STENSEN'S MYOLOGY IN HISTORICAL PERSPECTIVE

We think of truth as something that is invariable,
but add a new circumstance and we have a new truth.
WILLIAM J. MAYO[1]

A theory may be true even though nobody believes it.
KARL R. POPPER[2]

[1] Aphorism no. 19, 1938.
[2] *Conjectures and refutations*, p. 225.

1. Abstract

A MAIN WORK on muscular action, the *Elements of Myology*, by the Danish anatomist Niels Stensen (1638–1686), was written at a time when the teachings of Hippocrates, Erasistratus, Aristotle, and Galen were still the foundations upon which scholarly learning on the human body were built. In this work as in several other areas of research, Stensen described a structure versus time relation as a dynamic process. While declaring his ignorance as to the causes of contraction, he dissociated himself from contemporary anciently-derived speculations concerning an arbitrary force such as the animal spirit (Descartes, Croone) as well as from the idea of a globular microstructure of muscle (Borelli). From macroscopic observations of a number of muscles in several animal species, Stensen described the contraction of compound muscles arranged in unipennate structures with an angle between muscle fibers and tendons. *Overall shortening resulted from shortening of equally long muscle fibers between parallel tendons at opposite faces of the muscle belly.* The introduction of a model, the parallelepiped, enabled Stensen to introduce mathematics, and by geometric analysis to infer that *isovolemic contraction of the fibers of a unipennate muscle results in swelling mainly at one side of the muscle.* Therefore, the observed swelling of a muscle during contraction was not an argument for an expansion of its volume. The so-called "New Structure of Muscle" described in 1667 by Stensen, was evaluated by eminent scientists over the following century. Misunderstood and criticized with erroneous or irrelevant arguments (Borelli, Bernoulli, Boerhaave, Haller), the theory was rejected and disappeared from the scientific literature.

Anatomical studies and elaborate computer constructions published since 1980 from several scientific centers have confirmed the structural basis of Stensen's theory and applied it as a pivotal principle in muscular mechanics.[3]

2. Predecessors

2.1 Antiquity

THE FIRST KNOWN THEORY of the mechanism of muscular action,[4] was based on the evident swelling and hardening that occurs when muscles contract. According to Aristotle (384–322 B.C.) "The outputs of movement are pushing and pulling. Accordingly, the instrument of movement must be capable of expanding and contracting; and this is precisely the nature of breath. It contracts and expands without constraint, and so is able to pull and to push from one and the same cause."[5] Muscular shortening was thought to be caused by the inflation by derivatives of the breath, called *pneuma* or vital spirits, which entered the muscles. According to

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[3] Kardel, *Niels Stensen's geometrical theory of muscle contraction.* See also three overview articles in Danish, published 1991.

[4] Bastholm, p. 64; Needham, p. 7.

[5] Aristotle, *Motion of animals*, cf. Frampton, p. 316.

Galen (131–201 A.D.), this took place from the brain through hollow nerves as first formulated by Erasistratus of Julis (c. 330–250 B.C.). The influence of this theory lasted for no less than two millennia. Another important factor in early biology was the conflict between "Aristotelian" cardiocentric and "Galenic" cephalocentric models of animal sense-perception and locomotion, having its influence well into the seventeenth century.[6]

Galen identified and described a great number of muscles, considered as constituting the instruments of voluntary motion. He described the action of antagonistic muscle groups saying that each muscle had only one active movement. He described the paralysis of muscles when their nerve supply was cut. He also described the irritability of isolated muscle, a phenomenon that contradicted the theory of contraction by the inflow of pneuma, but frequently Galen shifted his position in his extensive writings in order to gain argumentative advantage.[7] Galen's conception of the structure of muscle has been summarized as follows:[8] The flesh, *caro*, merely acted as a filling material. It was formed from blood by a process of condensation. Nerves ran from the brain and spinal cord to the flesh, where they split up into ever finer branches—as fine as spiders' webs. The nerves dispersed through the muscle, assembled again into thicker branches, and finally left the muscle in the form of a tendon. The tendons leaving the muscles are often six to ten times larger than the neural fibers running to the muscle, thus something had been added to the nerves in the muscle. The tendons were thought to play an active part in contraction. The fact that sinews and nerves were named by one word, *neura*,[9] makes room for interpretations of ancient texts.

2.2 Renaissance

In 1536 the Venetian anatomist Niccolò Massa (1485–1569) gave the following account of the structure of muscle in his *Liber introductorius anatomicae*:[10]

> In each muscle that has a tendon the fleshy part draws the tendon to itself since the nerves, from which motion originates, come first to the fleshy part; then they proceed through the entire muscle. But muscles which have no tendon are contracted to their origin by means of fibers, or filaments.

This work was known to Stensen because he referred to Massa's description of the tongue as a muscle in *De musculis*.[11]

On the basis of animal experiments, Andreas Vesalius (1514–1564) also rejected any active part taken by the tendons and recognized that the

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[6] Ibid., p. 330.
[7] Wilson, *Erasistratos, Galen and the Pneuma.*
[8] Bastholm, pp. 82–84.
[9] Frampton, note 41.
[10] English translation quoted from Lind, *Pre-Vesalian Anatomy*, p. 210.
[11] Kardel, *A specimen of observations upon the muscles*, p. 109.

fleshy parts alone were responsible for the contractile force. Vesalius compared the structure of muscle with that of cheese:[12]

> That foundation and body is simple flesh covered with fibres, which is put into the fibres in exactly the same way as the experts in cheese-making put milk into baskets and other vessels when they are curdling it. So imagine that the fibres that flow from the nerve and tendon correspond to the rushes, the blood to the milk itself and the flesh to the cheese. For as cheese is made from milk, so is flesh from blood.

Hieronymus Fabricius ab Aquapendente (1537–1619) in works published in 1614 and 1618 expressed some views on animal motion. In contrast with Vesalius, Fabricius wrote that contraction takes place mainly in the tendons, they being the most prominent instrument of motion.[13]

The pennate structure of muscles is hardly discernable in Vesalius's magnificent plates in the *Fabrica* (Fig. 1), but were illustrated by Giulio Casserio Placentinus (1545?–1616) (Fig. 2).[14] A pennate structure can mainly be seen in planes cut parallel with the fibers of the muscle and to a lesser degree on the surface of the muscle. After Stensen and the immediate reactions on his work, muscles with a unipennate structure are seen in some later anatomical works without receiving attention, as in the plates of Jacques François Marie Duverney (-1748) from 1745, and also in the anatomical textbook that I used in my medical studies, the Spalteholz *Atlas* from 1953,[15] with typical examples such as the flexor pollicis longus and the gastrocnemius muscle, as already mentioned by Stensen [p. 53].

2.3 Contemporary Opinions

Stensen's teacher at Copenhagen, Thomas Bartholin (1616–1680), wrote on "what a Muscle is" in his widely distributed textbook *Anatomia reformata*, quoted here from a contemporary English translation:[16]

> A Muscle is an Organical Part, the Instrument of voluntary motion. For only this part can receive the Influx of the motive faculty. It consists 1. Of flesh. 2. Of a tendinous part (and these are the two parts, which perform the Action). 3. Of Veins to carry back the Nutriment. 4. Of Arteries preserving the inbred Heat, and bringing the Nourishment to the part. 5. Of Nerves, which contribute sense and especially motion. For the Brain sends the motive faculty through the Nerves into

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[12] *Fabrica*, p. 220: *Carnis in musculo usus*. Translation quoted from Needham, pp. 12–13.

[13] Bastholm, pp. 126–127.

[14] Borelli, Propositio VI: "Finally, there are multipennate muscles. They were first observed and described by Casserio of Piacenza [Placentinus]." It is an intriguing fact that Stensen, without making reference, must have known this work pretty well, since the 1656 Frankfurt edition of Placentinus's atlas was edited by Stensen's teacher at Copenhagen, Professor Simon Paulli. It is doubly intriguing that Borelli made reference to an atlas containing illustrations of several unipennate muscles but, as mentioned later, ignored the existence of this structure of muscle.

[15] Spalteholz, plate 401: *The flexor pollicis longus muscle;* and plate 303: *The gastrocnemius muscle.*

[16] *Bartholinus Anatomy*, p. 8.

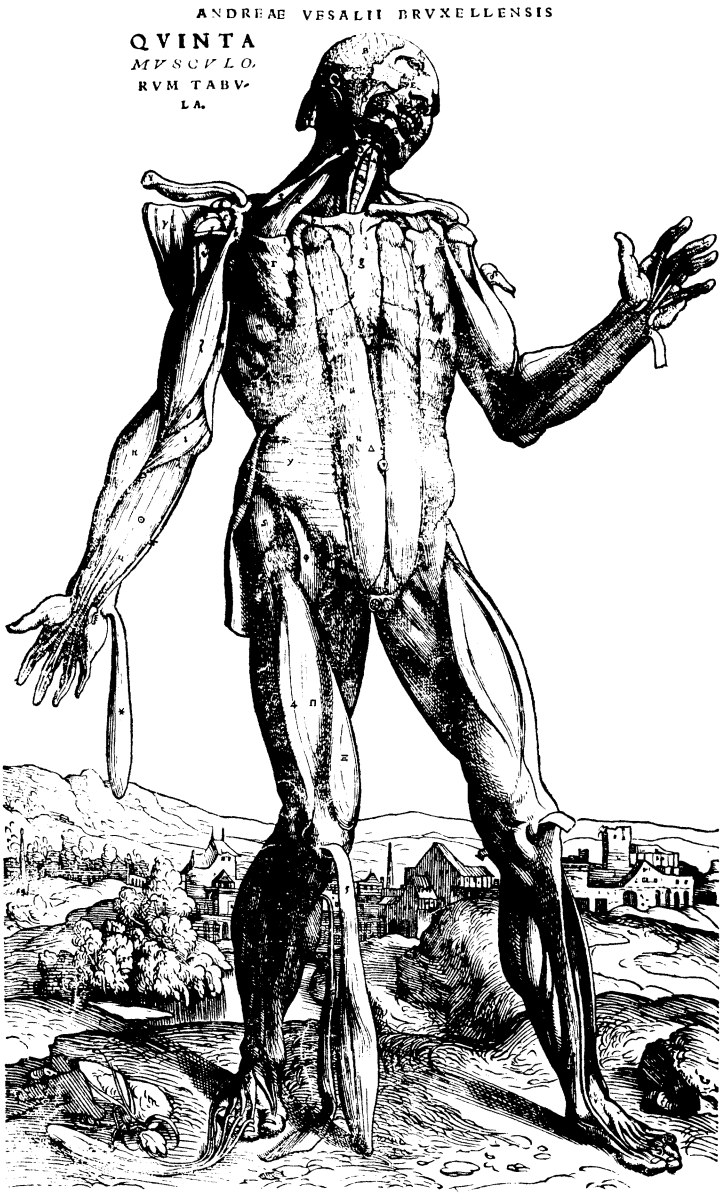

FIGURE 1. **Plate V from Vesalius' *Fabrica*, first edition Basel, 1543. Danish National Library of Science and Medicine (DNLSM), Copenhagen.**

the Muscles. 6. Of Membranes which encompass and keep the muscles together. 7. Of Fat which moistens them, and hinders them from being dried by over much motion.

