Who Was Borelli Responding To?

Nicolaus Steno in *De motu animalium* (Rome, 1680-1)

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Abstract

The theories of muscle contraction followed by Giovanni Alfonso Borelli and Nicolaus Steno have often been considered to be at odds with one another. This short essay, however, nuances the antagonism between Steno and Borelli's muscle theories. It also argues that Steno's work was more important to Borelli than previously acknowledged. In the end, Borelli's disagreement with Steno was more nuanced than what Borelli himself writes. Their differences in explanation are traced back to their different purposes in writing each book.

In 1680, readers in Rome witnessed the publication of one of the most famous books of seventeenth-century science: Giovanni Alfonso Borelli's *De motu animalium* (Rome, 1680-1). Borelli's posthumous work is often mentioned in history of science textbooks, modern texts of biomechanics, and in books about the history of anatomy and the mechanical philosophy.[2] Borelli's opening words may have contributed to the historical status of the book. As he put it, until his work "nobody has described or even suspected the innumerable, remarkable and interesting problems which are involved" in animal motion.[3] Ironically, and despite the book's fame, very few scholars have studied this book carefully both in its contents, editorial

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[2] For history textbooks see Richard Westfall, *The Construction of Modern Science: Mechanics and Mechanisms* (Cambridge: Cambridge Univ. Press, 1971), 94-96; and Andrew Wear, "Early Modern Europe, 1500-1700" in *The Western Medical Tradition: 800 BC to AD 1800*, ed. by Lawrence Conrad, Michael Neve, Vivian Nutton, and Roy Porter (Cambridge: Cambridge University Press, 1995), pp. 215-362, esp. 355-357. On Borelli's impact on modern biomechanics see Andreas Mayer, *The Science of Walking: Investigations into Locomotion in the Long Nineteenth Century*, trans. by Robin Blanton and Tilman Skowroneck (Chicago: The University of Chicago Press, 2020), p. 5; and C. Ross Either and Craig Simmons, *Introductory Biomechanics: From Cells to Organisms* (Cambridge: Cambridge University Press, 2007), pp. 6-8; On recent in-depth studies see Luciano Boschiero, *Experiment and Natural Philosophy in Seventeenth-Century Tuscany* (Dordrecht: Springer, 2007), pp. 89-92; and Domenico Bertoloni Meli, *Mechanism: A Visual, Lexical and Conceptual History* (Pittsburgh, PA: University of Pittsburgh Press, 2019), pp. 116-118.

[3] Giovanni Alfonso Borelli, *On the Movement of Animals*, trans. Paul Maquet (Berlin: Springer-Verlag, 1989), p. 6, "Introduction."

production, and reception.[4] In fact, it is almost always the book's figures that appear when Borelli is mentioned, because they provide a powerful visual description of the mechanization of the animal body in the early modern period. This article is an attempt to bring research on Borelli's *De motu animalium* forward by looking at one of its strongest, yet rarely acknowledged influences.

De motu animailum is a book about "the physiology of the motion of animals."[5] In the early modern period physiology was part of the discipline of anatomy.[6] However, a rapid glance at the book shows that it is as much about mathematics as about anatomy. Borelli – no anatomist himself – justified this approach by claiming that "in building the organs of animals, God exerts geometry."[7] But Borelli was not the first to have this insight. More than ten years earlier, the anatomist Nicolaus Steno (1638-1686) claimed that the body should be studied according to the laws of mathematics in the *Elementorum myologiæ specimen* (Florence, 1667).[8] Steno and Borelli's books were different in size, style, and in its various anatomical topics. But both authors dedicated most of their pages to the application of geometry to muscle motion. In fact, before the publication of Borelli's *De motu animalium* there was not another author that placed mathematics as much at the forefront of anatomy as Steno. Thus, it is impossible that Borelli was not influenced by Steno when writing his book. Strikingly, Borelli rarely quotes Steno or his other sources and opponents. This looks strange in light of modern citation practices, but Borelli's attitude was not uncommon in the early modern period.[9] Recent research identified sections of *De motu animalium* that show Borelli writing in explicit opposition to Steno on the field of muscle physiology. Eyvind Bastholm mentions that Borelli "differs from Steno on

[4] In the books mentioned in n. 1, *De motu animalium* is only briefly mentioned. For more robust studies see Maria Conforti, "Succo Nerveo e Succo Seminale nella Macchina del Vivente di Giovanni Alfonso Borelli" *Medicina nei Secoli Arte e Scienza* 13 (2001), 577-595; Domenico Bertoloni Meli, *Mechanism, Experiment, Disease: Marcello Malpighi and Seventeenth-Century Anatomy* (Baltimore, MD: Johns Hopkins University Press, 2011); and Margaret Nayler, "The Insoluble Problem: Muscle in the Mid to Late Seventeenth Century," Ph.D. Dissertation, University of Melbourne, May 1993, esp. 453-554.

