Foundations of Human and Animal Sensory Awareness: Descartes and Willis

Deborah Brown, Brian Key

Abstract: In arguing against the likelihood of consciousness in non-human animals, Descartes advances a slippery slope argument that if thought were attributed to any one animal, it would have to be attributed to all, which is absurd. This paper examines the foundations of Thomas Willis' comparative neuroanatomy against the background of Descartes' slippery slope argument against animal consciousness. Inspired by Gassendi's ideas about the corporeal soul, Thomas Willis distinguished between neural circuitry responsible for reflex behaviour and that responsible for cognitively or consciously mediated behaviour. This afforded Willis a non-arbitrary basis for distinguishing between animals with thought and consciousness and those without, a methodology which retains currency for neuroscience today.

Keywords: René Descartes, Thomas Willis, consciousness, animal soul, structuredetermines-function principle, immortality.

1. Introduction

1664 marked the year of publication both of René Descartes' *Traité de l'homme* and Thomas Willis' *Cerebri anatome*, although Descartes' treatise was written much earlier (between 1629 and 1633) and had appeared in Latin in 1662. Placed side-by-side the works are striking both for their similarities and their differences.

A strict mechanist, Descartes sets out to uncover the principles governing the functions of the human body as if it were a "statue or machine made of earth"— that is, to describe all "our functions which can be imagined to proceed from matter and to depend solely on the disposition of our organs" (AT 11, 120; CSM 1, 99). The contrast is with all those functions we possess as human beings that depend on the faculties of the rational soul. The rational soul is really distinct from this automaton that is the human body, and there is no other soul—vegetative or sensitive¹—needed to explain the vital and sensitive functions of an animal

¹ Tripartite divisions of the soul since Antiquity distinguished (1) the vegetative soul, which governs nutrition, cardiovascular functions, respiration and reproduction and associated motor functions, (2) the sensitive soul, incorporating all the functions of the external and internal senses, including the *communis sensus* (common sense), and corporeal imagination

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Deborah Brown, Brian Key, Foundations of Human and Animal Sensory Awareness: Descartes and Willis, © Author(s), CC BY 4.0, DOI 10.36253/979-12-215-0169-8.06, in Andrea Strazzoni, Marco Sgarbi (edited by), Reading Descartes. Consciousness, Body, and Reasoning, pp. 81-99, 2023, published by Firenze University Press, ISBN 979-12-215-0169-8, DOI 10.36253/979-12-215-0169-8 body. These functions include non-conscious sensory processing and appetite; the circulation of the blood and respiration; digestion, nutrition, growth; sensory processing and reflexive behaviours; indeed, any of the functions we share with animals. Here, as elsewhere in Descartes' anatomical treatises, the explanatory strategy relies on a kind of "reverse engineering," appealing to the same principles that one would apply in dissecting and analysing the movements of a clock or other automaton. He first identifies a function; then proceeds to identify the structure responsible for performing that function; and then attempts ultimately to subsume the explanation under the laws of mechanics.

Willis' explanatory strategy also involves a commitment to iatromechanics, but one tempered by his iatrochemistry (Arráez-Aybar et al. 2015). His explanations stop at the level of describing anatomical structures and chemical reactions that either promote or inhibit the activity of the animal spirits. Willis analyses the "nervous juices" or animal spirits that flow through the nerves and account for sensory processing, storage, and retrieval, as well as all muscular movement in the animal body, as mixtures of chemical particles. These include familiar active (Paracelsian) and passive principles (active: mercury or spirit, sulphur or oil, and salt; passive: water, phlegm, and earth) but also nitro-aerial particles (Eadie 2003, 16). Whether he thought that these chemical properties were basic or reducible to the properties like those of Cartesian physics (e.g., size, shape, motion) is obscure, but also probably irrelevant. The "nitrosulphureous particles" (Willis 1681a, 129) in the animal spirits are essential to explaining how the animal spirits go off with a bang in the brain when they need to produce a fast muscular reaction at a distance. The matter of the brain and nerves, Willis hypothesized, is too "tender" to account for the speed of reflexes—a simple opening of a valve to release animal spirits into the nerves wouldn't cut it. Where Descartes' central metaphor for the nervous system was the slowly unwinding clock,² Willis' was gunpowder—an explosive substance able either to propel a projectile a considerable distance at great speed or to displace the quantity of animal spirits or nervous fluid already in the nerves (Willis 1681b, 40; Willis 1681a, 129). This, according to Willis, is how the animal spirits control muscular movements.

In this paper, we examine how Willis responded—perhaps unwittingly—to a specific challenge laid down by Descartes' bête-machine hypothesis, namely, the problem of locating a non-arbitrary basis for distinguishing between those

and memory, and (3) the rational soul, responsible for the functions of intellect and will. Drawing on Plato's tripartite division, Galen divided the animal into three separated yet integrated systems or "souls" centred around the functions of the liver, heart, and brain. The terminology persisted, as evident from Willis, despite refutations of Galen's anatomy in the 16th century, including by Paracelsus (Temkin 1973, 118 and 123–25). Prior to Descartes, it was unusual to deny that the sensitive soul was the seat of consciousness or even a kind of judgement. See Brown 2006, chapter 2.

² Descartes describes a nociceptive reflex—withdrawing the foot from a fire—of the imaginary humanoid body lacking a rational soul in *L'homme* at AT 11, 141–44; CSM 1, 101–3.

non-human animals capable of thought and consciousness and those that are not. Descartes argues that to demonstrate consciousness or thought, an animal would have to exhibit flexible, non-deterministic behaviour and be able to communicate their thoughts via language (broadly construed to include gestures or nonverbal signs). His conclusion is that no animal is capable of thought or consciousness (see Brown 2015 for discussion). We focus on Willis' examination of the distinction between the involuntary and voluntary nervous systems as addressing the question of whether animals can perform more than reflex functions. Willis' recognition that higher, cortical brain structures are involved in voluntary motor control was, we argue, prescient. Philosophically, it allowed him to make a distinction between the types of sensitive soul different brutes can be said to possess—finer grade distinctions than Descartes was prepared to allow but proved useful in accounting for different kinds of animal behaviours. Willis is thus clearly opposed to Descartes, but he is also opposed to Descartes' chief opponents, the vitalists, who conflated any kind of sensory processing with conscious cognitive processing. While Willis allows that some non-human animals are conscious and capable of a specific kind of thought, he accuses Descartes of committing a *non sequitur* in supposing that the animal soul would, if it were thinking, need to be both immaterial and immortal. Significant challenges to Cartesian metaphysics were thus advanced on the back of Willis' empirical investigations into the "seat" of consciousness in the brain.

