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Early Modern Experimentation on Live Animals*

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Abstract. Starting from the works by Aselli (*De lactibus sive lacteis venis*, 1627) on the milky veins and Harvey (1628, translated in 1993) on the motion of the heart and the circulation of the blood, the practice of vivisection witnessed a resurgence in the early modern period. I discuss some of the most notable cases in the century spanning from Aselli's work to the investigations of fluid pressure in plants and animals by Stephen Hales (*Vegetable Staticks*, 1727). Key figures in my study include Johannes Walaeus, Jean Pecquet, Marcello Malpighi, Reinier de Graaf, Richard Lower, Anton Nuck, and Anton de Heide. Although vivisection dates from antiquity, early modern experimenters expanded the range of practices and epistemic motivations associated with it, displaying considerable technical skills and methodological awareness about the problems associated with the animals being alive and the issue of generalizing results to humans. Many practitioners expressed great discomfort at the suffering of the animals; however, many remained convinced that their investigations were not only indispensable from an epistemic standpoint but also had potential medical applications. Early modern vivisection experiments were both extensive and sophisticated and cannot be ignored in the literature of early modern experimentation or of experimentation on living organisms across time.

Keywords: Vivisection, Anatomy, Experiment, Life, Harvey

Introduction

Techniques of investigation are a crucial aspect of anatomical research, as shown for example by studies on microscopy and injections, both

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recent and less recent. Complex techniques require great skills, attention to detail, careful controls, patient and creative labor: far from being neutral tools, techniques helped define the horizon of research at different periods and interacted problematically with the results attained. Vivisection in particular required great dexterity and involved prior knowledge of the anatomy of the animal to be dissected, including the exact location of its vital parts. The early modern period witnessed a flourishing of anatomical researches based on novel methods of investigation such as microscopy, and the revival and refinement of ancient ones such as vivisections and injections, which were used only occasionally in the past; these and other techniques were often used in combination. The striking usage of vivisection in the early modern period and its interaction with other techniques call for a critical reflection on how and why anatomists and physicians used it and on the significance and implications of the animal being alive.[1]

Dissection and vivisection were the subjects of debate and controversy from antiquity right through the period covered in this study and beyond: although dissection and vivisection were practiced and the knowledge they provided was deemed essential, some argued that dissection was useless because the body changed with death, others believed that cutting open a living body altered it to such an extent that no reliable knowledge could be drawn from studying it, while others still were opposed to cutting the animal body altogether, whether dead or alive. Often, however, anatomists assessed the perceived merits and problems of vivisection implicitly and explicitly not in the abstract but with regard to specific issues and organs, such as the speed of decay of given body parts and their visibility in a dead or alive body, for example. At times vivisection involved prolonged observation of processes in animals and even plants requiring careful analyses from several perspectives and showing surprising connections between interventionist methods of inquiry and observation techniques typical of natural history.[2]

Anatomists advocated vivisection on the ground of its utility to understanding the structure and purpose of many body parts and of potential medical benefits. While some anatomists found the suffering of animals in artificial and cruel settings unbearable, many defended

[1] Cole, 1917–1921; Cook, 2007, pp. 281–285; Wolfe, forthcoming; Wilson, 1995; Ruestow, 1996; Fournier, 1996.

[2] Von Staden, 1989, pp. 234, 236; Carlino, 1999, pp. 131, 138, 158–159, 166–167; Rupke, 1987, especially the essay by Maehle and Tröhler. [Morgagni], 1705, pp. 166–169. See the essay by Allen Shotwell in this issue Guerrini (2003).

vivisection on the ground that it is permissible to treat animals the way we wish; paradoxically, Danish anatomist Nicolaus Steno did both. My focus in this paper is primarily on techniques and epistemological issues rather than on ethical ones, important as they are both historically and philosophically. In this respect Steno's observations are especially interesting: in his treatise on the anatomy of the brain, *Discours sur l'anatomie du cerveau*, delivered in 1665, he instantiated the claim that we can treat animals the way we want, by arguing that surgeons practice procedures like trepanning on them. However, he also warned that the brains of animals differ considerably from species to species, especially when humans are involved. His passage highlights the links between surgical and vivisection practices, as well as of the problem of variability in nature (Steno, 1910, vol. 2, pp. 25–26; Guerrini, 1989, p. 406; 2006; Oster, 1989; Bartholin, 1663–1667, III, p. 228; Kooijmans, 2010, pp. 32–35; Bertoloni Meli, 2011c).

Our knowledge of vivisection from antiquity includes treatises from the Hippocratic corpus, Aristotle, the Alexandria anatomists, and especially Galen. Iacopo Berengario da Carpi, Andreas Vesalius, and Realdo Colombo were key figures in the revival of vivisection in the Renaissance. Vivisection was traditionally performed to study motions, such as those of the heart, of the thorax in respiration, and of the peristalsis of digestive organs, as well as the role of nerves in controlling body parts; in addition, vivisection was used to ascertain the heat of several organs, the precise condition of body parts that decay rapidly with death, the contents of vessels, and matters associated with generation, just to mention some of the main areas examined by Allen Shotwell in this issue (see also von Staden, 1989, pp. 147, 247; Cunningham, 1997, Chapter 5 and p. 159; French, 1999, Chapter 6, pp. 193, 207).

The range of the investigations carried out in the early modern period was such that this brief essay cannot offer a comprehensive analysis; instead I seek here to provide a bird's eye view of experimentation on animals—and occasionally plants—with special focus on its purposes, and to highlight key features in the cases I investigate. Some of the experiments I discuss are well known today, others less so, but seen together, they provide a vivid picture of the issues and problems addressed.

Anatomists were fully aware of the profound changes their field was going through and of each other's works, which appeared in the widely circulating scientific journals of the time, in monographs that were frequently reprinted, typically in the Low Countries, and also in the imposing *Bibliotheca anatomica*, two huge folio volumes issued in 1685 and in expanded form in 1699 containing a critical compilation of the recent literature. Its contents date overwhelmingly from the second half of the century, the works by Gasparo Aselli of 1627 and William Harvey of 1628 being the two outstanding exceptions from the first half and those whence my analysis sets off.

There are additional reasons for starting my analysis from Aselli and Harvey, besides following contemporary perceptions: in their investigations they used vivisection in diametrically opposed ways, thus setting the stage for appreciating the wide range of motivations for which vivisection was practiced and its surprising outcomes. Aselli examined structures whose existence had already been predicted and conceptualized but which had not been fully uncovered; Harvey focused on motions without providing any new structural finding. Johannes Walaeus pursued their researches in creative ways, while Jean Pecquet brought Aselli's findings to dramatic new consequences and opened the door to the discovery of a new system—the lymphatics. The examples I selected from Marcello Malpighi's and Richard Lower's works reflect the differences between Aselli's and Harvey's, in that Malpighi used vivisection to investigate structures—not because of their ephemeral nature but to enlarge them as through a microscope—whereas Lower investigated the role and purpose of respiration without any new structural findings. In the Netherlands, Reinier de Graaf, Anton Nuck and Anton de Heide performed striking vivisections aimed at investigating a number of problems, including pathological issues. Johann Jakob Wepfer investigated the effects of hemlock and other poisons, while his son-in-law Johann Conrad Brunner excised the pancreas to understand its purpose. Lastly, Stephen Hales's celebrated experiments on blood and sap pressure in animals and plants first published in 1727 close a remarkable century, providing rich material for reflection on changing conceptualizations of life and experimentation more broadly.