[5] Borelli, *On the Movement of Animals*, p. 6, "Introduction."

[6] Peter Distelzweig and Evan Ragland, "Medicine and the Science of the Living Body," in *The Cambridge History of Philosophy of the Scientific Revolution*, eds. David M. Miller and Dana Jalobeanu (Cambridge: Cambridge Univ. Press, 2022), pp. 201-221, esp. 202-204.

[7] Borelli, *On the Movement of Animals*, p. 2, "Preface to Queen Christina."

[8] Nicolaus Steno, *Elementorum myologiæ specimen* (Florence, 1667), "Preface to the Grand Duke."

[9] Borelli once wrote that he did not mention his adversaries' names in Borelli, *On the Natural Motions Resulting from Gravity*, trans. Paul Maquet (Cham: Springer, 2015), p. v, "Foreword to the Reader." For practices of authorship and credit in the history of science see *Scientific Authorship: Credit and Intellectual Property in Science*, eds. Mario Biagioli and Peter Galison (London: Routledge, 2013); and Domenico Bertoloni Meli, "Authorship and Teamwork around the Cimento Academy: Mathematics, Anatomy, Experimental Philosophy," *Early Science and Medicine* 6 (2001), pp. 65-95. For the similar case of Newton, see Richard Westfall, *Never at Rest: A Biography of Isaac Newton* (Cambridge: Cambridge University Press, 1980), pp. 123, 380, 401.

several details" on this topic.[10] And Troels Kardel, the physician who first noticed similarities between Steno's muscle model and those used today in modern biomechanics, claimed that Borelli "fought [Steno] back even from his deathbed in Rome."[11] Indeed, this narrative of a clash with Steno is slightly favored by Borelli's own writings, both in his correspondence and book on animal motion. In this short essay, however, I nuance the interaction between Steno and Borelli's muscle theories and argue that Steno's work was more important to Borelli than previously acknowledged. I start by showing that Borelli was fully aware of Steno's anatomical research and publications through Borelli's letters. Some of these letters have not been previously considered in studies of Borelli's relationship with Steno. The second part documents Steno's possible, but hidden influence on Borelli, by carefully looking at claims about anatomy in which they shared the same opinion. Then, I show where exactly Borelli criticized Steno and why. I argue that this disagreement was more nuanced than what Borelli himself writes. Although only a preliminary research, this comparison between Steno and Borelli helps to address broader questions about authorship and the importance of an audience in shaping the authors' scientific claims. As this article suggests, although very different persons, Borelli and Steno's ideas were far more similar than a first reading may suggest.

Giovanni Borelli, Reader of Nicolaus Steno

Giovanni Alfonso Borelli was a mathematician by training and fame.[12] He studied mathematics with Benedetto Castelli (1578-1643), famous disciple of Galileo Galilei (1564-1642), and later taught mathematics at the University of Pisa, a chair previously held by Galileo. Borelli was in Tuscany from 1656 to 1667 and there he wrote about mathematics and astronomy under the patronage of the Medici court. In these years, Borelli also fostered an interest in anatomy, mostly due to his friendship with Marcello Malpighi (1628-1694) and Lorenzo Bellini (1643-1704).[13] Borelli not only read and discussed anatomy with them but also tried to follow the new

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[10] Eyvind Bastholm, *The History of Muscle Physiology: From The Natural Philosophers to Albrecht Von Haller*, trans. W. Calvert (Copenhagen: Ejnar Munksgaard, 1950), p. 164.

[11] Troels Kardel, "Steno's Myology: The Right Theory at the Wrong Time," in *Steno and the Philosophers*, eds. Raphaele Andrault and Mogens Laerke (Leiden: Brill, 2018), 138-173, esp. 158. On Kardel's reappraisal of Steno's myology, see T. Kardel, "Niels Stensen's Geometrical Theory of Muscle Contraction (1667): A Reappraisal," *Journal of Biomechanics* 23 (1990), 953-965.