We close this discussion by pointing to the legacy of Willis' scientific contributions for the science of consciousness today, including his recognition of the importance of the cortex to subjective experience, and his application of what was to become the foundational axiom of neurobiology, namely, that structure-determines-function.

2. Descartes' Wicked Thesis

L'homme is of a piece with other works by Descartes that describe the functions of the animal machine exhaustively in terms of mechanical processes without any mediation by conscious or cognitive processing. From the Discours de la méthode of 1637 onwards, he was widely known for what seemed to many a monstrous and repulsive thesis, namely, that all animals are simply unfeeling machines. Pushback was swift and deafening. As Leonora Cohen observed, each set of objections to the *Meditationes de prima philosophia* (1641) contains an objection to the bête-machine hypothesis despite the question being absent from the Meditationes itself (Cohen 1941). Criticism took various forms—from behaviorist assumptions that the complexity of animal behaviour and learning presupposed consciousness (at least that of the animal's awareness of its own wants (More; Cavendish)); from vitalist objections that the inertial quality of Cartesian matter could not explain the distinction between living (self-moving) and non-living (inert) things (Cudworth; More); and from teleologists committed to the irreducibly normative aspects of nature, which invoked God as the "other director" or his instruments-final

causes or "plastick natures" (Cudworth)—as basic presuppositions of physics (Gassendi; Cudworth; Leibniz).³

Descartes' reasoning for his wicked thesis is straightforward. First, behavioural criteria are too weak to ground the existence of souls as organising principles of living things. Since we can construct automata that satisfy the same criteria using only principles of mechanics that make no reference to minds or souls, this is easily demonstrated. If we built a doll that cried out when we touched it, we would not think it in pain (AT 6, 56; CSM 1, 140), so why would we suppose an animal crying out is in pain if we can explain its movements in the same terms we use to explain the construction of the doll? In regard to language, he wrote, "we see that magpies and parrots can utter words as we do, and yet they cannot speak as we do: that is, they cannot show that they are thinking what they are saying" (AT 6, 57; CSM 1, 140). Their lack of ability to communicate is not due to want of an organ of speech, but to want of a rational soul. Their responses lack the freedom of human action and speech. Animal behaviour is instead highly inflexible—it is either the exercise of a reflex or instinct (AT 4, 575; CSMK, 303) or behaviour "learned" through processes of (non-conscious) sensitisation and habituation, as when we train hunting dogs to respond to a secondary stimulus (a gunshot) to run towards not away from the direction of the shot. Nowadays, we would call this associative learning—conditioned responses that do not need to be mediated by cognitive processing to explain their existence. By contrast, our reason is a "universal instrument" that allows us to adapt our behaviour to changing circumstances without rehabituation (AT 6, 57; CSM 1, 140). Even in regard to what we would now think of as the more sophisticated operant conditioning models of behaviorism, this approach, by Descartes' reckoning, is dead in the water.

Second, if we can succeed in explaining the formation and development of organisms in mechanical, non-mentalistic terms, then postulating a distinct principle of life (soul) is redundant—a bit like postulating the existence of a gremlin to explain how the hands of a clock move. Descartes' account of embryogenesis—a zealous fable of how once particles are heated in the womb, they are stirred into circulation, compact (initially into the organs of the heart and brain as they cool), or being deflected by larger bodies and their containing membrane from their rectilinear tendencies, move into new areas to create all the diversity of organs that make up an animal body—is an example of this explanatory approach at full tilt (AT 11, 254, 274–76, 318, 516, and 599).

Finally, Descartes presents a host of dialectical arguments aimed at reducing his opponents' arguments to contradiction or absurdity. While it was orthodox to accept that the rational soul or mind of a human being was immortal, most would not have wanted to hold that the vegetative or sensitive souls of animals were immortal. While Descartes never professes to have proved that any soul

³ See Brown and Normore 2019, chapters 3 and 4 for a comprehensive discussion of the backlash against Descartes' views on animals.

is immortal, including the mind,⁴ he offers a slippery slope argument that if we accept that the rational soul is immortal and were to attribute it to any animals, then we would have to attribute it to all, including oysters and sponges, and that would be absurd (AT 4, 576; CSMK, 304). We can call the arrangement of matter in an animal that accounts for its self-movement and functions a corporeal or animal soul if we want, but we should not confuse that with the thinking and self-aware soul of the human being that can exist apart from matter (Letter to More, February 5, 1649: AT 5, 276).

There were various pressures on Descartes not to admit that consciousness or thought admit of degrees or that a soul could be sensitive but not intellective or volitional. His argument for the simplicity and unity of the soul is based on the assumption that anything which can sense, can form judgements and incite the will, and vice versa (AT 7, 86; CSM 2, 59). His seeming conflation of sensation and sensory judgement at the "third grade" of sensory response together with the volitional nature of judgement would entail that anything capable of sensory consciousness (at the second grade) must be capable of judgement and possess a free will (AT 7, 436–38; CSM 2, 294–95). The conflation of thought and consciousness (*Responsiones secundae*), and the implication of the *cogito* that anything which thinks/is conscious is simultaneously reflectively selfaware (CSM 2, 22), would have made it impossible for him to admit forms of consciousness that were not at the same time aware of the ego or mental substance that is doing the thinking.⁵ One cannot, on Descartes' view, be just a little bit conscious.

In advancing his slippery slope argument, Descartes did not, however, see the potential in his own forays into neurology for avoiding the regress from attributing consciousness and thought to a dog to attributing it to oysters and sponges. Descartes is right to be worried about *arbitrarily* drawing a line between conscious and non-conscious organisms, but his own commitment to what was to become the foundational axiom of the biological sciences—the *structure-determines-function* principle—should have afforded him the idea that such discriminations might at least be possible. While such a commitment appears to be excluded by his other metaphysical commitments, his tendency to rely on the assumption that if animals think or are conscious at all, they must meet the

- ⁴ He claims only that his argument for the real distinction of mind and body leaves open the possibility that the rational soul is immortal, an orthodox position, never that he has an argument for believing that it is immortal. What he does claim is that any argument for immortality depends first on a thorough understanding of physics, presumably to isolate those immaterial things which are candidates for immortality (AT 7, 13–4; CSM 2, 10), but this seems on the face of it to beg the question.
- ⁵ To our mind, Descartes was at least right to question the assumption that consciousness admits of degrees. As pointed out in Bayne et al. 2016, in much of the empirical work supporting the idea that consciousness comes in degrees, there is confusion over whether the evidence supports the existence of different degrees of being conscious or consciousness of stimuli with different degrees of clarity.

criteria for having immaterial, immortal souls like humans do, struck many, including Willis, as simply false—an ad hoc move designed to shore up his otherwise questionable metaphysical assumptions. Descartes uses physiological explanations based on the structure-determines-function principle in much of his work. For example, his explanation of the circulation of the blood in terms of the structures of the heart (chambers; valves; arteries; connecting fibres; etc) is a case in point. The question is why a similar approach to the nervous system would not enable us to make informed judgements about which animals do or do not have subjective experience.

