.

THE MICROCOSMIC EMBODIMENT OF MACROCOSMIC TIMINGS

Inasmuch as the circuits of the stars and planets across the sky were the very measures of the chief periodic regularities in nature in some of the oldest records in the Middle East, their motions would seem like an obvious choice to account for the earliest observed biological rhythms. Following the Babylonian and Egyptian astrologers, ancient Greek natural philosophers posited natural harmonic relationships between the motions of the stars and planets and mundane events. In his *Tetrabiblos*, Ptolemy went so far as to characterize the effects of planetary aspects on the developmental characteristics and personalities of individual people, based on the supposed influences of the planets and stars at the time of conception. Basic Aristotelian metaphysics supported the idea that a causal chain of celestial influences—beginning with the motion of the outer sphere, the prime mover—set the terrestrial elements in motion, continually stirring them up. Implicit in this cosmology is the idea that the causes of rhythmic changes and behaviors of living things are external to their bodies, exogenous in origin. This contrasts fundamentally with the current understanding that many biological rhythms, including the chief ones of interest to ecologists and evolutionary biologists, are endogenous or internally generated by biological clock mechanisms. The shift from regarding biological rhythms as caused by external causal factors to comprehending them as produced and regulated by internal agency was transformative for the incorporation of rhythms into biology and medicine. So, when were such timings attributed to organisms themselves rather than to the planets?

Rhythms and cycles in human health and disease, both in individuals and in populations, were evident to the early Greek physicians, so it is not surprising to find celestial cycles, mediated by seasonal weather cycles, implicated in the literature of Western medicine. By the High Middle Ages, the dependence of medicine on astrology in the European and Islamic realms provided much of the market for the production of accurate ephemerides, which showed the expected positions of the sun, moon, and planets within the zodiac. Medicine's dependence on these numerical tables for making diagnoses and planning treatments provided an impetus for refining the astronomical observations and mathematics on which they were based, provoking the achievements of the sixteenth-century astronomers Nicolaus Copernicus and Tycho Brahe.[2] Medical authors elaborated hypothetical links between the motions of the heavenly bodies and the qualitative states of specific organs and the relative mobility and abundance of the body's basic humors (blood, phlegm, yellow bile, and black bile), grounding astrological medicine in Aristotelian physics and motivating its legitimacy. The supposed regularity and cyclical shifting of the balance of the humors in the body undergirded the idea that there were predictable crisis points or critical days that could help physicians anticipate the course of an individual's disease. But, inasmuch as this concept of critical days on which a patient's health could make decisive turns was based on the "medical week," which was defined as one-fourth of an averaged lunar month, it was not based on either the periodicity or phase of actual lunar motions. This fact, which became more apparent as the precise measurement of the lunar period and other astronomical cycles became more important in the fifteenth century, led Renaissance physicians to question the connection between the course of diseases and the real motions of the planets, their aspects, and other details that complicated astrological practice.

From Saint Augustine forward, astrology was frowned on by Christian theologians as antithetical to divine omnipotence and human free will, casting astrological prophesy and horoscopy into a suspicious light. However, medical astrology was based on physical actions on the body and not on the willful soul. Thus it largely escaped charges of determinism and censure until Renaissance physicians and philosophers began to scrutinize it more carefully following Pico della Mirandola's late fifteenth-century attack on judicial astrology in his *Disputationes adversus astrologiam divinatricem*.[3]

Suspicion of the validity of astrology led to an increasing scrutiny of supposed physical macrocosmic-microcosmic links between celestial bodies and terrestrial creatures, and sixteenth-century medical writers began more explicitly to ground physiology and pathology in the materiality of the bodies themselves, citing bits of matter (*fomes*) and atoms or seeds (*semina*) and the supposed material increases and decreases of the humors in the body as causes of diseases. In his 1555 treatise on the causes of critical days, Girolamo Fracastoro attributed these cyclically recurring days not to lunar motions but, rather, to the aggregate ebbing and flowing of the principle Galenic humors with respect to the blood, each of which had its own natural periodicity: phlegm had a quotidian period, yellow bile a tertian period, and melancholia a quartan period. The interplay of these rhythms explained the different periodicities evident in fevers. The maxima and minima of an individual humor's fluctuation were not always significant in Fracastoro's system, but when the maximum of one humor coincided with the maximum of another, the synergy could produce a critical level, yielding a critical day. As an example, he showed how the tertian and quartan periods of yellow and black bile (choler and melancholia) tended to reinforce each other to produce the traditional critical days (see figure 1.1).[4] Fracastoro's explanation does not appear to have attracted much interest among his contemporaries, which is not so surprising when one considers that he did not question the existence or significance of critical days but merely provided a somatic explanation of them. But this in itself marked a significant intellectual shift, because it de facto located the rhythmicity of the bodily fluids in the fluids themselves rather than in rhythmic cosmic stimuli. This was a step toward internalizing biological rhythms.

The idea that timings and cycles might be internal to bodies, that individual living beings contain within them the causal principles of their biological rhythms, *endogenous* causes, was also implied in the writings of Fracastoro's near contemporary Theophrastus Paracelsus and was elaborated by later Paracelsian writers, who expressed an ontological supposition that has recently been termed "immanent vitalism," but which contemporaries called "vital philosophy."[5] The term *vital philosophy* (as both *philosophia vivente*