At Leiden another teacher of Stensen, Frans dele Boë Sylvius (1614–1672), wrote, "and the contraction of a muscle is nothing else than the

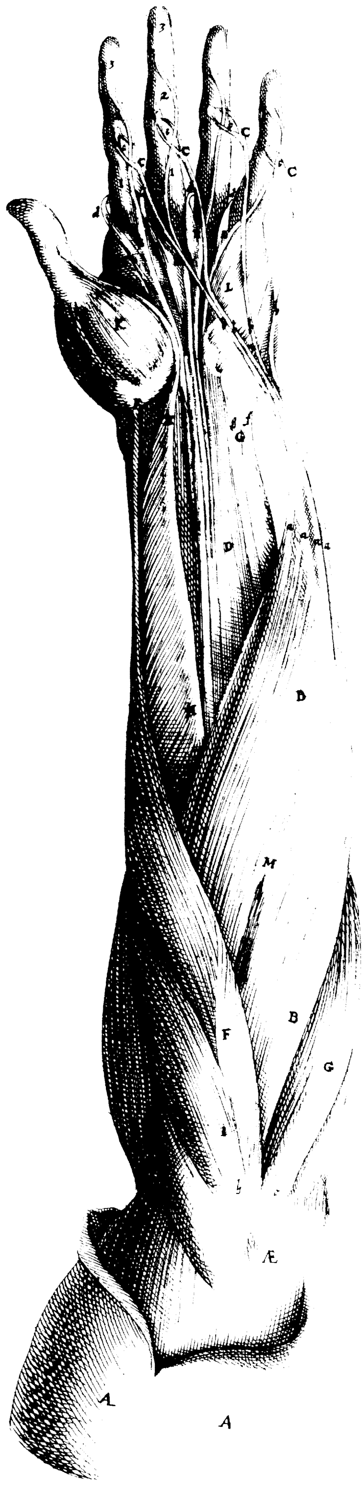

FIGURE 2. From one of several plates in Placentinus' *Tabulae anatomicae* in which the pennate structure of muscle can easily be recognized. Venice 1627. DNLSM.

distension of its fibers swollen with the Animal Spirit and hence its shortening."[17]

Similar ideas were expounded authoritatively by René Descartes (1596–1650) in *De homine* first published at Leiden in 1662 when Stensen was studying there:[18]

Now in the same measure that spirits enter the cavities of the brain they also leave them and enter the pores in its substance, and from these conduits they proceed to the nerves. And depending on their entering some nerves rather than others, they are able to change the shapes of the muscles into which these nerves are inserted and in this way to move all its members.

Descartes compared the flow of the animal spirits into the nerves with that of water flowing through pipes in fountains causing the fountains' figures to move. Descartes even supplied the nerves of his human machine with valves directing the flow of the vital spirits to and from antagonistic muscle groups.

In 1664, just two years after the publication of Descartes's treatise, William Croone (1633–1684) published anonymously a booklet *De ratione motus musculorum* in which he showed the strong influence of Descartes's "human machine":[19]

Having postulated these things, we shall consider the living body to be nothing else but a kind of machine or automaton and the Mind, which is in us, we may move meanwhile by its own thought, or at least we may arrange to sit in the brain merely as a spectator of this play which is acted out in the scene of the body.

Croone developed a theory of muscular contraction based on the ancient principle of a flow through hollow nerves of the Animal Spirits, the substance of which he described as "that most subtle, active and highly volatile liquor of the nerves." Croone added to the ancient principle that the impulse was transmitted along the nerve in the same way as vibrations are transmitted along the tightened string of a musical instrument.

The interaction of the spirits with the muscle, according to Croone, caused the muscle to swell in a kind of fermentation that occurred when the blood, flowing into the muscle through an artery, met in the cavity of the muscle the juice supplied by the nerves, P in Croone's Fig. 1 (Fig. 3). When in Croone's Fig. 2 the muscle swelled from E to D, it produced a moment of pull to the tendon. Croone built this theory on the *Experiments concerning the force of blowing with a man's breath* demonstrated by John Wilkins (1614–1672) for the Royal Society at one of its first meetings, 31 July 1661, but not published until 1756.[20] Thus, necessary preconditions for a muscle contraction according to Croone are

[17] Cf. Wilson, *William Croone's theory of muscular contraction*, p. 159.
[18] Descartes, p. 21.
[19] Cf. Wilson, p. 161.
[20] Birch, *The History of the Royal Society in London*. Vol. 1, p. 36. See also Hierons and Meyer 1964.

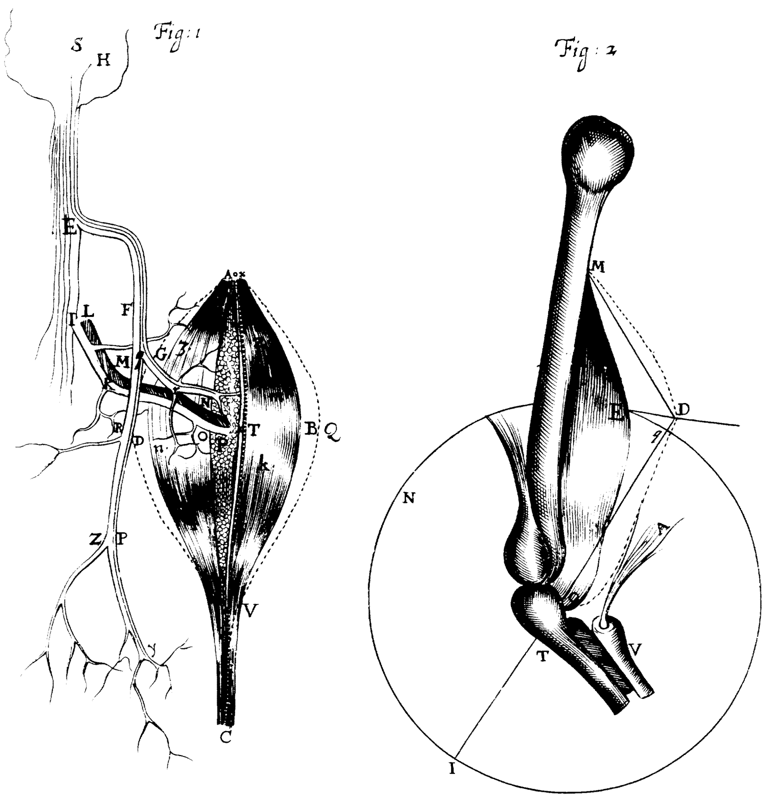

FIGURE 3. Croone's theory on muscular contraction based on volume expansion through the inflation of vital spirits. The Wellcome Institute for the History of Medicine, London.

1. something flowing from the brain or the medulla;
2. something flowing from the artery; and
3. a volume increase during contraction.

In 1658 Walter Charleton (1619–1707) took a somewhat inconsistent standpoint in his main work published in English the following year as the *Natural History of Nutrition, Life, and Voluntary Motion.* First he said, "We (with all the Ancients) conceive, that the *Animal Spirit* sent from the brain, by the Nerves, into the Muscles, are the Immediate instrument of the Soul, whereby she doth impress an actual motion upon the Muscles."[21] Later he argued that a geometrical inscription of an upper arm, the parallelogram A B C D representing (Fig. 4)

> the Muscle Biceps of the Arme, as it is extended; and a Square equal thereunto, *B E G F*, representing the same Muscle, as it is contracted . . . hath lost nothing of its bulk, that it had in the first Figure, or Extension: but, because the Square of the muscle, *B E G F* is equal to the Parallelogramme, *A B C D*; therefore it followes, that the superfice of the muscle is the same, and that the part *G D* changed

[21] Charleton, p. 183.

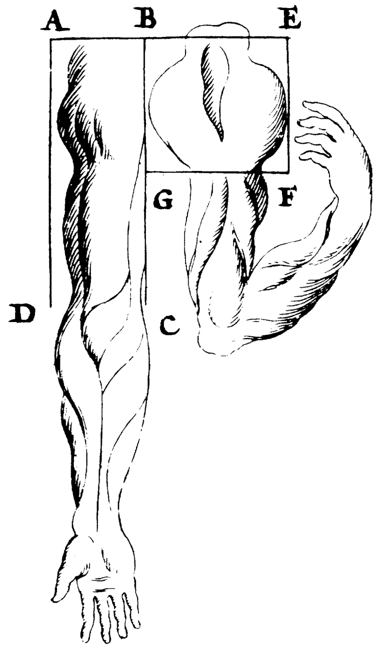

FIGURE 4. **Charleton's figure of muscles of the upper arm in contraction. DNLSM.**

in its Latitude, is in proportion to the Line *A D*, which determin's the Local motion.[22]

Like Bastholm and Hierons and Meyer, in my paper on Stensen's geometrical muscle theory, I included Charleton's work as one employing geometrical reasoning to suggest an unchanged muscle volume during contraction.[23] I am not quite sure that all readers will find Charleton's reasoning on the constancy of the muscle bulk, as described above, scientifically valid. However, after a more careful study of Charleton's text, like Gosch, I have come to the conclusion that Stensen himself denied Charleton's argument in the *Elementorum*: "nor does an explanation with rectangles agree with Nature."[24]

An account of the various ideas on muscular contraction at the time of Stensen is found in Thomas Willis's (1621–1675) work, reviewed in 1674 by Willis's compatriot John Mayow (1643–1679) in his *Tractatus quinque.*[25] The work may have added to Mayow's qualifications to be elected in 1678 as a member of the Royal Society of London of which Willis and Croone were founding members. Mayow wrote:

No one doubts that the movements of animals are produced by the contraction of the muscles, but how that contraction is brought about is the subject of varied

22 Ibid., p. 208.
23 Kardel, op. cit., p. 958.
24 P. 123.
25 Mayow, p. 230 ff.

controversy among authors. Still, the most generally received opinion is that the fibres of the muscles are inflated with some elastic matter, so that while they swell as to breadth they contract as to length.

And this inflation of the fibres is thus described by that very distinguished man, Dr Willis, in his Discussion on Muscular Motion.[26] This learned man thinks namely, "That the Animal Spirits carried from the brain by the channel of the nerves are stored up in the tendinous fibres, as in suitable repositaries; but that these spirits, on the incitement to motion being given, spring forth from the tendinous into the fleshy fibres, and there, meeting active particles of another sort, supplied by the blood, immediately effervesce with them, so that from the struggle and agitation of them both, the fleshy fibres, being lax and porous, are stuffed out and corrugated, and that the contraction of the muscle is produced by the corrugation at the same time at both ends of all these fibres. But when the contraction is over, the unused spirits that are left again in great part retire into the tendinous fibres, leaving the other particles within the fleshy fibres, and then the blood, as also their nerves repair the waste of these fibres. But as to how the spirits stored in the tendinous fibres are brought thence into the fleshy fibres for the production of motion," our learned author supposes "that an impulse transmitted by the nerves, as it were a token, is required, and that this is done by other spirits sent from the brain, while, namely, these inflowing spirits, by their varying approach to the muscles, regulate the innate spirits in their various movements, whether of expansions or of retreats." . . . Finally, as to the part of the muscle which primarily undergoes contraction, it is probable that not so much the fibres, as the fibrils inserted transversely into them, chiefly undergo contraction, as will be shown afterwards.

