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Brain and Cognition 51 (2003) 66–94
Brain and Cognition
www.elsevier.com/locate/b&c

The vibrating nerve impulse in Newton, Willis and Gassendi: First steps in a mechanical theory of communication

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Accepted 19 June 2002

Abstract

In later editions of his two major works, Isaac Newton proposed an electrical hypothesis of nervous transmission. According to this hypothesis, an electrical aether permeates the nerve and transmits vibrations along it. This implies that the nerve is a communication line, and potentially, an extension of the mind. The opposite view was held by Cartesian mechanists, who taught that the nerve is a power line, transmitting either pressure or tension, and that the mind is separate from the nervous system. The Newtonian model eventually supplanted the Cartesian model in the mid 18th century, and became a crucial part of the conceptual environment in which neuroscience originated. In this paper I examine the scientific origins of the Newtonian model of nervous transmission. I argue that Newton's model relies on prior work by Thomas Willis and Pierre Gassendi. Willis supplied the anatomical and physiological "hard data" upon which the model was built. But Gassendi, a generation before, laid out the conceptual foundations of the problem, including the principle of impulse-transmission, and the corrolary principle of the muscle as an autonomous generator of force. I conclude that Gassendi's work has been undeservedly neglected as a turning-point in the history of neuroscience.

Keywords: History of neuroscience; Electrophysiology; Nerve impulse; Nervous transmission; 17th Century science; Fermentation; Aether; Animal spirits

> All perception of truth is the detection of an analogy.
> —We reason from our hands to our head.
>
> Henry David Thoreau[1]

1. Introduction

Luigi Galvani is generally considered the founding father of neuroscience, and with good reason: he literally wired lightning into a dissected animal part. He cap-

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[1] In a journal entry dated September 5th, 1851: see *A Year in Thoreau's Journal* (Penguin Classics), p. 201.

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doi:10.1016/S0278-2626(02)00513-4

tured lightning from a thunderstorm, channeled it into a wire, and stimulated the severed limb of a frog. This was a dramatic gesture, and its repercussions in the intellectual world of Europe were enormous.[2] But this was not Galvani's only experiment, nor did it emerge fully formed from Galvani's mind as a dramatic performance. Galvani himself, and other scientists before him, had made previous and less famous attempts to understand the role of electricity in animal movement. These included many experiments with electrical fish, hand-powered spark generators, farm animals, human children, dissected animal parts, and other bizarre biomechanical combinations. Along with this work came a great deal of research on the nature of nervous transmission, and the nature of electricity itself.[3]

The fact is generally known, but not truly appreciated, that Isaac Newton's theory of nervous transmission was a fundamental influence on Galvani's work. Newton's theory was transmitted in the 18th century by a minority of physiologists, most of whom were English, and all of whom were opponents of the Cartesian theory. Against the Cartesian 'hydraulic' theory, Newton's theory focused attention on electricity as a possible mediator of nervous transmission. In fact, Newton proposed the first clear and balanced theory for how electrical and chemical mechanisms could interact to form the substrate of nervous transmission. Newton's theory would eventually be vindicated by history, but it remained a minority opinion for most of the 18th century. In spite of its many shortcomings the Cartesian theory was remarkably persistent, probably because it was less open to fanciful interpretation and therefore more attractive to experimentalists.[4]

Descartes described the body as a machine in which the nerves act as force transducers, materially involved in the transfer of force from and to the brain. In this machine, the brain is like a bellows which pumps air into the muscles, and sensory impressions are like ladies who pull on bell-cords for service. In modern terms, the motor function of the nerves is carried by pressure, while the sensory function is carried by tension. Both motor and sensory functions are carried on the same nerve. This Cartesian theory was the first mechanical model of the entire body, and as such it formed the background and gold standard against which all new theories were argued.[5]

[2] Emil DuBois-Reymond, the discoverer of the action potential, compared the 'storm' set off by Galvani's papers with the contemporaneous storm of the French revolution. The comparison is not far-fetched since one consequence of Galvani's fame was a widespread interest in the electrical stimulation of human corpses and severed limbs, with the intention of reviving them. Galvani's own nephew Aldini made an international career out of stimulating the severed heads of decapitated criminals. Not surprisingly, Mary Shelley's *Frankenstein* was influenced by such experiments, as Finger and Law (1998) have documented. See also Cohen (1953).

[3] On Galvani see Clower (1998), Cohen (1953) and Clarke and Jacyna (1987). On pre-Galvanian electrophysiology see Cohen (1953) and Home (1970); also see Fulton and Cushing (1936), Hoff (1936), and Walker (1937). Fulton and Cushing's piece is an annotated bibliography of primary sources which contains a few errors, as Walker (1937) and Clarke and Jacyna (1987) have pointed out. Marcello Pera's book *The Ambiguous Frog* (1986) is devoted to Galvani's experiments, and also explains the electrical theories and devices of the period. The book's primary focus, however, is Galvani's ill-fated controversy with Volta, the physicist who invented the electric battery based on Galvani's initial findings.

[4] The "Newtonian school" of physiologists, of whom Hartley is the most important, also included Kreill, Robinson, Tabor, Mead, Cheyne, Pitcairne and others (see Blastholm, 1950, p. 189 ff.; Coleman, 1967; Earles, 1961; Hall, 1968; Jackson, 1970). This school arose in England as a somewhat unfaithful medical development of Newton's ideas. A more rigorous medical application of Newton's method was developed by Haller in Switzerland, creating a powerful and highly influential system which was also, however, seriously flawed. Galvani's success can largely be attributed to his neglect of Hallerian arguments, and his simple-minded adherence to the earlier kind of Newtonian physiology (see Cohen, 1953; Home, 1970; Pera, 1986). One contemporary reader of Galvani even drew explicit attention to the similarities between Galvani's animal electricity and Newton's aether (Pownall, 1819).

[5] See Canguilhem (1955, Chap. II), Berthier (1914), Hall (1970), Wilson (1961).

The Newtonian theory became the principal rival of the Cartesian theory, and after a long period at the margins it eventually (though in altered form) supplanted it. However, the Newtonian theory benefited from several prior generations of scientists who had struggled against the Cartesian theory and ironed out an alternative picture. There were two great epochs in the pre-Newtonian concept of the nerve. Closest to Newton, both culturally and chronologically, was Thomas Willis: Willis prepared the way for Newton by compiling and shaping a chaos of clinical and experimental findings into the first comprehensive doctrine of the nervous system. This doctrine gave first expression to several fundamental pillars of modern neuroscience, including a molecular model of the nerve impulse and a theory of reflex action. But before Willis could undertake to build his new doctrine, another pioneer came before him to clear and survey the land: this was Pierre Gassendi. Gassendi was not, like Willis, active in medical practice or research. He was a theoretician, a reader—but a very careful one. He drew on classical Greek atomism, Renaissance alchemy, and contemporary medical literature, to arrive at the most basic principle of all: that the nerve is a carrier of information and not of force, a communication line and not a power line.

This principle, first articulated by Gassendi, was an unacknowledged turning point in the history of neuroscience, since it endowed the experimental study of the nervous system with a new and compelling mission: to understand the soul itself in mechanical terms, to look among the dissected parts of animals for a window into the soul. In the hands of Willis, Newton, Locke, Hartley and many others, Gassendi's principle became the first foundation from which a 'physiological psychology' could arise to challenge the Cartesian and Continental type of dualistic psychology.

Before proceeding further, let me acknowledge that some of the material presented here has been discussed by Georges Canguilhem in his book, *La Formation du Concept de Reflexe* (1955). It would be hard to overstate the justice and precision of everything Canguilhem has to say in this or in any of his books. A few inaccuracies have become apparent in his account of Newton, however, largely through new discoveries in Newton scholarship since the time of publication.[6]

2. Newton

Most of Newton's writing on the subject of nervous transmission is found in passages added to later editions of his two major works, the *Principia Mathematica* and the *Opticks*. The relative brevity of these passages did not prevent them from having a powerful influence on 18th century science.[7]

The most famous passage is the last paragraph of the "General Scholium," a section which Newton added to the second edition of the *Principia Mathematica* (published 1713). Here, in the dramatic style of a "short communication," Newton imparted to his readers the latest and most astonishing prediction of his system: this concerned nothing less than the ultimate unification of matter and soul.

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[6] In addition to Canguilhem's book there is a Ph.D. Thesis written in 1975, *The Matter of Motion and Galvani's Frogs* (Williams, 2000), which aims to be a comprehensive survey of neuromuscular physiology from the ancient Greeks to Galvani. The book dwells at length on the role of Newton and Willis in preparing the way for Galvani. However, this book contains important inaccuracies, particularly with respect to Newton. For instance it erroneously attributes to Newton the doctrine that the nerves themselves vibrate, as opposed to an aether contained within them. Furthermore it identifies Newton's muscular contraction model with Willis's, claiming that Newton's model required "sulphureous particles," although there is no evidence to support this. Finally, an inaccuracy which this book shares with Canguilhem's is the claim that Newton's doctrine of nervous transmission was not influenced by chemical thinking (see notes 75 and 76 below for further discussion).

[7] Earles (1961), Coleman (1967), Hall (1968), Jackson (1970).

Even without this ambitious finale, the General Scholium was not short on contentious material: the section begins with a refutation of planetary vortices which demolished the Cartesian model of celestial mechanics; following which Newton asserts that God is omnipresent not only virtually but substantially in every moment and at every place (another blow to the Cartesians); he then denounces the use of hypotheses in natural philosophy (striking the Cartesian method at its very root). After these arguments, and concluding the entire work, comes the paragraph under consideration. The passage is carefully worded, and bears quoting in full:

> And now we might add something concerning a certain most subtle spirit which pervades and lies hid in all gross bodies; by the force and action of which spirit the particles of bodies attract one another at near distances, and cohere, if contiguous; and electric bodies operate to greater distances, as well repelling as attracting the neighboring corpuscles; and light is emitted, reflected, refracted, inflected, and heats bodies; and all sensation is excited, and the members of animal bodies move at the command of the will, namely, by the vibrations of this spirit, mutually propagated along the solid filaments of the nerves, from the outward organs of sense to the brain, and from the brain into the muscles. But these are things that cannot be explained in few words, nor are we furnished with that sufficiency of experiments which is required to an accurate determination and demonstration of the laws by which this electric and elastic spirit operates.[8]

The passage begins in a very tentative voice. "And now we might add a few discreet suggestions," Newton seems to say, "concerning some rather interesting phenomena which some readers may find curious..." But this tentative language gives way suddenly to a grand hypothesis of the boldest nature—bolder still for being born under the very nose of the famous denunciation of hypotheses, which crowned the preceding paragraph.[9] Indeed, the properties of a 'subtle spirit' are proposed to account for the entirety of chemistry, electricity, and optics. And the vibrations of this spirit, conducted along the nerves, are responsible for all animal movement and sensation. This is a sweeping hypothesis, and as if to protect the reader from its destabilizing effects, Newton is quick to add a note of caution and respect for "that sufficiency of experiments which is required to an accurate determination and demonstration of the laws by which this electric and elastic spirit operates."

2.1. The Queries

If the General Scholium hinted at incredible things, the Queries confirmed them. The Queries were a series of hypotheses, formulated as rhetorical questions, which Newton added to the end of his second major work, the *Opticks*. They were composed during the final phase of Newton's life, and John Heilbron has called them "Newton's last guesses at the structure of the world." It may be that Newton agreed: his style in the Queries displays a combination of freedom and rigor which can justly be called poetic. In any case, historians are unanimous in believing that the Queries strongly influenced 18th century physics, serving as "a quarry of qualitative images in the style of Descartes' *Principia philosophiae*."[10]

The Queries grew in number and content as successive editions of the *Opticks* were prepared: 16 Queries in the first English edition (1704); seven additional Queries

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[8] Newton (1713). Koyré and Cohen (1960) give a short commentary on this passage.