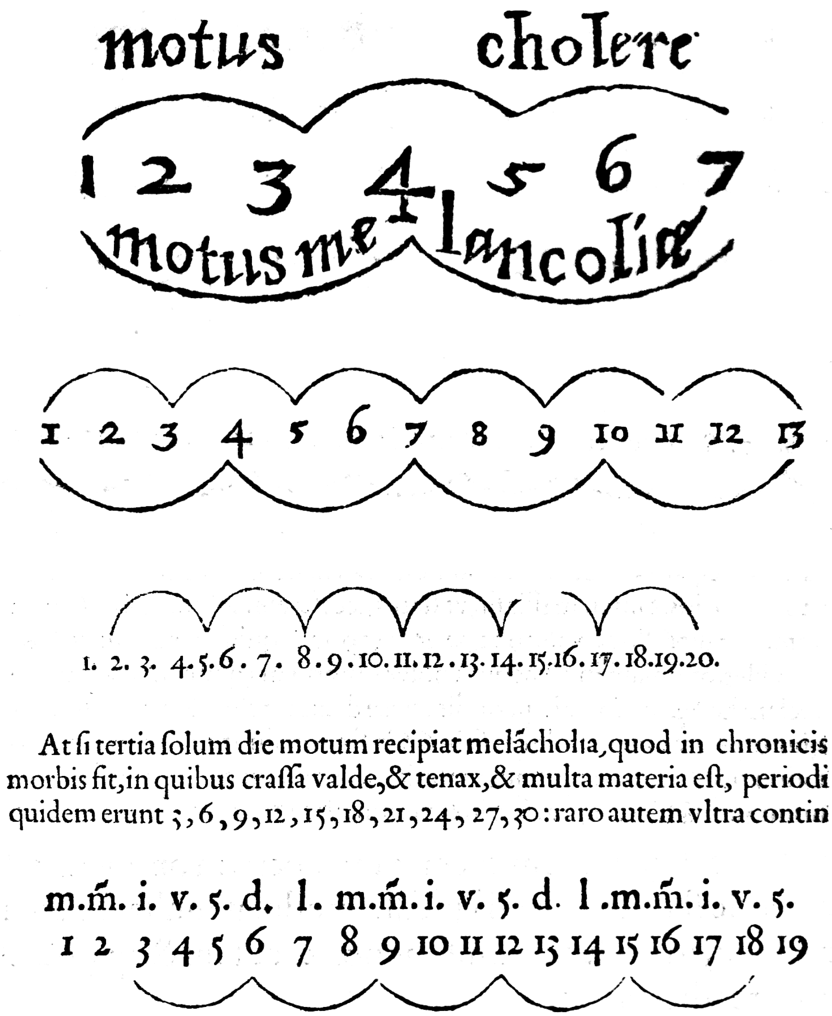

FIG. 1.1. The Hippocratic treatises codified the ancient concept of crises in some diseases, which were turning points at which a disease might take a turn for the worse or toward remission. The "critical days" on which these crises might fall followed cyclical patterns, reckoned from the first day of disease onset. The sixteenth-century Italian physician Girolamo Fracastoro explained the cyclical nature of these diseases as the result of interactions in the inherent cyclical nature of the Galenic humors, chiefly the fluctuations within the body of yellow bile (*motus choleræ*), which followed a tertian cycle (every other day from the third day after the onset of illness, day 1), and black bile (*motus melancholiæ*), which followed a quartan cycle (every third day). The tertian and quartan febrile cycles were well-known in antiquity, today associated with various kinds of malaria. The lower two figures indicate how the quartan periodicity of black bile, associated with melancholic diseases of old age and those who were excessively cold and dry, could be adapted to explain cyclical symptoms of chronic diseases. *Source:* Girolamo Fracastoro, *De causis criticorum dierum*, in *Hieronymi Fracastorii veronensis Opera omnia* (Venice: Giunta, 1555), ff. 72v, 74r, 76v. Copy in the Wangensteen Historical Library, University of Minnesota, Minneapolis.

and *philosophia vitalis*) was used by the prolific Paracelsian critic and alchemist Andreas Libavius in 1615 to characterize what he took to be the erroneous ideas of one of Paracelsus's followers, Petrus Severinus, which he criticized in his attack on another Paracelsian chemist, Johann Hartmann.[6] Severinus was the king of Denmark's personal physician and a widely read Paracelsian theorist and Hartmann was one of the earliest chemical physicians to offer a course of laboratory instruction in the preparation of chemical medicines, so Libavius's targets were significant.[7] Libavius was not the first to use the term *vital philosophy*, but it seems clear that he assumed his readers would readily understand it to apply to Paracelsus's chemical philosophy as interpreted by Severinus and other "vitalist" followers, in this instance Johann Hartmann, but perhaps also the less avidly Paracelsian Gregor Horst, who had used the term in 1612. It is within this vital philosophy that we find further hints that biological timings were beginning to be conceptualized not as responses to cosmic causal influences but as inherent characteristics of living beings and their parts—that is, as endogenous features.

Severinus's book *The Ideal of Philosophical Medicine* (1571) is at root an elaboration of Paracelsian philosophical and medical ideas in the context of Neoplatonic and Aristotelian metaphysics, intended to effect a new biological theory grounded in a fundamentally hylozoic conception—that is, that matter is inextricably bound to spirit, which gives it an internal agency, life.[8] The core of Severinus's theory is his supposition that all cosmic changes are developmental changes and are preordained by the Creator, who planted the seeds of all created things into the world at the beginning, as seminal potencies. These *semina*, as he called them, contain within them the knowledge of all ordained developments, including all the characteristics of the bodies they will produce, when they will produce them, and when they will decay back into potency. In modern terms, these developments comprehend both cyclically recurring timings and linear developmental timings, development and ageing. Within the broad scope of Severinus's vital philosophy, temporality is but one factor among many characteristics that define development and therefore entities. Nevertheless, it clearly does constitute a factor, the recognition of which is a striking innovation by Severinus, which he explicitly extended to the ontology of disease. In chapter 13 of his book, titled "On the location and timing of diseases, and other characteristics arising in the mechanical progress of generations," he wrote that diseases, like all seminal entities, are "bound by places and timings," by spatial and temporal limits—that is, they exhibit timings that are continuous or interrupted and swift or slow in carrying out their pathological functions and producing symptoms.[9]

Severinus's conception of developmental timing as being intrinsic to organic entities yet subject to alteration or reprogramming by external supervening factors contrasts strikingly with the medieval Aristotelian and Galenic teleological view of sublunary nature as being ultimately dependent on celestial causes. His realization that temporal behavior is an intrinsic part of life—that timing can be localized in the material organism itself—marks a significant turn in the history of physiology. It placed the Paracelsian concept of internal agency and efficient causation, personified as the inner alchemist or *archæus*, squarely into vital philosophy and, subsequently, into biology, where it remained as a possible explanation for the next two and a half centuries.

Severinus's Paracelsian attribution of characteristic "timings" to organic beings was but one explanation for the relationship between elements of the microcosm and the macrocosm, which can be broadly subsumed under the label Renaissance Platonism. A more general explanation was that a spiritual affinity or harmony linked things below to those above, a traditional idea that was repeated in Renaissance Platonism from Marsilio Ficino into the seventeenth century, when such affinities began to be abandoned in favor of material-mechanical explanations for causation. Jesuit polymath Athanasius Kircher elaborated an idea of this sort for the sake of illustrating every human's connection with God, applying it to the tropism of the sunflower. This and other plant movements would fascinate naturalists in the Enlightenment. As such, Kircher's "sunflower clock" is a historical curiosity worth mentioning, even if it neither exemplified nor explained biological rhythms.

According to the account he published, Kircher constructed what he described as a sunflower clock that could track the movements of the sun, even at night, by growing a sunflower and affixing its root onto a moveable cork flotation, so that the whole plant could rotate freely in a water bath. As depicted in his 1641 book on magnetism, he mounted an indicating stylus onto the blossom, which pointed out the time on a calibrated rim as the flower rotated itself on its float to remain oriented toward the sun. It is not known whether this device was actually built, but perhaps this is beside the point: Kircher evoked it on paper (see figure 1.2) as a virtual demonstration of the harmonic integrity of the cosmos. The device has variously been construed by historians as an artifice intended to inform cosmological debate in the years surrounding the condemnation of Galileo for teaching heliocentrism and as an elaborate baroque emblem of the spiritual forces that buttressed the Catholic church. In any case, inasmuch as the sunflower clock, as he described it, did not operate by movement of the parts of the plant but, rather, by the rotation of the whole plant as it floated in water, this sheds no light on early study of plant movement, let alone biological rhythms. It served instead as an exemplary vegetable version of a lodestone and thus demonstrated the universality