For his slippery slope argument to be cogent, Descartes must be entitled to suppose that between *any* two species, there is an inevitable indeterminacy or "gray zone" (Walton 2017, 1513) from which it follows that it is impossible to decide whether both are conscious or only one is. Gray zones are difficult to defend in comparative neurobiology and worse still, if they are presumed to be transitive so that if there is a gray zone between species A and B, and one between B and C, there is one between A and C. Otherwise, from the fact that one is pretty sure that oysters are not conscious, but unsure whether birds are conscious, one would not feel entitled to conclude that apes are not conscious. One might well have good reason to deny that oysters are conscious based on facts about their neurobiology while regarding the jury as out on birds but there being no question about the consciousness of apes. The slippery slope is beginning to look more like a staircase. Compare the following analogy. The gray zone between mammals and fish that might make it hard to decide whether the lungfish should count as having lungs in the same sense that mammals do is not a reason for supposing that every animal, down to oysters and sponges, either has lungs or none do. Taxonomic issues may be complex, but are not, for all that, a free-for-all.

One can see the tension clearly in Descartes' argument that animal behaviour is invariably inflexible, based on the fixity of their organs. Machines are constrained to produce actions according to the arrangements of their parts, and there are mechanical limits on what can be added to any machine to increase the number and variety of functions it can perform. Think of a 17th century clock with a specified number of gear chains for each of its functions. On could only add more gear chains within limits, and even then, each of those would be fixed in terms of the functions it performs. For Descartes, the pineal gland by contrast enables a great variety of human actions because it can be moved this way or that, not only by the animals spirits, which are fixed in their movements, but also by the rational soul, which because of its freedom is not so constrained. The precise mechanism for this freedom of movement of the pineal gland is that the soul (in some unspecified way) can control the release of animal spirits from the gland (where they are distilled or better, sieved, from the blood; AT 11, 129; CSM 1, 100), directing them back into the nerves controlling the muscles. Descartes draws this conclusion about the "adaptability" and "diversity" of motions of the animal spirits in humans from his anatomical observations of the brains of non-human animals:

both in our bodies and those of brutes, no movements can occur without the presence of all the organs and instruments which would enable the same movements to be produced in a machine. So even in our own case the mind does not directly move the external limbs, but simply controls the animal spirits which flow from the heart via the brain into the muscles, and sets up certain motions in them; for the spirits are by their nature (*ex se*) adapted with equal facility to many diverse actions (AT 7, 229; CSM 2, 161; trans. alt.).

Aside from the fact that it is highly implausible to suppose that the pineal gland is capable of accounting for the unlimited variety of actions Descartes attributes to it, Descartes here seems inconsistent. As Willis observes, that many non-human animals have pineal glands should give us pause in thinking that this gland is the seat of a soul that is supposedly exclusive to humans. But if the pineal gland were the seat of the soul in humans, here would be a structure that, being shared by many animals, might give animals the flexibility to adapt their responses to changing circumstances just as it does in humans. And if we do not see animals adapt their behaviour in this way while having a pineal gland, could this really be the function of this gland in humans? (Willis 1681a, 106). Yet, Descartes is unwilling to countenance doubt about this issue, preferring instead to treat the reflex behaviours of animals, like that of dogs and cats when they futilely scratch the ground to cover their excrement (AT 4, 575; CSMK, 303), not as evidence of the absence of the right organ for the job, but as evidence of the absence of conscious thought. And that is to beg the question. The same question arises for the unthinking humanoid body of *L'homme*. Is it too stuck performing merely reflex actions, or could it adapt its behaviour because of its pineal gland and animal spirits? Descartes does not say. In the end, it is arguably Descartes himself who is guilty of arbitrarily drawing a line between conscious (i.e., human) and non-conscious (i.e., non-human) animals.

3. Willis on the Various Seats of the Various Souls

The term "neurologie"—the doctrine of the nerves—first appears in Samuel Pordage's 1681 English translation of Willis' 1664 *Cerebri anatome* (Willis 1681a, 136; Eadie 2003, 14). Unlike Descartes, Willis was a practising physician, a neurologist with a specialty in nervous pathologies. Willis headed a team of anatomists at Oxford, which included the brilliant anatomist, Richard Lower, and the astronomer and architect, Christopher Wren, who illustrated *Cerebri anatome* with exquisite neuroanatomical illustrations. Willis and his team crafted new ways of performing dissections of the brain, removing it whole and unrolling it instead of slicing it while still in the skull as was common practice (Willis 1681a, 55; Meyer and Hierons 1965a, 9–10). He used a variety of methods, some similar to ablation and nerve-muscle isolation techniques still used today, to theorise about the sensorimotor functions of the nerves and structures of the brain. And he synthesised a substantial amount of zoological work, contributing both to comparative neuroanatomy and to the classification of species into groups. Dissections of the brains of many different animals revealed to Willis a "notable Analogy" between the brains of humans and four-footed animals, despite the fact that the human brain is both larger and thicker (Willis 1681a, 61). He noted a different kind of analogy between birds and fishes, concluding that the brains of humans and four-footed creatures are "more perfect" than those of birds and fish (Willis 1681a, 56). What proceeds is a remarkably detailed neuroanatomical description that improved in accuracy on preceding accounts. As Eadie remarks, Willis was "well aware of the general configurations of the cerebral hemispheres, cerebellum, brain stem, spinal cord and the peripheral and autonomic nervous systems" (Eadie 2003, 15); enumerated the cranial nerves more accurately than had previously been thought possible; and importantly, localised brain functions in the cerebrum and cerebellum rather than the ventricles, as Descartes had mistakenly done (cf. Willis 1681a, 97).