But so far I think we may agree with the learned author [Willis], for I believe that the contraction of the muscles is produced by particles of different kinds mixed with one another in the structure of the muscle, and mutually effervescing, as will be shown below.

This quotation tells two stories: first, what ideas on muscle contraction Stensen was up against; and second how little impact Stensen's works from 1664 and 1667, to be described below, had exerted in 1670 and 1674 in England. I shall return to Willis and Mayow in section 5.2.

3. Niels Stensen[27]

NIELS STENSEN became interested in studies of muscle contraction at Leiden during the winter 1662–1663 because of an interest in the structure and function of the heart. Stensen was born at Copenhagen in 1638. From 1656–1659 he studied medicine at Copenhagen University under Thomas Bartholin. Niels Stensen, or *Nicolaus Stenonis*, often shortened to *Steno*, continued studies at Amsterdam, where in his first dissection he discovered the excretory duct of the parotid gland named after him.[28]

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[26] Willis, *De motu musculorum*. 1670.

[27] The author's comprehensive review of Stensen's work and methods in science is in press in *Acta hist scient nat med* (Copenhagen) as vol. 42, 1994.

[28] The discovery resulted in a fierce dispute on priority with Gerard Blaes (1626-1682), Stensen's teacher at Amsterdam, and his supporters, Deusing and Hoboken, which is reflected in the texts presented. See pp. 73–75.

At Leiden University he continued studies of glands 1660–1664 under Frans dele Boë Sylvius and Jan van Horne (1621–1670). He distinguished between lymphatic glands with both afferent and efferent serous vessels and excretory glands with only efferent vessels, and he discovered the lacrimal ducts; accordingly, he concluded that tears are secreted by small glands and not by the brain. In 1664 he was back in Copenhagen for family reasons, but since there was no chair for him at Copenhagen University, he went abroad for further study. In 1665 he delivered at Paris a famous lecture on the anatomy of the brain. From 1666 he was at Florence where he became scientist to the Grand-Duke Ferdinand II of Tuscany and after 1670 to Ferdinand's son and successor Cosimo III, who became his friend and benefactor for life. In 1667 and 1669 Stensen published at Florence works considered to be basic to geology, paleontology, crystallography, and the study of female reproductive organs. In 1667 Stensen became a convert to Catholicism, thus disqualifying himself for a position at Copenhagen University, but in 1672–1674 he was in Copenhagen as anatomist invited by the Danish King. After his return to Florence Stensen prepared himself to become a priest and in 1677 was consecrated by Pope Innocent XI, as bishop and apostolic vicar to the scattered remnants of Catholicism in Northern Germany and Denmark. For the rest of his life he lived at Hanover, Münster, and Hamburg in self-inflicted poverty and religious renunciation and died at Schwerin in 1686. The body lies buried in the Church of San Lorenzo at Florence. In 1988 Niels Stensen was beatified in the Roman Catholic Church by the Pope, John Paul II.[29]

3.1 *New Structure of the Muscles and Heart*

Stensen wanted to compare the contraction of the heart with that of skeletal muscles. In 1664 he gave the following account in *De musculis* of how he started the studies on muscles:[30]

Meeting with so many various Doubts concerning the Doctrine of the Muscles, I was almost deter'd from proceeding any further in the Scrutiny of the Heart; but happening to have a dead Rabbet at Hand, I laid hold of its Legs, and separated its Muscles, with a full Resolution to try whether there was any Hopes left of attaining any greater Certainty in this Point than before. The first I happened to light upon being cut off and divided with one strait Section from one Extremity to the other, did represent itself in the most simple and plain Figure or Shape that ever I saw afterwards; for the opposite Tendons gather'd at the Extremities, as soon as they came to the fleshy Belly, were divaricated in such a Manner, that one being expanded thro' the superior, and the other through the inferior Surface of the middle Belly, grew slender by Degrees, the carneous Fibres met in a strait Course, each of them being contiguous to the tendinous Fibres.

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[29] Scherz, *Niels Stensen; eine Biographie.*

[30] The English translation from 1712, see Kardel *A specimen of observations upon the muscles: Taken from that noble anatomist Nicholas Steno.* pp. 108–109.

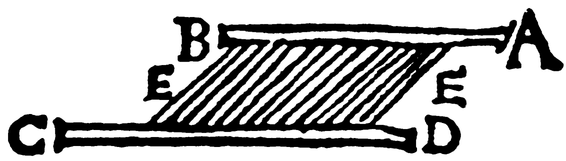

FIGURE 5. **Drawing from Stensen's letter, *Nova musculorum & cordis fabrica*, dated Leiden 1663. Published in Copenhagen 1667. DNLSM.**

Stensen presented the preliminary results of his study of muscle structure at Leiden in a letter to Thomas Bartholin, dated 30 April 1663.[31] The text of the letter and three sketches of the structure of muscles contain the structural essence of Stensen's theory of muscular contraction (Fig. 5). In 1667 Thomas Bartholin published the letter, entitled *Nova musculorum & cordis fabrica*, in one of his collections of letters.[32] Bartholin replied but made no comments himself on Stensen's new structure of muscle. But after Stensen's return to Copenhagen in 1664 he gave the young protégé opportunity to publish on these new ideas.

3.2 *Specimen of Observations on Muscles and Glands*

In this work, *De musculis et glandulis observationum specimen* (Fig. 6),[33] Stensen described clearly which structure contracts in a muscle:[34]

That which is contracted is not the Tendon, but the Flesh that is comprehended betwixt the tendinous Expansions, which by its Contraction produces this Effect, that the two or more opposite *Plana* of the Belly do approach nearer to each other, so that the Tendon is not the first Principle of Motion.

Stensen refrained from attempting to explain what caused the contraction:

But in what Manner this Contraction is accomplish'd it is hard to determine, considering there are many who deduce it from the Repletion of the Fibres, some others from the Inanition of them, and others again there are, who have Recourse to both. I should perhaps be looked upon as too forward and bold, if I should pretend to set up for an Arbitrator in so difficult a Point, and therefore am rather inclined to declare, that I am not satisfied yet as to the true Causes or Manner of this Contraction.

In *De musculis* Stensen used the argument of "detailed similarity"[35] comparing the structure of heart and muscle to confirm the hypothesis, that the heart is only a muscle. He thereby concluded that "there is nothing wanting in the Heart that is not met with in a Muscle; and further, that nothing is found in the Heart but what is contained in a Muscle."[36] He

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[31] E 13.

[32] Bartholin, *Epist. Medicin. Cent.* IV. Ep. 70: *Nova musculorum & cordis fabrica*, Copenhagen 1667. OPH 14. First English translation, see pp. 59–75.

[33] OPH 15, English translation in Kardel, op. cit., pp. 105–121.

[34] Kardel, p. 112.

[35] "Principle of molding" and "Detailed similarity" are two principles of Stensen's method in geological research, cf. Gould, *The titular bishop of Titiopolis*, pp. 23–24.

[36] Kardel, p. 115.

FIGURE 6. Stensen's illustration of the unipennate structure of muscle is seen upper left in the frontispiece of *De musculis et glandulis observationum specimen*, Copenhagen 1664, a work dedicated to Denmark's King Frederik III. DNLSM.

strengthened the hypothesis as a scientific theory by studying various muscles in several species of animals in which he found nothing adverse to his conclusion: "This done, I pursued my Scrutiny in other Muscles at different Times, and of different Sorts, all which confirm'd me in the Truth of my former Observations."[37] Stensen aimed at greater certainty[38] by repeating the observation in the same set or under changed condi-

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[37] Kardel, p. 109.

[38] Compare: . . . *num spes ad certiora perveniendi superesset.* OPH 1: 173. A discussion of Stensen's scientific method is given in "Reflections on Niels Stensen's scientific method," ch. 3 in the author's *Steno: Life, Science, Philosophy.*

tions, while he refrained from certainty through authoritarian belief—*ex authoritate*—or certainty through analogies.

Several contemporary readers reacted against Stensen's theory of the heart as a muscle, thereby suggesting its originality. Stensen's reply to such critics is found in his letter to Thévenot, p. 201 ff. *De musculis* contains Stensen's early attempt to describe the muscle contraction geometrically. Without accompanying illustrations, his description is hard to understand even for me after several years of work with Stensen's myology.

De musculis contains several statements or rules on muscle, which may be regarded as arguments for, or derivatives from, a still not yet fully formulated theory on the structure and function of muscle:[39]

> The Length of the Belly is not always to be measured by that of the carneous Fibres, because the longest Belly has oftentime the shortest Fibres. . . . The Action of the Muscle consists in its Contraction, but thence it does not naturally follow, that the strait interjacent Part of the Muscle betwixt its Extremities should become shorter; but that each of the Fibres of the same Muscle, which lie betwixt the said two extreme Points, should be shorten'd. . . . The shorter the Flesh is in a long Belly, the stronger is the Force of Contraction, because the Number of the Fibres is the greater.

Stensen exemplified the value of studying the relationship between normal and pathological physiology:

> How far the aforesaid Structure of the Muscle may be able to lead us upon further Enquiry, a right Understanding of the Causes as well as the Cures of certain Diseases, will appear more fully from what follows. I told you before, that the Flesh was contained betwixt the tendinous Expansions, and it is not long since that I observed in a Turky-Cock,[40] in several Muscles of the Legs, the tendinous Expansion so far freed from the Flesh that lay underneath it, that it only adhered to it by some very thin Fibrils, which by the least Touch or Force would break asunder immediately, and then the Tendon appeared like unto a Membrane. The carneous Extremities which had been continued to this Tendon before, in that Part where they appeared somewhat white, but firmer, came off from the rest of the fleshy Part, and contained also something of a Moisture about them. This Observation I made only once in such a Cock; and, What Reason can be given why such a Thing should not happen sometimes also in the humane Muscle?