[9] That is, the famous "Hypotheses non fingo," which immediately precedes this paragraph in the General Scholium.

[10] Heilbron (1979, p. 51 ff.). In spite of the indirectness of the Query form, Newtonians generally interpreted the Queries as realized scientific models, according to Koyré (1965, p. 50 note). See also Heilbron (1979, p. 51 ff., p. 55 ff.), Earles (1961), Coleman (1967), Hall (1968), Jackson (1970).

and revisions to the others in the first Latin edition (1706); further revisions and an additional eight Queries in the second English edition (1717).[11]

The "electric and elastic spirit" evoked in the General Scholium returns in the Queries as an "aether"[12] whose functions are no less general, but whose mech-

[11] Heilbron (1979, p. 51 ff.), Cohen (1956), Koyré (1960). I will quote here from the third English edition (1730), which is considered definitive.

[12] Newton apparently considered these terms synonymous (see Heilbron, 1979, p. 30 ff., 46 ff., 229 ff., 237 ff.). The word 'aether' derives from the Greek *aither*, from *aei theou*, "eternal movement." The word was used by philosophers such as Heraclitus and Aristotle to designate a divine fire more pure than earthly fire. This fire is found in the "outer heavens," a region which surrounds the world. It was thought to be the primordial origin of all things, but also the material of souls. (See Kirk, Raven, & Schofield, 1983, p. 198 ff.; Aristotle, *On the Heavens* I, 270 b 24; Canguilhem, 1955, Chap. 4.) This conception subsisted in the middle ages: for instance in the *Golden Legend* we read that angels lifted up Mary Magdalene into the aether every day, "and an hour later brought her back to her place with divine praises." (Voragine, c.1260, Vol. 1).

Scientists in the 17th and 18th centuries set out to redefine this ancient concept in corpuscularian terms. They measured its ancient connotations, but added other powers such as magnetism, electricity, and gravitation. One of Newton's early breaks with Descartes was to postulate a compressible or 'elastic' aether. ("Elastic," a Latinate word coined in the mid-17th century, denoted the "spontaneous expansion" of air or gases.) Thus Newton defined aether by analogy with air, in contrast to the Cartesian fluid or effluvium. See Heilbron (1979, p. 30 ff., 46 ff., 229 ff., 237 ff.), Koyré (1965), Hall and Hall (1967), Cohen (1958). On Newton's conception of the fundamental structure of matter see Thackray (1970). Willis discusses the composition of aether in his *De fermentatione* (1659), Chap. 10.

The word 'spirit,' from the Latin word *spiritus*, "breath," has a complex etymology. Medieval medicine used the term 'animal spirits' to denote the substance of the soul: this was inherited from Greek medical tradition, especially through the writings of Galen (2nd c. AD). Galenic medicine taught that the human body has three principal functions mediated by three *pneuma* or breaths: the natural spirit (*pneuma physicon*), the vital spirit (*pneuma zoicon*), and the animal spirit (*pneuma psychikon*). Nervous transmission was explained as a "flow of potency" through the *pneuma psychikon*, which resides in the nerve (see Hall, 1969, Vol. 1, p. 162).

The question of whether the *pneuma* were considered material entities is difficult to answer. Verbeke (1945) concludes that there were three distinct (though overlapping) pneumatic traditions in the ancient world, each of which assigned a different degree of "spiritualization" to the *pneuma*. In the medical tradition, the *pneuma* were considered exclusively material; with the Stoic tradition a "spiritualization" of the *pneuma* took place; and finally with the Christians the *pneuma* became exclusively divine and non-material. The earliest medical writings (e.g., of Erasistratus and the Hippocratics) described *pneuma* as a kind of hot breath. As it was spiritualized, the *pneuma* became increasingly identified with fire or *aither*, and with the tradition of the "igneous soul" (see Canguilhem, 1955, Chap. 4). Galen, who was both a Stoic and a medical writer, likened *the pneuma psychikon* to "fire mixed with air." In the Christian New Testament, the word *pneuma* gives us expressions such as "Holy Spirit" (*hagiou pneumatos*) or "wicked spirits" (*pneumatoon poneeron*): here the *pneuma* are understood as disembodied intelligent beings rather than primitive organic forces. (See also Long & Sedley, 1987, Vol. 1; Partington, 1961, Vol. 1; Solmson, 1961; Vol. 1).

The word 'spirit' was first applied to the products of distillation, such as spirits of wine or turpentine, in the early 17th century (*Oxford English Dictionary*). This usage must have then spread from the trades into the sciences, where the term 'animal spirits' was stripped of its Greek and Christian overtones, and given a crude materialistic interpretation. Thus Croone spoke of animal spirits "exactly as we speak of spirit of wine or of salt or of others of the same kind" (1664, s. 13). Descartes described the animal spirits as a "very subtle liquor," and treated them as a hydraulic fluid (see Canguilhem, 1955, Chap. 2). Willis, however, argued that animal spirits are not liquid, nor are they 'spirits' in the sense of distillation products, but rather, a kind of ineffable substance defined only by inference: thus spirit is not a *product* of distillation, but rather that which *disappears first* after distillation or combustion (Willis, 1664, Chap. 19). However, Willis did ascribe to this substance a corpuscularian basic structure, as he would for a material substance (Willis, 1659, Chap. 1; Willis, 1672, Chap. 4).

Willis's apparently unorthodox interpretation of spirits actually came out of an older alchemical tradition (see notes 75 and 76 below). In late alchemy, spirit was an alternative name for mercury, one of the three 'active principles' of matter, along with sulphur and salt. The three active principles were considered analogous to body, soul, and spirit in the human body. Thus the late alchemist Van Helmont taught that metals consist of body and soul held together by spirit. Body would correspond to salt, soul to sulphur, and spirit to mercury. But in addition to their analogical implication, the alchemical 'principles' also had a material implication in line with Willis's definition: thus spirit is the most volatile of the active principles, because it disappears first after distillation or combustion. Spirit is also the most active or 'mobile' principle, and therefore the primary cause of fermentation (see Bloch, 1971, Chap. 8; Partington, 1961, Vol. 2; Pagel, 1982; Willis, 1659, Chap. 1).

anisms are more specifically spelled out. Among its functions, the nervous system again figures prominently. Nervous transmission is mentioned several times in the succession of Queries, yet only in the last (1717) set of Queries is directly connected with the aether. This suggests that Newton's ideas on nervous transmission underwent change and modification during the period from 1704 to 1717. We can follow this change by reading the material of the Queries in chronological order.

Query 16 (published 1704) begins the series with an observation inspired from ancient Greek sources:

> When a man in the dark presses either corner of his eye with his finger, and turns his eye away from his finger, he will see a circle of colors like those in the feather of a peacock's tail. If the eye and the finger remain quiet these colors vanish in a second minute of time, but if the finger be moved with a quavering motion they appear again.

The Greeks took such flashes of light generated by pressure to demonstrate "that the eye has within it a native fire, and that on this native fire [...] its faculty of vision somehow depends."[13] Newton takes a more modern tack, talking of "motions" and "vibrations" within the solid structures of the eye:

> Do not these colors arise from such motions excited in the bottom of the eye by the pressure and motion of the finger, as, at other times are excited there by light for causing vision? And do not the motions once excited continue about a second of time before they cease? And when a man by a stroke upon his eye sees a flash of light, are not the like motions excited in the retina by the stroke? And when a coal of fire moved nimbly in the circumference of a circle, makes the whole circumference appear like a circle of fire, is it not because the motions excited in the bottom of the eye by the rays of light are of a lasting nature, and continue till the coal of fire in going round returns to its former place? And considering the lastingness of the motions excited in the bottom of the eye by light, are they not of a vibrating nature?

I imagine that these physiological speculations arose in Newton's mind during the years of prisms and dark chambers, when his experiments required him to distinguish visual phenomena belonging to the nature of light itself, from those which arise in the eye or the nervous system. But Newton's mind, childlike in its constant capacity for questioning, would not stop at this distinction, and began also to theorize about the causes of nervous transmission.

Newton's theory of nervous transmission is developed in Queries 17, 23, and 24 (all published 1717). Query 17 connects the vibrations of Query 16 with hypothetical tremors excited by the refraction or reflection of light:

> When a ray of light falls upon the surface of any pellucid body, and is there refracted or reflected, may not waves of vibrations, or tremors, be thereby excited in the refracting or reflecting medium at the point of incidence, and continue to arise there, and to be propagated from thence as long as they continue to arise and be propagated, when they are excited in the bottom of the eye by the pressure or motion of the finger, or by the light which comes from the coal of fire in the experiments above mentioned?

This idea is given more formal expression in Queries 23 and 24, where the sensory and motor functions of the nerves are described. Query 24 then seems to reiterate the hypothesis of the General Scholium, with a few additional details:

> Is not animal motion performed by the vibrations of this medium, excited in the brain by the power of the will, and propagated from thence through the solid, pellucid and uniform capillamenta of the nerves into the muscles, for contracting and dilating them? I suppose that the capillamenta of the nerves are each of them solid and uniform, that the vibrating motion of the aethereal medium may be propagated along them from one end to the other uniformly, and without interruption: for obstructions in the nerves create palsies [*paralysis*]. That they may be sufficiently uniform, I suppose them to be pellucid when viewed singly,

[13] Beare, 1906, p. 10.

> though the reflections in their cylindrical surfaces may make the whole nerve (composed of many capillamenta) appear opaque and white. For opacity arises from reflecting surfaces, such as may disturb and interrupt the motions of this medium.

Electricity is not specifically named in this passage, but recent scholarship has shown that Newton's aether in the Queries was both conceived and interpreted as an electrical aether. Therefore, Newton's model of nervous transmission was essentially electrical, with or without explicit mention of electricity.[14]

2.2. The second paper on color and light

The model presented in the Queries immediately suggests some difficult challenges. For instance, even if we grant that the nerves are composed of solid, pellucid and uniform capillamenta, how does Newton propose that the aether, which can travel freely through these solid structures, should cause the contraction and dilation of muscles? Wouldn't the aether leak out either from the capillamenta or from the muscles? And furthermore, assuming that the aether does not leak, how is a mere tremor in the aether translated into a powerful muscular contraction? The Queries are silent on these matters, and it might seem that Newton simply overlooked them: a theoretician cannot be expected to clean up every detail after all, the point of a model is its simplicity.

But I discovered to my surprize that Newton, far from having overlooked these problems, had already solved them. Within a well-known paper which he wrote early in his career, is embedded (somewhat incongruously) a discussion of muscular contraction. In this discussion, Newton proposes that nervous transmission is mediated by an aether. His hypothesis includes a chemical model which explains both how the aether is prevented from leaking, and also how a tremor in the aether causes muscular contraction.[15]

The argument begins with the supposition that the "animal juices" which comprise the active substance of a muscle are similar to a compressible aether:

> For though common water will scarce shrink by compression, and swell by relaxation, yet (so far as my observation reaches) spirit of wine and oil will; and Mr. Boyle's experiment of a tadpole shrinking very much by hard compressing the water in which it swam, is an argument that animal juices do the same.

Newton proposes that the compression or relaxation of the animal juices is brought about by the condensation or dilation of an aether which permeates them, an aether which he distinguishes from the "ambient aether" outside the muscle.