[12] For biographical studies of Borelli, see Thomas Settle, "Borelli, Giovanni Alfonso," in *Complete Dictionary of Scientific Biography*, vol. 2, (Detroit, MI: Charles Scribner's Sons, 2008), pp. 306-314; Boschiero, *Experiment and Natural Philosophy in Seventeenth-Century Tuscany*, pp. 59-92.

[13] Bertoloni Meli, *Mechanism, Experiment, Disease*, pp. 18, 40-45.

anatomical research published at the time. As part of these interests, in the fall of 1663, Borelli asked Antonio Magliabechi (1633-1714), chief librarian of the Medici court, to read the "anatomical observations of Steno."[14] Nicolaus Steno had just published a groundbreaking work on the anatomy of glands in which he showed how exactly the salivary glands functioned and where they were located. But when Borelli asked for Steno's *Observationes anatomicæ* (Leiden, 1662), he already knew of Steno's discoveries on the glands and saw Bellini trying to identify them during a dissection in Pisa.[15] In the years that followed, in two letters currently held at the Staatsbibliothek in Berlin, Borelli kept on talking about the salivary glands and manifested an interest in the muscular fibers of the tongue, a topic mentioned by various anatomists at the time, including Malpighi and Steno.[16] It is possible that Borelli read Steno's *De musculis et glandulis* (Copenhagen, 1664) around this time, because the muscular structure of the tongue and the heart takes a prominent place in the book.

Nicolaus Steno was also aware of the scientific activities taking place in Tuscany and sought them actively by visiting Florence and staying there for a few years.[17] In his first months in Florence, Steno met Borelli at the Medici court and went to his home asking for advice on mathematical matters.[18] Both Steno and Borelli were doing research on muscle motion at the time and it made sense to at least exchange ideas about it.[19] Since one was trained in anatomy and the other in mathematics they could benefit much from each other.[20] Borelli, however, had followed Steno's controversial dispute in discovering the parotid salivary duct.[21] Some authors thought that the original discoverer had been the physician Gerard Blasius (1627-1682) who hosted Steno in Amsterdam for a few weeks in 1660. For that reason, and given the apparent similarity of their research on muscles, Borelli avoided talking with Steno about myology,

[14] G. Borelli to Antonio Magliabechi, 22 November 1663, in Florence, Biblioteca Nazionale Centrale di Firenze, Magl.VIII.518, fols. 128r-128v.

[15] Borelli to Marcello Malpighi, 15 February and 22 March 1663, in Howard Adelmann, *The Correspondence of Marcello Malpighi*, 5 vols. (London: Cornell University Press, 1975), vol. 1, pp. 147-149, 152-154.

[16] Borelli to (possibly) Prince Leopoldo, 13 September 1664 and 29 August 1665, in Berlin, Staatsbibliothek, Darm 3a 1650, fols. 1r-4v. See also Howard Adelmann, "A Supplement to *The Correspondence of Marcello Malpighi*" *Journal of the History of Medicine* 33 (1978), 53-73.

[17] Nuno Castel-Branco, "Steno, The Traveling Anatomist: Physico-Mathematics and the Search for Certainty in the Seventeenth Century," Ph.D. Dissertation, Johns Hopkins University, 2021, pp. 176-179.

[18] Borelli to Marcello Malpighi, 17 July 1666, in Howard Adelmann, *The Correspondence of Marcello Malpighi*, 5 vols. (London: Cornell University Press, 1975), vol. 1, pp. 318-320.

[19] On Borelli's early work on *De motu animalium* see Boschiero, *Experiment and Natural Philosophy in Seventeenth-Century Tuscany* pp. 84-85.

[20] Domenico Bertoloni Meli, "The Collaboration between Anatomists and Mathematicians in the mid-Seventeenth Century with a Study of Images as Experiments and Galileo's Role in Steno's Myology," *Early Science and Medicine*, 13 (2008), pp. 665-709.

[21] Borelli to Malpighi, 10 July 1665, in Adelmann, *The Correspondence of Marcello Malpighi*, vol. 1, pp. 266-268.

fearing that the latter could steal his ideas.[22] This does not necessarily mean that they did not remain in good terms, as other have suggested.[23] Borelli continued to follow Steno's work and shortly after Steno's *Elementorum myologiæ specimen* was published, Borelli rejoiced in the fact that the book was different from what he expected.[24] The fears that Steno would publish similar things to him faded away. Once back in Messina, Borelli wrote to Prince Leopoldo de' Medici (1610-1675) telling him that Steno would be welcomed in Messina.[25] He also contributed to Steno's geological research by sending stones from southern Italy to Tuscany.[26] In short, Borelli knew not only Steno's work well but also had a personal relationship with him. For this reason, it is hard to believe that he did not think of Steno's work on the geometry of muscle motion when writing his own *De motu animalium*.