A review of *De musculis* was published in the *Journal des Sçavans* on 23 March 1665[41] during Stensen's stay in Paris. While the anonymous reviewer was willing to abandon the old concept that the heart is the seat of natural heat, of the production of blood, and of the vital spirits, he was reluctant to accept Stensen's dictum, that the heart is only a muscle, because of the heart's great vessels and valves, the irregularity of its structure, and the fact that the heart may be the seat of mortal diseases. In the review there is no mention of Stensen's ideas on the structure of skeletal muscle, but such mention is found in a letter dated 29 July 1665 by

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[39] Kardel, pp. 111–112.
[40] *Gallus africanus.* See also p. 100.
[41] *Journal des Sçavans* 1665, pp. 157–160.

the physician André Graindorge (1616-1676) describing Stensen's anatomical demonstration with a sketch of a unipennate muscle showing that in 1665 Stensen had demonstrated that structure at Paris.[42] Also, the *Philosophical Transactions of the Royal Society* in London brought an excerpt of Stensen's first work on muscles,[43] which was characterized as "a golden book-let" *aureus libellus* by Albrecht von Haller in 1774.*

3.3 The Influence of Swammerdam

When Stensen developed his geometrical muscle model, Jan Swammerdam (1637-1680) was doing basic research in muscle physiology. They were friends and sometimes worked together both at Leiden and Paris. Stensen later visited the Swammerdams, Jan and his father, at Amsterdam. Stensen and Swammerdam both refer to each other's writings on muscle contraction with respect.[44] Unfortunately, Swammerdam's account of his research report on muscle contraction was published not during his lifetime, but in 1737.[45]

Swammerdam's work was completed *after* the publication in 1669 of the second edition of Stensen's *Elements of Myology* to which Swammerdam referred.[46] He mentioned Stensen seven times in his treatise and did not speak about other research-workers at all.[47] From studies of isolated hind limb muscles in the frog Swammerdam drew conclusions, which undermined the very foundation of all anciently-derived theories on muscle contraction.

Swammerdam showed (Fig. 7) that touching the nerve to an isolated frog muscle caused the muscle to contract although nothing had flowed into the muscle from the brain or spinal medulla. When the muscle was encircled by a glass cylinder, during contraction the muscle swelled and filled the cylinder. Finally, when the muscle was enclosed in an air-tight syringe, an externally induced contraction resulted in no movement of a water droplet *e* blocking the capillary opening of the syringe, showing that there had been no change in muscle volume.

Thus, contraction had taken place, (1) without accession of any material from the brain; (2) without blood supply; (3) with a shortening and widening of the muscle: but (4) without any increase of the muscle's volume. Had Swammerdam's experiments been published, the basis for the ancient theories of muscle contraction would have been removed. But in the 1670s Swammerdam went into a deep religious and personal crisis, which paralysed his scientific work. We learn of this crisis because

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[42] Eighteen letters in the Royal Library, Copenhagen (Kgl. Bibl. Ny kgl. Samling 4660, 4°). See also Scherz, *Da Stensen var i Paris.*

[43] *Philosophical Transactions of the Royal Society*, vol. 1, pp. 176-178, 1665-1666.

* *Bibliotheca anatomica*, vol. 1, p. 492.

[44] Thévenot letter p. 207. Wilson, pp. 166-167.

[45] Swammerdam, *Biblia Naturæ*, 1737.

[46] Swammerdam referred to the Jansson edition, which means *Elementorum myologiæ specimen*, second edition published at Amsterdam in 1669 by Jansson.

[47] Schulte, p. 39.

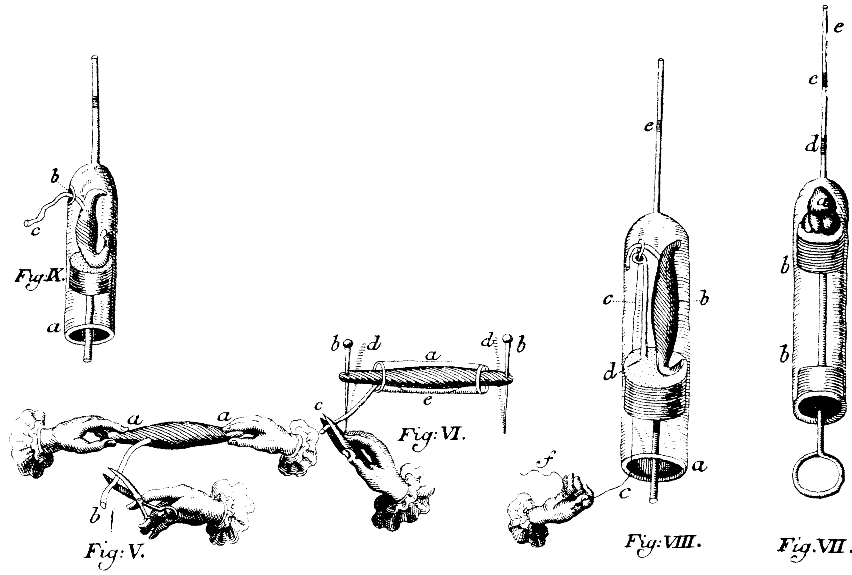

FIGURE 7. Swammerdam's experiments in frog muscles from the late 1660s. First published at Leiden in 1737. Mayo Foundation Library, Rochester, Minnesota.

Stensen sent some of Swammerdam's scientific drawings of silk-worms to Malpighi in Bologna with the accompanying letter:[48]

My very dear Sir.

Mr Swammerdam, while being on the point of abandoning his studies of nature, has forwarded me the enclosed drawings that I pass on to your lordship if you would kindly receive them. When he had written a treatise on this matter he destroyed it and he has only preserved these figures. He is seeking God, but not yet in the Church of God. Pray for him and have those friends known to be true servants of God pray for him too. Let me at this occasion remind you of my whole-hearted friendship and affection. I remain obliged and pray God for your eternal reward.

Florence, 18 July 1675. Unworthy Servant in Christ
Niels Stensen

4. *Elements of Myology*

STENSEN'S MAIN WORK on muscle was published at Florence in 1667. Different in style from that of 1664 in the *De musculis*, the *Elements of Myology* is a systematic and scholarly work with a formal geometrical argumentation accompanied by many illustrations. Stensen appears to have written it as a result of discussions among the learned circles at

[48] E 106, translated by T.K. On Stensen's correspondence with Malpighi, see also Malpighi 1697, pp. 59 and 110.

Paris, Montpellier, and Florence, in which his arguments from *De musculis* had been evaluated, polished, and sharpened. The cost of the illustrations and printing was a good reason for Stensen gratefully to acknowledge his benefactor, the Grand Duke Ferdinand II. In the preface Stensen praised in superb literary style the Grand Duke's hospitality and his interest in science. Now he proposed to apply mathematics, so valuable in astronomy, optics, and geography, in the study of the living organism, clearly a reference to the late protégé of the Grand Duke, Galileo's recommendation of 1623 in *Il Saggiatore.*[49]

The problem, which Stensen wanted mathematics to solve, was presented in the first two pages illustrated by two figures. The first figure shows the old muscle structure, a muscle formed like a spindle, with longer, curved muscle fibers surrounding a core of shorter, straight fibers. Stensen wanted to replace this structure, "completely unknown to Nature," with the second one, the new structure of muscle, which was a prismatic structure of flesh formed like a parallelepiped, with tendons formed like wedges at both ends. Stensen hoped that the reader before making any judgment would read the whole work without being alarmed by the shape of the new structure. In spite of the author's warning, such appears to have been exactly the fate of Stensen's new muscle structure.

To make a brief move forward in time, I should like to present an illustration from 1983 of the structure of a muscle in a modern textbook.[50] In several illustrations the structure is depicted in a manner identical with that called obsolete by Stensen! Fig. 8 is from a chapter on muscle physiology of a textbook given to me as an introduction to the study of muscle physiology at the Orthopedic Biomechanics Laboratory at the Mayo Clinic in Rochester, Minnesota during the winter of 1989. Quite simply, I had to conclude that *either* Stensen was wrong when rejecting the ancient structure; *or* that Stensen had presented "the new muscle structure" in vain.

4.1 The Geometrical Argumentation

The structure of the argumentation of *Elements of Myology* is as follows:

1. The outer shape and inner structure of a muscle model is determined by 44 *Definitions*, pp. 97–119;
2. The movement of the model by 5 *Suppositions*, p. 123. Definitions as well as suppositions were based on observations. Then, in a purely abstract geometrical deduction employing Euclidean mathematics, Stensen formulated 6 *Lemmas* or supporting propositions, pp. 125–137, to reach

[49] "Philosophy is written in this grand book—I mean the universe—which stands continually open to our gaze, but it cannot be understood unless one first learns to comprehend the language and interpret the characters in which it is written. It is written in the language of mathematics, and its characters are triangles, circles, and other geometrical figures, without which it is humanly impossible to understand a single word of it; without these, one is wandering about in a dark labyrinth." Galileo, *The Assayer*, pp. 183–184.

[50] Ottoson, Fig. 3.9 (middle section), p. 85.

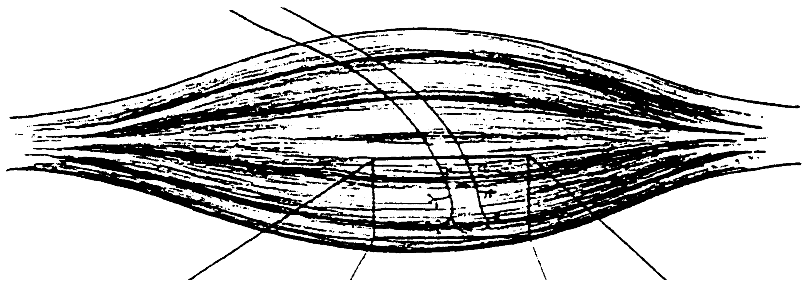

FIGURE 8. The muscle structure from a physiological handbook in 1983, see text. Oxford University Press, New York, by permission.

3. A main theorem, the *Propositio,* p. 139, which says: "Every muscle swells when contracting."

Involving that much brain work and ink, one would expect something to be proven just a little bit fancier than what children can demonstrate to each other by bending their arms. Possibly this is a major reason why *Elements of Myology* was little understood and later became ill famed.

What in fact Stensen had promised to demonstrate was presented on page 136, following a geometrical assessment in several paragraphs of the variable swelling in long and short muscles. His main conclusion was: "I thus think it is amply demonstrated in every muscle that when the muscle contracts a swelling occurs, even if no new substance enters the muscle." Thereby, the easily recognized swelling during contraction was not an argument for the volume increase of a muscle when it contracted, and neither was it an argument against contraction without change of volume: "Whatever clever arguments are proposed from several sides about an influx of new substance into the muscle, they are by no means proven."

Stensen was aware that a description of the relation between the structure and function of a muscle could be useful, since in the same paragraph he stated that he had made the geometrical analysis "in part to make clear the value of the new muscle structure to explain the movement of muscles."

According to Stensen, the motor fiber was "the true organ of movement." One long fiber had a middle, contractile part, with inextensible tendon parts at each end. This continuity in one long fiber has not been confirmed by microscopy. Moreover, recent investigation shows that tendons stretch slightly when exposed to tension.[51]

In definitions 3 through 10, pp. 98–105, Stensen defined a microstructure, the shape of the single motor fiber, as a long, thin parallelepiped. This shape was purely speculative without any counterpart in reality.

[51] See, for instance, Otten, *Concepts and models of functional architecture in skeletal muscle,* and Lieber et al., *J Biomechanics* 25 (1992):421–28.