This essay highlights the existence of a wide range of purposes, epistemic functions, and technical aspects in vivisection, calling for a reevaluation of the role of anatomy in early modern experimentation. Together with other examples in this special issue, the cases I discuss call for a reflection on changing conceptualizations and practices of animal experimentation from Antiquity to the Enlightenment.

Gasparo Aselli: Finding a Missing Structure

The posthumous work by the Pavia professor of medicine Aselli, *De lactibus sive lacteis venis*, announced the discovery of the milky veins, the vessels allegedly carrying chyle from the intestine to the liver. While performing a vivisection of a dog in front of several witnesses in order to study the recurrent nerves, which control the actions of the larynx and the voice, Aselli decided to investigate the motion of the diaphragm as well. The recurrent nerves had a dissection and vivisection history stretching from Galen to Vesalius and Colombo (see the essay by Allen Shotwell in this issue). Aselli's curiosity about the motion of the diaphragm too was quite traditional in a vivisection, Colombo having drawn attention to it as well in connection with respiration (Eriksson, 1959, pp. 291–293; French, 1999, pp. 207–208). In the course of his vivisection, however, Aselli noticed many white vessels, whose nature was at first unclear, but when he saw white milk exuding from an incision he had practiced with a sharp scalpel in one of them he exclaimed "eureka!", marking his joy at the belief that he had discovered the passage of chyle envisaged by Galenic anatomy from the intestine to the liver. His joy was short-lived, however, since the dog soon died and the milky veins suddenly disappeared in front of his eyes while he was observing them. Repeating the experiment on the following day on a different dog, Aselli failed to find the vessels altogether. He reasoned at this point that the dog in his first vivisection had recently eaten; therefore he performed a third vivisection approximately 6 h after the dog's last meal, finding the milky veins again (Aselli, 1627, pp. 19–21).

Aselli's finding in the course of what appeared to have been an entirely typical vivisection in the Galenic tradition was unexpected, more by chance than by design, or as he put it, "casu magis (ut verum fatear) quam consilio" (Aselli, 1627, p. 18). To his surprise, Aselli realized that vivisection made a difference not only to the study of actions—as was in his own and his friends' intention in revisiting the role of the recurrent nerves and the motion of the diaphragm—but also of structures so ephemeral that they could suddenly disappear after death. In dissecting a recently deceased man in order to investigate the moisture of the pericardium, Vesalius found that the heart was still beating; this borderline case between dissection and vivisection highlights the crucial role of freshness—if not life—in dissection (Park, 1994, p. 19. See also the essay by Allen Shotwell in this issue). Aselli's surprising finding in a live dog involved a new genre of vessels—the fourth after veins, arteries, and nerves—as well as the reliance on an unusual variable: thus Aselli made not only an important anatomical find but also highlighted the role and significance of the timing of the animal's last meal, accidentally reviving a vivisection technique that had been employed by Galen in order to investigate digestion (Galen, *On the Natural Faculties*, III, 4).

Aselli's perspective was that of completing the established Galenic system rather than subverting it; this, however, was a major contrast with Harvey.

William Harvey: Understanding Motions and Directionality

Unlike Aselli's treatise of the previous year, Harvey's *De motu cordis et sanguinis* presents no new anatomical structures. Rather, he reinterpreted recent findings, such as the *ostiola* or little doors in the veins found by his teacher Gerolamo Fabrizi, on the basis of anatomical observations, quantitative reasoning, and vivisection experiments. In particular, the *ostiola* in the veins and valves in the heart took on a major role in the study of unidirectionality. While Harvey's results were strikingly new, his vivisection techniques were not especially innovative, except possibly for their systematic nature and the wide number of animals involved. The originality of Harvey's findings is clearly not at stake here; in a sense, the largely traditional nature of the methods he employed would make—if possible—his achievement even more impressive.[3]

De motu cordis et sanguinis treats the motion of the heart in the first part, Chapters 1–7, and the circulation of the blood in the second, Chapters 8–17; since Harvey routinely relied on vivisection, my account does not pretend to be exhaustive. In the first part he dissected live cold-blooded animals "such as toad, serpents, frogs, snails, lobsters, shell-fish, prawns, and all small fishes", where the heartbeat is slower. Similarly, he closely observed the motion of the heart in dying warm-blooded animals in order to determine the active phase, or systole, and the passive one, or diastole, a procedure going back to Galen and employed also by Colombo. Harvey also experimented on eels, showing that their hearts keep moving not only after they have been extracted from the body but also after they have been chopped to pieces; we are going to encounter other instances of experimentation on body parts and cadavers below. It was certainly unusual to dissect such a wide range of animals, but it was not unique. Harvey's Padua teacher Fabrizi had promoted a broadly neo-Aristotelian comparative anatomy project and half a century before Harvey the Dutch anatomist and physician Volcher Coiter had vivisected the hearts of serpents, frogs, fishes, and cats. Harvey's work, however, stands out for its scope and systematic

[3] The study of generation too is relevant to vivisection and poses considerable problems. On these matters I refer to Ekholm, 2010.

nature (Harvey, 1993, pp. 19 and 26–27; Cunningham, 1985; Bylebyl, 1985, pp. 237–242).

Harvey also carefully observed the relation between the motion of the heart and arteries, finding that "arterial diastole is synchronous with cardiac systole" and vice versa. Initially he deemed the experiment with the reed in the artery, performed by Erasistratus and Galen in order to ascertain whether arteries fill because of a faculty transmitted by the heart or because of the impulsion of blood, impossible—though later in his 1649 second response to Riolan the Younger he succeeded in performing it, showing that arteries fill like leather bags rather than bellows, against Galen and in agreement with Erasistratus. Harvey confirmed the same result also through an "experiment" performed by nature through disease: he found in a gentleman that the descending aorta with its two femoral branches had turned into a pipe-like bone. Despite this, Harvey could still feel the pulse in the arteries of the leg, as he knew very well because the gentleman was his patient; indeed, he preserved a span of the bony artery removed from the corpse. In this remarkable case Harvey used a diseased state as a form of control of a vivisection experiment, confirming his findings through different means. Harvey showed his methodological awareness about the problems of vivisection in other instances too: he argued that some small shrimps found in the Thames have a transparent body, enabling the anatomist to study their heart motion "with the least possible impediment", without cutting and interfering with the body. In conclusion, in the first part of *De motu cordis et sanguinis* Harvey relied extensively on vivisection, so much so that he stressed its role in several chapter headings. In one crucial respect Harvey used vivisection for the same reason for which Galileo had used the inclined plane, in order to slow down what he wanted to observe and investigate, in this case the heartbeat rather than free fall.[4]