Scientific resonances between Giovanni Borelli and Nicolaus Steno

In order to grasp the impact of Nicolaus Steno's work on Borelli it is better to situate it in relation to the long *De motu animalium*. The latter work was published in two parts printed one year apart in Rome. According to their titles, the first part deals with "external motions of animals."[27] In this first volume Borelli deals with the motion of limbs, muscles, and animal locomotion: walking, jumping, flying, and swimming. The second part is on the "internal motions of animals."[28] Here Borelli addresses physiological problems like blood circulation, respiration, and reproduction. Interestingly, Borelli also explores the internal structure and motion of muscles in the second part, which speaks to the importance this topic had for him. Above all, and according to Borelli, all these topics were to be studied with mathematical demonstrations. His aim was to "enlist anatomy into physics and mathematics not less than astronomy."[29] Steno himself made a similar claim in the *Elementorum myologiae specimen*. He

[22] Borelli to Malpighi, 17 July 1666, in Adelmann, *The Correspondence of Marcello Malpighi*, vol. 1, pp. 318-320.

[23] Gustav Scherz, *Niels Stensen: eine Biographie*, 2 vols. (Leipzig: St. Benno-Verlag, 1987), as translated into English in *Nicolaus Steno: Biography and Original Papers of a 17th Century Scientist*, ed. Troels Kardel and Paul Maquet, 2nd ed. (Berlin: Springer, 2018) (hereafter, BOP), pp. 1-410, esp. 185-186, 191; and Kardel, "Nicolaus Steno's New Myology (1667): Rather than muscle, the motor fiber should be called animal's organ of movement" *Nuncius* 23 (2008), 37-64, esp. 54-56.

[24] Castel-Branco, "Steno, The Traveling Anatomist," p. 204.

[25] Borelli to Leopoldo, 1 December 1667, in Florence, BNCF, Gal. 278, fols. 95r-96v.

[26] Borelli to Leopoldo, 3 August 1667 and 4 October 1667, in Florence, BNCF, Gal. 278, fols. 42v, 73r-73v. See also Dominici, "A Man with a Master Plan," p. 68.

[27] Borelli, *On the Movement of Animals*, p. 1.

[28] Borelli, *On the Movement of Animals*, p. 203.

[29] Borelli, *On the Movement of Animals*, p. 6.

wrote that the study of muscles, or myology, should be "part of mathematics" and that anatomists should give to the muscles "what astronomers give to the sky."[30]

But despite having the same aim, Borelli's book was different from Steno's in many ways. It was much longer and more systematized. For instance, unlike Steno, Borelli divided his work into multiple chapters and all his work was about physiology and mathematics. Steno, on the other hand did not have chapters and the last parts of the book were not related to mathematics. More importantly, Borelli applied mathematics to many physiological questions, whereas Steno applied mathematics only to the structure of muscles and their motion. Nevertheless, Borelli addressed the structure and motion of muscles in both parts of his work, showing that muscle motion took a central place in his work. Indeed, by 1680, Nicolaus Steno's myology was still one of the most important works on the application of mathematics to muscle contraction.[31] Thus, it is normal that Borelli would consider it when writing *De motu animalium*.

Strikingly, Borelli mentions Steno's name only once in *De motu animalium* and almost in passing. When describing what he calls radial muscles as a multiplicity of feather-like or pennate fibers, Borelli quotes Steno for an empirical confirmation of his description. He says that the structure he proposed "could not be confirmed experimentally," but that he was "very happy to see that the famous anatomist Steno … observed exactly the same structure in the human deltoid muscle."[32] Indeed, Steno had described the deltoid muscle as a composite of simple muscles. But Steno's description of the deltoid is but a minor detail inside a book that Borelli must have mastered.[33] One reason for that is the many similarities between Steno and Borelli's understanding of muscles. For instance, Borelli describes muscles in the same way as Steno, distinguishing between fibers and tendons, and choosing fibers as the main motor of muscular motion. As Borelli put it, "n a muscle, we see that only the fleshy threads [i.e. fibers] … contract when the muscle acts."[34] And Steno wrote "the muscle does not act unless its single fibers act."[35] This distinction runs contrary to the claim of Fabricius ab Acquapendente (1537-1619), one of the main authorities on muscle motion in the early modern period. Fabricius wrote that the

[30] Steno, *Elementorum myologiæ specimen*, "Preface to the Grand Duke."