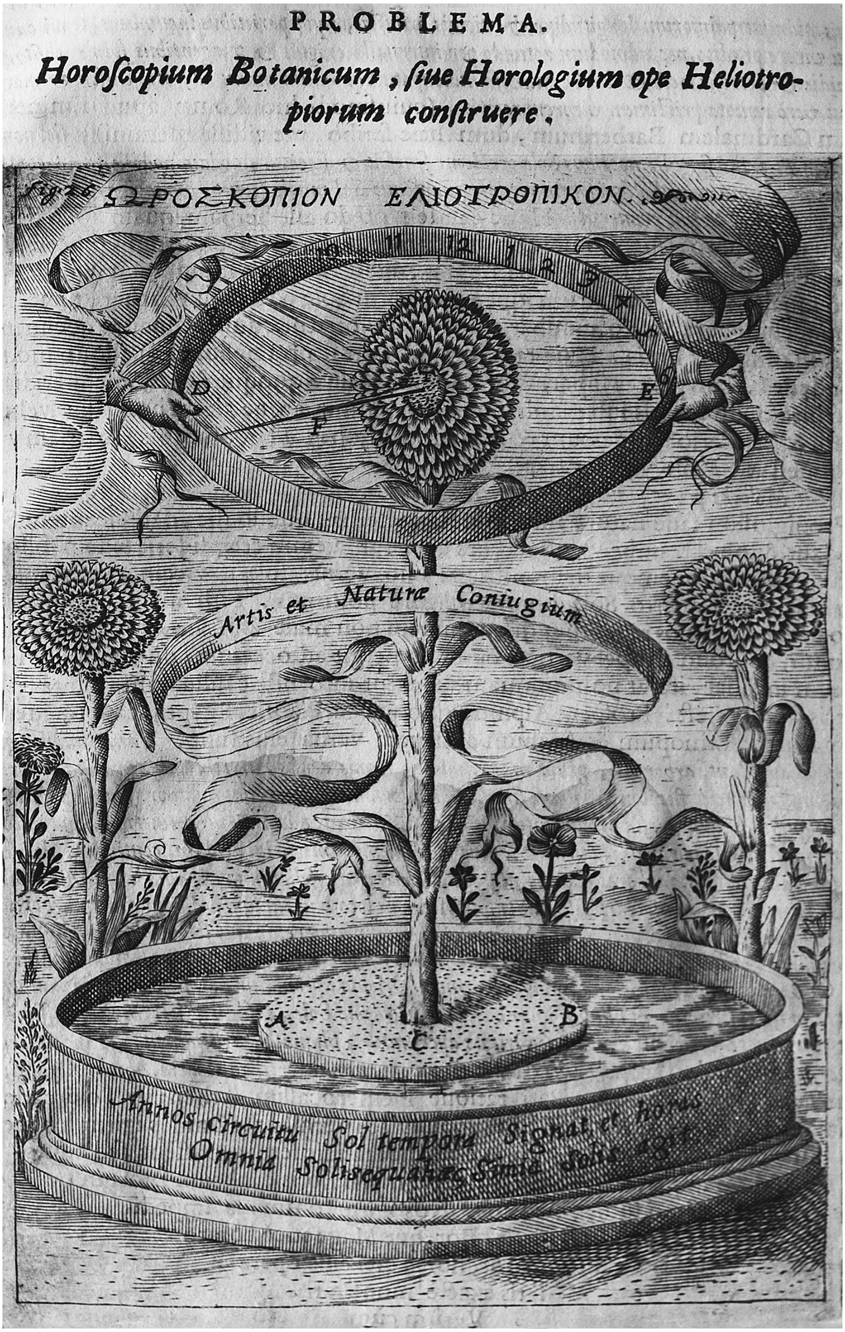

FIG. 1.2. The seventeenth-century Jesuit polymath Athanasius Kircher depicted a kind of clock based on the principle of vegetable magnetism, presumably a rationalization of the observed behavior of heliotropes to orient toward the sun as it moves across the sky during the day. Here, the sunflower is grown on a base that is floating in a water-filled basin, and its daily rotation is used to depict the time of day on the circular band at the top. *Source:* Athanasius Kircher, *Magnes, de arte magnetica opus tripartitum* (Rome: V. Mascardi, 1654), 508. Image from Andersen Library Rare Books, University of Minnesota Libraries, Minneapolis.

of magnetic affinity through the extension of mineral magnetism to vegetable magnetism.[10]

THE CLOCK AS METAPHOR

The Paracelsian philosophical legacy, fragments of which persisted in the intellectual formations of Romantic philosophy into the modern period, was largely eclipsed by a turn toward a more materialist and mechanical conception of the physical world in late sixteenth- and seventeenth-century developments in science and technology. A new attention to mixed mathematics and pseudo-Aristotle's *Mechanical Problems* in the late Middle Ages, coupled with the revival of Archimedes's statics, provided the mathematical and philosophical foundations for Simon Stevin's applications of mechanics to large-scale technological problems in hydraulics, ship design, and machine design, as well as for Galileo's interest in materials science and a new science of mechanics. These are all part of a reorientation of Western science that is captured by the term *mechanical philosophy* and by phrases such as *the mechanization of the world picture* and subsumed under Cartesian mechanical philosophy. Clearly a turn toward mechanical thinking and mechanical approaches to scientific research antedated René Descartes, who has repeatedly been credited with introducing mechanical philosophy.[11] Also, as recent studies have shown, mechanical philosophy was not as thoroughgoing and resolutely "mechanical" in the sense of denying vital agency as was once imagined.[12]

Nevertheless, a materialist mechanical philosophy was elaborated by those who followed Descartes—Robert Boyle, for example, who gave it the name "mechanical philosophy." Natural philosophers of the northern European Enlightenment of the late seventeenth and particularly the eighteenth centuries entrenched Descartes as the pioneer of a new materialist-mechanist approach to nature. But, far from eliminating vital agency from the new science, Descartes's dualism defined mind as outside of natural philosophy and the physical sciences and rendered mind and behavior intractable to experimental philosophy, which empowered a long dialectic between materialistic mechanists and vitalists that now and then surfaced as heated controversy.[13] Dualism served natural philosophers well, especially those pursuing what has been termed natural theology, insofar as Cartesian mechanism came to be closely associated with the deistic view of the physical world as a kind of machine or system of machines, lacking internal agency or volition and therefore fairly characterized as clockwork. Willy-nilly, the clockwork became the central emblem of the mechanistic side of Cartesian dualism and with it a powerful metaphor for the nature of biological timing in the modern period.[14]

Mechanical philosophies of all types reduced the objective phenomenological world to the motions of pieces of matter and their consequent collisions, adhesions, and so on. Implicit in this view was a narrowing of the concept of motion from the medieval and Renaissance Aristotelian notion that motion is change of any sort—developmental as well as local—to a conception of motion as only local. Machines and material components could rotate and translate, but they could not transform and grow, except through the translation, collision, and adhesion of their corpuscular components. Moreover, the implied definition of motion as local motion invited attention to speed and thus to consideration of time intervals and timing, preparing the ground for quantitative measurement of rhythm. The Cartesian definition of motion by itself ruled out Aristotelian teleological principles situated in the interior and essence of bodies, where the Paracelsians had placed them, and post-Cartesian "mechanical philosophers" sought mechanistic explanations not only for animal machines but for plant motions too, once these came under scrutiny. But transition to a mechanistic paradigm was neither simple nor decisive, and there was dissent.

SENSITIVE PLANTS AND IRRITABILITY

The observation that specific organs and tissues react autonomously to stimuli—the peristaltic contractions of intestines when they are subjected to salts, for example—defied easy explanation in terms of the mechanics of internal matter. In these instances, whatever caused the at times rather abrupt and violent responses to stimuli appeared to be internal to the parts or tissues themselves, an internal agency, which fit well with the Paracelsian archæus and other Neoplatonic conceptions of imminent agency and vitality but was antithetical to the mechanical philosophy of the late seventeenth century. William Harvey, no mechanist, famously pointed to the heart of a snake and other cold-blooded animals, which would continue to beat for hours after being excised from its host body as evidence of some sort of internal sense that moves organic parts. Whatever caused such actions was clearly not a property of the whole animal, an animal soul or spirit of some sort, but was evidently a property of the organ itself, a property that his contemporary Francis Glisson termed irritability and assigned to the fibers that constitute the body's solid parts. This concept proved to be very durable in biology, remaining a challenge for materialist-mechanist philosophy into the early twentieth century.[15]

Irritability explained tissue reactivity in animals, which had been allotted movement and therefore agency in Aristotelian biology, so the problem confronting seventeenth-century natural philosophers was partly to explain how such a moving soul could be a property of the parts rather than of the whole animal and to reconcile such an explanation within the metaphysical restrictions of mechanical philosophy. But when naturalists learned of plants that appeared to show irritable reactions to mechanical stimulus, the problem they faced was compounded by questions of defining distinctions between plant and animal life forms. Attribution of an "animal" moving soul to plants confounded the Aristotelian distinction between vegetable and animal organisms and presented a new question to mechanical philosophers: if plants and animals are merely reaction machines possessing a property called irritability, then was the difference between them reduced to a matter of complexity on a scale of material organization rather than owing to categorical distinction? These were problems that engaged scientific observers of the reactive behaviors of so-called sensitive plants in the seventeenth century and were extended to plants' rhythmic motions in the eighteenth.