[14] Heilbron (1979, p. 239 ff., 237 ff.). tells the fascinating story of how Newton came to imagine a connection between light and electricity, a connection which he advertized in the Queries with his theory of the unified aether. More generally, Heilbron notes that the Queries were interpreted in the 18th century as "a guide to the hidden mechanics of electricity" (p. 51 ff., p. 55 ff.). When the neurological speculations of the Queries are read in this light, one can begin to understand the powerful influence which the Queries exerted on 18th century physiology (see Coleman, 1967; Earles, 1961; Hall, 1968; Jackson, 1970). An interesting footnote to the electrical interpretation of Newton's physiology is supplied by Koyré and Cohen (1960), who point out that the phrase "electric and elastic spirit" is not found in the original Latin text of the General Scholium. The words "electric and elastic" were supplied by the English translator Andrew Motte in 1729, i.e., after Newton's death. However, the addition was not unauthorized, since Newton himself added the words "electric and elastic" in a marginal note to his copy of the 2nd edition of the *Principia*. Why Newton's addition was not included in the third Latin edition of 1726 remains a mystery.

[15] The second paper 'on color and light' (Newton, 1675) was sent in writing by Newton to the Royal Society, and read aloud at a meeting. Its text was entered into the minutes of the Royal Society and therefore published. Hall and Hall (1967) have called attention to this passage, describing it as "an explanation of a mysterious phrase in the General Scholium of forty years later." But no one to my knowledge has studied the passage in detail.

But the question remains: what causes the condensation or dilation of this internal aether? By what means does the will act upon this aether? As if to review the state of Cartesian hydraulic physiology, Newton makes a long inventory of possible means, forgetting no option however absurd:

> Some may be ready to grant that the soul may have an immediate power over the whole aether in any part of the body, to swell or shrink it at will: but then how depends the muscular motion on the nerves? Others therefore may be more apt to think it done by some certain aethereal spirit included within the dura mater, which the soul may have power to contract or dilate at will in any muscle, and so cause it to flow thither through the nerves. But still there is a difficulty, why this force of the soul upon it does not take off the power of its springiness, whereby it should sustain, more or less, the force of the outward aether. A third supposition may be that the soul has a power to inspire any muscle with this spirit, by impelling it thither through the nerves. But this too has its difficulties, for it requires a forcible intending the spring of the aether in the muscles, by pressure exerted from the parts of the brain: and it is hard to conceive how so great force can be exercised amidst so tender matter as the brain is. And besides, why does not this aethereal spirit, being subtle enough, and urged with so great force, go away through the dura mater and skins of the muscle, or at least so much of the other aether go out to make way for this, which is crowded in?

For every Cartesian option, Newton finds a fatal flaw. Like the magician who demonstrates to his audience that the man he is about to chop in half is really alive, that the sword he will use is sharp, and that the box through which the man will be severed has no false bottom, Newton scrupulously demonstrates that no adequate explanation can be found in the realm of Cartesian hydraulics. The soul cannot act either directly on the whole body, or directly on the muscles, or directly on the brain. The audience is cast down, depressed, discouraged even from believing in science. But like the doctor who rises at midnight to rescue a family in distress, Newton undertakes to restore order.

> To take away these difficulties is a digression; but seeing the subject is a deserving one, I shall not stick to tell you how I think it may be done.
>
> First then, I suppose, there is such a spirit; that is, that the animal spirits are neither like the liquor, vapour, or gas of spirit of wine; but of an aethereal nature, subtle enough to pervade the animal juices, as freely as the electric, or perhaps magnetic, effluvia do glass. And to know how the coats of the brain, nerves, and muscles, may become a convenient vessel to hold so subtle a spirit, you may consider how liquors and spirits are disposed to pervade or not pervade things on other accounts than their subtlety. Water and oil pervade wood and stone, which quicksilver does not; and quicksilver metals, which water and oil do not: water and acid spirits pervade salts, which oil and spirit of wine do not; and oil and spirit of wine pervade sulphur, which water and acid spirits do not. So some fluids, as oil and water, though their parts are in freedom enough to mix with one another, yet **by some secret principle of unsociableness** they keep asunder; and some, that are sociable, may become unsociable, by adding a third thing to one of them, as water to spirit of wine, by dissolving salt of tartar in it. The like unsociableness may be in aethereal natures, as perhaps between the aethers in the vortices of the sun and planets.[16] [Emphasis added.]

Thus the first step in overcoming the Cartesian impasse is to posit a non-hydraulic aether, one which can move freely through solid objects. But this aether can be confined in the muscle by a kind of chemical phobicity against the muscle wall. Here we begin to see Newton's originality: if the aether is confined, it is essentially hydraulic—but if it can be released from confinement by a chemical transformation, then it can transgress the rules of Cartesian mechanics and behave in a completely new way. The remaining course of the argument is already clear.

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[16] Newton (1675). At this early date Newton still employed the Cartesian model of gravitational vortices, though his aether already differed from the Cartesian in being compressible, whereas the Cartesian aether was dense and incompressible (see Heilbron, 1979).

> For knowing how this spirit may be used for animal motion, you may consider, how some things unsociable are made sociable by the mediation of a third. Water, which will not dissolve copper, will do it, if the copper be melted with sulphur: aqua fortis, which will not pervade gold, will do it by addition of a little sal armoniac, or spirit of salt [. . .] in like manner, the aethereal animal spirit in a man may be a mediator between the common aether and the muscular juices, to make them mix more freely; and so, by sending a little of this spirit into any muscle, though so little as to cause no sensible tension of the muscle by its own force; yet, by rendering the juices more sociable to the common external aether, it may cause that aether to pervade the muscle of its own accord in a moment more freely and copiously than it would otherwise do, and to recede again as freely, so soon as this mediator of sociableness is retracted.[17]

This is a chemical model of muscular contraction, coupling the intangible aether to the tangible muscle by means of the chemistry of animal spirits. The model involves three basic ingredients: (1) a gas-like "common aether;" (2) muscular juices; and (3) animal spirits (which are "of an aethereal nature, subtle enough to pervade the animal juices, as freely as the electric, or perhaps magnetic, effluvia do glass"). A tremor in the animal spirits spills a drop of the animal spirits into the muscle. The muscle then contracts due to a chemical reaction between the animal spirits and the muscle juices. This reaction causes the omnipresent common aether to rush into the muscle, attracted by a dramatic change in its binding affinity for the muscle juices, and the muscle contracts by inflation.[18]

This model is not in all points identical to that of the General Scholium and the Queries, primarily because it requires two distinct aethers, or at least a bound and a free state of aether, which have different chemical properties (i.e., the animal spirits and the "common aether"). The General Scholium and Queries call for a single universal aether or spirit. However, there is a strong continuity between the models, especially in their basic electro-chemical premise.

3. Willis

The Newtonian theory I have just reviewed was not invented by Newton, but rather, perfected from an earlier, more convoluted, and less precise model developed by Thomas Willis (1621–1675). In particular, three important features of Newton's model can be recognized in Willis's writings: the solid nerve, the vibratory and light-like nerve impulse, and the autonomy of the muscle from the nerve. These features emerge less saliently from Willis's writings than from Newton's—we could perhaps say that they are less confidently asserted. But, on the other hand, they are supported by so much real anatomical and physiological data that they seem to carry more weight.

Willis's name is best known today for the "circle of Willis," a vascular structure at the base of the brain, but his influence was much greater than this suggests. He was a student of Harvey and Boyle, and counted among his own students Locke and Hooke. An eminent physician and Oxford professor, Willis was also a founding member of the Royal Society, and his influence on that body was considerable during its first generation. Willis's books were pathbreakers in clinical and

[17] Newton (1675).

[18] Even 10 years after this paper, Newton continued to be interested in the mechanism of muscular contraction, since in 1684 he suggested to Boyle that he should place a muscle in his air pump, to investigate the effects of pressure on muscle contraction. See Birch, *The History of the Royal Society* (1756, reprinted 1968), Vol. IV, p. 320.

comparative neurology and neuroanatomy, but also in psychiatry, pharmacology and biochemistry.[19]

Willis developed his theory of nervous transmission in chapter 19 of his great textbook *Cerebri anatome* (published in 1664, when Newton was 22 years old), and subsequently in two other works: *De motu musculari* (1670); *De anima brutorum* (1672).

Willis's writing style has often been called fanciful. This impression is probably due in part to unfamiliarity with his chemical vocabulary, which departed from the common usage of his time.[20] However, Willis's style is especially problematic if one reads him in English, since the standard English translations, made by the poet Samuel Pordage after Willis was dead, are couched in a rather turbulent 17th century idiom. To alleviate this problem, I have used non-Pordage translations when possible.[21]

3.1. The solid nerve

The first element of Newton's theory which can be traced to Willis is the "solid nerve." This was not a minor point for Newton or his followers, and in fact, one reason for the relative marginality of Newtonian physiologists in the 18th century was their steadfast adherence to the concept of a "solid, uniform" nerve.

The terms "solid nerve" and "hollow nerve" are slightly misleading since it is clear that neither side believed the nerves to be completely solid or completely hollow. But

[19] For an introduction to Willis's life and works, see Finger (2000, Chap. 7), Dewhurst (1980), or the more complete biography by Isler (1968). Isler gives summaries of several of Willis's books, and explains the context in which they were written, both social and scientific. For background on other prominent medical men of this period see Debus (1965, 1974), especially Chapters 8 and 13–16 of the latter. On Willis's role in the Royal Society, see Hall (1974, Chap. 16). On his contributions to neuroanatomy, neurology and psychiatry, see Isler (1968) and Diamond (1971). On his contributions to pharmacology and biochemistry, see Davis (1974, p. 81 ff.) and Isler (1968, p. 45 ff.). On his comparative anatomy, see Isler (1968), who also reproduces several beautiful illustrations from Willis's dissections of invertebrates.

Canguilhem devotes a chapter of *The Formation of the Concept of the Reflex* (1955) to Willis; this chapter contains a synopsis of earlier scholarship on Willis, and a synopsis of Willis's doctrine of nervous transmission. Blastholm (1950) and Hierons (1964) give succinct, but sometimes hasty overviews of the technical content of Willis's neurophysiology. Sherrington's teacher Foster devotes some space to Willis in his *Lectures on the History of Physiology* (1901, p. 269 ff.); his judgment is highly pejorative, however, and plays into a tradition of Willis as an opportunist and a dandy. Isler (1968, p. 105 ff.) Persuades us to abandon this view, tracing its origin to a disputatious neighbor of the Willis family, one Anthony Wood, who wrote a history of Oxford (*Athenae Oxonienses*, 1721) in which, animated by neighborly jealousy, he claimed that Willis owed all his fame to the work of his assistant Richard Lower.

[20] See Isler (1968, p. 105 ff.). Willis himself admits that Chap. 18 of *Cerebri Anatome* is "a troublesome and intricate sea of disquisition." (Willis, 1664, Chap. 19). Foster goes further: "He caught up the phrases of his friends, Boyle and others, without understanding them, and when he comes to explain nervous phenomena, he mixes up the properties of light with other physical phenomena, and indeed with chemical phenomena." (Foster, 1901, p. 275) However, as discussed in notes 75 and 76 below, the chemical content of Willis's neurophysiology was by no means a mistake, but rather a bold and speculative move. I tend to agree with Canguilhem (1955), who interprets Willis's style as the sign of "an open and curious mind," endowed with "theoretical audacity and a quasi-poetic intuition."

[21] Stevenson (1978) observes that Pordage often translated Latin words by using the most similar-sounding English word, rather than the most accurate with respect to meaning. Unless otherwise noted, I have re-translated the Latin myself, using Pordage for support. In some cases I have used the extensive excerpts of Willis's writings translated by Foster (1901), Ciarke and O'Malley (1968) and Isler (1968).

these nicknames do help to contrast the Newtonian and Cartesian views.[22] The primary importance of this distinction was not anatomical correctness, but the functional question of whether a hydraulic mechanism could account for nervous transmission. In general, the proponents of a Newtonian "solid nerve" favored a vibratory type of transmission, and considered transmission based on hydraulic pressure to be mechanically impossible.[23]

Lest it seem that 17th century anatomists were abnormally prone to validating the functional theories they happened to favor, we should remember that functional theories have continued to exert a determining influence on nerve histology in more recent times. For example Clarke (1968) argues that the discovery of the electrical action potential in the early 1800s led to the dominance of a solid-nerve histology in the 19th century, which "conclusively denied to the nerve fiber a canalicular form and a movement of its contents." This notion of "inflexibly static nervous tissues" was overthrown in the mid-20th century, when axoplasmic flow was first observed. But the late 20th century has brought back solidity, with the conception of a polymer-like cytoskeleton which "anchors" signalling proteins.