[31] There were however other authors who made similar, but more modest claims on anatomy and mathematics such as Walter Charleton (1619-1707), William Croone (1633-1684), Thomas Willis (1621-1675), Richard Lower (1631-1691), and John Mayow (1641-1679). See Nayler, "The Insoluble Problem;" and Troels Kardel, *Steno on Muscles: Introduction, Texts, Translations* (Philadelphia: The American Philosophical Society, 1994), 25-33.

[32] Borelli, *On the Movement of Animals*, pp. 94-95.

[33] Steno, *Elementorum myologiæ specimen*, pp. 37-38.

[34] Borelli, *On the Movement of Animals*, pp. 9-11, esp. 11.

[35] Steno, *Elementorum myologiæ specimen*, p. 4.

contractile element was in the tendons and not in the fibers.[36] But Steno and Borelli were not the only ones privileging fibers over tendons in muscle contraction. William Croone and Walter Charleton, for instance, followed a similar approach.[37] But unlike the latter two, Steno had a different understanding of muscle fibers and did not distinguish them from simple flesh. For him, muscle flesh is precisely a group of muscle fibers joined together.[38] Borelli again followed Steno here by dedicating an entire proposition to show that "flesh cannot be different from muscular fibers."[39] Finally, Borelli shared ideas first advanced in print by Steno, such as the muscular structure of the heart, the role of the muscles of respiration in venous return, the importance of angles to distinguish intercostal muscles, and the newly discovered ovaries in female mammals.[40] The reason that he does not quote Steno probably relates to the fact that other anatomists also made similar claims.[41]

But perhaps the greatest resonance between Borelli and Steno is in the actual description of the muscle structure. Steno writes that "there can be two descriptions of a muscle" according to the disposition of fibers in it, namely rectilinear muscles and oblique muscles.[42] One of Steno's main claim is that oblique muscles resemble two-dimensional parallelograms (i.e., rhomboids) or, in three dimensions, oblique parallelepipeds (fig. 1).[43] For Steno, this rhomboidal structure of muscle fibers is the key constituent of all muscles. Strikingly, Borelli agrees with Steno by writing that some muscles are "rectangular prisms," but almost all others are either "a rhomboid" or a "rhomboidal bundle" (fig. 2).[44] Borelli insists in this structure in a proposition about the "true picture of muscles" in which he writes that there are muscles made of parallel fibers and then others made of "oblique fibers" or rhomboids.[45] Just like for Steno, rhomboids are more central to Borelli's understanding of muscles than meets the eye. After identifying the different types of muscles, Borelli writes that muscle contraction "results from the structure of

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[36] Nayler, "The Insoluble Problem," p. 5.

[37] Nayler, "The Insoluble Problem," p. 106, 117, 181-182.

[38] Steno, *Elementorum myologiæ specimen*, p. 3, 5.

[39] Borelli, *On the Movement of Animals*, p. 10.

[40] Borelli, *On the Movement of Animals*, pp. 243-249, 103-104, 392.

[41] Honoré Fabri and Richard Lower also spoke on the muscular structure of the heart, see Honoré Fabri, *Tractatus duo: quorum prior est de plantis et de generatione animalium et posterior de homine* (Paris, 1666), p. 371 and Kardel, *Steno on Muscles*, p. 28. Jean Pecquet was the main authority on venous return, see Nuno Castel-Branco, "Physico-mathematics and the life sciences: Physico-mathematics and the life sciences: experiencing the mechanism of venous return, 1650s–1680s," *Annals of Science*, doi:10.1080/00033790.2022.2086301. For a recent account of the discovery of the ovaries, see Bertoloni Meli, *Mechanism, Experiment, Disease*, pp. 208-233, esp. 215-224.

[42] Steno, *Elementorum myologiæ specimen*, p. 13.

[43] Steno, *Elementorum myologiæ specimen*, p. 3.

[44] Borelli, *On the Movement of Animals*, pp. 10-11.

[45] Borelli, *On the Movement of Animals*, p. 13.

the little machines of which the fibers are made."[46] Later into the work Borelli explains what these machines are. According to him, muscular fibers are similar to "a series of small machines of … rhomboidal shape like a chain made of rhombs."[47] Therefore, Borelli attributes to muscle fibers a similar geometrical structure as the one used by Steno. Why then did he not acknowledge Steno in these parts? The answer lies in the differences between Steno and Borelli on muscle contraction.