Willis embraces many of the features of Descartes' and other mechanists' account of nerve function—the role of the animal spirits as matter that travels through the nerves causing the contraction or relaxation of muscles; the role of the brain in integrating and storing sensory information in a "natural (i.e., corporeal) memory" and issuing motor commands; the idea that the "corporeal soul" of animals is material and thus distinct from the intellectual soul of humans; and, crucially, the structure-determines-function principle. While others (e.g., the Dutch anatomist and microscopist, Jan Swammerdam) not long after were conducting experiments that questioned both the essential role of the brain in producing muscular movements and the idea that animal spirits cause muscular contraction by swelling up in the nerves of the muscles and relaxation by their sudden exodus from the nerves, Willis retained both of these distinctively Cartesian ideas. Swammerdam's experiments in the 1670's with an isolated nerve and thigh muscle (belonging to that "old martyr of science,"⁶ the frog) showed that a muscle would contract when an adjacent nerve was rubbed with a scalpel.⁷ This is purported to have shown that the brain was not a necessary cause of motor responses (Cobb 2002). When the same experiment was performed on a muscle immersed in water, the Cartesian view would predict that the volume of animal spirits in the muscle by displacement of water should increase. The fact that no increase in volume of the muscle was observed is reputed as having shown that the doctrine of the animal spirits is false. Cobb thus concludes that Swammerdam made a significant contribution to "exorcising" animal spirits from science (Cobb 2002, 397–98). But interestingly, Willis had performed similar nerve-muscle isolation experiments and provided an explanation consistent with the doctrine of the animal spirits. In his *De motu musculari* (1670; Discourse of Musculary Motion, 1681), he describes experiments in which the muscles of decerebrate animals move of their own accord, but infers that this is

⁶ As Hermann Helmholtz (Holmes 1993) apparently referred to the frog.

⁷ According to Sleigh (2012), Swammerdam's frog work was only published posthumously in 1737, in which case Willis would not have known about it.

due to the presence of animal spirits in the remaining nerves, which, containing "motive Particles" retain some of their explosive force and can cause slight movements. Indeed, the contraction of the muscle was hypothesised to be caused by the explosion within the muscle itself, which, expanding its girth, draws its ends together. Eadie attributes this idea even earlier to Gassendi (Eadie 2003, 16). Thus, for Willis, it is not just the volume of animal spirits but their activity that is responsible for muscular movements. Nor would Swammerdam's experiments have cast doubt on the role of the brain in controlling muscle movements. Very small reflexive muscular movements can occur in isolation but for any larger movements, the brain is necessary. The muscles of animal bodies could thus only "act," he writes, if the brain and nerves and a significant volume of animal spirits are involved (Willis 1681b, 40–1).⁸

In Willis' neuroanatomy, the cortex of humans and higher animals is the principal site for voluntary brain functions, being responsible for both the procreation of animal spirits and their circulation. Animal spirits—pure and highly active particles of matter—are distilled and "subtilized" from the blood which reaches the brain via the "sanguiducts." This blood has already undergone some distillation. Thinner and more volatile blood can only reach the head of an animal whose head is held high (Willis 1681a, 87–8). Humans and horses, for example, will thus have more superior faculties than those whose head is mostly near the ground and whose blood is, as a result, thicker and more sluggish. The brain is likened to an alembic (a still) or Balneo Marie, separating through heat and constant stirring the more rarified particles (Willis 1681a, 88; Willis 1683, 30). It is the *circulation* of the animal spirits and interaction between the corpus callosum and cortex, however, that is responsible for consciousness. We can feel the "endeavour or striving motion"—a nod in the direction of conatus or active motive force that one sees in the mechanics and psychology of Descartes, Hobbes and Spinoza—in the forebrain when we rub our forehead or temples in trying to recall something (Meyer and Heirons 1965b, 142–43). Indeed, Willis uses the same language as Descartes to describe this active force—as a "tendency" or a "stretching forth" (e.g., Willis 1683, 30; Brown 2021). All voluntary motions depend on the activity of the animal spirits in these sites, whereas the "Spirits inhabiting the Cerebel [in the hindbrain] perform unperceivedly and silently their works of Nature without our knowledge or care" (Willis 1681a, 111). The motions issuing from the cerebel are fixed, like those in an "artificial Machine or Clock" (Willis 1681a, 111).

It is thus not the cortical organs per se but the way the animal spirits interact with them that is responsible for consciousness and voluntary motions. The slowing or wearying of the motion of animal spirits in this location caus-

⁸ It is thus not obvious that, as Georges Canguilhem assumes, there was the equivalent of a Copernican Revolution in the physiology of movement revolving around the "dissociation of the notions of the brain and of the sensori-motor centres, the discovery of eccentric centres, the formation of the reflex concept," Canguilhem 1977, 127; also 77. At least Willis did not take his own ablation experiments to show that the brain was not necessary to explain reflexes.

es drowsiness and then sleep. Although their ceasing to flow to the "streaked membrane" (i.e., striatum of the subcortical basal ganglia) halts voluntary movement, their continued motion in the cerebellar cortex ensures continuation of vegetative functions during sleep (Eadie 2003, 21). Willis hierarchically orders and explains five pathological disturbances to consciousness—somnolence, coma, lethargy, carus, and apoplexy—in terms of different degrees of immobility of the animal spirits in the cortex or in terms of their dilution, as in the case of cerebral oedema, which Willis discovered through autopsies (Willis 1683, Second Discourse; Eadie 2003, 22). This could be brought on through head injury or narcotic or morbific matter that inhibits the mobility of the animal spirits or displaces them from their place in the cortex. Reflex behaviours—e.g., rubbing an injured spot while asleep—can be triggered by the striatum alone without the animal spirits passing from there to the callous body (i.e., corpus callosum). Without the engagement of the callous body, imagination is not engaged, and without the engagement of a second structure, the Appendix, to which animal spirits flow from the callous body, the functions of appetite and locomotion, are not consciously engaged. If the animal spirits reach the cortex, phantasy (imagination) and memory become involved, and voluntary conscious action is possible (Willis 1681a, 96). Through the cortex, the rational soul (which Willis regards as immaterial) can also direct the sensitive soul, although Willis does not explain by what power or mechanism it achieves this effect.