In the second part of *De motu cordis et sanguinis* Harvey established the circulation of the blood through a series of cogent reasons and experiments, including vivisections. Most brutally, he killed animals by drawing their blood, something he argued could not happen in less than a quarter hour if blood did not circulate (Harvey, 1993, pp. 9, 50, from *De motu cordis*, 1628). More subtly, he employed ligatures in order to observe the direction of blood flow inside the body through vivisection and outside without any need for the knife; the only figure in his book relies on this notion, showing the motion of blood in the external veins

[4] Bylebyl, 1985, pp. 229, 237, is a valuable study of heart vivisections before Harvey. Harvey, 1993, p. 29, from *De motu cordis*, 1628, pp. 112–114, from *Exercitatio anatomica de circulatione sanguinis*, 1649.

of the arm. While traditionally anatomy books focused on structures and were replete with figures, Harvey's figure shows a process in four parts but no new structures. Significantly, the most effective visual representation of his findings is in the form of a film shot in 1928 for the tercentenary of the *editio princeps*, highlighting motion and processes. In Chapter 10, Harvey described a vivisection experiment on a snake, where the vena cava goes into the lower part of the heart and the artery leaves from the upper part. By seizing with a forceps or ligating the vena cava, the heart becomes pale and is emptied of blood by its pulsation; conversely, by releasing the vein and ligating the artery, the heart will turn purple and then livid in color in becoming engorged with blood. Ligatures were well known from antiquity for surgical operations such as amputations and even simple bloodletting. Contrary to standard beliefs, Harvey argued that ligatures do not draw or attract—*attractio* being the Latin term—anything, they simply block—one could add mechanically—blood flow: tight ligatures block both arterial and venous blood, medium tight ones only the latter.[5]

Although most previous anatomists assumed they already knew the direction of flow of fluids in the body, using ligatures to investigate directionality was not a new procedure: Galen had used them in a vivisection experiment described in *On the Natural Faculties* in order to argue that urine reaches the bladder via the ureters. Harvey revived Galen's procedure to investigate directionality: as we are going to see, his way of proceeding became standard in later seventeenth-century vivisection in the study of the direction of flow of other fluids such as lymph and bile.[6]

Harvey's work on the circulation led to a revival of vivisection experiments and opened up the field: the question now was no longer to complete an established system, as for Aselli, but to put together the pieces of an entirely new one.

Johannes Walaeus: Joining Aselli and Harvey – and a Harveyan Coda

In the 1630s and 1640s Dutch circles were especially active in anatomical research, in the wake of Aselli's and Harvey's works: it is no

[5] von Staden, 1989, index *sub* ligation; French, 1994, pp. 107–110, 168–178, 348–371 and index *sub* "attraction"; Bylebyl, 1982; Biagioli, 2006, pp. 136–143; Lawrence, 1987.

[6] French, 1994 is useful but not always reliable. Galen, *On the Natural Faculties*, I.13. Shank, 1985. Galen had relied on ligatures of the umbilical cord during vivisection experiments: *On the Usefulness of the Parts of the Body*, VI.21. Harvey's teacher Gerolamo Fabrizi too applied ligatures to the umbilical cords, Fabrizi, 1600, pp. 110–111 and 119–120. I am grateful to Karin J. Ekholm for these important references.

accident that both Harvey's and Aselli's books were reprinted at Leiden in 1639 and 1640, respectively. In 1633 the renowned atomist Isaac Beeckman, for example, proposed – though did not perform, as far as we know – a vivisection experiment to investigate the circulation of the blood: he argued that by replacing a section of a vein with a glass tube, one would be able to see whether venous blood was flowing away from or towards the heart; one may even inject with a syringe some extraneous bodies some as a little fluff or a small ball to be used as markers to visualize the direction of blood flow (van Lieburg, 1982, p. 167). The Leiden physician Johannes Walaeus did not simply propose but also performed vivisections to study Aselli's milky veins, the circulation, and digestion: he often relied on ligatures. His study of digestion highlights his attempt to investigate experimentally operations traditionally associated with Galen's natural faculties, such as nutrition. While initially opposed to Harvey's views, Walaeus became convinced of their soundness by the experiments by the physician Sylvius dele Boë in Leiden. He later performed some himself in which he showed that arteries filled on the proximal side of a ligature, between the heart and the ligature, veins on the distal side, away from the ligature. In a vivisection experiment that synthesizes Aselli's and Harvey's procedures, Walaeus ligated the milky veins of a dog, showing that they filled between the intestine and the ligature and emptied on the other side: the figure is clearly derived from Aselli's and shows ligatures applied to the milky veins, leading to a bulge on the side of the intestine (see Figure 1). His work was published in 1641 in the form of two letters to Thomas Bartholin and soon established itself as a classic that was often reprinted; his letters were issued in a revised and expanded form in 1645, though curiously with their original date. Be that as it may, vivisection in the traditions of Aselli and Harvey was becoming a standard technique that was developed and combined with other techniques in creative ways (Lindeboom, 1975, pp. 2117–2119, 1939–1943; Schouten, 1974; French, 1994, pp. 153–162, 206–208).

Here I would like to mention another experiment performed by Walaeus on a dead dog: although strictly speaking this experiment was not on live animals, its implications and subsequent history make it relevant to my story. The purpose of the experiment was to infer the inosculation of arteries and veins, which could not be seen directly. To this end Walaeus laid bare an artery and a vein in a leg of the dog; he emptied and ligated the crural vein, then after ligation of the main vessels, both arteries and veins, he was able to press blood from the artery, which thus emptied, into the vein, which became filled, thus

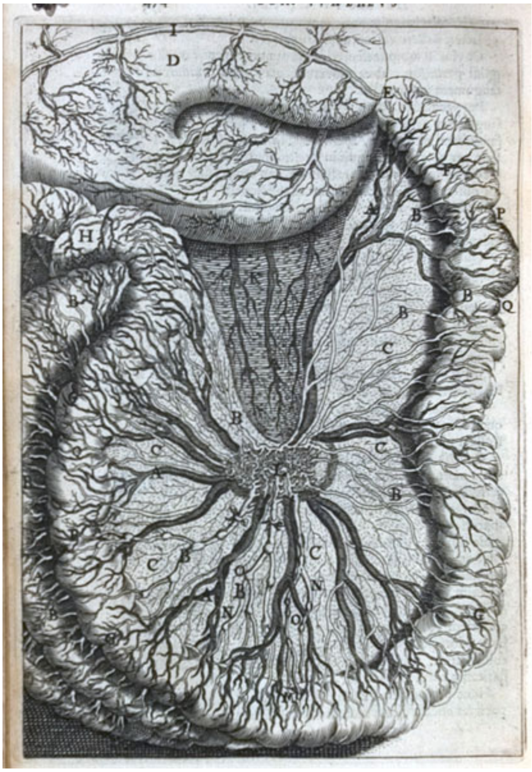

Figure 1. Johannes Walaeus, ligated milky veins, from Thomas Bartholin, *Instituti-ones anatomicae* (Leiden, 1645). By courtesy of the Lilly Library, Indiana University, Bloomington

providing visual evidence in support of his claim (Schouten, 1974, pp. 262, 271; Lindeboom, 1975, p. 281).