Insert Figure 1 and Figure 2

Disagreement on Muscle Contraction

The main point in which Giovanni Borelli apparently disagrees with Nicolaus Steno is not on the "true shape of muscles," but rather on "its mode of action."[48] Steno had argued that the rhomboidal structure of muscles was enough to explain muscle contraction. Almost all anatomists until then thought that the swelling of a muscle meant that a fluid entered into it. But Steno concluded that such a fluid was not needed. His reasoning was geometrical and based on Euclid's *Elements*. If muscles really can be described as rhomboidal prisms, then with a simple variation of angles their shape changes without changing the volume of the prism. This means that no new mass is needed for muscle contraction to happen. Steno's theory has been extensively studied by Troels Kardel, Raphaele Andrault, and Domenico Bertoloni Meli, among others and I refer to their work for further details.[49] In short, and to use Steno's words, "it is amply demonstrated in every muscle that when it contracts swelling occurs, even if no new substance enters the muscle."[50] The muscle's geometrical structure alone was sufficient to explain contraction.

Borelli, on the other hand, challenged this claim. He acknowledged that "new thoughts on the true shape of muscle and on its mode of action have appeared in the last few years."[51] He did not mention Steno by name, but he was clearly thinking about him when stating that some authors "assume" that muscular action "is carried out by the tension of the fibers without addition of a new body."[52] Moreover, according to Borelli, such authors stated that "the

[46] Borelli, *On the Movement of Animals*, pp. 13-14.

[47] Borelli, *On the Movement of Animals*, p. 119.

[48] Borelli, *On the Movement of Animals*, p. 11.

[49] Kardel, *Steno on Muscles,* pp. 11-23; Bertoloni Meli, "The Collaboration," pp. 696-706; Raphaële Andrault, "Mathématiser l'Anatomie: La Myologie de Stensen (1667)," *Early Science and Medicine*, 15 (2010), pp. 505-536.

[50] Steno, *Elementorum myologiæ specimen*, p. 30.

[51] Borelli, *On the Movement of Animals*, p. 11.

[52] Borelli, *On the Movement of Animals*, p. 11.

rhomboid … remain[s] unchanged in dimension and the mass of solid substance mentioned above is neither increased nor decreased, only the oblique fibers … are shortened."[53] Borelli, however, thought that this conclusion was wrong and provided several arguments against it. Troels Kardel explains Borelli's counter arguments in detail and rightly concludes that some arguments do not necessarily apply to Steno's theory.[54] Borelli's strongest claim was an experiment in which "the moving power of the fibers cannot raise the resistance R by using a single rhomboidal muscle."[55] That is, a rhomboidal structure can hold a weight, but is unable to lift it by itself.

It is possible that Borelli had in mind other authors saying similar things to Steno. These were possibly some of Steno's readers, such as Honoré Fabri (1608-1688) and Michelangelo Ricci (1619-1682), some of whom lived in Rome alongside Borelli before the publication of *De motu animalium*.[56] Maybe for that reason, some of Borelli's arguments do not exactly match Steno's claim. Regardless, Borelli clearly preferred the so-called inflation theory of muscle motion, shared by almost all anatomists at the time and other famous authors such as René Descartes (1596-1650).[57] Much of Borelli's writings on the muscles relied on his theory that muscles move due to a substance coming from the brain into the muscles through the nerves. Borelli's inflation theory also undergirded the calculation of forces that permeates almost all of the first part of *De motu animalium*. Nonetheless, there were other factors shaping Steno and Borelli's theories of muscle contraction.

Borelli's Paradoxical Agreement with Steno

The problem with Borelli's disagreement with Steno is that at some other times Borelli seems to endorse Steno's view. In the second part of *De motu animalium*, when explaining the internal motion of muscles, Borelli describes muscle contraction in terms very similar to Steno's. He writes that muscles

[53] Borelli, *On the Movement of Animals*, p. 11.
[54] Kardel, *Steno on Muscles*, pp. 33-37.
[55] Borelli, *On the Movement of Animals*, p. 12.
[56] Castel-Branco, "Steno, The Traveling Anatomist," pp. 204-205.
[57] Kardel, "Steno's Myology: The Right Theory at the Wrong Time," pp. 154-161; Nayler, "The Insoluble Problem," 14-89. See also Matthew Cobb, "Exorcizing the animal spirits: Jan Swammerdam on Nerve Function" *Nature Reviews Neuroscience* 3 (2002), pp. 395-400; and Smith, Frixione, Finger, and Cover, *The Animal Spirit Doctrine and the Origins of Neurophysiology* (Oxford: Oxford University Press, 2012).