In Cerebri anatome, the cortex of humans and four-footed animals is described as lying on the outside of the brain, whereas in fish and birds it appears inverted relative to the ventricles (Willis 1681a, 75). Willis then describes the brains of fishes and birds as mostly "Cortical and Ashy" with very little medullary (i.e., white matter or nerve tracts), which is why when boys perform the "Experiment" of passing a needle through the head of a hen, she "lives and be well for a long time" (Willis 1681a, 93). Lacking the power to circulate animal spirits between the callous body and cortex robs these animals of phantasie and memory; it is instead from their striatum that the animal spirits issue forth to meet the sensitive and locomotive needs of these animals (Willis 1681a, 75–6). In later work, Willis locates the seat of the soul principally in the activity of the spirits in the Imagination or Phantasie and associated structures "for this is where all sensible species may be beheld" (i.e., become conscious) (Willis 1683, 41). Animal spirits that do not proceed higher than the striatum are reflected back through the nerves and produce only involuntary, reflex motions. When this happens, the animal spirits are reflected to the brain stem and spinal cord and from there to peripheral nerves and muscles without conscious or cognitive mediation (Eadie 2003, 26–7). The similarity in brain structure between fish and fowls accounts for the similarity of some of their bodily movements. Although fish have even less brain and blood than birds, the flight of birds is likened to "swimming in the air" (Willis 1681a, 77). Similarly, the optic chambers of both are almost as large as their brains, which accounts for their keenness of sight (Willis 1681a, 104). These are nice examples of the structure-determines-function principle at work in Willis' comparative neurobiology.

Imagination consists in the undulation or wavering of animal spirits that radiates out from the middle of the brain towards its circumference; memory consists in the reflecting back of animal spirits in the opposite direction from the outer reaches back to the mid-brain. There, appetite is stirred up and spirits flow to the nervous system (Willis 1681a, 91). Both imagination and memory are needed for consciousness and thought. The "gyrations and turnings" of brain structure create a "spiral circuit" from the forebrain to the back. The cortical substance is "uneven and rough with folds and turnings" that contain "cells or storehouses" in which "sensible species" (the forms or phantasmata of sensible things) are stored for recollection (Willis 1681a, 92). Memories consist in the animal spirits carving tracks of the object perceived in these cells, an idea similar to Descartes' account of corporeal memory as involving carved channels in the brain (AT 11, 360; CSM 1, 343–44). Willis states (Willis 1683, 36) that "a Character being affixed on the Brain, by the sense of the thing perceived, it impresses there, Marks or *Vestigia* of the same, for the Phantasie and the Memory then affected [...]." And

when the Prints or Marks of very many Acts of this Kind of Sensation and Imagination, as so many Tracts or Ways, are ingraven in the Brain, the Animal Spirits, often of their own accord, without any forewarning, and without the presence of an Exterior Object, being stirred up into Motion, for as much, as the Fall into the footsteps before made, represents the Image of the former thing [...] (Willis 1683, 36).

When these engravings on the cortex are triggered by association, animals can think of things not immediately present.

Like Descartes, Willis notes that humans have an advantage over other animals in their freedom of movement, but attributes this to a difference in the size and complexity of their brains, not to the operations of an immaterial soul:

hence these folds or rollings about are far more and greater in a man than in any other living Creature, to wit, for the various and manifold actings of the Superior Faculties; but they are garnished with an uncertain, and as it were fortuitous series, that the exercises of the animal Function might be free and changeable, and not determined to one. Those Gyrations or Turnings about in four footed beasts are fewer, and in some, as in a Cat, they are found to be in a certain figure and order: wherefore this Brute thinks on, or remembers scarce any thing but what the instincts and needs of Nature suggest. In the lesser four-footed beasts, also in Fowls and Fishes, the superficies of the brain being plain and even, wants all cranklings and turnings about: wherefore these sort of Animals comprehend or learn by imitation fewer things, and those almost only of one kind; for that in such, distinct Cells, and parted one from another, are wanting, in which the divers Species and Ideas of things are kept apart (Willis 1681a, 92).

Where there is less diversity of flexibility in behavioural response or where animals appear only to respond to things immediately present, there is less reason to suppose that they have sensitive souls that would presuppose cognition or consciousness.

Willis' attention to the differences in brain structures that serve as the "hypostases" of the involuntary and voluntary systems respectively afforded him a principled way of drawing a distinction between reflexive and voluntary behaviour. Reflexes are wholly explained in terms of sub-cortical neural activity directed by the striatum, whereas voluntary—consciously and cognitively mediated-behaviour is under cortical control. This, in turn, afforded him a non-arbitrary basis for halting Descartes' slippery slope. Where a species lacks a cortex, it can reasonably be inferred that it lacks imagination, memory, and thus the capacity for voluntary, conscious behaviour. That having been said, whether Willis always applied this finding consistently is less clear. If one reads the Cerebri anatome, one could well infer that fish and birds are not capable of consciousness or voluntary movements. But in a later text, De anima brutorum (1672; Two Discourses Concerning the Soul of Brutes, 1683), birds are cited as teaching other birds songs, which they recall from memory (Willis 1683, 37). Nor is it always clear when Willis speaks of the "soul" of various animals whether he is talking about the vital (non-sensitive) soul or a sensitive soul but one lacking imagination and memory or a sensitive soul featuring imagination and memory which may thus be supposed to be conscious. The details though are perhaps less important than the fact that the overarching framework is one that at least allows for such discriminations to be made.

While Willis' contribution to the medical sciences was profound, he seems to have made little dent on debates about the nature of the soul in philosophical circles. On a superficial reading, Willis can appear to be simply reinstating the tripartite division of souls from Antiquity, only grounding the division in a clearer understanding of the structures and functions of the brain. Willis thought, however, that his empirical results required us to rethink Descartes' twin metaphysical assumptions that no sensitive soul could be rational without being capable of intellectual abstraction and that no soul could be both rational and corporeal. While this, Willis acknowledged, was essentially the same view as Gassendi's (Willis 1683, 42–3), Willis' distinctive contribution was to provide an empirical foundation for Gassendi's distinction among corporeal souls.⁹ What was left to ground the distinction between the souls of brutes and human beings remained, however, a vexed question.