The initial acquaintance of Europeans with the American plant *Mimosa pudica*, the leaves of which contract fairly quickly when touched, a sensitive and reactive behavior previously associated only with animals, presented seventeenth- and eighteenth-century mechanical philosophers with a phenomenon that begged explanation in mechanical terms. *Mimosa* was described by Spanish physician Cristóbal Acosta in his 1578 *Tractado de las drogas y medicinas de las Indias Orientales*, which was translated by Charles de l'Ecluse and rapidly became popular with gardeners who fancied exotic species.[16] A specimen of the plant was cultivated in St. James's Park in London, where it attracted King Charles II's attention, and he requested an explanation of its movements from the Royal Society, whose members sought to give the phenomenon of plant movement a purely mechanistic and materialist explanation, much as Francis Bacon had done in *Sylva sylvarum* (1627).[17] Their observations in 1661 were reported to the Royal Society by Timothy Clark and were included by Robert Hooke in his *Micrographia* (1665), along with an illustration depicting the open and closed position of the leaves (see figure 1.3). It is plain from Hooke's presentation of these observations that the *curiosi* were looking for vegetable analogs to animal vascular systems, which in the wake of Harvey's work were given functional descriptions in terms of fluid dynamics.[18]

Hooke explicitly related to his readers that Clark gave these plant motions a purely mechanical explanation, though he had not yet reached a satisfactory conclusion as to the mechanism involved. Hooke may have had a hydraulic mechanism in mind when he observed that the *Mimosa* plant was composed of "*Fibres,* and visible *Canales*, through which this fine liquor circulateth," which invited a comparison with animal tissues at a time when William Harvey and Francis Glisson attributed irritable contraction to the Galenic property of irritability possessed by the fibers composing organs.[19] Harvey had already suggested in his *De generationi animalium*, which was written in the 1640s and published in 1651, that both plants and animals might possess sensitivity, but Glisson's interpretation of irritability transcended Galenic

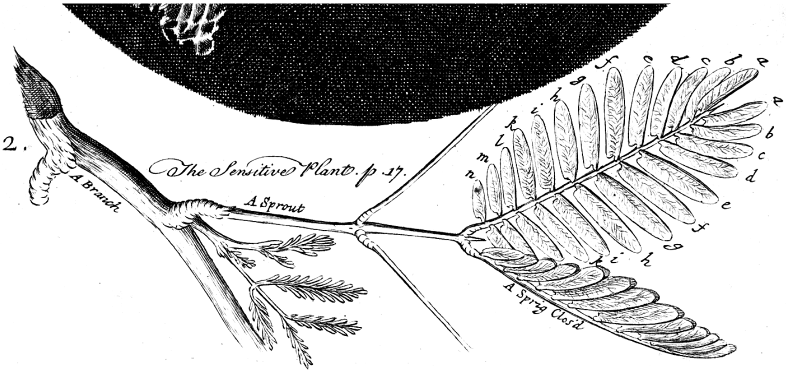

FIG. 1.3. The seventeenth-century English experimental philosopher Robert Hooke included an image of a branch of "The Sensitive Plant" in his famous 1665 book *Micrographia: Or Some Physiological Descriptions of Minute Bodies Made by Magnifying Glasses with Observations and Inquiries Thereupon*, where it appears in the lower part (fig. 2) of plate 11, and reprinted as plate 8 in *Micrographia Restaurata: Or, the Copper-Plates of Dr. Hooke's Wonderful Discoveries by the Microscope, Reprinted and fully Explained* (1745). *Source:* Robert Hooke, *Micrographia Restaurata: or, the Copper-Plates of Dr. Hooke's Wonderful Discoveries by the Microscope, Reprinted and fully Explained* (London: John Bowles, 1745), plate VIII. Image from Wangensteen Historical Library, University of Minnesota Libraries, Minneapolis.

attribution of the faculties of attraction, retention, and expulsion to longitudinal, oblique, and transverse fibers and instead drew on the Paracelsian archæus as an inner agent of irritable reaction. For Glisson, irritability implied perception.[20] The phenomena attributed to irritability remained a pressing problem for mechanical explanations, which was made more complicated by the attempt to discern specific boundaries between plants and animals. The so-called plant-animals (zoophytes) had already complicated this problem for naturalists, but now if plants reacted irritably to stimuli were they also possessed of sense?

When John Ray published his *Historia plantarum* in 1693, he did not attribute *Mimosa*'s irritability to the plant's ability to sense a stimulus, which implied an Aristotelian sensitive soul, but rather to a mechanical reaction to the physical stimulus, whether the touch of a human hand or a stick.[21] Giovanni Alphonso Borelli, the Italian iatromechanist, had similarly attributed the irritable reactions of *Centaurea* stamens to mechanical action in 1653. Ray extended this mechanical stimulus-response explanation to the observed diurnal periodic leaf movements of certain kinds of plants and the periodic opening and closing of certain flowers, such as *Calendula,* which he attributed to changes in ambient temperatures, affecting the turgidity of their parts.[22]

In the late 1720s the French astronomer Jean-Jacques d'Ortous de Mairan observed that the rhythmical behavior of *Mimosa* plants, which in addition to exhibiting the common phototropism both fold and unfold their leaves on a diurnal basis, seemed to be coordinated with the movements of the sun even while the plants were experimentally maintained in complete darkness. He compared the plants' sense of day and night in the absence of exposure to natural alternations of light and dark to bedridden patients who were said to know the difference between day and night when kept indoors and away from natural lighting conditions. De Mairan's observations were reported to the Académie (the royal academy of sciences) in Paris in 1729 by a friend and member, the botanist Jean Marchant, who pointed out that the astronomer's experiments had not extended to observing the plants in various artificially regulated heat environments, which might decide whether the plants are truly dependent on the sun, and he recommended further research by the "botanists and physicists."[23] Almost immediately, society members Charles François de Cisternay du Fay and Henri-Louis Duhamel du Monceau set about repeating them. Examination of the attention devoted during ensuing decades to the phenomenon that De Mairan reported reveals that the movements of sensitive plants and the diurnal changes in leaf position in particular intrigued botanists, even if they presented no obvious novelty or challenge to the then current scientific paradigm of mechanical explanation. In the main, diurnal plant movements and sensitivity were absorbed into the persistent debate about the distinction between plants and animals and the unity of life.

De Mairan was a Cartesian astronomer and was therefore likely well-disposed to a mechanistic explanation for the plant's ability to react rhythmically in the absence of any obvious mechanical stimulus. There is no indication that he considered the possibility that the plant might have internal agency or that he attempted any of the experiments that later researchers would employ to study rhythm, nor did he apparently observe any deviation from a cosmically determined twenty-four-hour cycle, an observation that would point later researchers in the direction of an autonomous inner clock. Nevertheless, he had put the problem before the Académie, and it soon came to the attention of Swedish, German, and English investigators, who participated with the French in the growing international network of Enlightenment science.

Charles du Fay reported to the Académie on July 24, 1736, that he and Duhamel were studying the sensitive plant. An anonymous contribution to the *Histoire de l'Académie royale des sciences* that same year under the heading "Botanique. Sur la Sensitive," refers to Du Fay's report in the *Mémoires*, suggesting that it, too, was written by Du Fay. These articles cite previous observations by Hooke and De Mairan and note that Du Fay and Duhamel were observing *Mimosa* already in 1729.[24] Du Fay's study was cut short by his death in 1739, but Duhamel persisted in his research, which he reported in the context of his 1758 two-volume study of the physiology of trees, *La physique des arbres*.

In the meantime, in 1748, Carolus Linnæus took an interest in the daily and seasonal temporal patterns manifest by the flowers and leaves of certain plants, reporting his observations in his 1751 *Philosophia Botanica*. There he systematically recorded the timing of plants' growth, germination, leafing out, flowering, opening, fruiting, and loss of leaves, pointing to their variability and association with climates.[25] Those plants he termed "solar flowers" (*solares flores*) exhibited fixed and distinctive daily "waking" times (*vigiliæ*) when their blossoms opened, expanded, and then closed. He subdivided these into three types according to their temporality: meteorical, tropical, and æquinoctial. The variability and predictability of the "equinoctial" flowers particularly interested him, and he included a list of their timings.[26]

In 1750 Linnæus composed a treatise in which he described how certain plants fold up in anticipation of rainy weather, which must have taken him deeper into the study of plant responses to changes in illumination and diurnal leaf movement, and after the academic custom of the times, he engineered a thesis defended by his student Peter Bremer in 1755, in which he introduced the term *plant sleep* to characterize the nighttime folding down movement of the leaves.[27] Also interested in plant seasonality, Linnæus published a treatise on vernalization (*Vernatio arborum*) in 1753 and the seasonality of blooming (*Calendarium floræ*) in 1756.