become tense and hard. But careful examination does not show any increase in volume of the muscles. The length of a muscle contracts and shortens but its width and diameter actually do not seem to increase. They retain the same size. … [T]he volume of flesh contained in the muscle when elongated and flaccid is also contained in the same muscle when contracted, since both correspond to the same quantity of muscular tissue.[58]

Borelli then argues geometrically by showing that two cylinders "of unequal heights" can have the same volume (fig. 3). In the book's first part, Borelli speaks again of a muscular contraction that "results from the structure of the little machines of which the fibers are made," as if the structure alone explained this contraction.[59] How can this be squared with Borelli's previous comments against Steno's theory of muscle contraction, which also relied on structure alone?

Insert Figure 3 here.

The answer lies in the fact that Borelli seems to agree with Steno but only partly. As Borelli writes, "experience shows that muscles exert two forces. One is due to the fibers themselves and results from their normal structure. The other results from an external cause and is used by the muscles and by instruments to carry considerable weights."[60] According to Borelli, Steno's explanation is only valid for the first type of muscle force, but not for the second. That is why his strongest argument against Steno was that the rhomboidal structure was not enough to move certain weights. According to him, something else was needed for the muscle to be able to lift heavy weights. The difference of their views becomes clearer when writing about the contraction of the masseter muscles in the jaw. Whereas Steno insists that "the swelling … of the muscle by clenching one's teeth … is easily explained without the arrival of new material," Borelli calculates the magnitude of the muscle's resistance to motion (figs. 4 and 5).[61] In short, Borelli takes Steno's model of contraction with rhomboids to explain basic muscle contraction but adds his own forceful contraction on top of it.

Insert Figures 4 and 5 here.

But why, then, did Borelli attack Steno's model in the first place? The problem lies not on muscle contraction itself, I argue, but on Borelli's use of a slight distortion of Steno's view and Borelli's own goals. According to Borelli, Steno held the view that the geometrical

[58] Borelli, *On the Movement of Animals*, p. 218.
[59] Borelli, *On the Movement of Animals*, p. 14.
[60] Borelli, *On the Movement of Animals*, p. 13.
[61] Steno, *Elementorum myologiæ specimen*, p. 38; Borelli, *On the Movement of Animals*, pp. 101-102.

rhomboidal structure excluded a substance causing muscular motion, such as animal spirits. This was untenable for Borelli because one of the main quests of his work was to find out "what is actually transmitted to the muscle by the nerves."[62] He thought that "the nerve is the path through which the motive faculty transmits from the soul to the muscle the order to be stimulated, to move, or to carry."[63] Indeed, if most muscular motion is voluntary, there needs to be some trigger in the muscle related to the nervous system. Something has to arrive from the brain into the muscle so that the muscle contracts. Borelli was thus convinced that the principle of motion of animals, i.e. the soul, "is supposed to reside in the animal spirits."[64] When Borelli wrote about this topic it was not yet clear what these spirits were. For Borelli, muscle contraction occurs due to the mixture of "some material substance transmitted through the nerves," or nervous juice, with something already present in the muscles, such as blood or lymph, which creates an explosive fermentation that moves the muscle.[65]

Steno did not necessarily deny this explanation. His main claim was only that "swelling occurs even if no new substance enters the muscle" and that whatever has been said "about an influx of new substance into the muscle, they are by no means proven."[66] His goal was only "to show the usefulness of the new muscle structure to explain the movement of muscles."[67] Steno was responding to the uncertainty associated with the doctrine of animal spirits with rigorous new knowledge about muscles. As he puts it, many authors call muscle fluids "animal spirits, the more subtle part of the blood, its vapor, juice of the nerves. But these are mere words, nothing proved by experiment."[68] In short, it is not that Steno denied the existence of animal spirits. He merely suggested that they were not necessary for muscle contraction to happen. Indeed, he bluntly states that if his new geometrical structure of muscle "cannot determine the true mode of contraction, it can at least distinguish what is certain in it from what is uncertain."[69]

Therefore, the main difference between Steno and Borelli is in their epistemological aims, which in turn are shaped by the audiences they were writing to. Steno was writing to fellow anatomists who knew well the problems of anatomy and medicine of their period. As he