4. Psychologie or the Doctrine of the Soul

In the Preface of his *Two Discourses*, Willis affirms that the sensitive soul is corporeal, shared between humans and brutes, and distinct in kind not merely in degree from the rational soul, which he accepts is immaterial and immortal. He dismisses the idea that matter is incapable of perception and the idea that there cannot be two forms (rational and sensitive) actuating matter, finding

⁹ For a detailed exposition of the relationship between Willis' and Gassendi's ideas, see Meyer and Hierons 1965a.

more absurd the idea that two immaterial souls might compete to be united to the same matter and integrate their functions. Better to consider the sensitive, inferior soul as immediately conjoined with matter as its form (admitting of no real distinction) and as subordinate to a second but distinct kind of form in humans—the rational soul. Willis is thus a hylomorphist about the sensitive soul and a dualist about the rational soul. In chapter 1, Willis also dismisses the Cartesian objection that if we suppose that the souls of humans and beasts differ only in degrees of perfection, they "must alike be either Mortal or Immortal, and alike propagated *ex traduce* or from the Parent" (Willis 1683, 3). Neither horn of this dilemma was tenable. Holding the rational soul to be mortal and to proceed from the potentiality of matter would have been heretical, whereas holding the animal soul to be immaterial and potentially immortal was absurd. The idea that fishes and insects have immaterial and immortal souls is ludicrous, when their main function, Willis says, is to be "pickled" (i.e., preserved) in water for consumption by other animals (Willis 1683, 4). But how does Willis propose to avoid impaling himself on the first horn of this dilemma if the kind of cognitive and conscious capabilities we think of as definitively rational and, therefore, human, make their way in some form into his conception of the animal soul?

Willis acknowledges Descartes' and Digby's equation of the corporeal soul with the arrangement of the parts of the machine but regards this as too passive a model for understanding animal motion. The clocks and fountain automata on which Descartes models his animal body move only when moved by something else (the winding of a cord or spring). Animals, by contrast, contain the principle of life and movement within themselves. Willis describes a second slippery slope argument we see in the background of the Cartesian view—one based on the slide from attributing some cognitive faculties to brutes to attributing all cognitive faculties to them. People who deny cognition to brutes, suppose that:

for otherwise, if Cognition be granted to the Brutes, you must yield to them also Conscience [consciousness], yea and Deliberation and Election, and a Knowledge of Universal Things, and lastly a rational and incorporeal soul (Willis 1683, 3).

Descartes and Digby, despite their differences, come to the same wrong conclusion in Willis' mind, underestimating the power of God to make that of which they cannot conceive (Willis 1683, 3). They underestimate the workmanship of the divine craftsman in creating the providential order and the capacity for some form of thinking among brutes (Willis 1683, 29).

For Willis, the corporeal soul is extended throughout the body, a fact which can be seen when by cutting a worm, eel, or viper into segments, each part curls up of its own accord. But more specifically, the soul is a fiery substance, which, as we learned from the earlier *Cerebri anatome*, are the explosive animal spirits distributed by the nerves throughout the body (Willis 1683, 5). The spirits permeate the body like a "spectre or shadowy hag," which cannot be seen but only known through their effects and operations (Willis 1683, 6). What proceeds in *Two Discourses* is a long, anatomical discussion of the vital operations of blood-

less insects, molluscs, and crustaceans, and the question whether they should be attributed a soul at all, especially given that they live under water, an element "deadly to fire" and, hence, deadly to Willis' gunpowder analogy for the animal soul (Willis 1683, 13). This is resolved subsequently where it is explained how the nitrosulphuric particles in the animal spirits can burn "in the dark like a live Coal" (Willis 1683, 15). The case is clearer with bloody fishes, for where blood exists, so too do the organs of sense, and fish have brains (Willis 1683, 13).

Chapter 6 is titled "Of the Science or Knowledge of Brutes." This attribution is quickly qualified. While some animals appear to choose between actions and have Deliberation, they do not have rational souls like humans or they would rise to the level of having science or the knowledge that humans possess, but they do not (Willis 1683, 32). This was not by any means either an inconsistent or radical position. Avicenna and Aquinas each thought that animals were capable of a rudimentary form of judgement—a function of their vis estimativa (estimative power) for discerning the aetiological properties of objects. The sheep may lack both reason and will, but its sensitive soul can judge the malicitas of the wolf as much as the wolf's colour or shape, and flee accordingly (see Brown 2006, 42-3). Willis too acknowledges that animals can, in addition to sensing properties through the five external senses, sense the utility or disutility of external objects, prompting in them the experience of various passions and subsequent self-preserving actions. Species of the same object sensed by the external senses that appear "Congruous or Incongruous, produce the Appetite, and local motions its Executors" (Willis 1683, 36). On the question of animal deliberation, Hobbes, in his Leviathan (1651), had already diluted the notion of deliberation to the alternation of passions representing the pros and cons of a certain course of action, and thus to something we share with brutes. The notion of deliberation circulating in England was thus far from anything resembling Aristotle's syllogisms of practical reasoning.

Willis' view likely sits somewhere in the middle of these views. Higher brutes are "Knowing and Active"; have a faculty of "Varying their Types [of actions], and of Composing them in themselves"; and use methods of "ratiocination" that involves considering "Propositions" as "Premises" in simple "arguments." A four-footed animal can form ideas of singular things and associate them with other ideas: "she is taught through various Accidents, by which she is wont to be daily affected, to know afterwards other things" (Willis 1683, 34). Some of these ideas are innate, geared towards conservation of the animal, which is a "Law of Divine Providence." These ideas are correlated with fixed, deterministic responses to external stimuli. Other ideas arise, however, out of the interplay of Sense, Imagination and Memory. Sometimes, innate and acquired ideas interact. Instincts can be "complicated" by notions acquired by sense—e.g., when a dog comes to associate a stick with pain through being struck by one (Willis 1683, 38). Acquired ideas are typically sparked by contingent experiences, but the animal is then able to store or put them together with other ideas to reproduce an action from memory or produce a novel action to achieve its wants. In these cases, Willis claims that we are dealing with a kind of knowledge, one which requires a clear brain and lucid animal spirits. When this material is transmitted to the striatum, reaches the common sensory, and then,

as a sensible Impulse of the same, like a waving of Waters, is carried further to the Callous Body, and thence into the Cortex, or shelly substance of the Brain, a perception is brought in concerning the Species of the thing admitted, by the Sense, to which presently succeeds the Imagination, and marks or prints of its Type being left, constitutes the Memory (Willis 1683, 35–6).