In 1650, in the aftermath of Walaeus's letters, William Harvey too performed an experiment on a dead animal, the cadaver of a throttled man: as he wrote to the Hamburg physician Paul Marquard Schlegel, Harvey wished to refute Jean Riolan the Younger's denial of the pulmonary transit, a debated point since Colombo's times (see the essay by Allen Shotwell in this issue). Colombo had denied that venous blood seeped through pores in the septum of the heart and argued instead that blood moved from the right ventricle to the lungs, and then back to the left ventricle. Having ligated the *vena arteriosa* (pulmonary artery), the *arteria venosa* (pulmonary vein), and the aorta, Harvey fastened an ox bladder to a tube, as was usually done in clysters, and injected warm water into the vena cava; the usage of warm water was presumably a precaution against the objection that the pores in the septum of the heart had closed because of lack of heat. While the right ventricle filled with water, not a drop reached the left ventricle, thus showing that there were no pores in the septum. Having released those ligatures, Harvey inserted the tube into the *vena arteriosa* and ligated it between the tube and the heart, to prevent water from returning to the right ventricle. On pressing the bladder, this time water came out from the left ventricle of the heart, thus revealing an easy passage through the lungs to the *arteria venosa*.[7]

There are similarities between Walaeus's experiment on the dead dog and Harvey's second experiment on the throttled man: both sought to provide evidence for the passage of blood through the flesh and lungs, though Walaeus was more explicit about the existence of anastomoses.

Jean Pecquet: Tracing Ephemeral and Subversive Structures

The experiments performed in Paris by Jean Pecquet while still a medical student and published in the 1651 *Experimenta nova anatomica* share several features with Aselli's. Both worked on related structures having started vivisections aimed at investigating motions. As Pecquet put it, the main difference between dead and live animals is motion, whose chief seat is the heart; therefore he set out to perform vivisections of dogs in order to study the heart (Pecquet, 1653, p. 7). On noticing a milky fluid from the vena cava, Pecquet at first thought it was pus, but upon reflection he realized that this was unlikely because the animal appeared very vigorous: by closer inspection and tasting he concluded that what he had found was chyle. Aselli's findings were widely known by then and Pecquet was also well acquainted with the topic through conversation with Pierre Gassendi, who had told him how Nicolas-Claude Fabri de Peiresc had arranged for a criminal to be executed after an abundant meal, in order to find the milky veins in man. With further investigations and vivisections of animals about 4 h after they had eaten, Pecquet found that chyle reached the subclavian vein in the vicinity of the heart through a vessel departing from a previously unknown receptacle located between the kidneys; chyle reached the receptacle through a network of vessels he compared to a spider web (Pecquet, 1653, pp. 29, 34–35; Gassendi, 1641, book five). His work extended over a three-year period and involved over one hundred

[7] Harvey, 1993, pp. 140–145, at 140–141, from the letter to Schlegel dated London, 26 March 1651; French, 1994, pp. 279–285; Cole, 1917–1921, pp. 290–291; French, 1985, p. 54, deals with injections using a syringe in order to study the passageways of fetal anatomy.

vivisections of many different types of animals. Ligatures engorged the chyle vessels with fluid, enabling him to trace their path and to study the direction of flow (Pecquet, 1653, pp. 15–16, 32). Pecquet had traced an entirely new way through which chyle entered the bloodstream: not via the liver, which according to Galen and Aselli received chyle and transformed it into venous blood, but directly from the intestine, bypassing the liver. The largest internal organ was thus deprived of its primary role of sanguification. Thus retrospectively Aselli's work appeared problematic in that he had seen new structures but interpreted them through Galenic eyes—or perhaps he had waited too long after the animal's meal and had detected additional minor vessels of the lymphatic system as opposed to the main ones seen by Pecquet. Timing the vivisection after the last meal was becoming increasingly important. There is another aspect to Pecquet's research: the French anatomist argued that the motion of chyle occurred purely mechanically through pressure, without any need for attraction, on the example of a number of phenomena observed in experiments on the air and its elasticity that were being debated at the time in the wake of Torricelli's barometric experiments (Bertoloni Meli, 2008, pp. 670–677).

Once the anatomists knew what to look for and where to look, subsequent researches could be carried out in special circumstances also on dead animals with the help of injections; the initial stimulus to this area, however, came from vivisections. Vivisections continued to represent an important research tool in two related areas: on the one hand, the anatomist and physician Richard Lower investigated the purpose of the thoracic duct by resection, showing that the animal died even if it was fed normally because food could not reach the blood stream. On the other hand, the thoracic duct was seen as part of an entirely new system—the lymphatics—that became more evident at a slightly longer interval after the animal's last meal in the investigations by Thomas Bartholin and Olaus Rudbeck. Conscious efforts to find the receptacle of the chyle, thoracic duct, and lymphatic system in humans highlight the widespread awareness that anatomical features may vary from species to species and results could not be automatically generalized (Frank, 1980, pp. 197, 201, 209; Eales, 1974, pp. 280–282; Kooijmans, 2010, pp. 56–59; Bertoloni Meli, 2011c).

Marcello Malpighi: Magnifying the Invisible

Marcello Malpighi received his training in dissections and vivisections at Bologna in mid-century when he was still an Aristotelian and continued to perform vivisections until the end of his life in 1694. He claimed that the initial stimulus came from Harvey's discovery of the circulation and other recent findings, in all probability Aselli's and Pecquet's. While at Pisa between 1656 and 1659 under the philosophical tutelage of Giovanni Alfonso Borelli, Malpighi converted to the new corpuscular and mechanical philosophy; his reliance on vivisection irrespective of his philosophical allegiance highlights that this technique crossed philosophical boundaries. It was at Pisa, Borelli recounts in *De motu animalium*, that he performed a brutal vivisection experiment by inserting first a finger and then a *thermometrum* into the viscera and the heart of a live stag, thus proving against traditional doctrines and Descartes that the heart was not hotter than the rest of the body. The idea of investigating the heat of body parts through direct experience in vivisection was not new: Colombo had argued that blood in the left ventricle was hotter than in the right ventricle by inserting a finger in them. Borelli's usage of an instrument, rather than relying on direct sensory experience, is noteworthy here: he argued that the temperature was 40°, or the temperature of a hot summer day.[8]