Linnæus's work suggested that the regularity of diurnal plant movements and the diversity of the timings with different species could serve the knowledgeable observer as a kind of natural timepiece, a floral clock. He began to tinker with this idea in a 1750 Swedish treatise on certain flowers' anticipation of rain (*Regnblomman*) and referred to a *horologium floræ* in the 1651 *Philosophia Botanica*. His son, Carolus Linnæus junior, exploited this idea in a draft for a dissertation that he planned to present circa 1756 at the University of Uppsala, under his father's direction.[28] The content of this dissertation is derivative of his father's work, and he specifically cited the *Philosophia Botanica* and replicated Linnæus senior's division of solar flowers into *meteorici*, *tropici*, and *æquinoctiales*. Although the concept of a floral clock would capture the imagination of twentieth-century chronobiologists, it was Linnæus's concept of plant sleep—which was redolent with questions about plant sensitivity and the analogy, and possible biological relationship, of plants and animals—that attracted the attention of late eighteenth-century natural philosophers.[29]

EXPERIMENTS ON THE SLEEP OF PLANTS

One early reaction to Linnæus's identification of diurnal plant movements as "plant sleep" was conceived as an epistolary response to Linnæus, *The Sleep of Plants and the Cause of Motion in the Sensitive Plant, Explain'd*, published by English naturalist John Hill in 1757.[30] Hill did not mention De Mairan in this letter, but he noted that the phenomenon "has long been known," having been described by Acosta and Prospero Alpini among others, that Linnæus had been chiefly responsible for describing it for Europeans, and that it was Linnæus who applied the term *plant sleep* to it. Hill bristled at Linnæus's use of the term "sleep" in this context as being "an affected, as well as improper term," but he excused it and maintained it on the basis of Linnæus's authority.[31] Hill did not explain why he thought the term "affected" and "improper," but we can guess that the anthropomorphism imputed a willful, vital agency and a sensitivity to plants that did not square with his Cartesian materialist view of nature; for he sets out not merely to disprove that sleep movements of leaves are responses to changes in the temperature or humidity of the ambient air but to prove that they are direct mechanical effects of the presence and absence of incident light. His account is resolutely corpuscular, explaining causation in terms of the inertial motion of material bodies, and he claimed that it also explained on a physical basis the irritable reaction observed in the sensitive plants.[32]

Hill argued that plant movements must be a response to a stimulus, and he narrowed these down to the influences of air, heat, humidity, and light. He quickly dismissed the possible causal influences of the first three by noting many observations by himself and others that plants exhibiting sleep movements do so in various climatic situations and in heated as well as unheated experimental rooms. By elimination, this left light, and here Hill claimed originality.[33]

Hill regarded light as a stream of corpuscles that affected plants through their physical impact on the plants' fibers, thus altering their tension: "The change produced in the position of the leaves of plants by light, is the result of a motion occasioned by its rays among their fibres: to excite this motion, the light must touch those fibres."[34] The vibrational motion thus induced in the plant fibers was the immediate cause of both plant sleep movement and the reactivity of the sensitive plants to touch. This was in keeping with the solidar physiology created by the mechanist Hermann Boerhaave and his students, which explained bodily health and disease in terms of the cohesion and tension of its tissues.

Hill's account was not merely a priori Cartesian speculation but was also grounded in his experiments, which showed him that the movement effects were only present and absent when the light was present and absent, affirming the causal relationship: "We always know the cause of those effects we can ourselves produce; and experiments are the true test of reasoning."[35] In this case, Hill carefully observed a plant he placed in a windowsill, correlating the general timing and amplitudes of leaf motions with the variations in illumination, noting, for example, that on cloudy days the leaves did not raise fully to the day position. But this was passive observation. The English Baconian experimentalist demanded active intervention: "On the seventh day I made the final experiment. It appeared to me that if light were the sole cause of the motion, and change of position in the leaves, then denying the plant the benefit of light at any time, must bring on that change. . . . This experiment appeared as a just proof of the foregoing reasonings: if darkness would at any time throw down the lobes, the system of that motion before delivered must be true; if not, that all the reasonings must be false."[36] He put the plant in a bookcase equipped with opaque doors and faced it toward the window, so that he could open or close it at pleasure and thus give or deprive the plant of light at will. No matter what time of day he closed the doors, when he came back later he found the plants in the sleep position; whenever he opened them, they were found to be in the day position after a short time. He concluded from this that "we know that in these experiments, light alone is the cause: we are therefore certain, that what is called the sleep of plants, is the effect of the absence of light alone, and that their various intermediate states are owing to its different degrees."[37] Hill did not identify sleep movement as an endogenous rhythm but, rather, as a direct mechanical response to incident light. Although he did not discuss the rhythm of the sleep movements per se, it follows that he would have regarded any such rhythm as exogenous or cosmic, owing to its causal dependence on the natural day/night light alternation.

In 1758, the year after Hill published his account of the sleep movement of plants, Henri-Louis Duhamel included the results of work he had begun in collaboration with Du Fay in his much larger book on plant physiology, *La physique des arbres*.[38] In order to ensure that his "spiny sensitive plant" (*Mimosa*) was properly isolated from any changes in daylight, he placed it in a cellar designed for aging wine, which admitted no light. Here he observed the plant folding and unfolding its leaves as if still in natural lighting conditions, just as De Mairan had reported. However, when he restored the plant to a natural diurnal lighting regimen, he noticed that during the first night the plant leaves remained unfolded, that their movements had failed to resynchronize immediately with the new lighting conditions. Moreover, in order to determine if temperature changes caused the plant rhythm, he followed Linnæus's procedure and put it in an artificially heated greenhouse, where the nighttime fall in temperature could be negated. He concluded that the diurnal temperature cycles were not the effective environmental stimuli.[39]

Also in 1758, Richard Pultney's "Observations upon the Sleep of Plants" was read before the Royal Society of London and then published in its *Transactions*.[40] Pultney ascribed the observation of diurnal plant leaf movement to Acosta and Alpini in the sixteenth century but noted that it was not termed "plant sleep" until Linnæus, who listed many more species exhibiting this behavior. Pultney added to this list clover-grass (*Trifolium pratense purpureum majus*) and the common bean *Phaseolus vulgaris*, which became an important object of chronobiological study in the twentieth century. He reported that Linnæus's experiments on plant sleep had revealed that these movements occur also in the dark and are not dependent on fluctuations of heat and cold.[41]

The following year, Johann Gottfried Zinn published a report of his observations and experiments on the phenomenon of plant sleep in *Hamburgisches Magazin*, a scientific journal published in Hamburg and Leipzig. Zinn, a professor of medicine at Göttingen, noted that what Linnæus and others called plant sleep had long been of interest to naturalists and he referred to recent literature by De Mairan, Duhamel, Du Fay, and Hill by name. He commented that many observers had attributed the daily leaf movements to changes in heat and humidity, but that Hill and others who had studied the phenomenon closely had ruled out those as causes.[42] Using a good thermometer and observing the sleep movements of his plants, both in the cellar and in the much warmer greenhouse, Zinn affirmed that temperature had no obvious effect on the movements. But he also observed that the differing light conditions seemed to have no effect, and he explored this more closely. Confined to the cellar, where no light at all reached the plants, they raised and lowered their leaves at the same time as in the greenhouse, where light conditions varied. This observation ran counter to what he read in several journals in 1758, in particular Hill's confident assertion that plant sleep was a direct response to the removal of incident light.[43]

Zinn repeated Hill's experiments with *Mimosa* and found that placing it into darkness could indeed trigger the onset of the leaves' movement to their night position, but he remained skeptical about the causal relationship, in part because the plants did not readily resume their day position when moved back into the light and in part because he had observed that the sleep movements of plants appear to remain more or less the same regardless of season, independent of the actual time of the sun's rising and setting, and therefore they did not seem to be in a clear causal relationship with the presence and absence of light.[44] He concluded from his various experiments and observations that neither heat, humidity, nor light could be directly responsible for plant sleep, but that its cause must lie elsewhere. Indeed, if plant movements were directly dependent on incident light, how could Linnæus's flower clock possibly work?[45] Without committing himself to a metaphysical position on the matter of plant sleep, Zinn refuted Hill's mechanical-corpuscular explanation and supported the findings of De Mairan and Duhammel that the timing of the phenomenon did not correlate with obvious environmental stimuli. In particular, the persistence of daily plant sleep movements in the absence of apparent rhythmic stimulus and the failure of the rhythm of these movements to conform immediately to the natural rhythm of day and night when they were again exposed to the normal environmental stimuli frustrated mechanical explanation and left the door open for vital agency.