In any case, during the years of Newton's working life, solid-nerve histology was enjoying a period of widespread acceptance. The best anatomists, including Willis, Leeuwenhoek and Borelli, described a solid nerve fiber. Willis was one of the early pioneers of microscopic anatomy, and was also, in 1664, the first person to describe the nerve based on observation through a microscope. In contrast to Descartes (who did not use a microscope), Willis described a solid fiber. Similar descriptions were published by Leeuwenhoek in 1678 and Borelli in 1681 (in fact, Borelli's description even seems copied from Willis).[24] Thus, Willis's description can serve as a paradigm of the accepted view:

> The passages of the nerves are not hollowed out like those of the arteries and veins, because their substance is not only impervious to any stylus, but the use of a lens or microscope confirms that there is no cavity present in them. [...] The nerves are clearly formed of a compact and firm substance so that the subtle humor, which is the vehicle of the spirits, may pass through their structures not otherwise than spirits of wine through the tensed cords of a lute, only by slowly creeping through. Hence it may be argued that the animal spirits require no manifest cavity within the nerves for their expansion. [...]
>
> The nerves are white, smooth, and round bodies. Within the skull and near their beginnings, being covered only with the pia mater, they are soft and easily broken; but distal to this they become somewhat hard and more tenacious, since many of them are usually gathered to-

[22] Descartes had proposed two different mechanisms of nervous transmission, one based on pressure and the other on tension, both acting within the same bidirectionally conducting nerve. The pressure mechanism acted by hydraulic flow through the whole tube of the nerve, channeled according to a system of valves. This was the mechanism for outgoing, motor commands from the brain. The tension mechanism, transmitting sensations acted by pulling on individual fibers within the nerve tube, each of which was connected to a separate sensory receptor. Thus for Descartes, the sensory and motor systems were structurally dissimilar, the motor system being tubular and branched, like the vascular system of a mammal, whereas the sensory system was fibrous and unbranched, like the vascular system of a plant. See Canguilhem (1955, Chap. II), Berthier (1914), Hall (1970), Wilson (1961). Newton, as we have seen, considered the nerves to be bundles of solid capillamenta. For him the sensory and motor systems were structurally similar, and both systems were fibrous and unbranched. Each nerve fiber was a 'labeled line' connecting directly from the periphery to the center.

[23] Nerve histology in the 17th and 18th centuries is reviewed by Clarke and Jacyna (1987, Chap. 5), Clarke (1968), Cole (1937), and Grmek (1970).

[24] Borelli wrote: "The nerve fibres are neither entirely solid, filled and impermeable, nor are they empty, tubular hollows similar to reeds, but are channels filled with a certain spongy substance, like the pith of the eider tree." (Borelli, 1681, cited by Clarke & O'Malley, 1968, p. 164) Leeuwenhoek's description in 1675 was slightly more Cartesian, but was interpreted as a "solid nerve:" he described a bundle of vessels filled with "soft fluid globules." He estimated that 10,000 of such globules could fit into a grain of sand (Cole, 1937; Grmek, 1970).

> gether, and also clothed with the dura mater.[25] The nerves themselves (as may be discovered with the aid of a microscope) are formed throughout with pores and passages like so many holes densely packed one next to another; thus their tubelike substance, like sugar cane, is porous and pervious throughout. Within these little spaces the animals spirits, or very subtle corpuscles, by their nature always ready for movement, are in gentle agitation.[26]

Willis called the individual fiber a "nerve" or a "nerve fiber" indifferently. In this he followed the anatomical norm of his day.[27] Thus, his description suggests a solid nerve fiber. But there is a long way from this to Newton's "uniform and pellucid capillamenta." According to Willis the nerve fibers are neither uniform nor pellucid, but spongious, like sugar cane: a solid yet porous material which moves a 'subtle humor' along its permeable interior. Similar descriptions were published by Leeuwenhoek in 1675 and Borelli in 1681. Borelli's description even seems copied from Willis. Clearly, Newton's idea of the nerves as fascicles of clear and uniform fibers draws support from the anatomical literature of his time, but clearly it abstracts from it as well. (Newton admits as much in Query 24, when he calls the filaments "pellucid" as a *supposition* introduced for the sake of simplicity.)

Was it a coincidence of history that Newton found support for his solid nerve in the anatomical publications of his day? Did blind chance favor, then chasten, the simplicity of Newton's scheme—or did a knowing God deliberately part the seas of hollow nerve histology for a span of four decades, so that Newton could move unhindered towards the electrical nerve impulse? Whatever the case may be, the tide turned in 1717, when Leeuwenhoek, after a hiatus of four decades, revised his earlier solid nerve description: he now represented the nerve as a sheaf of hollow tubules. Leeuwhenhoek's revised description was confirmed by other anatomists, and was disseminated by Boerhaave in his textbook *Institutiones Medicae,* which was taught in medical schools throughout the 18th century—except in England, where a solid nerve doctrine persisted among the "Newtonian physiologists."[28]

3.2. The nervous juice

In contrast to his anatomical description of the nerve, Willis's physiological theory of nervous transmission was not a single, unequivocal doctrine. Rather, it was a series of metaphors. The same process was redescribed from different points of view, until clarity was (hopefully) attained. Like Descartes, Willis often compared the nervous system to a fountain proceeding from the brain, and like Descartes he sometimes compared it to a church organ blowing air into its pipes. Like Descartes he also compared the nerves to the strings of a lute, which conduct vibrations when struck. But above all, and in contrast to Descartes, Willis emphasized the similarity of nervous transmission to the transmission or radiation of light.[29]

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[25] Here Willis echoes the opinion of those anatomists who claimed that all "sensitive membranes" (i.e., the sheaths of nerves and muscles) originate from the dura and pia mater (cf. Croone, 1664, Section 16).

[26] Willis (1664, Chap. 19), translated by Clarke and O'Malley (1968, p. 160), translation altered.

[27] See note 30 below.

[28] On Boerhaave, see Lindeboom (1970). On Newtonian physiology see Earles (1961), Coleman (1967), Hall (1968), Jackson (1970). A striking example of the English 'holding out' for a solid nerve is David Hartley in his *Observations on Man* (1749): "The nerves are rather solid capillaments, according to Sir Isaac Newton, than small tubuli, according to Boerhaave." Another example is Bryan Robinson, who wrote in 1734 that the nerves "are not only impervious to the smallest stylus, but when viewed through the microscope, evidently appear to have no cavity." (Cited from Pera, 1986.) Robinson's statement reveals the continuing influence of Willis within Newtonian physiology, since Robinson's words appear to have been lifted straight from Willis's *Cerebri anatome,* as can be ascertained by comparing them with the excerpt cited above. Therefore it seems that anachronistic reliance on old data was instrumental in preserving the theoretical consistency of Newtonian physiology.

[29] See Canguilhem (1955), and Willis (1664, Chap. 19). See also Willis (1672, Chap. 6) and later chapters.

Before examining his arguments, I should note again that for Willis and his generation, a 'fiber' was not synonymous with a nerve fiber. The muscles, tendons and other innervated organs, which Willis groups together as *genus nervosum*, "the nervous kind," are all supplied with fibers. In fact the tendons were thought to be nothing other than enormous bundles of fibers.[30] Willis argued that such fibers cannot simply be branches given off by the nerves: they must be partially distinct from the nerve fibers.

> In addition to the nerves themselves, fibers are, also sparsely interwoven in musculous flesh, parenchyma, and other parts, and united in the tendons, and all of these are motile and sensate organs. Indeed the actions of their faculties are-more principally and immediately carried out by the fibers than by the nerves; for clearly, by drawing together the muscles and other moving parts, they produce the movement itself; and the nerves only carry away from the encephalon the impulse [*instinctum*] for executing that action.[31]

Thus it is these fibers, rather than the nerves, which make an organ capable of movement and sensation. The nerves are merely relays, carriers of impulses: the motile and sensate organs must be there to give or receive the impulses. These impulses travel within a "nervous juice"[32] which is contained in the nerve fibers.

> This nervous juice, being channeled from the brain and cerebellum into the medullary appendix [spinal cord], is then carried outward, gently wending its way into every part of the nervous kind, and irrigating the whole of the nervous system. The expansion of the animal spirits throughout the whole depends upon the equal emanation of this juice; and the substance of these spirits, in fact the hypostasis of the Sensitive Soul itself, is founded on the diffusion of this humor.[33] If the animal spirits are left to themselves, they follow the motion of this juice, flowing with it on the same circuitous course, and are quietly spread about. But meanwhile, when occasion is given, the same spirits assume a different and more rapid evolution, like a breath moving upon those waters. For just as in a river, various kinds of waves are thrown up by the winds or by things cast into it, so the animal spirits, when awoken by objects, go forth to carry out the functions of sense and motion, stretching hither and thither within the nervous kind, and being agitated there in other ways.[34]

The analogy to waves could imply that the animal spirits are materially similar to water. But here Willis considered the metaphor misleading, and switched gears, comparing them to rays of light:

> But since it is not trivial to distinguish spirits and waters by their motions and consistency, perhaps it will better illustrate the matter if the spirits [...] are compared to the beaming forth of different rays of light. [...] The animal spirits irradiate and swiftly cross all parts of the nervous system, both primary and secondary, so that light is scarcely carried faster through a diaphanous medium, than the communication of spirits is made from one end of the nervous system to the other.[35]

Thus, according to Willis, the animal spirits are like light dissolved into a nervous juice. This juice, "itself of very subtle parts," is a vehicle for the even more subtle

[30] The fiber, rather than the cell, was at this time thought to be the basic unit of physiological function. Related to this was the commonly accepted notion—which lasted well into the 18th century—that the tendon, a fibrous tissue, is the contractile organ of muscle. The non-tendinous 'flesh' of the muscle was thought to be a nutritive packing material which moves aside as the tendon contracts. See Canguilhem (1992), Grmek (1970), Clarke (1968), Hierons (1964), Wilson (1961). On ancient sources of this idea see Solmson (1961).

[31] Willis (1664, Chap. 19).

[32] Or "humor" or "latex." "Latex" and "humor" were Latin terms for "fluid," but medical tradition had given them the specialized meaning of a bodily fluid or secretion. "Nervous juice" is Pordage's translation of the Latin "succus nervosus." A better rendering might be "nerve sap," which preserves the sense of a nutritive fluid and a branching, fibrous structure. However, for its poetic appeal, as well as its currency in the literature on Willis, I prefer the expression "nervous juice." See Blastholm (1950, p. 205 ff.).

[33] *"Ab aequabili hujus emanatione, spirituum animalium per totum expansio dcpendet; atque horum substantia, imo ipsius* Animae Sensitivae hypostasis, *in* ejusdem humoris diffusione fundatur." (Willis, 1664, Chap. 19, emphasis in original.) "Hypostasis" is discussed in note 65 below.

[34] Willis (1664, Chap. 19).

[35] Willis (1664, Chap. 19).

animal spirits, which diffuse through it "like a breath moving upon those waters." But the juice is also a "rope" (*retinaculo*) "whose viscosity retains them so that they cannot dissipate, but remain in the same place, as in a pattern or connected series."[36] This is a chemical model, and the role of the nervous juice as both vehicle and obstacle to the movement of spirits is not far from the chemical mechanism Newton would later propose in his second paper on color and light.