Nevertheless, since Stensen used the micro-structures only descriptively to fill up the macrostructure, and he made no use of them in his geometrical argumentation, the error did not invalidate the conclusions. Among the five suppositions, Stensen wrote that he intended to demonstrate suppositions no. 1-3, probably in a planned extension of *Elements of Myology*, which he never did. As mentioned above, tendons are slightly stretched as force is applied to them and the motor fibers bend slightly according to the local pressure and stress.[52] Thus, Stensen's suppositions 1 and 2 are approximations. Even if Stensen did not like to explain "problems in complex and extraordinary things by means of ordinary and simple examples," p. 103, that is, however, what he did here.

During this research, Stensen noticed the varying colors of different muscles in the leg of a rabbit. His description in definition 2, p. 99, is the first distinction between red and white muscles recorded in the literature.

The geometrical argumentation in which Stensen proceeded from definitions and suppositions, through lemmas, to the main proposition, is that of traditional Euclidean mathematics with the application of a deductive *ergo* no less than 18 times. As Borelli put it, Stensen used "that worn-out proposition from Euclid, that two prisms upon the same base between two parallel planes are constituted as equal to each other."[53] Borelli is right that there is nothing innovative in Stensen's geometrics. What distinguishes Stensen's study and was ignored by Borelli and later investigators, however, are that Stensen carefully tested the consequences of his theoretical considerations by observation: he sought after special cases; and he searched for the described structure in different species of animals. On pp. 143–145 he described the geometry of the contraction in very long muscles, on pp. 145–147 in very short muscles, and on page 149 in more complex muscles. On pp. 157 ff., illustrated by Plate II and III, he gave typical examples of the pennate structure of different muscles: the gastrocnemius and semimembranous are formed as unipennate structures and the deltoid muscle as a multipennate structure. The typical bipennate structure was described in muscles of the lobster's claw (Fig. 9). In the shark Stensen described the complex pattern of a multipennate structure with curved myosepts. (When describing the contraction of muscles of the lobster's claw, Stensen did not mention the straightforward argument that any volume increase inside the bone-hard claw of a lobster would be hard to believe.)

An old dogma, that the volume increases when muscles contract, had been at issue. Stensen went a long way to deliver an indirect counter argument. It would take more than one hundred years to change the dogma, partly because Swammerdam's experiments with the direct evidence, were not published until 1737. It would take more than three hundred years before the new muscle structure was to become useful for the expla-

[52] Ibid.
[53] Borelli, Proposition 5.

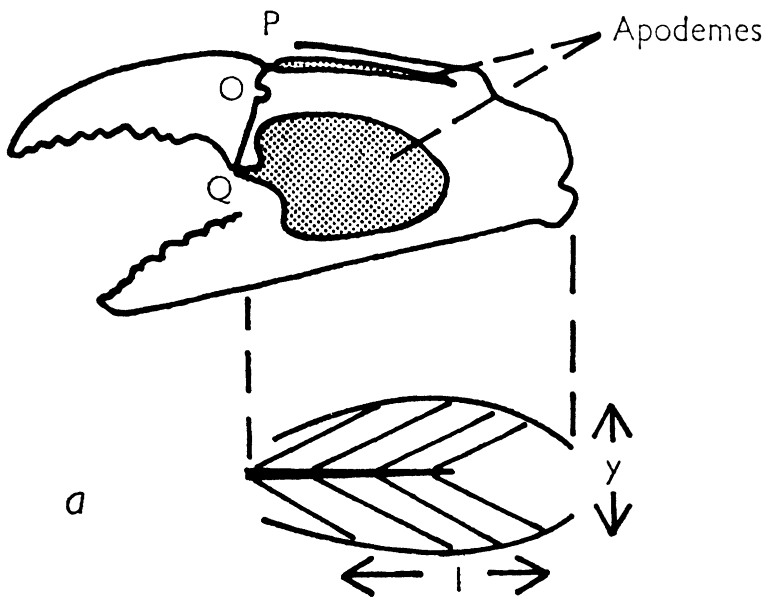

FIGURE 9. The skeleton of a crab chela and a diagram showing the pennate arrangement of the muscle that closes the chela. The lower claw is fixed, and the upper one pivots at O. From McNeill Alexander (1968) by permission from the author. Compare with Stensen's Plate III, Fig. iv and with p. 158.

nation of the movement of muscles according to the author's written intention.

Is there any priority conflict between Swammerdam and Stensen when looking today at their published works on muscle? The answer must be a clear *No!* The two authors described equally important but clearly different aspects of muscular contraction. Swammerdam showed convincingly that contraction of an isolated leg-muscle of a frog was not associated with any change in the muscle's volume, while he paid no attention to the structure of muscle. Stensen showed the relation between structure and function in compound muscles, that is, how a muscle can swell during contraction without any increase in volume.

One remarkable feature of *Elements of Myology* is the description at pp. 173–175 of how to compare different compound muscles by equalizing their geometry. Similar principles are in use today. Finally the geometrical part of the treatise includes on pp. 177–183 the description and schematic illustration of the complicated build-up of muscles of the back in man. For the purpose a similar scheme, *Des Releveurs de Stenon,* was used by Jacques François Marie Duverney.[54]

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[54] Duverney, *Myotomologie,* pp. 91–92.

4.2 The Letter to Thévenot

The second half of *Elements of Myology* is a bread-and-butter letter to Melchisédek Thévenot, Stensen's benefactor at Paris in 1665. The letter was apparently written during the first few months after Stensen had arrived in Tuscany in March 1666.[55] It creates the impression that Stensen had received very strong criticism of his ideas on muscle contraction and other discoveries, and that he now wished to counter such criticism. Since the *Elements of Myology* and the Thévenot letter are written by the same clerk in the MS, it is suggested that they were written almost in continuation as a consequence of the criticism and as a result of the support Stensen received at the court of the Grand Duke.

As in the 1665 lecture at Paris on the anatomy of the brain, Stensen proposed in the letter to Thévenot a full program for research on muscles, pp. 217–225. Muscle research, even if heavily criticized, had a high priority for Stensen: "It is a frequent experience that what displeases other people is often what pleases the authors most," p. 93. Most remarkable in the Thévenot letter is perhaps Stensen's clear considerations on science methodology, pp. 193–199, exposing the limitations in scientific practice of the inductive method of empiricism. Stensen also described the limitation of the deductive method, hoping for great results if reason accepted what has been only demonstrated, p. 93. Otherwise Stensen's emphasis on what is *not* known on muscles with a whole section called "Demonstration that much is still unknown about the muscles," p. 211, clearly distinguishes the work from contemporary writings, except, of course, from Stensen's much more famous lecture on the anatomy of the brain: "Gentlemen, Instead of promising you to satisfy your curiosity concerning the anatomy of the brain, I confess sincerely and publicly here that I know nothing about it. . . ." Both to scientists on the Continent, increasingly influenced by the rationalism of Descartes, and to the British empiricists, ignorance was to become a sin,[56] perhaps blocking the readers' attention to much of the "positive" knowledge contained in the treatises.

In the *Canis carchariæ* accompanying the *Elements of Myology* but not included in this translation, Stensen briefly mentioned that temporary ligation of the abdominal aorta in a dog caused a reversible paralysis of the animal's hindlimbs, presuming to show the need of a blood supply for the muscular contraction.[57] Stensen's ultra-short report on the so-called Stensen-experiment caused both vivid discussions and several futile attempts to reproduce the experiment by members of the Royal Society,[58] thereby also diverting the attention away from the author's main issue. Two centuries later, two German theses showed that the tran-

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[55] P. 185: ". . . in France, through which I traveled last autumn and the following winter."
[56] Karl R. Popper, *Objective knowledge*, p. 68.
[57] GP, p. 89.
[58] Poynter, pp. 275–277.

sient paralysis was caused by ischemia of the spinal cord,[59] which was in fact already suggested in 1670 by Thomas Willis.[60]

Stensen considered his *Elements of Myology* to be a preliminary report, a "specimen," but "if it does not displease the public, on some occasion I intend to give a complete description of the muscles according to these new principles," p. 93. He never did this, however. In view of the reception given the *Elements of Myology*, Stensen had had little incentive to fulfill his promise.

5. The Contemporary Reception

AS SUGGESTED by Thomas S. Kuhn, "If a paradigm is ever to triumph it must gain some first supporters, men who will develop it to the point where hardheaded arguments can be produced and multiplied."[61]

Prospects were favorable for a quick success when Stensen published the *Elements of Myology* in 1667; the subject was of universal interest; the author was well known in scientific circles; the theory had been discussed at several centers and a forerunner had been reviewed by newly created scientific journals. The printing was well done and sponsored by no less than Ferdinand II, the patron of Galileo's famous *Dialogue on the two chief world systems* from 1632.

The reception was substantial; there were long reviews in scientific journals at London and Rome and some favorable comments in letters.[62] One proponent, Thomas Willis, came forward in 1670. The first apparently critical response came in 1674 from John Mayow in Oxford followed in 1680 by Borelli's devastating criticism in Rome. Stensen kept silent. No one among friends and scientific colleagues in Italy, France, the Netherlands, England, or in Denmark[63] felt obliged to counter the criticisms on behalf of the then bishop to save a theory which they barely understood. Strangely enough, over the following one hundred years, one after

[59] Faller, *Zur Diskussion um das Stensen Experiment*.

[60] "From the observation of Doctor *Steno*, in a live Dog the trunk of the descending Artery being tyed, all the lower or posterior members were suddenly deprived of motion. And though it doth not yet appear plainly to me, whether the exclusion of the blood from the spinal Marrow, or from the Muscles themselves, or from both together, be the cause; yet however it comes almost to the same thing, for as much as the animal Spirits being procreated within the Head, and stretched out by the medullary and nervous Appendices into every member, without the concourse of the blood, they should not be able to perform the loco-motive power." Willis, *Practice of Physick* (1684), "Two medico-physical exercitations" 1670, sect V, p. 35.

[61] Kuhn, p. 158.

[62] Scherz, *N.S. Eine Biographie*, vol. 1, p. 169 has listed letter responses to third persons from the mathematicians P. Stefano Angeli of Venice and Michel Angelo Ricci of Rome, and by the anatomist Molinetto of Padua.

[63] The only existing source to the reception in Denmark of Stensen's work on muscle is a short epigram by Thomas Bartholin, In *Librum de Musculis Nicolai Stenonis*, published in 1669: *Ecce moves validos post experimenta lacertos,/ Robur et ingenii monstrat habere liber.* Cf. Olden-Jørgensen, *Thomas Bartholin og Niels Steensen*, p. 289. Plate I from *Elementorum myologiæ specimen* was reproduced 1677 in Th. Bartholin, *Anatome*, Lyon, pp. 42–43.

another, eminent scientists took up Stensen's muscle theory for discussion. From four different points of view, all came to the same conclusion: it contained fundamental errors. Stensen's geometrical theory of muscle contraction was side-tracked from the mainstream of science. In 1873, Stensen's theory and the arguments by which it had been refuted were evaluated by the Danish zoologist and diplomat C.C.A. Gosch (1832–1913), in 1910 by the physiologist and later professor of history of medicine at Copenhagen, Vilhelm Maar (1871–1940), in 1950 by the general physician Eyvind Bastholm (1904–1989), and recently by me,[64] also a general physician.