PLANT IRRITABILITY, SENSITIVITY, PERCEPTION, AND SPONTANEOUS MOVEMENT

Charles Bonnet experimented with plant movements around the same time as Duhamel and Du Fay, Hill, and Zinn, bringing the concept of plant irritability to bear on the vitalist-mechanist debate. In his 1764 *Contemplation de la nature* he wrote that the various motions of plants "which may be called spontaneous, arise no doubt from a pure mechanical cause, but which is hitherto unknown to us." However, he also considered that they might be irritable responses, similar in nature to the irritability attributed to animal matter by Glisson in the seventeenth century and more recently developed as a concept by Bonnet's cousin Albrecht von Haller: "*Irritability* then seems to be what constitutes the *vital power* in the animal. This property has not yet been perceived in the vegetable. Can it be that *distinguishing* character we seek for? But is it indeed certain that vegetables are not irritable? . . . Are we quite certain that those motions, apparently so spontaneous, of roots, stalks, leaves, flowers, &c. . . . are not in any degree owing to irritability? . . . A sound logician advises us still to suspend our judgment."[46] Bonnet's attribution of irritability to plants spoke directly to the question of the unity of life and was amenable to vitalist explanations of coordinated movement and growth in organic nature.

Bonnet's suggestion that plants may possess irritability similar to that established for animals by Glisson and Haller and that this implied a vital property of some sort was widely accepted by early nineteenth-century biologists, including Charles Darwin's teacher John Henslow, but Enlightenment naturalists only slowly yielded to a vitalist perspective.[47] In Colin Milne's 1770 *Botanical Dictionary*, for example, we find only a purely mechanical explanation. Milne summarized Linnæus's report of plant sleep and wakefulness under entries *Motus* and *Vigiliæ Plantarum*. His entry for the Linnæan order *Lomentaceæ* takes up the phenomenon of the sensitive plant, parsing the motions into two kinds: a "natural" motion "occasioned by the action of warm nourishing vapours," and an "artificial" motion, which is a response to mechanical stimulus (touch). Although he characterized these movements as "muscular" and attributed them to a "sensibility" that resides in the base of each stem, he judged that all such movements were mechanical in nature: "To conclude, the cause of this and the other motions of plants is merely external. The motions themselves, therefore, are not spontaneous, as in perfect animals, which have that cause dependent on their choice and will."[48] But the similarity of irritable reactions of plants to animal behaviors was a nagging problem.

Richard Watson, a professor at Cambridge and later bishop of Llandaff, followed up on Bonnet's query about the distinguishing characteristics of plants and animals in an essay on chemistry in 1771: "If rejecting spontaneous motion and figure as very inadequate tests of animality, we adopt perception in their stead; He would be esteemed a visionary in Philosophy who should extend that faculty to vegetables; and yet there are several chemical, physical, and metaphysical reasons which seem to render the supposition not altogether indefensible."[49] Watson had in mind the opening and closing of "solar flowers" and the sleep of plants described by Linnæus, which he concluded "should be equally derived from mechanism, or equally admitted as criterions of perception."[50]

A little over a decade later, Thomas Percival had no doubts about ascribing perception to plants. His "Speculations on the Perceptive Power of Vegetables" was read before the Literary and Philosophical Society of Manchester on February 18, 1784, and was published in the society's *Memoirs* later that year. Adducing the geotropic behavior of plant roots and shoots, the sudden capturing of insects by the carnivorous plant *Dioniæ muscipula* from North Carolina, and other plant motions, Percival argued that, "If the facts and observations, which have been adduced, furnish any presumptive proof of the instinctive power of vegetables, it will necessarily follow, that they must be endued with some degree of spontaneity. . . . And such volition presupposes an innate perception, both of what is consonant, and of what is injurious to the constitution of the individual."[51] Percival's logic was that if chemical stimuli cause the plant's fibers to contract, then they must be possessed of irritability, and "the presence of irritability can only be proved by the experience of irritations, and the idea of irritation involves in it that of feeling."[52]

Working in ignorance of Bonnet's contemporary research in France, the colonial English clergyman and botanist John Lindsay began experiments on *Mimosa pudica* in Jamaica with the aim of investigating plant sensitivity and movement in the context of the debate about the essential differences between plants and animals. Lindsay was an ordained minister and served as rector of a church in Jamaica, but he was also an accomplished naturalist, artist, and illustrator and had served as chaplain to an expeditionary vessel along the coast of Africa in 1758, just prior to assuming his post in Jamaica, where he pursued botanical study as an avocation.[53] Sometime during the next thirty years Lindsay drafted "An Inquiry into the Nature of the motions of the Sensative, Sleeping and Moving Plants." In 1788, the year of the Reverend Lindsay's death, his son John, a surgeon and botanist in West Jamaica, revised the first part of this treatise and submitted it to the Royal Society, followed two years later by the original, neither of which was published by the society.[54]

Lindsay opened his treatise with a quotation from Linnæus's *Somnum plantarum* about the apparent similarity between the movements of plants and animals, which are characterized by sense and volition. This quotation, standing as the epigram to his experimental report, along with another quotation from Linnæus's treatise on plant sleep and also an added note reporting that he first saw Hill's 1757 *Eden, or, A Compleat body of gardening* after writing his account, all reinforce Lindsay's assertion that he believed his inquiry into the physiology of plant movements to be original.[55] The epigraph also positions Lindsay's research in the context of the debate about the formal boundaries between plant and animal kingdoms or the unity of living beings in the lead up to modern evolution theory.

Lindsay determined from his experiments that the leaf movements of *Mimosa* are produced by the alternating hydraulic tension and relaxation of soft "cellular" tissue in the pulvinus, a body of tissue at the base of the leaf stem, which, although he conjectured to be not wholly passive, does not compare to the contraction of animal muscles.[56] He offered no explanation for the observed fact that the stimuli that caused these plant movements were sometimes transmitted to the pulvini from significant distances in the plant, but he clearly expected that it was a purely mechanical process, which resulted in the turgidity and collapse of the "cellular" substance in the pulvinus.[57] An appropriately Jamaican experiment of dosing the soil around the root of the *Mimosa* with "a spoonfull or two of Rum," which also produced the sensitive reaction, suggested to Lindsay "that it is sufficiently probable, that the cellular substance in every part of a young healthy plant is susceptable of excitement."[58] If this were the case, it stood to reason that the diurnal leaf movements that Linnæus had characterized as plant sleep were also produced by a similar excitement of the pulvini, and Lindsay next turned to study plant sleep.