3.3. The communication of spirits

Willis went to considerable lengths to define what he called the "communication of spirits" which takes place along a nerve. The primary or most simple form he envisioned was that of a wave. This metaphor seems to arise from the same considerations that would later suggest it to Newton:

> We notice, that as often as the exterior part of the soul being struck, a sensible impression, as it were the optic species, or as an undulation or waving of waters, is carried more inward.[37]

In addition to a wave, Willis also refers to a vibration, as in the plucking of a stringed instrument. Here his examples are drawn from sensation as opposed to motion.

> In sensation, the fibers receive first and most immediately the impressions of sensible things, and retain their forms by a modification of the internal particles (as musical strings do the pluckings of a pick or thumb), and represent the various approaches of the object by similar motion of the fibrils, as by a moveable and fluid stamp, whose idea the nerves convey as far as the head.[38]

Willis did not propose, as Descartes had, that the nerves or nerve fibers are actually pulled tight. He used the figure of a stringed instrument, but he imagined a different kind of tension, a tension created by the continual and tonic flow of animal spirits.

> [The animal spirits] being distributed by the brain, as from a fountain, along the nerves over the whole body, imbue, irradiate, and fill all parts, inducing in each a certain tenseness. So that the ducts of the nervous structures, like cords lightly strung, are extended from the brain and its appendages in every direction to all peripheral parts. And these are so strung and so actuated by a certain continuity of the soul, that if either extremity be struck, the blow is forthwith felt throughout the whole.[39]

As for the waveform of the vibration itself, Willis compared it to "a moveable and fluid stamp" (*mobili and fluido charactere*): more literally, a movable printing block whose shape is continually adjustable. In other words, this vibration is not of a uniform character, its waveform is not stereotyped. Instead, various kinds of forms and figures can be carried by it. This explains how the nervous juice can carry not only raw impulses or sensations, but "the determinations also of form and figure."

Taking the final step into a corpuscularian model, Willis proposed that the pattern or *systasis* (combination, configuration) of spirit particles can be imprinted with forms. When such particles are "concatenated and adhering to each other," they form *species*, i.e., molecular units. To describe the organization of such units, Willis uses the metaphor of soldiers in phalanxes and formations. But in addition to such static arrangements, the spirits can undergo *metathesi* (changes of sequence, transpositions), and *gesticulatione* (gesticulations, gestures). Not accidentally, these dynamic attributes are described in semantic terms: a transposition of letters in a word forms a different word, and a change of conformation of limbs in a gesture forms a different gesture. The pattern and dynamic motion of the animal spirits is therefore a kind of language, which is transmitted in the nerves.

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[36] Willis (1664, Chap. 19), translated by Clarke and O'Malley (1968, p. 161), translation altered.
[37] Willis (1664, Chap. 11), translated by Pordage.
[38] Willis (1664, Chap. 19).
[39] Willis (1672), translated by Foster (1901, p. 275).

> The animal spirits being stationed at intervals within the individual muscles, beside the fibers in series, seem like so many distinct troops or companies of soldiers. When a new impression comes to them through the nerves, either outward from objects, or inward from the encephalon, then immediately, as if stationed in a watch-tower, they are ordered into various special groups and formations, to carry out movements or sensations of this or that kind. [...] The disposition and arrangement of the animal spirits constitutes the hypostasis or essence of the Sensitive Soul, which truly is just a certain configuration or shadowy subsistence of those spirits (which like atoms or subtle particles, concatenated and adhering to each other, are configured into certain species). Furthermore, the faculties of that soul arc derived from the various transpositions and gesticulations of the same spirits within the aforementioned organs of the encephalon and nervous system.[40]

3.4. The muscle as an autonomous generator of force

Descartes understood the nerve as a conduit of force, a structural entity materially involved in a transfer of force from the brain to the muscle. In contrast, Willis understood the nerve as a conduit of *information*, not involved in the transfer of force but only in its *signification*. But to make this model work on the motor side, the muscle had to have its own autonomous capacity to generate force. The nerve could not carry anything more than an impulse, which would have to trigger or release an independent mechanism in the muscle. A physiological model for this process was devised by William Croone (1633–1684) in his treatise *De ratione motus musculorum*. Croone's treatise was published anonymously as a monograph, but was later appended to Willis's *Cerebri anatome*, again anonymously, giving rise to a confusion of authorship.[41]

Cartesian physiology explained muscular contraction as an inflation of the muscle, with consequent shortening of its length. Descartes never tested this idea, but many scientists in the mid-17th century took it up, and set out to test it experimentally. One type of test was to verify whether a real muscle did in fact change its volume after contraction. Another, more popular kind of test, was to demonstrate that a heavy weight could be lifted by filling a non-elastic bladder with water or air. (The bladder would be attached to the heavy weight, and upon inflation, would lift the weight off the ground.) The Royal Society records that Croone carried out a demonstration of this kind three years prior to the publication of his treatise.[42]

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[40] "Spiritus animales *intra singulos musculos juxta fibrarum series dispositi, totidem quasi militum turmae, seu manipuli distincti videntur; qui omnes veluti in specula constituti, prout nova impressio iisdem, vel exterius ab objectis, vel interius ab enkephalo per Nervos advehitur, illico in varias formas and taxeis peculiares, pro* motu *aut* sensu *hujus out illius generis obeundis, ordinantur.* [...] *In* Spirituum animalium diataxi *and ordinatione, qualis modo describitur*, Animae Sensitivae hypostasis *sive essentia consistit, qua nempe solummodo est spirituum illorum* (*qui velut Atomi, seu particulae subtiles sibi mutuo adhaerentes and concatenae, sub certa specie configurantur*) systasis quaedam *sive* umbratilis subsistentiae. *Porro istius Animae* facilitates *ab eorundem spirituum intta praedicta enkephalon and systematis nervosi organa* varia metathesi and gesticulatione *dependent*." (Willis, 1664, Chap. 19, emphasis in original.)

[41] Croone's treatise is reviewed by Wilson (1961) and has recently been reprinted with an English translation (Croone, 1664). The reprint contains a rather contemptuous analysis of the treatise (Nayler, 2000). In fact, Croone's treatise is quite rigorous: considerably more so than *Cerebri anatome*, for instance, in terms of physical and physiological reasoning. Its only shortcoming is a perhaps excessive attention to detail. On the confusion of authorship with Willis see Hall (1974, Chap. 16), Nayler (2000, note 52).

Croone and Willis did not collaborate, since Croone was at Cambridge and Willis was at Oxford. But they probably did attend meetings of the Royal Society together. A brief biography of Croone is included in the reprint of his treatise (Croone, 1664). He was a founding member of the Royal Society and did experimental work in both medical and physical sciences. In contrast to Willis, his foundation was primarily in physics rather than chemistry: he has been called "one of the earliest iatrophysicists" (Blastholm, 1950, p. 190). In his will he provided funds for two lecture series, the famous Croonian Lectures: one on the nerves and the brain, and the other on the nature and laws of muscular motion.

[42] Croone's demonstration, entitled "Experimental account of the raising up of a weight hung at the bottom of an empty bladder," took place on November 6, 1661. Nayler (2000) reviews this and other demonstrations in detail. See also Wilson (1961), Hierons (1964) and Blastholm (1950), who review the science of muscle physiology in the 17th century.

In his published treatise, Croone proposed a mechanical model of muscular contraction, based on the principle of inflation. He emphasized that the nerve transmits a tiny force not at all commensurate with the force required to lift an object. Croone used the words *vis* (force) or *impetus* (violent impulse) to describe this force.[43] In the details of his description we can see that he identified this force as a signal, and not what we today would call a force. First, he says, the nerve fibers are "agitated" (*concutiuntur*), and then "droplets of liquor" are ejected from their ends, "just as liquor leaps out at once when the piston of a syringe is pushed in very lightly."[44] This is still a hydraulic model, but here the piston needs to be pushed in only very lightly—just enough to cause a tiny droplet to come out—a much smaller force than would be required to inflate the whole muscle.

Croone seems to have hesitated between a hydraulic and a vibratory model, and he mentioned both in the main statements of his treatise, including the final summary. The vibratory signal which he proposed is transmitted through the membranes of the nerves and muscles, which are under tension: "It must be understood that these membranes while they maintain their tensions and due tone can be considered as behaving like a bell or as the purest glass."[45] (Here perhaps is a precedent for Newton's comparison of the nerve fibers to glass.)

But for such droplets to be effective, the entire work of muscular contraction must be activated by them. For this, Croone proposed that a chemical reaction takes place between the nervous liquor and the blood contained in the muscle. This reaction produces an effervescence in the blood, which pushes blood out of the arteries and into the flesh of the muscle. This effervescence—a chemical phenomenon—is the energy source for the independent force of contraction of the muscle. Croone defended this chemical hypothesis with a provocative jab at Cartesian mechanists:

> No one is such a novice in chemistry as not to know how great a commotion and agitation of the particles usually occurs from different liquors mixed with each other. This can be seen in the example just mentioned [*spirit of wine mixed with the spirit of human blood*] and also in plain water mixed with oil of vitriol, or in butter of antimony dissolved with spirit of nitre, and in an almost infinite number of other cases of this kind.[46]

Croone was confident, but the story did not end there. The science of muscle physiology was a fast-changing one in the 1660s, and the principle of muscle inflation was quickly challenged by theory and experiment, both in England and on the Continent. Foremost among the challengers was Nicolai Steno, whose *Elementorum myologiae specimen* (1667) sufficiently discouraged Croone that he refrained from revising his treatise for its second edition.[47]

In contrast, Willis held tenaciously to the Croonian theory and developed it further, in spite of the countervailing evidence. In *Cerebri anatome* (1664) chapter 19, Willis had proposed a model of muscular contraction very similar to Croone's, though less detailed: where Croone had likened the reaction in the muscles to an effervescence produced by a sulphureous substance (oil of vitriol, i.e., concentrated sulphuric acid) or a nitrous substance (nitre, i.e., saltpeter), Willis likened it to an *explosion*, produced by a *nitrosulphureous* substance, i.e., gunpowder.[48] In *De motu musculari* (1670), Willis elaborated on this model, defending the idea of chemical inflation with new arguments

[43] Croone (1664, Section 27).
[44] Croone (1664, Section 35).
[45] Croone (1664, Section 17).
[46] Croone (1664, Section 27), translated by Paul Maquet, translation altered. According to Canguilhem (1955) Descartes was contemptuous of chemists' vocabulary, which he considered to be 'outside of common sense.'
[47] See Wilson (1961).
[48] As Willis explained in *De Fermentatione* (Willis, 1659, Chap. 10), gunpowder was prepared by mixing nitre and common sulphur with charcoal dust.

and experimental evidence. He cited Steno with apparent relish, dishing out praise for his anatomy, but only to undermine his physiology. Willis even claimed to have observed an increase in the volume of a single excised muscle fiber placed under the microscope. In fact, his only deference to the criticism that had defeated Croone was to withdraw his specific claim about nitrosulphureous particles.