Examples of the first kind of action, produced from knowledge stored in memory, include the horse that upon seeing hoofprints leading out of its meadow, recalls the greener pastures further away and embarks on a journey going hither and yon to find them. Examples of the second include draft beasts who, from drinking water and observing its cooling effects, proceed to lie down in it to reduce their heat (Willis 1683, 37). Perhaps the most striking case of animal ingenuity is that of the fox, which feigns death to fool the hen into coming closer, or more hilarious yet, being aware that the turkey up in the tree is watching it with a keen eye, runs at great speed around the base of the tree until the turkey, getting giddy, falls to the ground (Willis 1683, 38). This kind of "acquired Knowledge of the Brutes, and the Practical Habits introduced by the Acts of the Senses, are wont to be promoted by some other means to a greater degree of perfection." It teaches them "to form certain propositions" and "draw certain conclusions" (Willis 1683, 36). Things that come to them by accident that are repeated become habits. And such cases show animals to have "Cunning and Sagacity" (Willis 1683, 37). Willis refers to the case of the fox as evidence of "a kind of Discourse, Ratiocination or Argumentation" (Willis 1683, 38):

the reason of the whole thing done, or the Endeavour, is resolved into these Propositions; the Fox thinking now to take the prey [suggested by natural instinct], that is before his eyes, after what manner he may, remembers how he had taken the same formerly, by these or those sorts of Cunning ways or Crafts, found out by some chance.

Animal reasoning is thus grounded in experience and confined to being about particulars, but the animal soul can think beyond the immediately given through the powers of association afforded by Imagination and Memory.

We have left only to consider why Willis is adamant that such powers are corporeal. First, he argues that it is absurd to reject the idea that a sensible thing can be composed of insensible material, citing a chemical analogy of how we have no trouble conceiving how a "kindled thing" (a fire) can be made from "inkindled things." Animal spirits are nothing more than their material parts, just as light is nothing more than a kind of fire:

Animal spirits as Rays of Light, proceeding from this fire, are Configured according to the Impressions of every of their objects, and what is more, as it were meeting together with reflected irradiations, cause divers manners of motions (Willis 1683, 33).

Nor is it problematic to suppose that animal spirits may constitute perceptions, any more than it is to accept that light coming through a pinhole can project an image onto a surface behind it (Willis 1683, 33).

Second, Willis offers a lengthy discourse in chapter 7 on what is unique to the rational soul of humans, and why it cannot therefore be accounted for in terms of the composition or faculties of the brain (Willis 1683, 38ff). Willis sees us sharing Phantasie and Memory and the capacity for practical habits with four-footed creatures at least, but we excel brutes both in the variety of objects we can think about and in our "Acts and Modes of Knowing." For, as Aristotle observes, our thought is not restricted to objects of sense, but extends beyond the sublunary to consider all beings (ens) (de Anima, 3.4). The reasoning of brutes is analogical; that of humans scientific. Our reasoning is logical; we reason from first principles—i.e., about the causes of things; demonstrative; mathematical; and mechanical (Willis 1683, 39–40). There is also a normative dimension to our thinking that brutes lack. Brutes have only a few simple notions of particulars and intentions to act, but know nothing about rights or laws of political society (Willis 1683, 40). Human reason corrects its imagination and abstracts universals, and brings those universal concepts to bear on its actions when it counteracts or diverts the effects of the passions. The rational soul considers immaterial things, such as God and the angels, which it could not do if all its ideas were sensory; it composes and divides; deduces; comprehends virtue; and perceives itself, which neither imagination nor memory alone can do. The rational soul is, therefore, clearly immaterial, and although Willis, like Descartes, offers no argument for it, clearly also immortal (Willis 1683, 38-9).

5. Conclusion

Our reading does not reveal any dramatic inconsistencies between the earlier work of *Cerebri anatome* and the *Two Discourses* (cf. McNabb 2014). Willis is consistently a materialist about the corporeal soul, whether that be the vital soul of insects, molluscs and crustaceans, or the sensitive-but-involuntary souls of fish and (possibly) birds, or the sensitive-and-voluntary souls of higher animals. Willis' inattention to the rational soul in his *Cerebri anatome* is consistent with his later insistence that the rational soul of humans is immaterial and immortal, since the purpose of the *Cerebri anatome* is to uncover the neural bases of reflexive versus "voluntary" (meaning: consciously mediated) animal behaviour. It is also consistent with other investigations throughout the history of anatomy—particularly Galenism—into the "seat" of the soul in the brain, the principal organ of the body that the soul relies upon for its sensitive and appetitive functions. In this regard, Willis is not doing anything fundamentally different from Descartes, except drawing different conclusions about where that seat is located and what kinds of souls can be attributed to which kinds of animals.

With hindsight from the perspective of contemporary neuroscience, there is much to admire in Willis' neuroanatomy. As Meyer and Hierons note, "In 1946 [C.S.] Sherrington wrote: 'The notion of reflex action is traceable to Descartes,

but the term hardly. The term is traced more clearly to Thomas Willis'" (Meyer and Hierons 1965b, 142). There was in the 17th century nothing comparable to Willis' understanding of the reflex, even if he failed to understand how the sensory and motor components of the reflex arc connected. It would take another 100 years "until Whytt introduced the spinal cord for this purpose and thus prepared the way for Unzer, Prochaska and above all Marshall Hall to build the modern concept of reflex action" (Meyer and Hierons 1965b, 143). In the meantime, it was Willis, not Descartes, who remained the authority.

There is much else besides his analysis of the reflex for which to applaud Willis. When he writes in *Two Discourses* (Willis 1683, 7) "that as there are Various kinds of Bodies, in the diverse Habitats of this world, and offices of those Bodies destined to life, so also Various Souls" he is very much in tune with the sentiment of a much later evolutionary biology that took a comparative approach to the question of what the soul is. When Willis considers that the passages or tracts in the nervous system allow for the flow of "some subtle particles" "most thin, invisible, and nimble" (Willis 1683, 23), he is not that far off from the view held today that it is the flow of ions through the nerves that creates neural activity. For Willis though, these structures and the animal spirits that move within them are the "Constitutive parts of the sensitive Soul" and the "Authors of the Animal Function" (Willis 1683, 23). Similarly, when he introduces the idea that these tracts or pathways carved out by the excited spirits become strengthened in the brain, he is describing a precursor to modern thinking about the strengthening of synapses and memory and how imagination and voluntary action arises. And when he describes the cortex as necessary for the kind of thought and consciousness implicated in "voluntary," conscious actions, and speculates that perception involves "images or pictures" being sent via nerves from the cortex to the "streaked body," projected onto the corpus callosum like a screen, and then projected back to the cortical folds where they are stored as memories (Willis 1683, 25), he is again not too far off the mark. Memory continues to be a challenge in neuroscience today, but the cortex certainly contains representations and is, by all telling, the "seat" of consciousness. Willis' neurologie thus represents not only an important progression from the Cartesian account of nerve function, but one that served as a catalyst for rethinking the very foundations of Cartesian metaphysics of the mind.¹⁰

References

Arráez-Aybar, Luis-Alfonso, Navia-Álvarez, Pedro, Fuentes-Redondo, Talia, and José-Luis Bueno-López. 2015. "Thomas Willis, a Pioneer in Translational Research in Anatomy (on the 350th anniversary of *Cerebri anatome*)." J. Anat. 226: 289–300.