Beginning anew with a quotation from Linnæus about the analogy of plant sleep to animal sleep, Lindsay wrote that "this property of Plants has been long known and professedly treated of, but writers have not agreed about the cause of it, and the manner *how* it was performed," which suggests he was not wholly unaware of his predecessors' work.[59] Now citing Hill's claim that light is the only cause of these diurnal leaf movements, Lindsay reported his own experiments with what today would be called altering the phases of the cycles of movement. He even made observations in continual darkness to affirm that sleep movements do not seem to be dependent on direct exposure to light changes, nor are they caused by "visisitudes of heat and cold, or of dryness & moisture."[60] Lindsay's conclusion foreshadowed nineteenth-century assessments that the movements of *Mimosa* and other plants exhibiting sensitive reactions or diurnal alterations of leaf position are biologically mechanical in action, but not in the Cartesian sense of mechanical. That is, the immediate cause is not an external energy or force that is imposed, but rather, there is an endogenous power to respond that is internal to the plant tissues and somehow mechanically triggered: "I think we may therefore conclude that this diurnal change, called the sleep of plants, is a property inherent in the plants themselves, intimately connected with, perhaps necessary to, and wholy depending on their life; and which, though it may be affected by external influence, is not dependent on any cause whatever without the plant itself."[61]

The fact that the Royal Society failed to publish the Lindsays' manuscripts does not indicate a lack of interest in their research or in its quality. Other researchers, closer at hand, were also engaging the question of vegetable irritability at this time and submitted work for the Society's consideration. Under these circumstances the Lindsays' provincial work may have been regarded as of secondary importance, or perhaps unwanted competition. In particular, James Smith had also contributed his "Observations on the Irritability of Vegetables" to the *Philosophical Transactions* in 1788, noting the findings of Linnæus and his communication with Bonnet and concluding that "there still remains then this difference between animals and vegetables, that although some of the latter possess irritability, and others spontaneous motion, even in a superior degree to many of the former, yet those properties have hitherto in animals only been found combined in one and the same part."[62]

The problem of the boundary between plants and animals and the ascription of a *vis insitus* or vital agency to living matter persisted to the end of the century, exemplified in the contrasting perspectives of those two great naturalists of the period, Jean Baptiste Lamarck and Erasmus Darwin. Lamarck resisted ascribing irritability to plants, whereas Darwin not only did so but used plant movements as evidence for their perception.[63] Section 8 of Part 1 of Darwin's *Phytologia* (1800) is titled "The Muscles, Nerves, and Brain of Vegetables" and develops the earlier argument that the irritability of plants such as *Mimosa pudica* implies sensitivity and volition—will—and that this in turn implies a "common sensorium" or brain: "That plants possess in some degree the power of volition would appear first from the *hedysarum gyrans* [Indian telegraph plant, now generally called *Desmodium gyrans* or *Codariocalyx motorius*], which moves its leaves in circular directions when the air is too still. . . . But there is an indubitable proof of plants possessing some degree of voluntarity, and that is deduced from their sleep."[64] Darwin did not examine any of these phenomena in detail and did not comment in this context on the autonomy of plant sleep from the stimuli of light and heat. But his propositions illustrate the importance of periodicity, in this case specifically the diurnal sleep movements of plants, as an indicator of an internal vital agency that cannot be reduced to mechanical explanation. This was a problem that would continue to vex the vitalist-mechanist debates of the nineteenth century, notably in the context of the philosophical, theological, and moral consequences of physicochemical reductionism for the concept of free will.[65]

VITALISM, PHYSICOCHEMICAL REDUCTIONISM, AND FREE WILL

The reaction of some scientific authors to the consequences of mechanical philosophy, specifically to the reduction of spontaneous behaviors such as are manifest in plant sleep movement to physicochemical stimulus-response explanations, is readily apparent in an exchange that appeared in the Philadelphia journal the *Port Folio* between Thomas Cooper and his anonymous interlocutor J.R.W. in the years 1814–1815. Cooper is little known in the history of science today, which makes this exchange all the more interesting—inasmuch as it indicates the breadth of concern for the consequences of mechanical reductionism in late Enlightenment learned circles, which in this case reached across the Atlantic to inform philosophical, religious, and political discussion in the new republic. *Port Folio* served the new US political and literary elite during its short life from 1801 to 1827, and this exchange therefore reflects the supposed interest of a broad intellectual readership.

The context for this exchange was a passing comment that Humphry Davy had made in his lectures on agricultural chemistry about the mechanical nature of plant movements. Davy briefly treated the topic of plant motion in his 1813 *Elements of Agricultural Chemistry*, where he wrote that Linnæus's idea that the pith of plants functioned as the brain and nerves functioned also in animals—a notion that he attributed to the Swede's "lively imagination"—had been disproved by recent experiments.[66] These pertained to heliotropic movements, which Davy regarded as "in a great measure dependent upon the mechanical and chemical agency of light and heat." Applying this also to the sleep movements of plants, Davy asserted that "what Linnæus has called the sleep of the leaves, appears to depend wholly upon the defect of the action of light and heat, and the excess of the operation of moisture."[67] He based this conclusion in part on an experiment in which Augustin Pyramus de Candolle had put a specimen of *Mimosa* in a darkened room, causing its leaves to fold, and then caused them to unfold again under artificial illumination. Davy did not comment on the persistence of these behaviors in constant conditions; like his contemporaries, he was mainly engaged with the issue of irritability and was unaware of or uninterested in the rhythmicity of these movements. What Cooper apparently reacted to was Davy's dismissal of any vitalist explanation for these sleep movements or for the shock reactions of sensitive plants.

Although Thomas Cooper was a chemist and taught chemistry in America, he is obscure in the history of science, but he was well-known in his day to the early presidents of the United States as a political writer in the service of Thomas Jefferson. Cooper was born in England, educated at Oxford, and became a close friend of James Watt Jr., the son of the inventor, and the chemist Joseph Priestley. When Priestley and his family moved to Pennsylvania to establish a utopian Unitarian society on the Susquehanna River, Cooper and his family moved with them. In America Cooper parleyed his training in law and early pursuit of science into careers in law and education, teaching chemistry as a professor first at Dickinson College, then the University of Pennsylvania, the University of Virginia, and finally the University of South Carolina, where he became its president.[68] He was, therefore, well informed about chemistry as well as actively engaged in religious and political discussions.

In the course of his life as a political and scientific writer, Cooper contributed to the Philadelphia serial the *Port Folio* and assisted the editor around the time of the War of 1812, during which time he also took charge of editing John Redman Coxe's *Emporium of Arts and Sciences*. In 1814 Cooper contributed a long article "On Vegetable Life" to the *Port Folio*, which apparently was occasioned by his reading of Davy's 1813 *Elements of Agricultural Chemistry* or similar exposition:

> Professor Davy in his Chemical Principles of Agriculture, p. 217, quarto, has the following passage: ". . . . In calling forth the vegetable functions, common physical agents alone seem to operate; but in the animal system, these agents are made subservient to a superior principle. [. . .] The imagination may easily give Dryads to our trees, and Sylphs to our flowers, but neither Dryads nor Sylphs can be admitted in vegetable physiology: and for reasons nearly as strong, irritability and animation ought to be excluded." . . . According to this passage, a plant, though a living system has no title to irritability or even to animation. I wish sir H. Davy would condescend to explain to us, how life can exist without animation: or what life he knows of, devoid of irritability in the living parts![69]

Cooper understood Davy to be defending the traditional Cartesian proposition that humans differ from other forms of life because of their animation by a transcendent immortal soul. He was careful not to deny this proposition directly but, rather, sought to establish in "Vegetable Life" that all living matter was animated not by an immaterial principle (soul) but by a vital principle that was a property of the organization of living matter: "The vis vitæ, the vital principle, the vis mediatrix naturæ, and similar expressions of physiologists from the archæus of Van Helmont and the school of Hoffman inclusive, down to the school of Edinburgh, were never considered by the authors of them, as anything more than terms, like attraction and repulsion, used to express the unknown cause of a known set of motions in an organized body; and not immaterial beings separate from the body itself."[70] Cooper drew on the fact that plants are able to organize material nutriments, coordinate growth, and exhibit tropisms—and that those like *Mimosa* are able to react to stimulus in a way similar to animals' local motion—to establish the claim that plants possess irritability. Irritability in turn implied internal sensitivity and volition: "There can be no power of voluntary motion unless what arises from a sensation *ab intra*"—that is, endogenously. And "if there be voluntarity, the immediate motives of pleasurable and painful sensations, are of themselves, quite sufficient to determine it," without, he implied, requiring an immortal soul as a guide to moral behavior.[71]