In 1661 Malpighi performed his most famous vivisection, when he observed with a microscope the contrary motion of blood in the arteries and veins of the lungs of a frog: in this case vivisection combined with a new instrument enabled him to witness motion, arguably the most important motion in the body, that of blood. It would be impossible to provide a characterization of Malpighi's vivisection experiments in a short paper. His treatise *De viscerum structura* alone, dated 1666, contains many reports of vivisections relating to several organs. In the first essay on the liver, for example, *De hepate*, Malpighi mentions several experiments seeking to refute the views of those like Sylvius dele Boë and Jacobus de Back, who had argued that bile is formed in the gall bladder and moves to the liver. Relying on ligatures of the neck of the gall bladder and the coledochus—the bile vessel to the intestine—, Malpighi refuted these views. In this case his experiments follow Harvey's study of directionality; indeed, he even tried to show that he could not push the bile back towards the liver, much like Harvey had shown that venous blood could not be pushed back away from the heart. In another "vivisection" experiment clearly inspired by Harvey, Malpighi removed the bark from the trunk of a tree and applied a tight ligature: he then kept the tree under observation and noticed an enlargement above the ligature, thus showing that in the outer vessels sap flows

[8] Borelli, 1680–1681, vol. 2, prop. 96; French, 1999, pp. 194, 209; Siraisi, 1990, p. 104; Bertoloni Meli, 2011b, p. 46; Manzoni, 2008.

downwards. In this remarkable case Malpighi relied on experimental and observation techniques drawn from anatomy and natural history combined.[9]

The experiment I wish to focus on concerns the kidneys. Malpighi's discovery of the glomerules by means of injections and microscopy provides the context: by injecting the emulgent artery with ink mixed with spirit of wine, and then removing the renal membrane and cutting the kidney longitudinally, one sees with the help of a microscope the glands or glomerules where urine is filtered, hanging like apples from an apple tree. This was a new anatomical feature that had not been previously observed and that localized the exact site where filtration occurred. In line with views developed through the 1660s by the Danish anatomist Nicholas Steno, Malpighi thought all secretions to occur in glands through filtration (Bertoloni Meli, 2011b, Chapters 4 and 6; Cunningham, 1996). Malpighi tried desperately to grasp the connection among the vessels involved inside the glomerules by means of a vivisection experiment he repeated many times. He ligated the renal veins and ureter of a dog, in the hope of increasing the size of the kidney's microstructures. The animal survived a long time—Malpighi does not state how long—and when the kidney was examined again, it was found filled with blood. But even this technique failed to reveal the microstructures and connections Malpighi was after (Bertoloni Meli, 2011b, pp. 123–124). I have chosen this vivisection experiment because it captures a key aspect of Malpighi's investigations in many areas and over several decades: the attempt to make visible and therefore understandable the mechanism of separation of several fluids in the body. In this instance Malpighi used vivisection with a double ligature in order to magnify the glomerule, or the site of separation of urine he had previously identified, and to understand its mode of operation: whereas the microscope magnifies the objects through refraction, Malpighi sought to enlarge them for real.

Richard Lower: Preventing Motion and Locating Color Change

The mid-1660s witnessed a sustained body of research on respiration carried out at Cambridge, Oxford, and the Royal Society in London. I shall focus on a number of vivisection experiments performed by the Oxford anatomist and physician Lower, with the assistance of Robert Hooke, curator of experiments at the Royal Society, seeking to prove a

[9] Bertoloni Meli, 2011b, pp. 114–117 and 253. The entire book provides a more detailed study of Malpighi's vivisection experiments. Holmes, 1993, pp. 314–315.

chemical role for respiration against the so-called mechanical view of respiration put forward by Borelli and defended by Malpighi, Walter Needham, and others: according to them, the purpose of respiration was to mix properly all the components of blood, including chyle. In order for this mixing to occur, it was thought that the motion of the lungs was required. Additionally, Lower wished to determine whether blood changed color from dark to bright red in the heart or the lungs. In an initial vivisection experiment reported in the 1665 *Vindicatio*, Lower had found blood in the pulmonary vein, after it had passed through the lungs, to be dark or venous—probably because the lungs had collapsed and contained no air. Colombo had performed a similar vivisection in the previous century but his aim was to determine whether the pulmonary vein contains blood or smoky waste, an easier task than determining the precise color and nature of blood. Lower's task was especially challenging, so much so that even one of the leading experts in this area—as Lower unquestionably was—had trouble and had to recant his views shortly thereafter (Frank, 1980, pp. 188–192; Lower, 1669, p. 167; Colombo, 1559, p. 224; Bertoloni Meli, 2011a).

Initial vivisection experiments relied on insufflation, blowing air either with a straw into the heart through the thoracic duct, or with a pair of bellows into the lungs, to study the role of air in respiration, the motion of the heart, and the life of the animal. Insufflation experiments with a pair of bellows had been performed by Galen since antiquity—as Harvey reminded readers of *De motu cordis*—and were to be lampooned by Jonathan Swift in *Gulliver's Travels* (Harvey, 1993, p. 13, from *De motu cordis*, 1628; Bertoloni Meli, 2011b, p. 45; Steintrager, 2004, pp. 66–67). In 1668 Lower and Hooke performed a striking experiment with two pair of bellows instead of one. They opened the chest of a dog, cut the trachea, and attached the two pairs of bellows blowing alternately so as to produce a constant air flux. Air could escape the lungs that had been punctured at the opposite end, thus the animal could be kept alive for a long time without any motion in its lungs. This experiment presents paradoxical and counterintuitive features: traditionally vivisection was used in order to investigate motions, including those associated with respiration. In this case, however, Lower and Hooke used vivisection in order to keep an organ—the lungs—still: only in this way could they investigate whether motion of the lungs was a necessary component of respiration, in mixing blood, or rather fresh air was all that was needed. Thus the purely mechanical view of respiration was refuted in favor of a chemical one according to which respiration was seen as analogous to a burning flame (Lower, 1669, pp. 170–171; Frank, 1980, Chapter 8).

Some of these vivisection experiments appeared exceedingly cruel and many spectators expressed their unease and discomfort at witnessing or performing them. In light of Descartes's claims that the animals were automata without a soul, those feelings had a philosophical significance too (Frank, 1980, pp. 159–160, 201; Maehle and Tröhler, 1987; Maehle, 1990).

In order to investigate the site of the change of color of blood, Lower performed other experiments: he opened the chest of a live dog, cut the trachea and corked it; then he opened the cervical artery, after the blood had passed through not only the lungs but also the heart, and found that the blood was venous. This showed that if no air enters the lungs, no change of color occurs in the blood even after it passes through the heart, thus refuting those who attributed change of color of blood to a ferment or heat in the heart.