In making his stubborn defense of the Croonian mechanism, Willis was drawn to spell out in greater detail why such a mechanism was theoretically required. His argument reveals that he clearly understood the principle of the muscle as an autonomous generator of force. He pointed out that the conception of the nerve as a pressurized conduit of force makes the nerve equivalent to a lever: even if a lever gains some mechanical advantage, so that a smaller applied force can exert a greater effective force, the lever must bear the full effective force in the form of deforming stress. But the nerve is simply not a strong enough lever to withstand the stress required of it:

> In a crow or lever, and in other things reducible to a lever [...] the same force or impression may be continued, without the addition of any new force, from one term or end to the other, or from the first mover to the thing moved, which notwithstanding may be much increased in the way. [...] But to this there is required that the instruments of motion be sufficiently strong and tenacious in their whole tract; for otherwise the motive force being increased, the same breaking falls down before the designed action be performed.
>
> [...] There is another way of multiplying the motive force to a great degree, and also at a great distance, which is performed with the addition of new forces or fresh supplies, to wit, when the elastic particles, or those making the force, being disposed and shut up in private places, as it were little cells, afterwards, as occasion serves, are sent forth by a light contact or blast of a remote agent, into the liberty of motion, which they readily perform.
>
> [...] It seems impossible that a contraction so strongly performed by a muscle should be begun by the tender and immoveable brain, and continued through the small and fragile nerves, but that it must necessarily be supposed some motive particles are hid in the muscle, which, as occasion is given, are stirred up according to the impulse.[49]

Here Willis uses the word *instinctus*, the Latin equivalent to our modern word "impulse," a word which connotes not a force but a signal. Croone's word *impetus* was less modern since it still connotes an explosion, a violent and force-generating movement. But lest there be any doubt that Willis had fully understood the implications of his own theory, we see that in this 1670 treatise Willis speaks interchangeably of the impulse and the *symbol*, as when he says, "the inflowing spirits carry the symbol of performing contraction," or "the animal spirits, carrying the symbol of the motion to be performed."

With this word Willis had clearly cast aside all Cartesian moorings, and had firmly committed himself to a theory of communication.

4. Gassendi

In *De Anima Brutorum* (1672) Willis frequently cites a certain "skillful and cause-expressing man," "the most learned Gassendus," as an authority on whom he is alternately proud and reluctant to stand.[50] This man is Pierre Gassendi (1592–1655), a French savant known in his day as the principal adversary of Descartes. According to Canguilhem (1955), Willis's numerous citations are merely show, a scholarly flourish "to allege some authority for a theory which he knows to be novel and surprising to his contemporaries." But why second-guess Willis? If by his own admission he was influenced by Gassendi, maybe he was. In fact, a cursory comparison of their writings on nervous transmission reveals so many similarities between Willis and Gassendi

[49] Willis (1670), translation by Pordage, translation altered.
[50] See for example p. 2, 4, 5, and 41 in the Pordage edition (Willis, 1672).

that they are too numerous to catalog.[51] It can be said without exaggeration that the entirety of Willis's doctrine, including the chemical theory of muscular inflation, was directly imported from Gassendi and only slightly elaborated.

Pierre Gassendi, when his name is known at all in our own day, is generally depicted as an unsuccessful adversary of Descartes, an 'alternative' mechanist whose misfortune was to be weak in mathematics. If Descartes' name belongs to a universal coordinate system, Newton's to a unit of measurement, and Willis's to a landmark of brain anatomy, Gassendi is commemorated only by a crater of the moon and a back street of Paris. Little of Gassendi's writing is available in English translation, and English scholarship on him tends to be confined to non-biological subjects.[52] His work, it is claimed, was less original than it was archival: he sought in the writings of Democritus and Epicurus an alternative to the medieval Aristotelian system of nature; but in contrast to Descartes (a revolutionary modernist and a purely original thinker), Gassendi is cast as a pedant, a commentator on the ancients, a humble and tentative spirit.[53] However, this assessment has been gradually changing, at least among scholars, with a growing realization of Gassendi's contributions to the genesis of modern physics and chemistry, and a new appreciation for his biological theory of mind.[54]

In the decade before his death, Gassendi compiled all of his learning into a lengthy Latin treatise, the *Syntagma Philosophicum* ("System of Philosophy"), published in 1658.[55] This book was abridged by Francois Bernier into a more readable French version, the *Abrégé de la philosophie de Gassendi* (Bernier, 1684). The *Abrégé* became quite popular in its day, far surpassing the influence of the *Syntagma*, and it was on the basis of the *Abrégé* that Gassendi gained a considerable following in the late 17th century. For the purpose of this study I have used the *Abrégé* rather than the *Syntagma:* among other reasons, Gassendi's Latin is notoriously prolix and labyrinthine, whereas the style of the *Abrég*é is clear and its structure is more transparent.[56]

[51] For example compare Willis (1664, Chap. 19) with Bernier (1684, Vol. VI, book 6, Chap. 1; & Vol. V, books 5 & 6).

[52] A selection of Gassendi's writings is translated by Brush (1972). The *Institutio Logica* is translated by Jones (1981a). Some other portions of Gassendi's works are translated in unpublished dissertations by Clotfelter (1997) and Johnson (1993). English-language scholarship includes: Brett (1908), Jones (1981b), Joy (1987), Brundell (1987), Lennon (1993), Osler (1994). A better body of scholarship exists in French: I recommend the book by Bloch (1971), especially for Gassendi's sources in alchemical and classical Greek writings. The work of Rochot is highly respected, notably his book on atomism (1944); an older study by Thomas (1889) is also good. As a general introduction to Gassendi I recommend the book edited by the Centre international de synthèse (1955), which includes essays by a number of prominent scholars. An almost identical book was published by the Comite du Tricentenaire de Gassendi (1955), but is harder to find. See also Rochot (1964); Murr (1992); Colloque (1994); Colloque (1997); Mazauric (1998).

[53] Koyré goes as far as to say: "Gassendi was not a very good physicist, a bad mathematician, and a rather second-rate philosopher. [...] In the history of science, in the strict sense of the word, his place is not very important. He invented nothing, discovered nothing, and as M. Rochot (who cannot be suspected of anti-Gassendi sympathies) has observed, there is no law of Gassendi. Not even a law that would be proven false. But the judgment cannot stop there, it is even worse. For as strange as it may seem, this stubborn adversary of Aristotle, this resolute partisan of Galileo, remained entirely alien to the spirit of modern science, particularly to the spirit of mathematization which animates it." (Kogré, 1955, and 1965 p. 176).

[54] See Bloch (1971), particularly Chapters 7 and 8. Probably Gassendi's most fundamental contribution to science was his synthesis of the ancient physical systems of the Epicureans and Stoics (see notes 75 and 76 below). Both Boyle's chemistry and Newton's physics are heavily indebted to Gassendi in this regard.

[55] The *Syntagma Philosophicum* was published as volumes 1 and 2 of Gassendi's *Opera Omnia* (Lugduni [Lyon]: Sumptibus Laurentii Anisson and Ioan. Bapt. Devenet, 1658). This *Syntagma* should not be confused with an earlier *Syntagma* also by Gassendi, the *Syntagma philosophiae Epicuri.*

[56] See Brush (1972, p. 281), Koyré (1955), Thomas (1889, p. 24 ff.). Of Gassendi's Latin, Thomas says: "His style is pithy and tangled to excess; his quick and abundant phrases, rich with epithets and subordinate clauses, are too frequently redundant if not diffuse. One is reminded, in spite of oneself, of that 'windy loquacity' evoked by Tacitus, and which he identified with the meridional verve of his time." On the other hand, Koyré states that the *Abrégé* is a faithful exposition of Gassendi's scientific ideas, although it does contain distortions of his philosophical ideas. Since his philosophical ideas will not be discussed in the present study, the *Abrégé* can be considered a reliable source.

4.1. The nerve impulse

Gassendi's theory of the nerve impulse is developed in Vol. VI, book 6, Chap. 1 of the *Abrégé:* a section entitled, "What is the motor faculty of animals." This corresponds to *Syntagma Philosophicum*, Vol. 2, *Physics*, Section 3, part 2, book 11.[57] The arguments in this section are deliberate and rigorous, although free of mathematical formulas. Gassendi has been faulted for his non-mathematical style of reasoning, but in fact his method is quite consistent with modern practice. The goal of his reasoning is not to calculate, but to dissect: to reveal a hidden sequence of events, by carefully organizing a multitude of observations according to simple principles of exclusion. His approach is abstract and nonspecific, reminiscent in style of early 20th century genetics with its "germ plasm" and "factors." This style of reasoning has found greater success in contemporary biology and physiology than the axiom-laden style of Gassendi's contemporaries.

Gassendi begins his analysis of the nerve impulse with a review of in vivo experimental findings involving ligature or section of arteries, nerves, and spinal cord, and their respective effects on paralysis above and below the point of interference. He concludes that the nerve, not the artery, is the "mediating organ" of movement (the muscle being the "immediate organ"), and that a "virtue" must flow from the brain to the muscle via the nerve. He then addresses the same question which we have seen both Newton and Willis address, namely whether the nerve can conduct a force, or only a signal.

> For if the nerves, as is sometimes said, issued from a firm and solid origin, the attraction which occurs between the part that is moved and the origin of movement could truly be attributed to the nerves; but since the nerves issue from the marrow, which is a soft, tender and slack material, and since the nerves themselves at their origin are both very soft and very tender, consequently they cannot be fit for attracting the [*moving*] parts, nor for being the true and physical organs of movement. [...]
>
> What then can we say comes to the muscle from the brain, by the intermediary of the nerve, without which the muscle is not capable of moving? Certainly this seems to be nothing other than the commandment to move, which is somehow signified to the muscle by the arrival of the spirits transmitted by the nerve, such that without this front of spirits [*cet abord d'esprits*], the muscle remains sleeping, but if it has been excited thereby, as if awoken, it acts.[58]

Gassendi's manner of putting the question is both clearer and more complete than Newton's and Willis's. He condenses and brings together arguments which Willis makes in separate chapters and separate books. Furthermore, his use of the words "command" and "signify" clearly specify an information-bearing role for the nerve, and Gassendi drives home this point with the metaphor of a slave obeying the orders of a beautiful mistress:

> Nothing is transmitted from the brain to the muscle by the intermediary of the nerve, except this order, and this commandment, which is like the Will or the Appetite. And the Understanding, or Phantasy as mistress and directress, signifies to the tendon or to the muscle as to a slave, so that it should make such and such a movement, and that it should move such and such a body part.[59]

In designating the tendon as a contractile organ, Gassendi follows the standard medical opinion of his day.[60] However, in endowing it with its own force-generating capacity he explicitly differs from the Cartesian view, as he himself points out:

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[57] For commentary see Canguilhem (1955, Chap. 4). Bloch (1971) gives little additional information, noting only that it would be "interesting" to study Gassendi's biology more closely (see p. 439 note 27, and p. 268 note 162). Bloch cites three studies on that subject, one being Canguilhem's, and the other two being unrelated to the nervous system: Martin-Charpenel (1955), and Roger (1963, p. 135–140).

[58] Bernier (1684), Vol. VI, book 6, Chap. 1.

[59] Bernier (1684), Vol. VI, book 6, Chap. 1.

[60] See note 30 above.

> I know that most people attribute [*muscular contraction and tonic movements*] to spirits that come from the brain, which are transmitted with such impetuousness, and in such great abundance, that they inflate the nerves and the fibers like a kind of wind, or impetuous blowing, and by the disposition of the machine, compel the muscle to tense itself, and the tendon to retract itself, such that the movement will follow.
>
> But it is much more probable that the tendon, as I have said, should be able by itself to execute the commanded movements, and that the spirits which come from the brain are destined only to signify the commandment to the muscle, so that having been excited thereby, and alerted, the muscle should act by the natural force which it has. For as Aristotle says, the animal body is like a republic, in which every member it taught by nature to have enough sense and intelligence to understand and distinguish the orders which are signified by the superior and commanding faculty, and enough force within itself to execute these orders.[61]

4.2. The Sensitive Soul

The mention of Aristotle is characteristic of Gassendi, for it shows him willing to respect a thinker whose influence he himself had diligently combated (notably with his *Exercises in the Form of Paradoxes Against the Aristotelians*, 1624), and whose very name was anathema to most 17th century scientists (being associated with the inflexible dogma of medieval scholasticism). In fact, Gassendi's allegiance to Aristotle was one of his important contributions to modern science, since it was later absorbed by the British empiricists—whether consciously or not is another matter—and by their numerous modern offspring: Associationism, Behaviorism, Analytic Philosophy, Evolutionary Psychology, to name the most salient. This diverse collection of intellectual movements derive their origin, through Willis, from Gassendi.