Cooper took the irritability that produced internal stimulus to be a vital principle that resists reduction to principles of physics and chemistry: "Chemistry can afford us nothing, but the analysis of dead matter, the *anatomie cadavérique* as Bichat appropriately terms it: vital energy produces effects far more striking."[72] *Mimosa* and other sensitive plants provided evidence for his argument: "Here is a motion produced—a folding over and shutting up of leaves and petals by the contraction of a contractile and irritable fibre, not from the application of stimulus, but the absence of it. This can be accounted for, from an internal sensation, but in no other way." Linnæus's plant sleep, too, pointed to vital action. Following Anthelme Richerand's definition of sleep as "the repose of the organs of sense and of voluntary motion," Cooper concluded that plants that sleep must be possessed of volition.[73]

Cooper's essay elicited a response sent to the *Port Folio* by the otherwise anonymous J.R.W. of Bedford, who readily identified Cooper's "extensive view of the analogies between vegetable and animal life" as ideas that were "elegantly unfolded in Darwin's Phytologia. T.C.'s paper is not much more than a condensed view of the first nine sections of that work."[74] J.R.W. perceived in Cooper's piece an atheistic materialism like that imagined by Julien de La Mettrie in his *L'Homme Machine* (1748), which for Christian apologists was the dark beast: "But it may be asked, how is the hypothesis of the sensibility and voluntarity of vegetables hostile to the immateriality of the soul? It is supposed that no one will presume to attribute to vegetables an immaterial principle. If, then, sensibility and voluntarity can be proved to exist where there is nothing more than organized matter, there will be afforded a strong presumption that man is merely an organized, material machine."[75] The author found the weakness of Cooper's argument in his ready assumption that a reaction without an evident exogenous stimulus *ab extra* left no alternative but an irritable excitement *ab intra*, implying an internal vital agent or principle. "What then?" he asked. "When the magnetic needle points to the north pole, as a means to direct the surveyor and the mariner, are we to suppose that the needle really intends to answer that purpose? We know of no impulse from without." If this be the case, he wrote, then clocks must also be judged sentient and voluntary beings, since there is no evident impulse from without for their operation.[76] He saw no reason to deduce from the diurnal movement of plant leaves an interior agency any more than an interior agency is implied by the term "magnetic attraction" to explain the orientation of the compass needle: "We might give it the name of vegetable attraction. It would mean, at least as much as magnetic attraction."[77] The problem, as he saw it, was in Linnæus's unfortunate choice of the term *sleep* to characterize this phenomenon: "To call this folding of the leaf by the name of sleep has something in it fascinating."[78]

Cooper defended himself from the implied charge of atheism with a weak appeal to the orthodoxy of Charles Bonnet and others whose work he had drawn on for his essay. He also adduced another essay in which he summarized an 1813 article by "La Metherie" noting that plants have "the same (organic) systems that Pinel, Bichat, and others have demonstrated in animals," by which he meant that plants and animals have analogous tissue types.[79] J.R.W. wrote one more rejoinder to the editor of the *Port Folio*, in which he declared that "the friends of the Darwinian theory have made no progress in the establishment of their hypothesis" until they have demonstrated that plants have nerves, which are a prerequisite for sensibility and "voluntarity" (volition). Moreover, he contested both that irritability and sensitivity are essentially linked and that irritability is ipso facto an indicator of vitality: "The flesh of an animal will contract and expand, with very considerable force, several hours after death, and that merely upon being touched with the finger, as every one has often seen. Here is irritability separated from sensibility. It may be so in the sensitive plant."[80] The editor countered this point in his introduction to J.R.W.'s final reply to T.C. by plainly asserting that, although it is not strictly speaking the case that life and irritability are synonymous, "yet it must be conceded, we think, that there can be formed no rational idea of the existence of the former, independently of that of the latter. Irritability is a fundamental property of life—a sine qua non of vital action."[81]

We can see in this brief exchange in the *Port Folio* a long-standing intellectual problem that troubled theologians and philosophers alike—namely, the existence of free will and the reduction of organisms to the scientific principles of inorganic mathematics, physics, and chemistry. The diurnal movements of plant leaves and the reliability of the opening and closing of blossoms of certain types of plants, those that Linnæus had grouped as *flores æquinoctiales*, were among the key phenomena that complicated this issue. The focus of this debate was on irritability, a concept that was defined in animals by Francis Glisson in the seventeenth century but that was grounded in a long tradition of faculties in Galenic physiology. The more or less contemporary observations of autonomous plant movements raised the question as to whether irritability extended to plant fibers as well and ultimately was attributed to the organization of their matter by the eighteenth-century French philosophes. Lost in all of this was concern for the rhythmicity of these movements, the temporal nature of which also needed explaining in the course of understanding what constituted a vital mechanism. Thomas Cooper and J.R.W. perhaps inadvertently characterized the problem in a dichotomy that resonated through mid-twentieth-century debates about the nature of biological rhythmicity: Does it arise *ab intra* or is it a reaction to a cause *ab extra*, a rhythmic factor acting on organisms from without?

Internal agency was built into Aristotelian natural philosophy as enteleche, but this internal nature was generally subordinated to external causation in a cosmological scheme in which all terrestrial movements, all generations and decays, including mixing and growth, were caused by motions originating in the outer sphere of the cosmos and transmitted and mediated by the motions of the celestial spheres that also moved the sun, moon, and planets. This supposition does not appear to have been challenged within Western natural philosophy until the sixteenth century, when a measure of materialism that was inherent in Hippocratic-Galenic medicine reemerged in consideration of the causes of disease. In Girolamo Fracastoro's analysis of medical critical days, this took the form of compounding the cyclical ebbing and flowing of the body's humors, which produced cyclically recurring patterns of some illnesses. These were not biological rhythms in the modern sense, but Fracastoro did locate the immediate causes of the timings of diseases in rhythmic material fluxes within the body.

Around the same time, Paracelsus imagined the timings evident in healthy and diseased behaviors of the body to be owing to internal *immaterial* principles, the *archæi* or inner workmen who reside in the various parts of the body and carry out its chemical processes. These archæi were sometimes identified by Paracelsus and his followers with *astra*, stars that are internal to the body but which cycle in harmony with their celestial counterparts. This complementarity between the stars of the macrocosm and the stars of the microcosm was poignantly emblematized by the sixteenth-century Danish astronomer Tycho Brahe as two complementary astronomies—celestial astronomy and terrestrial astronomy (alchemy). This Neoplatonic harmonic relationship between the "tasks above" and the "flasks below," as James Joyce paraphrased the medieval *Emerald Tablet of Hermes*, permitted the breakdown of the Aristotelian exogenous causal scheme and facilitated speculation about causation internal to organic bodies.[82]

This late Renaissance natural philosophy was not biology in the modern sense and is perhaps better characterized as "vital philosophy," the term applied to Severinus's Paracelsian biological theory by the chemist Andreas Libavius at the beginning of the seventeenth century. But the Paracelsian archæus and its internal efficiency persisted into the modern period under the concept of irritability, long a viable vitalist explanation for biological phenomena that were not easily reducible to the materialist explanations offered by mechanical philosophers. Rhythmic, spontaneous cyclical behaviors of sensitive plants, along with the carefully articulated and coordinated biological processes of generation, nutrition, growth, and senescence presented the chief obstacles to physicochemical reductionism in physiology and other biological sciences in the nineteenth century. By the end of that century, vitalism was in general disrepute among a new generation of laboratory scientists, whose efforts were bent on experimentally controlling stimuli, applied to organic and inorganic specimens alike, to understand their effect on responses. Within this environment, the causes of rhythmic responses of organisms were supposed to be rhythmic fluctuations in exogenous factors—which were thought to set up persistent biological rhythms much as a hammer sets up the rhythm of a pendulum or a tuning fork, which may then persist for a time in the absence of the stimulus—but were clearly not produced by an active internal agency or mechanism.