5.1 Two Reviews: 1668 and 1669

The first review appeared less than a year after the *Elements of Myology* was published.[65] The anonymous reviewer in the *Philosophical Transactions* may have been none other than Croone.[66] The review gives a fair description of Stensen's muscle theory, with emphasis on Stensen's programmatic intention to employ mathematics in the study of the living organism:

The Author of this *Book* declareth, that his design in composing it was, to shew, that in a *Muscle* neither the *Parts* of it can be distinctly named, nor its *Motion* duely consider'd, unless the Doctrine thereof become a part of the *Mathematicks*. And he is of opinion, that there is no other cause of the many Errors, which spoil the History concerning the *Humane Body*, than that *Anatomy* hath hitherto disdaind the *Laws* of the *Mathematicks*. And therefore inviteth those that are studious in that part of *Philosophy*, to consider, that our Body is an *Engine* made up of a thousand subordinate Engins, whose true knowledge whoever thinks that it can be investigated without *Mathematical* assistance, must also think, that there is matter without *Extension*, and Body without *Figure*.

Hereupon he shews, that the very *Fabrick* of the *Muscles* imposeth a kind of necessity upon *considering* Writers to explicate them *Mathematically:* In conformity whereunto he pretends to have found, that in every Muscle there is One *Parallelepiped* of Flesh, and Two *Tetragonal Prismes* of Tendons; defining a *Muscle* to be a Body composed of divers series's or ranks of Fibers equal, like, and parallel among themselves, and so immediately placed upon one another, that whole ranks are congruous to whole ranks. Here he explains the *Dimensions* of a Muscle, its Contraction, and Strength, and says that the *Use* of this new discovery of the structure of the *Muscles*, is, to demonstrate, That they *may* swell in their Contraction without the Accession of new matter.

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[64] Kardel, *N.S.'s geometrical theory.*

[65] *Phil. Trans. R. Soc.* 1667/68;2:627–628.

[66] At the meeting of the Royal Society on 6 February 1668 "Mr. Oldenburg produced Nicholas Steno's new book entitled, *Musculi Descriptio Geometrica*, printed at Florence 1667, in 4to, which was delivered to Dr. Croune to peruse it, and to give an account of it to the society." On the meeting 13 February "Dr. Croune gave an account of Mr. Steno's *Musculi Descriptio Geometrica*, that the author pretended only to compose an essay on that subject, and reckoned up the desiderata in the doctrine of muscles; adding several good experiments, among which was one tying up the artery descending from the head, and thereby depriving the animal immediately of all motion: Which experiment was ordered to be tried before the society at the next meeting, by Dr. Lower." T. Birch, *The history of the Royal Society*, vol. 2, pp. 246–247. See also Poynter, p. 277.

He subjoyns a Letter to Monsieur *Thévenot,* in which, among other things he alledges several Experiments, to shew, that the Motion of the *Heart* is like the Motion of *Muscles* and answers those, who pretend that the true Fabrick of the *Heart* hath already been observed heretofore; and those likewise, who think that these new Observations of the Muscles are uncertain, concluding this Subject with an Enumeration of the particulars, yet remaining to be search'd into, in the *History* of the *Muscles.*

Members of the Royal Society devoted Stensen's experiment of producing paralysis of the hind legs in the dog during temporary ligation of the aorta an overwhelming interest, one after another trying to reproduce the experiment.[67] This was apparently due to the experiment's potential for explaining the origin of the substance thought to expand the contracting muscles. But I have only found one short early notice in the minutes of the Royal Society dealing with the structure of muscle: "[Mr Hooke] produced a muscle, to shew how it consists of mere fibres or strings lying close together, longwise, like the fibres of talc."[68]

In 1669 a four-page review, very favorable to *Elements of Myology,* appeared in *Giornale de'Letterati* of Rome.[69] The review contains a correct illustration of Stensen's parallelepiped of flesh. The review emphasized the value of the work to support the atomic theory of Democritus and Epicurus in the contemporary debate.[70]

5.2 Members of the Royal Society

5.2.1 Discussions with Croone

In the autumn of 1665 Stensen met William Croone (1633–1684) at Montpellier, France. The year before they had both published treatises on the muscle contraction. There are clear indications that they discussed the subject at Montpellier.[71] Even without agreeing, they later corresponded on friendly terms.[72] In *Elementorum myologiæ specimen,* published two years later, Stensen did not quote Croone by name. Nevertheless, the earlier quoted anonymous review in the *Philosophical Transactions* of the Royal Society of London, probably written by Croone,[73] was fair enough to Stensen's work.

From Wilson's analysis of the encounter at Montpellier,[74] Croone must

[67] See also Faller, *Zur Diskussion um das Stensen Experiment.*

[68] Birch, vol. 2, p. 271.

[69] 1669, pp. 5–9.

[70] Cf. Gardair, p. 194–196: "l'Elementorum Myologiæ specimen de Stensen lui inspire des transports lyrique, scandés par le seul point d'exclamation que nous ayons rencontré dans tout le périodique. . . . En associant les noms de Stensen et d'Epicure, il semble donc que les rédacteurs du "Giornale de'Letterati" entendaient moins forcer la pensée du savant danois que s'autoriser de son exemple, dont la prudence était particulièrement appréciée en haut lieu, pour combattre le discrédit attaché à la pensée atomiste."

[71] Martin Lister's description, see Scherz, *Nicolaus Steno and his Indice,* supplement 3, p. 292.

[72] Birch, vol. 2, pp. 100 and 102.

[73] Poynter, *Nicolaus Steno and the Royal Society of London,* p. 277.

[74] Wilson, *William Croone's theory of muscular contraction.*

have felt rather crushed by Stensen's arguments, including the knowledge of Swammerdam's experiments in frog muscles. So when Croone was asked by the publisher, Commelin of Amsterdam, to publish a second edition of his treatise on muscle—the first edition had been published anonymously at London together with Thomas Willis's *Cerebri anatome*—he wrote back a letter, which was added as a foreword to the 1667 edition:[75]

> Although your letter came to me directly my dear Commelin I would certainly have answered it more fittingly and so would have acted according to your wish, except that, almost at the same time, I also received a letter from Paris by which it was made known to me that a Treatise on Muscles of that distinguished gentleman my very good friend Dr. Steno is now in press there. One or two years ago there took place a considerable intercourse between that gentleman and I at Montpellier and we talked much together on this question. I wished to know fully what he, who is remarkable for the highest ingenuity, and diligence, had contributed to this very obscure matter from his store. For I do not have such faith in my opinion that I would not wish to test it first by the judgement of others. (which was my strongest reason for writing) before I shall bring into the light those things which themselves (as it seems to me) the mind must ponder further to confirm. You see dear Sir that I do not have any improper reason for publishing this Edition; meanwhile I am very unwell, my affairs are such that I am compelled to deny you that which, if it were of any value or moment, I would think it glorious to be struck with your imprint, the Commelin Press and to be ornamented with your type.
>
> Yours most devotedly,
> William Croone
> M.D. and Fellow of the Royal College
> of Physicians and of the Royal Society
>
> For if you are certain to print this treatise again, lest your edition seem to the ordinary reader to be a very faulty one of Willis (also a fellow of the same Society), you may if you like add this letter in place of a preface.

In 1674 and 1675 Croone read lectures in the Surgeon's Theatre at London, and had them published in summary form in 1680 by Robert Hooke.[76] Croone stuck to the idea of expansion of the muscle as cause of contraction, and to meet objections, instead of having the muscle swell like one bladder as suggested in 1664, he now supposed:

> each distinct Carneous *Fibre* to consist of an infinite number of very small *Globules*, or little Bladders. . . . From each ramification of the *Nerve* within the *Muscle*, that second sort of Matter much more fluid and active than the former is extravasated, and these mixt together as I said, enter into each little Bladder, and by these constant agitations, ebullition, or effervescence, which with the natural heat that is partly the cause, and partly the constant assister of this motion, and makes that which we call the very life of every part, as long as the Animal lives, keeps these Globules or small Vesicles always distended. How it enters in, and sends out its effete Particles again into the mass of Blood to be discharged by Transpiration,

[75] Quoted from Wilson, op. cit., note 38, p. 177.
[76] Croone, *An Hypothesis of the structure of muscle*, p. 22 ff.

and every moment takes in fresh, I endeavoured in those Lectures to shew at large.

As source of the idea of the microglobules he mentioned that "Mr. *Lewenhook* has since told us, That he finds by his Microscope the Texture of a carnous Fibre to be of innumerable small Vesicles or Globules, which gives an appearance of reality to the said Hypothesis." Croone appeared disillusioned, presenting this idea, "only in the way of an *Hypothesis*, not as if I did presume to believe I had found out the true Secret of *Animal Motion*, when I am almost persuaded, no Man did or will be able to explicate." In this late publication Croone referred neither to Swammerdam nor to Stensen, but to "that long expected Work of *Borelli, de Motu Animalium*," which had just arrived in London, and to which we shall return later.

It is noteworthy also that Croone did not recognize an experiment showing the limb's volume during contraction, carried out before the Royal Society on 16 December 1669, but mentioned several times in the Society's Minutes, by Jonathan Goddard (1617–1674). The experiment is often ascribed to Francis Glisson (1597–1677), who in the *Tractatus de ventriculo et intestinis*, 1677, gave an account of it. The experiment of Goddard designed to show "whether the muscles of an Animal, in their action, are bigger or less in their summe of Dimensions" was not published until 1756 in T. Birch's *The History of the Royal Society* (Fig. 10):[77]

A Case was made of lattin capacious and convenient to receive immersed in water the arm of a man, so as the large orifice or entrance into it might be stopped close by the part of the arm next the shoulder, with a small glass pipe cemented to it towards the other end, opening into the cavity, (according to the figure.) Upon putting in of water first a little warmed, and afterwards of the arm, so as it closed the wide orifice of it, and the water did rise into the small glass canal; first it was visible, that the water rose upon every pulsation of the artery, and subsided upon every intermission; and then the person being ordered to make a contraction or clutching of his fist of both arms, that within the case and that without at the same time; upon every such contraction the water in the glass canal did descend much more, than upon the intermissions of the pulse beforementioned.

Apparently Goddard's experiment did not shake his listeners' faith in the ancient theory:

Upon reading this paper, it was suggested by Mr. Hooke, that it would be worth considering what it is, that by its influx makes the muscles act by contraction; and then how the muscles are again relaxed by nature's discharging that liquor or spirit, which contracted them. To illustrate this, he mentioned that spirit of wine (for example) poured upon gut-strings contracts and shortens them, and being thence evaporated relaxes and lengthens them again. So that, he said, there must be a very subtile volatile spirit, that enters into the muscles; and the same must very quickly be discharged again to cause the contraction and expansion of the muscles.