[62] Borelli, *On the Movement of Animals*, p. 8.
[63] Borelli, *On the Movement of Animals*, p. 8.
[64] Borelli, *On the Movement of Animals*, p. 7.
[65] Borelli, *On the Movement of Animals*, p. 232.
[66] Steno, *Elementorum myologiæ specimen*, p. 30.
[67] Steno, *Elementorum myologiæ specimen*, p. 30.
[68] Steno, *Elementorum myologiæ specimen*, p. 63.
[69] Steno, *Elementorum myologiæ specimen*, p. 66.

put it, “it cannot any longer be ignored how incomplete our knowledge of what is common to all muscles has been and still is, and how great an area of investigation lies waiting for those who are not shy of work.”[70] Borelli, in a way, took on this legacy, but he did so by writing to a completely different audience, mostly made of mathematicians and natural philosophers. For instance, unlike Steno, Borelli proposed his theory of muscle motion in probabilistic terms because he, like Steno claimed, did not have an experimental confirmation. He wrote that the fermentation of nervous juices in the muscle is a possible mechanism and that it “must be admitted since it explains precisely the phenomena which is neither possible nor easier otherwise” to explain; moreover, he continues, “we can conclude with a high degree of probability that the operation carried out by Nature in muscles is not different.”[71] Borelli was showing his readers – mathematicians and natural philosophers – that his mechanical, chemical, and corpuscularian view of nature could also be applied to animal motion. As Borelli writes,

> some people claim that Nature dares, and can, use something beyond the laws of mechanics. They speak as if the laws of mechanics were not necessary and as if Nature could carry out impossibilities against the laws of necessity prescribed by Divine Wisdom.[72]

But for Borelli these people were naive, in part because, as he continued, they did not know mathematics and philosophy as well as they knew anatomy.[73] Mechanical laws were part of nature. And Borelli took on the task to show it even within the human body.

Conclusion

In his introduction to the second part of *De motu animalium*, Carlo Giovanni Pirroni (c. 1645-1685), the book’s final editor, advises the readers to “not fear difficulty because the author involves mathematics.”[74] One may wonder how many readers stopped reading the book’s first part due to the mathematical calculations it contained. Indeed, *De motu animalium* was divulged as a work of physiology, as the cover of the book shows. But it was written by a mathematician whose previous books were mostly targeted at mathematicians and natural philosophers, not

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[70] Steno, *Elementorum myologiæ specimen*, p 64.
[71] Borelli, *On the Movement of Animals*, p. 232.
[72] Borelli, *On the Movement of Animals*, p. 219.
[73] Borelli, *On the Movement of Animals*, p. 220.
[74] Borelli, *On the Movement of Animals*, p. 203.

anatomists. On the other hand, Steno was an anatomist writing a book filled with mathematical proportions to physicians. This difference in the book's audience is, I suggest, the key to understand Borelli's critical reception of Steno's theory of muscle contraction.

As this essay argued, Borelli's *De motu animalium* depends more on Steno's anatomical ideas about muscles than previously acknowledged. This resonance of ideas, however, was left unnoticed because of the way with which Borelli attacked Steno's geometrical model of the muscle. What is striking is that, as this article showed, Borelli used a very similar model. As I showed, neither Borelli denied Steno's rhomboidal structure altogether nor did Steno deny that there must be something moving the muscle. They seemed to clash because they were writing with different purposes in minds – Steno wanted to combat uncertainty in anatomy and Borelli wanted to apply the laws of mechanics to the body.

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Figure Captions

Figure 1. The muscle as an oblique parallelepiped. Steno, *Elementorum myologiæ specimen* (Florence, 1667), p. 3. Courtesy of the Institute for the History of Medicie, Johns Hopkins University.

Figure 2. The prevalence of rhomboidal structures. Borelli, *De motu animalium pars prima* (Rome, 1680), Tabula prima. Courtesy of Bodleian Libraries, Oxford University.

Figure 3. Two cylinders of unequal heights with the same volume. Borelli, *De motu animalium pars altera* (Rome, 1680), Tabula decima quinta, fig. 12. Courtesy of Bodleian Libraries, Oxford University.

Figure 4. Structure of the jaw muscle. Steno, *Elementorum myologiaæ specimen* (Florence, 1667), Tabula III, fig. II. Courtesy of the Institute for the History of Medicie, Johns Hopkins University.

Figure 5. The resistance of the jaw muscles. In Borelli, *De motu animalium pars prima* (Rome, 1680), Tabula IX, fig. 2. Courtesy of Bodleian Libraries, Oxford University.

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