Finally, Lower performed the last experiment, one I can no longer call a vivisection because the dog was strangled. Soon after the animal died, while keeping its lungs inflated with the two pairs of bellows and letting the air out through the incision in the lungs, venous blood was injected into the vena cava; one can gain a sense of the complexity of this setup by considering that at least three people must have been involved at the same time, two operating the two pair of bellows and one injecting blood. The venous blood went through the right ventricle, the pulmonary artery, and the lungs, coming out bright red from the pulmonary vein, as if it had been drawn from the artery of a living animal, says Lower. Thus color change in blood from dark to bright red occurred not in the heart because of the heart's heat—or indeed of any vital flame or property, since the animal was dead—but in the lungs purely as a result of fresh air. Similarly, color change in blood from bright red to dark was not due to lack of heat, since the blood going through the dead animal and collected in a dish clearly was not heated and yet it had not turned dark or venous (Lower, 1669, pp. 165–166; Frank, 1980, pp. 214–215).

The experiment on the dead dog had precedents in the ones carried out by Walaeus and Harvey and described in the letters to Bartholin and Schlegel. Since Harvey had performed his experiment in front of several colleagues and his letter to Schlegel was known to the physician and anatomist George Ent, a friend of Harvey's who remained active at the Royal Society for several decades, it is possible that Lower and Hooke may have known about it and may have been inspired by it. But whereas Walaeus was investigating the existence of inosculations between arteries and veins and Harvey the plumbing of the heart and lungs in order to deny the existence of intra-ventricular pores, Lower was doing something different. Respiration had been traditionally associated with life and motion: this is why it had been investigated through vivisection since antiquity. Performing a vivisection in order to keep an organ still was not the only paradox in their respiration experiments: Lower enacted respiration in a dead animal by blowing air through its lungs, thus implicitly showing that one of the key operations associated with life involved only chemical and mechanical processes.

Reinier de Graaf and Johann Conrad Brunner: The Role of Pancreatic Juice

The young Delft physician and anatomist Reinier de Graaf performed one of the most celebrated yet problematic vivisection experiments of the seventeenth century. De Graaf was a student of the Leiden professor of medicine Franciscus Sylvius dele Boë, who had made the chemical analysis of the fluids associated with digestion a central area of his research. Another of his students, Steno, in writing on salivary glands and secretion, for example, provided a brief chemical characterization of saliva. Sylvius's understanding of chemical processes relied on the dichotomy acid-alkali; as to digestion in particular, he sought to attribute acid and alkaline properties to the fluids at play, such as pancreatic juice and bile: their coming together would produce effervescence, enabling digestion. Following the discovery of the pancreatic duct by Johann Georg Wirsung two decades earlier, pancreatic juice was a key piece of the puzzle and while Sylvius's theories predicted that it would be acid, direct evidence was lacking (Ragland, 2008, pp. 624–631).

Therefore de Graaf set out to collect a sufficient amount of pancreatic juice as to allow assaying. Whereas saliva is readily available and bile can be easily collected from the gall bladder, pancreatic juice is produced in such small quantities as to render assaying arduous. For this reason de Graaf devised an elaborate contraption to collect pancreatic juice from a live dog; in a stunning vivisection experiment he managed to insert in the pancreatic duct of a dog a quill leading to a container attached to the dog's belly, where the fluid slowly collected. It took de Graaf six attempts in which many things went wrong before he could collect enough juice to allow assaying—by tasting. His medical dissertation under Sylvius's direction, *Disputatio medica de natura & usu succi pancreatici* was turned into a small treatise in the same year in which it was defended (1664) and went through two further editions with important additions in 1666 and 1671. Overall De Graaf found pancreatic juice to be acidic as his mentor had expected. In this case vivisection was required to collect a sufficient quantity of an elusive but important fluid; it was not the process of secretion, as in Malpighi's case, that concerned de Graaf, but the nature of the fluid. One may argue that vivisection in this case was merely enabling de Graaf to collect an elusive juice, but in fact matters became more complex when anatomists, following the failure to observe effervescence between bile and pancreatic juice in a flask, debated whether chemical reactions occurred in the intestine inside the body exactly as they do outside: in this case some unspecified feature inside the body—possibly heat—may have enabled a reaction that was not occurring outside (Ragland, 2008, pp. 660–662; Lindeboom, 1975).

Following de Graaf's experiments, others too sought to collect pancreatic juice and assay it by tasting, finding contradictory results. Eventually, its alleged key role in digestion was challenged by another vivisection experiment coming from an entirely different tradition. In the 1683 *Experimenta nova circa pancreas*, Brunner reported having removed most of the pancreas from several dogs without noticing serious adverse reactions, except possibly increased urination; Brunner stated that he had learnt the procedures necessary for vivisection operations, such as dealing with wounds, from a surgeon, thus highlighting the valuable lessons offered by surgical practices. Brunner's vivisections posed a serious challenge to de Graaf's views. The tradition of vivisection by excising organs was not new: in order to refute the Aristotelian claim that the voice came from the heart, for example, Realdo Colombo had ligated the major vessels of the heart and removed it from a dog, which continued to bark for a few moments before dying (see also the essay by Allen Shotwell in this issue). Others too in the seventeenth century performed excision of organs in vivisection experiments involving vastly different technical skills in order to investigate the consequences on the animal; in a sense, the old procedure of ligating or cutting the recurrent nerves to silence an animal and Lower's more recent resection of the thoracic duct in dogs, leading to their starvation, share common features with Brunner's work. Brunner stated that he was inspired to perform the excision of the pancreas—or most of it—from recent reports of splenectomies, since the pancreas had no more vascular connections than the spleen. But whereas excising the heart led to a swift death, excising the pancreas and spleen required careful observation of the animal's behavior over several months in order to ascertain any differences in its behavior (French, 1999, pp. 208–209; Webster, 1971; Bertoloni Meli, 2011b, pp. 156–158).

Johann Jakob Wepfer: Tracing the Poison's Paths

In 1679 the Swiss physician and anatomist Johann Jakob Wepfer published a remarkable work by many standards, *Cicutae aquaticae historia et noxae*. Wepfer reported in tragic detail a case of hemlock poisoning of young children dating from 1670, resulting in two fatalities. There is no indication that Wepfer performed postmortems on the deceased children. In order to investigate the effects of poisoning and the path the poison took inside the body, however, he subjected the digestive system to renewed study and described for the first time a number of glands (Maehle, 1987). In addition, Wepfer undertook a number of tests on animals, such as dogs, wolves, and others, which he poisoned with hemlock and other toxic plants and minerals. His book is so rich in themes and problems that a comprehensive analysis of its contents must fall outside the scope of this paper. Here I shall outline some of his vivisection experiments: he administered his poisons to the animals orally rather than through intravenous injections—a technique that had gained great notoriety in the 1660s—and sought to trace the poison's path inside their bodies by examining its effects on the lymphatic system, the circulatory system and the heart, and the animal as a whole by examining its behavior. He advocated vivisection or at least immediate dissection after the animal's death as the best method for tracing the poison's effects. Some of Wepfer's descriptions of the effects of poisoning are quite chilling in their detached observation and recording of the animal's final suffering, as in a natural history fashion. His followers, such as his son-in-law Johann Conrad Brunner, a Swiss anatomist and physician whom we will encounter below, pursued his researches by injecting poisons intravenously (Wepfer, 1679, preface and p. 299; Maehle, 1987).