[77] Cf. vol. 2, p. 412, and Mayow, pp. 231–232. See also Hierons and Meyer, 1964.

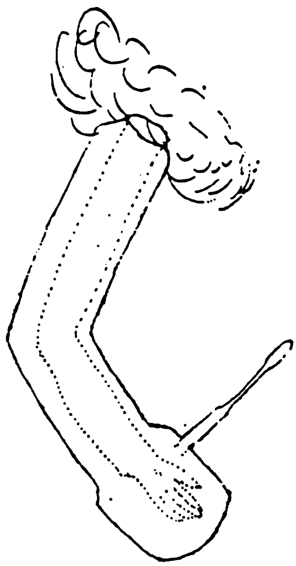

FIGURE 10. Goddard's experiment from London 1669, published 1756, showing no increase of volume of a working extremity. Royal Society of London.

5.2.2 Richard Lower: 1669

Richard Lower (1631-1691) published in 1669 at Oxford an account on muscle, heart, and circulation, the *Tractatus de corde.* Without quoting Stensen, Lower reflected on the similarity of the structures of skeletal and heart muscle. Lower is, however, unmistakably close to Stensen's description of the new structure of muscle, as is evident from the following excerpt and illustration (Fig. 11):[78]

> [Heart muscle] has this in common with [skeletal muscles], that its fabric and movement are based on exactly the same kind of fibres and mechanical devices, even if these are differently arranged. . . . It is certain that any muscle you like in the whole body, whose fibres and whose movement are straight, is not provided with a single belly only (as Anatomists have stated hitherto . . .), nor with a head and a tail; it is equally certain that the fibres are not carried directly from one tendon to another (as they are usually pictured: see Plate 3, Fig. 1). But all have two bellies and their fleshy fibres are carried from a different origin to different and opposite terminations. This is shown in Plate 3, Fig. 2. This is the structure of all the Muscles throughout the body, whether in the upper or lower part of the leg, the arm, or the neck of Man.

Lower made no geometrical considerations on contraction.

5.2.3 Thomas Willis: 1670

Thomas Willis's description of muscular action, *De motu musculari,* from 1670 became widely distributed through reprints in the *Opera omnia*

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[78] Lower, *Treatise on the heart,* pp. 18–19.

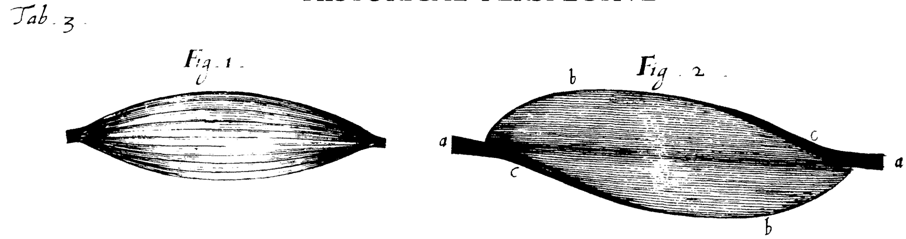

FIGURE 11. From Plate III of Richard Lower's *Tractatus de corde*, London 1669. DNLSM.

and through Samuel Pordage's translation of *Dr Willis's Practice of Physick*. Unlike his assistant, Lower, the year before, Willis referred to Stensen no less than seven times as the only author on muscle quoted:[79]

Moreover, although the Doctrine of the Nerves hath been much described by the most skilful Anatomists of every Age, so that the Muscles of the whole Body (as it is thought) have been exactly recounted, and offices assigned them, and monstrous names fitted for expressing them, yet the true frame of a Muscle, not yet shewed by others, first began to be delivered lately by the most ingenious Doctor *Steno*. He hath found out in every Muscle two opposite Tendons, into which both the Fibres go; yea, and hath taught, that the same Fibres wholly, which compose strictly on one side, the Tendon of the knitting being more loosely joyned, do constitute the flesh; yet so, that some being laid upon others, compose the thickness or profundity of the Muscle, and some laid nigh to others, its breadth or latitude: he calls the former Fibres *Ordines* or Orders, but the other *Versus* or Turnings; then the parts and composition of a Muscle being after this manner laid open, he aptly reduces its Figures to Mathematical Rules, and according to Canons thence taken, shews the action to be unfolded: because he advertising, that in a Muscle with a simple right line, all the fleshy Fibres, parallel within themselves, and for the most part equal, are carried from one Tendon obliquely into another; and that those Tendons are sowed in the opposite ends or angles of the flesh, whereby he most ingeniously describes a Muscle to be, *a Collection of moving Fibres, so framed together, that the middle flesh constitute an oblique angular Parallelopipedum, but the opposite Tendons compose two quadrangular Prisms or Figures.* The instrument which Painters use for the describing many Examples of the same thing, fitly represents the figure of this delineated in a plain: because the styles being fixed to the opposite Angles, express the insertions of the Tendons and the Parallelogram it self the fleshy part of the Muscle: for when the opposite Angles are diduced to a great distance from one another, and made sharper, the two sides come nearer together, and render the *Area* or middle of the Figure longer, but narrower, a Muscle not contracted is denoted: But if the same Angles are brought nearer, and made more obtuse, the two sides go farther apart, and so make the middle of the Muscle shorter, but also wider, a contracted Muscle seems to be represented. In the mean time, in either site of the aforesaid *Parallelogram* the quantity or longitude of the sides is not changed, but only their position, and the largeness of the Angles is varied: whether it may be also so in a Muscle, shall hereafter appear. In the mean time, we shall take notice, out of the observation of the same most Learned *Steno*, that a Muscle is either simple, which consists of one belly and two Tendons, of which sort there are many in the Arm and Leg,

[79] Willis, 1684, *Muscular Motion*, ch. 111, pp. 29-30.

which are the movers of the fingers and toes, yea and almost every where in other parts of the Body; or compounded, that hath many bellies, to every one of which, two opposite Tendons are hung; yet so, as when those compounded Tendons, to wit, two together, shall be joyned, one compound Tendon enters the middle of the flesh, and the other embraces the middle on both parts. This is evidently discerned in the Masseter or Throat-muscle, the Deltoid, and divers others, in all which, even as in a simple Muscle, whilst the fleshy Fibres (to which only the motive power belongs) are contracted, the opposite Angles are enlarged according to the insertions of the Tendons, and so the bellies being made shorter, and at the same time thicker, do swell up.

Stensen's influence on Willis's illustrations (Fig. 12), probably drawn by Christopher Wren, was explicitly mentioned:

I had designed Figures, almost of every kind of Muscles, to be engraved according to the natural appearances: but the Printer making haste, I had not the opportunity to dissect an humane Body, having only taken some few Muscles from the Leg of an Ox, we have caused them to be delineated to the life, which are to be seen at the end, although the famous *Steno* hath already accurately performed this task.

Willis wrote that "even the most ingenious Steno" abstained from erecting a hypothesis of muscular action, but this could not keep Willis from trying on his own. As remarked by Isler, "something like a Willisian Daimonion makes its presence felt,"[80] which is evident from the following short review of Willis's work on muscles written by a fellow member of the Royal Society in the *Philosophical Transactions*:[81]

The second Discourse treateth of the *Muscular Motion*, where, having declared, that Dr. *Steno* hath been the first that hath delivered aright the Structure of Muscles, and that the Figures described by him are visible in them; and also made out the motions of the Fibers by divers Anatomical Experiments; besides many other considerable particulars: He asserts, that the Motion of Muscles depends from a constant Influx both of the Bloud and the Animal spirits; and that the latter alone, without being associated by the former, cannot perform that moving function; maintaining, that as the Spirits (or Springy particles) in the contraction of a Muscle rush out the Tendons into the Fleshy parts of it, and in the relaxation, skip back from these into those, so those Spirits, lying quit within the Tendons, do swell the Fleshy fibres by conflicting and strugling these with the particles of Bloud.

In 1674 the structure and mechanics of muscle were taken up for discussion by members of the Royal Society as revealed by the minutes.[82] Although not explicitly being mentioned, some influence of Stensen is evident:

Mr. Hooke declared, that he had made some discovery of the structure of a muscle by inspection with a microscope. Dr. Grew supposing, that that discovery

[80] Isler, *Thomas Willis*, p. 147.
[81] *Phil. Trans. R. Soc.* 25 March 1670, vol. 5, p. 1178.
[82] Birch, vol. 3, p. 180.

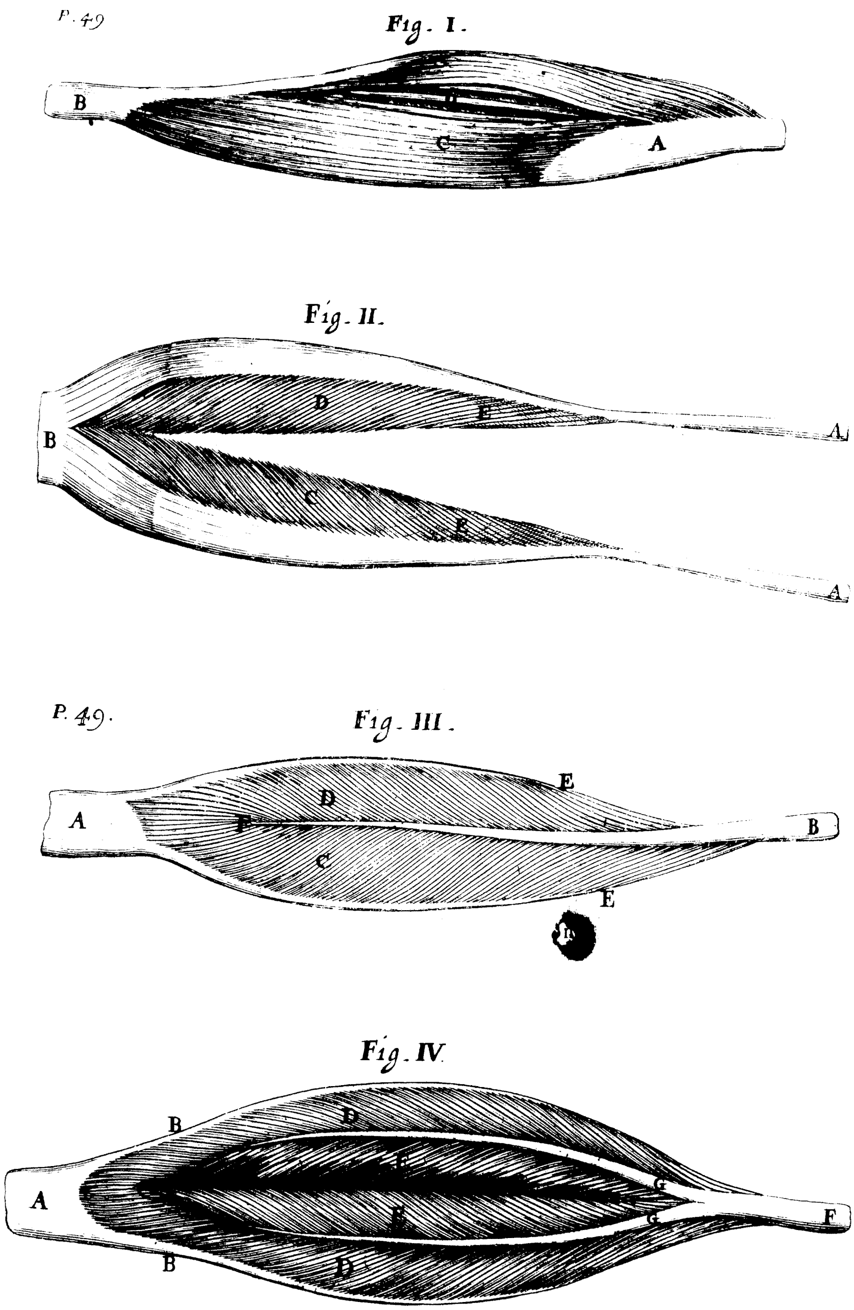

FIGURE 12. **Structure of muscle from the leg of an ox from a plate, probably drawn by Christopher Wren, in Willis's *De motu musculari*, 1670. The Wellcome Institute for the History of Medicine, London. Willis's Fig. I must be recognized as the earliest anatomical preparation demonstrating the unipennate structure of skeletal muscle according to Stensen, 1667.**

might have been the same with what he had some time since discovered, acquainted the Society, that he had some time since discovered, that the fleshy part of a muscle was divided into a sort of long parallelopipeds by the cross interweaving of small membranes and vessels crossing the said fleshy part.