In this context, the most important Aristotelian concept which Gassendi can be credited with saving is that of the "Sensitive Soul," the soul which man shares with beasts.[62] Aristotle (and the medieval scholastics) had divided the soul into three components: the vegetative or nutritive, the sensitive or appetitive, and the rational.[63] Descartes would discard the Sensitive Soul and propose only two entities: the body (a machine) and the rational mind (an immaterial soul). But the Aristotelian system was richer, in that certain cognitive faculties, such as memory and fantasy, were granted to some of the beasts. These faculties were both denied to beasts, and denied a physical basis by the Cartesian system. The concept of a Sensitive Soul enabled the Aristotelian system to mediate between mind and matter in a complex way which the Cartesian system deliberately renounced. And in the end the Aristotelian system, though more complex and less well grounded epistemologically than the Cartesian, left more room for scientific development.

Gassendi argued that if the Sensitive Soul is the cause of material effects, the Sensitive Soul must itself be material. It cannot be just a set of relations, as would be maintained by a Platonic view, since this would make the soul entirely passive. If the soul is able to effect material changes (such as muscular movements), it must also consist of a substance and thereby become the origin of action.[64] Therefore, what is really at stake in a theory of the nerve impulse is the material basis of the Sensitive Soul. This explains Willis's many allusions to "the hypostasis of the Sensitive Soul," a concept which Willis never coherently defines, but which we might render as "the formal model of the Sensitive Soul." Willis tells us that this formal model is

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[61] Bernier (1684), Vol. VI, book 6, Chap. 1.

[62] Willis himself (1672, Chap. 1) credits Gassendi with this concept.

[63] Aristotle, *On the soul* II, 3, 414 a 29 ff.; St. Thomas Aquinas, *Summa Theologica* Part I, Qu. 75.

[64] Bernier (1684), Vol. V, book 6, Chap. 2 ("What is the Soul of Brutes"), which corresponds to *Syntagma Philosophicum*, Vol. 2, *Physics*, Section 3, part 2, book 3.

equivalent to the anatomical structure of the nervous system, together with a corpuscularian description of its dynamic states.[65]

But this concept of the Sensitive Soul runs into difficulty when one considers the results of experiments with dissected muscles which, though living, are removed from the animal body. In such preparations, the nerve is not even necessary for the muscle to contract, provided that a sensory stimulus of some kind is given. It follows that not only the nerve, but the muscle too is in possession of a Sensitive Soul, since the muscle is independently capable of sensing and acting upon stimuli. This is just what Gassendi does argue, giving full rein to the vitalist and anthropomorphic implications of the idea.

> When one has freshly and skillfully dissected a muscle, and one holds it by the two extremities, and pricks it with a needle, it contracts, and brings together its two ends towards the middle. Can one say or think that the needle sends an abundance of spirits which go into the muscle to inflate it, and compel it to contract? Is it not more reasonable to imagine that the muscle is like an oyster, and that having like the oyster a Sensitive Soul, and consequently enough sensation and intelligence for knowing what is right or harmful for it, so also like the oyster it is excited, awoken, and determined by the pin-prick, as by a kind of message, to act, and to contract? One can say more or less the same thing for the heart, especially since Anatomy teaches us that it is nothing more than a double muscle, and since anyone can see that when a piece of the heart of a sea turtle, one hour after having been torn from the body of the animal, is still capable of sensation when pricked with a needle, this pin prick is probably doing nothing other than exciting what is left of the soul in there, and as if alerting it to contract itself, and to flee from the lesion which threatens its entire destruction.[66]

Such speculations entangle Gassendi only briefly, for in true philosophic spirit he transcends them through generalization. Ultimately he casts all interpretation aside and takes refuge in a kind of pre-Newtonian positivism, renouncing all but the basic premise that the muscle must have an autonomous mechanism of contraction:

> But I propose, you will say, that the muscle should be animated either by the Sensitive Soul alone, as with beasts, or by the Sensitive Soul and the rational soul, as with men, that it should have its own kind of sensation and understanding, such that it needs only to be pushed, excited, and alerted in order to understand what to do; I even propose that what should come to the muscle from the brain to excite and alert it should be very little, that it should be, for example, a lone and isolated little spirit, or perhaps if you will that this pulsion should occur by propagation, and by the continuity of spirits with which the nerve is filled from brain to muscle, in the manner of the light-stick of the Stoics which cannot be pushed at one end without the impression being felt at the other: I even propose that the Sensitive Soul is like a kind of very active and very mobile little flame, or if you prefer, with the authors of Atomism, that the muscle is composed of corpuscles or of atoms all in a very rapid agitation, and in frequent comings and goings, so that all these atoms being thus in continual and undissipating movement, need only some light pulsion to be directed to travel, to work, and to demonstrate and impress themselves towards a given place, and in a word, I agree to whatever story you please, but if the movement of the muscle occurs mechanically, it still remains to be explained how this takes place.[67]

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[65] Pondage's "Table of hard words" (see Willis, 1664) defines "Hypostasis" as "a substance or settlement, such as is in the bottom of an Urin." This indeed is the first meaning reported by the Oxford English Dictionary; but several others seem more pertinent: "2. Base, foundation, groundwork, prop, support;" "3. *Metaphorical.* That which subsists, or underlies anything; substance: (a) as opposed to qualities, attributes, or 'accidents'; (b) as distinguished from what is unsubstantial, as a shadow or reflection;" "4. Essence, principle, essential principle." (The last of these is most similar to the original Greek word, used frequently by Plato.) In *De motu musculari* (1670) Willis refers to "the moving animal spirits, whose companies or throngs constitute the hypostasis of the bodily soul." See also Willis (1664, Chap. 19), and Willis (1672, Chap. 1). In place of "companies or throngs," Willis also uses the word "contexture" (arrangment), borrowed from Gassendi who borrows it from the Epicurean atomists. I interpret Willis's statements to mean that the hypostasis of the Sensitive Soul is the ensemble of all possible arrangements and sequences of arrangements, of the corpuscles which take part in nervous transmission.

[66] Bernier (1684), Vol. VI, book 6, Chap. 1.

[67] Bernier (1684), Vol. VI, book 6, Chap. 1.

4.3. The nerve and muscle

If I understand this statement correctly, Gassendi reasoned that speculative hypotheses about the material nature of the Sensitive Soul cannot be tested until the mechanical basis of muscular contraction is discovered. In what follows, he seems to provisionally accept one particular model of the Sensitive Soul, and then to theorize about muscular contraction based upon that premise. This leads him to the explosion theory of muscular contraction which would later be taken up by Willis.

> May one not say, supposing the opinion of those who hold that the Sensitive Soul is a kind of very mobile and very active little flame, and that all parts of the muscle are composed of corpuscles in a kind of tonic movement, and ready to be directed at the slightest impression towards a given place; may one not imagine that the thing should happen,as is said nowadays, by a kind of explosion, such that what is transmitted from the brain to the muscle is like a tiny spark which suddenly causes, as in a canon, a movement, an agitation, in a word a kind of conflagration strong enough and powerful enough to tense the fibers and other parts of the muscle, and even to hold them for some time in this tension, but in such a way that it should not be with this conflagration in the muscle as with the sudden conflagration that occurs in canons, and in mines, but rather that the corpuscles of fire, or igneous spirits which arc in the muscle, being retained in the little fibers, and not able to leave suddenly, should be like a kind of wind, or very violent blowing, which strains toward a given place, and which holds the entire muscle inflated and tense, until the soul, alerted by another and different pulsion, should direct them into another movement which would go towards a different place, or should herself abstain from any effort, such that the spirits should be slackened, and should no longer cause this universal tension of the fibers, and other parts of the muscle? This is more or less what one might perhaps answer, but to tell the truth, this is still far from giving full satisfaction, though in my opinion we cannot hope for full satisfaction, since it would depend on knowing the nature of the soul, which is infinitely above the reach of our senses.[68]

Here we see that the entire model which Willis and Croone had so laboriously spelled out in their respective treatises, was sketched out almost as a throwaway argument by Gassendi, an hypothesis which he claimed could never be verified, since the nature of the soul is "infinitely above the reach of our senses."

Interestingly, in spite of this inherent limit to empirical knowledge of the soul, Gassendi's physiological exposition continues for another seven pages in Bernier's version. He adds details to his preliminary model, employing as a foil for his arguments the artifice of three "admirable things" concerning the nature of the soul: (1) that muscular movement is precisely controlled, though a single nerve gives off branches to numerous muscles; (2) that the nerve impulse is fast enough to govern the simultaneous and successive movements of the fingers of a Lute player; (3) that something so ethereal that its disappearance after death is undetectable (i.e., the soul), is capable of such power that it can lift and move an elephant (i.e., when acting via the muscles of an elephant).

In answer to the first riddle Gassendi argues:

> The interior substance of the nerve is nothing other than a mass of small independent cords which are as many little nerves joined together into the total nerve, such that, according to Aristotle's observation, the nerve can be cut lengthwise. For by this means it may happen that the spirits do not enter from the brain into the entire nerve, but only into the little nerves which are strung from the brain to the parts which must be commanded and moved.[69]

Here then is a precedent for the Newtonian "solid nerve" a half century before Newton. Another Newtonian concept, the light-like medium of nervous transmission, appears in Gassendi's answer to the second riddle:

> The nature of the spirits, which derives from that of the soul, is like rays of light no less speedy than those of fire, or of the sun. And since the nerves are continuous and stretch not only

[68] Bernier (1684), Vol. VI, book 6, Chap. 1.
[69] Bernier (1684), Vol. VI, book 6, Chap. 1.

from the brain to the heart, but even out to the muscles, and to the tendons of every part, the impression made at one of their extremities is immediately sensed and expressed at the other.[70] Canguilhem (1955, Ch. 4) attributes this concept to a Greek tradition of the "igneous soul," found in the writings of Plato, Aristotle, and the Stoics, and revived by Gassendi.

As for the third "admirable thing," the origin of the force of contraction, Gassendi states that it must resemble an explosion. He chooses this metaphor explicitly for its relevance to the *multiplicative* amplification of force which occurs in an explosion, which he explains by means of a corpuscularian argument:

> Even though [*the soul*] is a kind of very subtle and very minuscule flame, it can nevertheless by its extreme mobility do proportionately to the body of the animal what the flame in a canon does to the powder when it evicts the cannonball with such impetuosity, and makes the whole machine spring backwards from the force. We have shown in meteorites that this great force of the flame must be drawn from the frequency and the multiplication of the shocks of each corpuscle of which the flame is formed. However, the same must be said of this force by which the body of an animal is agitated, and one must conceive that it takes place and is excited by the frequent and multiplied agitation of the spirits, such that when we push against solid ground to be projected from it, or when one part presses itself against another to be reflected by it, or in a word, when the entire body, or any one of its parts is moving, the spirits inside it must be moved and agitated with a speed and frequency sufficient for this movement.[71]

In conclusion, the basic lines of Gassendi's argument are as follows: First, the nerve mediates muscular contraction, which can be inferred from lesion and ligature experiments. Second, the nerve carries a signal and not a force, since it is structurally too weak to withstand a sufficient force. Third, the medium of nervous transmission is like light or fire, because the signal travels too fast to be mediated by a fluid or solid medium. Finally, the muscle is capable of autonomous contraction in response to the nervous signal, and the mechanism of contraction is like an explosion, since only such a mechanism can provide the multiplicative amplification of force required. These arguments would go on to form the essential core of the neurophysiology of Willis and Newton.