Wepfer's vivisection experiments are of interest for his study of the movements of the digestive system and for study of the effects of poisoning. He relied on an eclectic combination of notions of disease—Galenic, Helmontian, chemical, and mechanical—and offered thoughtful comments on how to conceptualize it. His work of the effects of poisoning adds another striking dimension to the vast field of early modern vivisections, that of the study of pathology and cause of death; despite the obvious suffering inflicted on animals, the potential medical applications of his investigations were especially prominent in his concern with understanding and hopefully offsetting a poison that had recently killed young children.

Anton Nuck and Anton de Heide: Explaining Processes

The Dutch retained a leading role in anatomical research despite the apparent refutation of de Graaf's work on the pancreas. Anton Nuck taught anatomy and surgery at The Hague and, from 1687, medicine and anatomy at Leiden. In addition to his medical degree, Nuck was a skilful surgeon who published a book on surgical operations (Lindeboom, 1984, pp. 1442–1445; Nuck, 1692; French, 1999, pp. 206–210). No doubt, his surgical skills came in handy in his vivisection experiments. I am going to mention briefly three experiments performed and discussed by Nuck, on the operation of glands, the location and nature of fecundation, and the origin of bladder stones.

Nuck was the heir of the tradition of Sylvius dele Boë and Nicholas Steno: his first publication dealt primarily with a new salivary duct and the chemical analysis of saliva. There were different ways to approach the study of glands: by structural analysis, involving both the microscope and injections of different fluids; by chemical analysis of their secretions; by vivisection experiments, involving ligatures for example; and by remarkable case histories and pathology. Nuck relied on a creative combination of all these methods. In his study of saliva, for example, *De ductu salivali novo* (Leiden, 1685) he reported the opinion according to which secretion occurs by means of a ferment provided by a nerve and proceeded to test the claim by ligating the nerve to the salivary gland: saliva was still secreted, though in smaller quantities. Ligating the efferent vein, however, led to increased salivation, thus supporting the view that saliva originates from arterial blood and nervous action determined which proportion of arterial blood turned into saliva and which became venous blood. In this case Nuck's purpose was neither finding structures nor chemical composition—as for Malpighi and de Graaf—but the mode of operation of glands: we have thus encountered three different purposes for studying glands through vivisection.[10]

In his 1692 treatise of Glands, *Adenographia*, Nuck reported a number of striking vivisection experiments only tangentially related to glands but remarkable in their own right. In one of them he ligated the left uterine horn in a bitch 3 days after copulation; on the 21 day after the operation he dissected her and noticed two fetuses between the

[10] Nuck's *De ductu salivali novo* was republished with additions as *Sialographia et ductuum aquosorum anatome nova*, also in Le Clerc and Manget, 1699, vol. 2, pp. 797, 808b, 809a; Steno, 1910, vol. 1, pp. 25–26, 35–36, 38–39; vol. 2, pp. 100–101. Steno too performed resection and ligation experiments of the nerves and blood vessels connected to muscles to study their contractions.

ligature and the ovary: thus the vivisection experiment enabled him to locate the site where fecundation occurred. In his view his finding showed that fecundation occurs through an "aura seminalis" rather than male semen directly, which he believed could not reach so high. In the other experiment he investigated the origin of bladder stones, suspecting that they formed through the accretion and incrustation of successive layers. He opened the bladder of a dog and inserted a wooden globule in it; the dog survived the operation and lived happily for several weeks; after this time he reopened the bladder and found it covered with incrustations, thus proving his point and also showing the origin of the celebrated bezoar stone—a calculus found in the stomach or intestine of some animals—that were once believed to be antidotes to poison (Nuck, *Adenographia*, in Le Clerc and Manget, 1699, vol. 2, pp. 838b, 839b–840a; Lindeboom, 1975, pp. 290–291; Needham, 1959[2], p. 144).

Much like Nuck, Anton de Heide too was a physician with surgical skills who published an important contribution on the anatomy of mussels, *Anatomy mytuli* (Amsterdam, 1684). In a series of *Observationes* attached to his treatise, de Heide discussed a variety of themes, including the regeneration of bones; to this end he relied on a number of frogs, broke their hind legs, and then followed the process of repair on a daily basis. His procedure resembled studies of the formation of the chick in the egg by Harvey and others: in the studies on generation eggs were opened at successive intervals to investigate growth stages, whereas in the studies on regeneration frogs were dissected at successive intervals to investigate how far the bone had been repaired. Other relevant parallels can be found in the regeneration experiments on the tails of lizards or the claws of lobsters carried out by Robert Boyle in the late 1650s. De Heide traced the process of regeneration from blood effusion after 1 day, to a harder lamina after 5 days, to cartilage after 27, and to solid bone after 4 months; he concluded that the new bone originated from extravasated blood. Although such experiments were to prove crucial in later debates between mechanical and vitalist views, de Heide eschewed philosophical discussions (de Heide, 1684, pp. 123–126; Lindeboom, 1984, pp. 807–808; Frank, 1980, pp. 140–141; de Moulin, 1988, p. 104).

Stephen Hales and the Behavior of Fluids

In the first decades of the eighteenth century the clergyman and natural philosopher Stephen Hales carried out an extensive series of investigations on many aspects of plant and animal physiology, especially to do with the behavior of fluids. Despite the fact that his treatment of animals seems especially gruesome, Hales was careful to inform his readers that the animals he was using for his experiments were often diseased or about to be culled; at one point he also claimed that he had stopped his researches because of the "disagreeableness of anatomical dissections." Although he was not a professional anatomist, Hales was aware of obvious problems related to vivisection procedures, as when he discussed and measured differences in the heartbeat rate of a horse when it is not in pain or terrified and under vivisection. He focused with painstaking detail on the absorption and transpiration of water in plants and the pressure of sap and blood in plants and animals, providing extensive numerical tables: his experiments seemed inspired by Robert Boyle, who had studied the pressure of fluids in different experimental settings using similar devices, and the iatromathematical tradition then flourishing in Britain. Already in *Vegetable Staticks* of 1727, he provided details of his animal experiments, which were later expanded in the 1733 *Haemastaticks*. A feel for the question addressed by Hales can be gained from the following quotation[11]:

> Which force [of the rising sap] is near five times greater than the force of the blood in the great crural artery of a Horse; seven times greater than the force of the blood in the like artery of a Dog; and eight times greater than the blood's force in the same artery of a fallow Doe: which different forces I found by tying those several animals down alive upon their backs; and then laying open the great left crural artery, where it first enters the thigh. I fixed to it (by means of two brass pipes, which run one into the other) a glass tube of above ten feet long, and 1/8th of an inch diameter in bore: In which tube the blood of one horse rose eight feet, three inches, and the blood of another Horse eight feet nine inches. The blood of a little Dog six feet and half high: In a large Spaniel seven feet high. The blood of the fallow Doe mounted five feet seven inches.