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- Bayne, Tim, Howhy, Jakob, and Adrian M. Owen. 2016. "Are There Levels of Consciousness?" *Trends in Cognitive Sciences* 20(6): 405-13.
- Brown, Deborah J. 2006. *Descartes and the Passionate Mind*. Cambridge: Cambridge University Press.
- Brown, Deborah J. 2015. "Animal automatism and Machine Intelligence." Res Philosophica 92 (1): 93-115.
- Brown, Deborah J. 2021. "Agency, Force and Inertia in Descartes and Hobbes." In *Reconsidering Causal Powers: Historical and Conceptual Perspectives*, edited by Benjamin Hill, Henrik Lagerlund, and Stathis Psillos, 94–120. Oxford: Oxford University Press.
- Brown, Deborah J., and Calvin G. Normore. 2019. *Descartes and the Ontology of Everyday Life*. Oxford: Oxford University Press.
- Canguilhem, Georges. 1977² (1955). La formation du concept de réflexe aux XVII^e et XVIII^e siècles. Paris: Presses Universitaires de France.
- Cobb, Matthew. 2002. "Exorcizing the Animal Spirits: Jan Swammerdam on Nerve Function." *Nature Reviews/Neuroscience* 3: 395–400.
- Cohen, Leonora R. 1941. From Beast-Machine to Man-Machine. Oxford: Oxford University Press.
- Descartes, René. 1637. Discours de la méthode pour bien conduire sa raison, et chercher la vérité dans les sciences. Plus la Dioptrique, les Météores et la Géométrie qui sont des Essais de cette méthode. Leiden: Imprimerie de Ian Maire.
- Descartes, René. 1641. *Meditationes de prima philosophia*. Paris: Paris: Apud Michaelem Soli.
- Descartes, René. 1662. *De homine,* figuris et latinitate donatus a Florentio Schuyl. Leiden: Apud Petrum Leffen et Franciscum Moyardum.
- Descartes, René. 1664. L'homme [...] et un Traité de la formation du foetus, édité par Claude Clerselier. Paris: Chez Charles Angot.
- Descartes, René. 1964–1974² (1897–1913). *Oeuvres,* éditées par Charles Adam et Paul Tannery, édition révue par Joseph Beaude, Pierre Costabel, Alan Gabbey, et Bernard Rochot ("AT"). Paris: J. Vrin.
- Descartes, René. 1984–1991. The Philosophical Writings of Descartes, volumes 1–2, edited and translated by John Cottingham, Robert Stoothoff, and Dugald Murdoch ("CSM"); volume 3, edited and translated by John Cottingham, Robert Stoothoff, Dugald Murdoch, and Anthony Kenny ("CSMK"). Cambridge: Cambridge University Press.
- Eadie, M. J. 2003. "A Pathology of the Animal Spirits The Clinical Neurology of Thomas Willis (1621–1675). Part 1 Background, and Disorders of Intrinsically Normal Animal Spirits." *Journal of Clinical Neuroscience* 10 (1): 14–29.
- Hobbes, Thomas. 1651. Leviathan, Or, The Matter, Form, and Power of a Common-wealth, Ecclesiastical and Civil. London: Printed for Andrew Crooke.
- Holmes, Frederic L. 1993. "The Old Martyr of Science: The Frog in Experimental Physiology." *Journal of the History of Biology* 26 (2): 311–28.
- McNabb, Jody. 2014. "Thomas Willis: The Faculties and His Two Cognitive Frameworks." *Brain and Cognition* 91: 131–37.
- Meyer, Alfred, and Raymond Hierons. 1965a. "On Thomas Willis's Concepts of Neurophysiology [Part I]." *Medical History* 9 (1): 1–15.
- Meyer, Alfred, and Raymond Hierons. 1965b. "On Thomas Willis's Concepts of Neurophysiology [Part II]." *Medical History* 9 (2): 142–55.

- Sleigh, Charlotte. 2012. "Jan Swammerdam's Frogs." Notes and Records of the Royal Society 66 (4), 373–92.
- Temkin, Owsei. 1973. *Galenism: Rise and Decline of a Medical Philosophy*. Ithaca: Cornell University Press.
- Walton, Douglas. 2017. "The Slippery Slope Argument in the Ethical Debate on Genetic Engineering of Humans." *Science and Engineering Ethics* 23: 1507–28.
- Willis, Thomas. 1664. *Cerebri anatome: cui accessit nervorum descriptio et usus*. London: Typis Jo. Flesher, impensis Jo. Martyn et Ja. Allestry.
- Willis, Thomas. 1670. Affectionum quae dicuntur hystericae et hypochondriacae pathologia spasmodica vindicata [...]. Cui accesserunt exercitationes medico-physicae duae: 1. De sanguinis accensione, 2. De motu musculari. London: Apud Jacobum Allestry.
- Willis, Thomas. 1672. *De anima brutorum quae hominis vitalis ac sensitiva est, exercitationes duae*. Oxford: E Theatro Sheldoniano, impensis Ric. Davis.
- Willis, Thomas. 1681a. "The Anatomy of the Brain [and] the Description and Use of the Nerves." In Willis, Thomas, *The Remaining Medical Works*, edited and translated by Samuel Pordage, volume 2, 51–192. London: Printed for T. Dring, C. Harper, J. Leigh, and S. Martyn.
- Willis, Thomas. 1681b. "Discourse of Musculary Motion." In Willis, Thomas, The Remaining Medical Works, edited and translated by Samuel Pordage, volume 2, 34– 49. London: Printed for T. Dring, C. Harper, J. Leigh, and S. Martyn.
- Willis, Thomas. 1683. *Two Discourses Concerning the Soul of Brutes*, edited and translated by Samuel Pordage. London: Printed for T. Dring, C. Harper, and J. Leigh.