5. Conclusion

According to Canguilhem, ancient Greek theories of neurophysiology were 'magical,' in the they invoked intelligent communication between the different parts of an organism, like the communication between a king and his subjects, or a republic and its citizens: i.e., a discourse between intelligent beings using signs or words.[72] Cartesian physiology broke from this vision entirely, since it invoked nothing other than direct mechanical linkages between parts. Newtonian physiology, on the other hand, seems to have preserved something of the ancient view by calling for a signal rather than a mechanical linkage. This signal must be encoded or decoded by an organ which 'communicates' using the signal. However, in the Newtonian version, the nature of this communication is not verbal, but entirely mechanical.

Through the writings of Gassendi, Willis and Newton, we can trace the evolution of this concept of mechanical communication. Gassendi first made the critical distinction between signal and force, since he displaced the primary force-generating element from the brain to the muscle: this means the brain is not a pump, like the heart, but rather, a command center whose signals must be executed peripherally. In Gassendi's metaphor, the muscle is a powder-keg waiting for the spark of the nerve to ignite it. But a spark is not a weightless and immaterial substance, or else it could not affect material outcomes. The spark is equivalent to a weak force transmitted across a weak material, with subsequent amplification. The crucial difference between signal and force, or between

[70] Bernier (1684), Vol. VI, book 6, Chap. 1.
[71] Bernier (1684), Vol. VI, book 6, Chap. 1.
[72] Canguilhem (1965, Chap. III, Section 2), "Machine et Organisme." See also Espinas (1903).

Gassendi's model and Descartes', is the requirement for an effector organ, i.e., a distinct mechanical system with its own energy supply, which can amplify the signal.

In spite of his materialistic concept of a signal, Gassendi remained partly attached to the verbal or 'magical' kind of communication, since he thought that organs such as muscles have a 'Sensitive Soul' which endows them with quasi-intellectual faculties of interpretation and prediction. (For instance, they contract in response to a pinprick because they anticipate their potential demise.) In contrast, Willis spoke of a "symbol" traveling on the nerve, but he understood the properties of this symbol (or at least its motor properties) in purely mechanical terms. He did not invoke anthropomorphic faculties for the effector organ. However, he did impute anthropomorphic tendencies to the spirit corpuscles themselves, in fanciful passages where he described the spirits rushing about the nervous system like platoons of soldiers, growing restless and wild after too much confinement, becoming spasmotic, etc.[73]

Willis also made another important step beyond Gassendi, with his concept of the 'hypostasis of the Sensitive Soul'. By this he meant the formal basis, or the corpuscularian model of its function. The notion of a formal model of the soul was one of Willis's chief contributions to the emergence of physiological psychology. By casting the Sensitive Soul in corpuscularian terms, Willis called for a "thinking machine" in a way that Descartes could not. Descartes' machine was a walking machine, a talking machine, a behaving machine, but not a thinking machine. The notion that memory itself is mechanical would have been unacceptable to Descartes.

But in what sense was Willis's formal model really different from the Cartesian—other than in the wider scope it could grant to mechanical explanations? In a corpuscularian model of the Sensitive Soul, is not the soul reduced to a machine exactly as Descartes reduced the body to a machine? And is not this just a more extreme form of the basic Cartesian doctrine? If so, then in Willis as well as in Descartes there is still an inherent dualism. This is a fundamental obstacle to the science of Physiological Psychology founded on Willis's example, and I think it explains the alleged 'relapse' of gifted physiologists such as Sherrington or Eccles into metaphysical dualism.

The human mind, especially the mind of the physiologist, is not containable in a mechanical model which the human mind itself has originated. Furthermore, and as Descartes himself understood three centuries before Freud, *symbolic* thought is very resistant to a physiological description.[74] Thus, the Cartesian system of mind and matter is more tenacious than it appears at first inspection. But the Cartesian system had one fatal flaw: the Cartesian machine.

Descartes and Newton gave radically different definitions of what it means to be a machine, due to their different assumptions about the fundamental structure of matter. According to Descartes, every movement of a machine is the result of collisions between inert corpuscles which fill space completely. Descartes did not recognize the existence of void space, nor did he allow matter to have intrinsic activity or dynamism. Newton, on the other hand, recognized void space between corpuscles, and as a corollary, he allowed corpuscles to have intrinsic activity, endowing matter with dynamic properties such as cohesion, gravitation, and fermentation. Therefore, a Newtonian machine can be intrinsically active and even non-deterministic, whereas a Cartesian machine can only passively execute the consequences of its prior state. The concept of

[73] For example Willis writes in *Cerebri Anatome*: "The air or aerial particles, so long as they are free and unmixed, create no rush or tumult, yet when closely confined in clouds, or in machines, or brought into contact with sulphurous and other elastic corpuscles, being forthwith made wild, burst forth into often dreadful meteors, namely winds, whirlwinds and thunder. In the same way the animal spirits, so long as they are pure and are carried in the open spaces of the brain and its appendages, behave tranquilly enough, but when shut up within muscles, and these permeated with sulphurous particles from the blood, and sometimes with heterogeneous matter in other places, become exceedingly impetuous, that is elastic, or spasmodic." (Willis, 1664, translated by Foster, 1901, p. 274.)

[74] See; Riese (1972).

intrinsic activity—the notion that matter has its own intrinsic tendency to change—that change comes from within as well as from without—was Newton's radical break from the Cartesian system. Newton's chemistry and optics both depend crucially on matter that is intrinsically active. Even gravitation, according to Newton, depends on a force transmitted by active particles acting at a distance. Newton's neurophysiology, built upon a foundation of chemistry and optics, is no exception.

But this concept of intrinsic activity, which proved so indispensable to Newton, had long roots in alchemical modes of reasoning.[75] In fact another current that flows through Newton, Willis and Gassendi is their chemical and alchemical work, and this connects them at least as strongly as their theories of the nerve impulse. The synthesis of alchemy with Greek atomism, which gave birth to modern chemistry, was not performed overnight by Newton and Boyle. Its concepts and models were laboriously weighed and tested for a half century or more by many other thinkers, among whom the most prominent were (strangely) Willis and Gassendi. The new corpuscularian science of chemical transformations required a new model of the fundamental structure of matter—one which combined the theoretical consistency of Greek atomism with the practical wisdom of medieval alchemy. This project was a primary and career-long focus for Gassendi, Willis, and Newton, each in turn.[76]

[75] The alchemists, following the ancient Stoics, represented nature in a biological rather than a mechanical way. They did not make the modern distinction between organic and inorganic matter. For them the phenomenon of fermentation was the paradigm for all types of substantial transformations. The infamous Philosopher's Stone was a product of this kind of reasoning. It was thought to be a kind of leaven, "capable of fermenting, converting and altering metals by means of a certain digestive heat which brings out the potential and latent properties," according to Walter Pagel (1982, p. 261). See also Isler (1968, p. 59 ff.); Partington (1961, Vol. 2, Chap. 6). On Stoic physics see Long and Sedley (1987, Vol. 1), Partington (1961, Vol. 1), Sambursky (1956), Verbeke (1945).

[76] Willis's first published book, *De Fermentatione* (1659), was a corpuscularian theory of fermentation. It was one of his most influential works, and was read well into the late 18th century: see Isler (1968, p. 57 ff.); Davis (1974, p. 81 ff.); Canguilhem (1955, Chap. 3). Those influenced by Willis's fermentation theory included Newton, Hooke and Huygens; Stahl and Boerhaave adopted his theory completely (Finger, 2000; Partington, 1961, Vol. 2, Chap. 8). Willis was especially famous for applying corpuscularian chemistry to clinical diagnosis. He was one of the founding fathers of the iatrochemical, or medical-chemical school. See Isler (1968, p. 57 ff.); Debus (1965, 1974); Davis (1974); Foster (1901, Chap. 5); Thackray (1970). Isler (p. 119) speaks of "the tendency toward kinetic and energetic explanations of natural phenomena" which underlies Willis's "revolutionary ideas on nerve action." Canguilhem (Chap. 3) more conservatively sees in Willis "a vague and distant premonition of energetics [i.e., Lavoisier's science of heat and respiration]."

Willis's debt to Gassendi is demonstrated by Bloch (1971), who argues that Gassendi made "the first serious attempt" to give alchemy a corpuscularian basis. In fact, according to Bloch, it was Gassendi who coined the term "molecule" (Bloch, 1971, p. 267 ff. & p. 445 ff.). The corpuscularian chemists of the late 17th century, including Boyle, Sylvius, Glisson and Willis, were openly followers of Gassendi. An amusing example is the title of a treatise written by one of Willis's mentors, Walter Charleston: *Physiologica Epicuro-Gassendo-Charlestoniana: a Fabrick of Science Natural upon the Hypothesis of Atoms* (published 1654). See also Kuhn (1952).

Newton's interest in alchemy is the subject of a recent mass-market biography, *Issac Newton: The Last Sorcerer*, by Michael White (Addison-Wesley, 1997), as well as the more scholarly studies of Dobbs (1975), Rattansi (1972), Westfall (1972), Basu (1991). During the academic phase of his life, Newton was continually involved in alchemical experiments. In the 1670s he worked with particular intensity on experiments aimed at a corpuscularian theory of fermentation (Dobbs, 1975, p. 202, 218; see also Heilbron, 1979, p. 64 ff.). In Query 31 of the *Opticks*, Newton spoke of fermentation as "a general law of nature" on par with gravity and the cohesion of bodies; this view is also found in manuscript drafts of the *Principia* (Dobbs, 1975, p. 202). In his second paper on color and light (Newton, 1675), Newton gave chemical powers to light: thus accounting for the interaction between light and matter. In addition he spoke of the "sociabilities" of aethers: Willis had used similar language in *De Fermentatione* (see Willis, 1659, Chap. 12, e.g.: "Salts love to be united to the rest, and to be made into hard and solid substances; and being destitute of the company of the rest, presently to enter into new friendships, and desire only not to be joined to any opposite.").

This and other connections between Newton and Willis have been obscured by a misinterpretation of the role of chemical concepts in Newton's thinking. For example Canguilhem (1955, Chap. 4) and Williams (2000) either ignore or actually deny the chemical aspect of Newton's neurophysiology. This is not only factually wrong, but obscures important insights into the origins of Newton's ideas.

Thus the same people and the same historical period which gave us a revolutionary new concept of the soul, also gave us a new concept of the fundamental structure of matter.

This may be nothing more than a fascinating symmetry of history—but more likely it has a lesson to teach us. One way to interpret this lesson would be to say that the different disciplines of science are linked at their conceptual foundations, so that a change in the basic premises of one discipline can have unforeseen consequences on the development of another discipline. A more general, and perhaps more profound interpretation, is to say that knowledge is a tree with many branches, all of which stem from a single trunk—this trunk is the human mind with its inherent and inherited limits.

Acknowledgments

I gratefully acknowledge the four teachers and historians who fired my imagination and encouraged this work. Dr. Samuel Greenblatt, M.D., taught me the history of neuroscience, fostered my first attempt at historical research, and gave me the example of his own work, which is of the highest intellectual caliber. Dr. Hansruedi Isler, M.D., heard a preliminary version of this paper at the 2000 meeting of the International Society for the History of the Neurosciences, after which he discussed the paper with lively spirit and profound erudition, and emphatically urged me to investigate Gassendi. Dr. Robert Glassman fired my imagination with his poster, "Counterpoint between parsimony and conjecture about neural "vibrations" from 1749 to 1884: Paradigm gap at the mind/brain junction?" (Society for Neuroscience Abstracts Vol. 24 (1998), #95.1.) Dr. Harry Whitaker, editor of *Brain and Cognition*, backed this work with the confidence of an investor, and suggested ways to clarify and concentrate its thesis. I also thank Dr. James McIlwain, M.D., and (soon to be Dr.) Steven Thomas for reading drafts of the manuscript and providing valuable suggestions.

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