Figure 2 shows a plant set against a wall, with three s-shaped tubes attached at different points of the trunk. By means of mercury, Hales measured the changing pressure of sap along the trunk: his experimental set-up shows a striking resemblance to that of Bernardino Ramazzini in his investigation of the wells around Modena, a work well known in England at the time. In both cases the device measured differential pressure along a fluid conduit (Bertoloni Meli, 2006, pp. 187–189). The analogy with Boyle's and Ramazzini's works highlights that in his

[11] Hales, 1733, Introduction and pp. xviii, 2, 10, 13; quotation from Hales, 1969, p. 61.

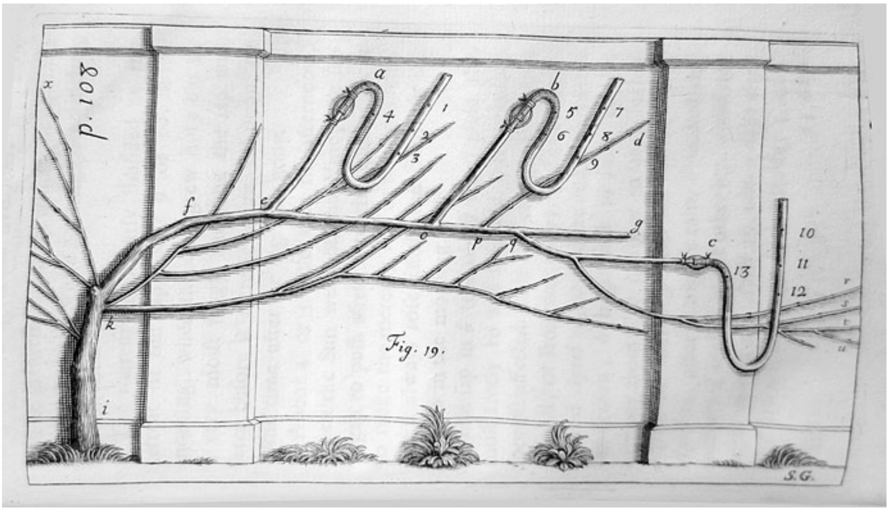

Figure 2. Stephen Hales, sap pressure in plants, from *Vegetable Staticks* (London, 1727). By courtesy of the Wellcome Library, London

experiments on plants and live animals Hales saw his subjects as hydraulic apparatus.

Conclusion

My overview of the complexity and richness of early modern experimentation on live animals shows that anatomists, surgeons, and physicians used vivisections on many grounds in a way that perhaps has not been fully appreciated either by historians of anatomy and physiology or by scholars of experimental practices. The fact that vivisection dates from antiquity may have led to the misleading impression that the early modern period offered little that was new. I hope that my brief study will contribute to dispelling this myth and to showing the range of techniques and purposes for which vivisection was used. Take de Graaf, for example: in the early nineteenth century his experiments were deemed impossible to reproduce by François Magendie; when Claude Bernard succeeded in replicating them he was so impressed that he dedicated one of his works to de Graaf. Yet one would look in vain for an account and analysis of de Graaf's work and of most other anatomical experiments—with the exception of Harvey's—in standard accounts of early modern experimentation (Ragland, 2008, pp. 616–617).

Vivisection experiments raise a number of issues about experimentation on live animals. Traditionally vivisection was used primarily to study motions, especially those related to the heartbeat and respiration—or the emotional reaction of a bitch in seeing her puppies, as in the examples of Vesalius and Colombo discussed by Allen Shotwell. While Walaeus, Harvey, and Lower focused precisely on those motions too, they also studied both blood flow and respiration itself in dead animals. Aselli, Pecquet, and Malpighi – at least in the examples we have seen – relied on vivisection primarily to investigate structures, while de Graaf was unique in the group I selected in focusing on collecting a sufficient amount of pancreatic juice to enable chemical assaying by tasting. Studies of directionality by Harvey, Walaeus, Malpighi, and Lower; the effects of poisoning investigated by Wepfer; the purpose and mode of operation of organs through excision and ligation explored by Brunner and Nuck; the exact localization of processes sought by Nuck; the regeneration of body parts investigated by Boyle and de Heide; and the presence of fluid pressure in the vessels invoked by Aselli, Walaeus, Pecquet, and Hales; all necessitate the animal to be alive.

Vivisection raises key questions at the intersection between practices of active intervention and observation: on the one hand, vivisection appears as the archetypal interventionist experimental technique; on the other, some experiments were associated with careful observation, at times resembling practices of natural history, as with Malpighi's observation of the ligated tree trunk or Brunner's observation of the effects of excising the pancreas, both involving several months at least. Perhaps few examples could emphasize more convincingly that observation intersects a variety of other techniques of investigation, including a quintessentially interventionist one like vivisection (Daston and Lunbeck, 2011).

Other problems concern the variability across species: since human vivisection was not allowed, in order to draw conclusions on human subjects it was necessary to generalize from animals, as we have seen in the examples of the brain, milky veins, the lymphatics, and bone regeneration, thus raising the questions of the uniformity of nature and differences across species. These themes were debated at the time and are relevant to current debates on early modern experimentation, posing a broader set of concerns than those typical of the physical sciences. Early modern anatomists were very much aware not only of animal suffering but also of the problematic nature of vivisection, which dramatically altered the object of inquiry: from Harvey's concern with the transparent shrimps in the Thames and the reed in the artery experiment to Hales's measurement of different rates of heartbeat during vivisection, anatomists displayed considerable sophistication (Dear, 1995; Bertoloni Meli, 2011a, b, c).

Perhaps it is not surprising or accidental that in the heyday of mechanistic anatomy, when the body was seen as a mechanical, pneumatic, and chemical machine, issues like structure, localization, directionality, assaying, and pressure took center stage; Boyle's and de Heide's regeneration experiments occupy a relatively marginal position in the late seventeenth century, though the role of similar experiments was to change dramatically in the eighteenth. However, in no way should one take all anatomists mentioned in this essay as mechanists forming a homogeneous community from a philosophical standpoint. Further, philosophical differences did not constitute a barrier or prevent borrowings and dialogue: Aselli and Harvey were not mechanists, yet large portions of their works, procedures, and results were widely accepted and used by mechanists such as Pecquet and Malpighi, for example. While there was no unanimity about the reliability and usefulness of vivisection, techniques and results traveled across many philosophical divides.

The material covered in this essay can be usefully contrasted with the other essays in this special issue, seeking to correlate the chief questions addressed about experimental techniques and philosophical perspectives in vivisection experiments to the key features attributed to life in different periods; in this regard one could argue that vivisection was especially significant with respect to other techniques of investigation such as microscopy and injections.

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