Dr. Croune supposed these fleshy parallelopipeds to consist of a chain of bladders, which being blown up by certain liquors shorten the said springs, and so contract the muscles. But Mr Hooke affirmed, that he could not discover any such texture in the said fleshy part, but that his observation was, that the fleshy part of a muscle consists of an infinite number of exceedingly small round pipes, extended between the two tendons of the muscle, and seem to end in these: which tendons in the muscles of beef boiled would be easily stripped off from the ends of those pipes, and so leave the ends of the round pipes very distinct. He said, that the reason of the moving of a muscle might be from the filling and emptying of those pipes, whose sides seem to be flexible like those of a gut.

5.2.4 John Mayow: 1674

In his *Tractatus quinque*, John Mayow discussed Stensen's theory on muscular contraction (Fig. 13), following the review of Thomas Willis's theory quoted earlier:[83]

I am quite aware that the learned Dr Steno, in his *Myologiæ Specimen*, published not long ago, thinks that there is no need that any elastic matter should be added in order to start the contraction of the muscles; which, in this learned author's opinion, can be effected by a mere change of their form. Thus, "If a muscle should change from an oblique-angled parallelogram into a parallelogram the angles of which are less acute, as is supposed to happen in the contraction of the muscle, then it will be contracted in length, and will also swell up, without the addition of any new matter"; as is shown in Plate III, Fig. I, in which, let *a, b, c, d,* be the muscle, *c, d, a, f,* the same contracted, and although it be of the same magnitude as before, and has had no new matter added to it, has yet undergone contraction as to length, and besides, rises at *f* into a tumour. But, indeed, it is hardly to be believed that muscular fibres should be ready to start this sort of motion unless some new matter were added for that end; for, as the structure of an uncontracted muscle is lax, it would seem that the fibre *b, d,* in its contraction should not be carried outwards towards *f*, but rather, on the contrary, should go inwards. Again, if the contracted muscle is of the same size as before, and if no new matter has come to it, how is it that in its contraction it becomes so hard and tense, as any one can find out in himself by placing his hand on a contracting muscle? And finally, what indeed could contract the fibres and cause a change of this sort in the muscle if nothing flowed into it? Nay, it is quite evident that some new matter brought by the channel of the nerves is required for starting the contraction of the muscle, inasmuch as, if the nerve distributed to a muscle be cut, the contraction of that muscle becomes impossible.

I confess, for my part, that if we concede the arrival of new matter for accomplishing the contraction of the muscle, its contraction can be produced by a mere change of its shape; as will be seen in the figure referred to, in which, when the muscle *a,b,c,d,* is inflated by the motive influx, it necessarily follows that the fibres *a, c,* and *b, d,* are brought towards a position at right angles to the tendon *c, d,* which we assume to be fixed, and that the other, the more mobile tendon, is

[83] Mayow, pp. 233–235.

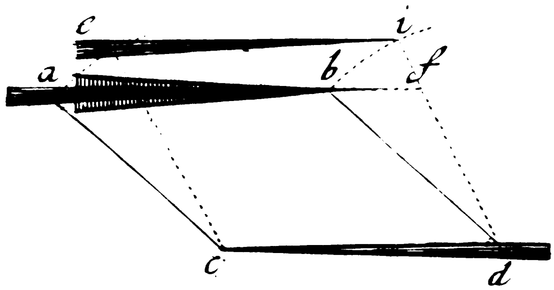

FIGURE 13. **Part of plate III from John Mayow's *Tractatus quinque*, London 1674. DNLSM.**

drawn outwards so that the inflated muscle will be *c, d, e, i*. For that muscle could, by no other change produced in it, be enlarged for the reception of new matter and be thus inflated. But while the muscle is thus changed as to shape, it swells as to breadth, but becomes less as to length; and in this way a muscle can be shortened, although its fibres suffer no contraction.

But whether a change of this kind takes place in a muscle, and its contraction depends on this alone, I shall not say for certain. Still, it does appear to me that a contracted muscle does not swell up so much as would be required if its contraction were caused in this way. Besides, I do not see what part of the muscle should sustain the attack of the motive matter in such contraction, for some kind of membranous vesicles, rather than muscular cords, would be suitable for bearing the force of contraction, and yet the strength of a muscle seems to proceed from its fibrils and cords rather than from any kind of vesicles or membranes.

To Mayow, Stensen's theory did not work, not because of errors or contrary observations, but simply because it differed from Mayow's own concept that some matter was flowing into the muscle making it hard and tense and thereby making it contract. With no other supporting argument than two questions, Mayow changed Stensen's model to fit his own concept.

Summarizing these communications from members of the Royal Society, I conclude, (1) that muscular action was a matter of concern to the founding members, and (2) that Stensen's theory was a core issue and great inspiration. From an accurate review in the *Philosophical Transactions* to matching illustrations in the works of Lower and Willis, Stensen's message became distorted in Mayow's account and was virtually ignored by Croone.

5.3 Giovanni Alphonso Borelli: 1680

In his *De motu animalium*, published posthumously in 1680, Giovanni Alphonso Borelli (1608–1679) did not mention Stensen's name, when in Proposition V he rejected his theory. In fact, Borelli's only named reference to Stensen is found as a comment to Proposition no. 80 on an issue of such small importance that no mention had been less offensive. But since both Bernoulli and Haller later made reference to the fifth proposition as a discussion of Stensen's theory, we can take it for granted that

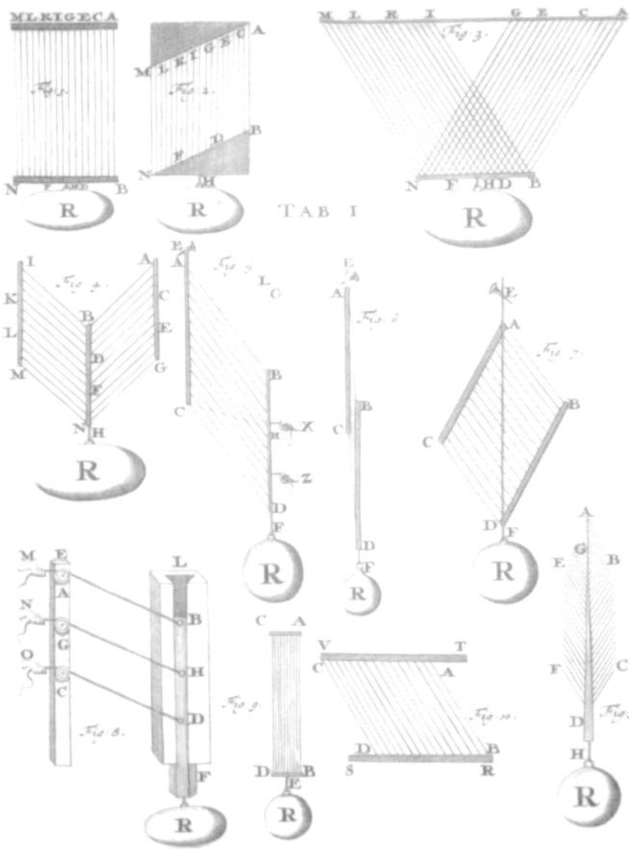

FIGURE 14. Tabula I from Borelli's *De motu animalium*, 1680, here from the 1710 edition. Mayo Foundation Library.

"these famous men" denotes mainly, if not exclusively, Borelli's reference to one person, Niels Stensen.

Chapter I of *De motu animalium* includes "a description and use of the muscles." In Proposition IV, Borelli presented his own concept of muscular mechanics (Fig. 14):[84]

Proposition IV. *The action of the muscle is contraction.*

We see in the muscle that only the *fleshy filaments* AB, CD, EF, and C of these figures 1, 2, 3, 4 of Tab. I are shortened when the muscle is set in motion; indeed the extreme tendons BH, to which the *fleshy fibers* are attached, are not contracted, but remain as long as they were before. It is clear in this sense from the anatomy of the living.

Hence it follows that only the *fleshy fibers* AB, CD, EF, GN and C [sic] produce the force in supporting huge weights by means of energy when contracted. In fact, the *tendons* BH are the recipients of the force insofar as they are drawn by

[84] The quoted passages from Borelli are translated from Latin by M.E.C.

the single local movement by the contracted *fleshy fibers*, and those [the tendons] serve as handles to which the *fibers* are attached.

The subsequent Proposition V is a discussion of the unipennate structure of muscle, called the rhomboidal instrument. It is necessary to study this proposition in full to discuss the arguments which led to the rejection of Stensen's theory.

Proposition V. *Critique on the recently published structure of the Muscle and its mode of action.*

In these last years a new concept of the true structure of the *muscle* and of its mechanical mode of action, about which in the love of truth, we express our opinion. Tab. I. Fig. 5, 6, 7 and 8.

They posit that there are found simple, rhomboidal muscles in animals, as ABCD, Fig. 5, Tab. I, whose *tendon* AC is firmly attached to the *bone* EAC, or is affixed to the end E; indeed the opposite *tendon* BD is equidistant to AC, and they are separated from each other. Afterwards, two contrary forces are present: one of which is the weight of R drawing the tendon BD downwards from B toward F; the other is the contractive force of the *fibers* which acts by drawing the weight R obliquely upwards from B toward A and from D toward C. They also posit that such action is caused by the tension of the *fibers* without the addition of a new substance in that neither inflation, nor increase of mass, nor decrease is observed in them [the fibers]. Yet they say, that at all times in the oblong prism ABDC, whose two opposite sides AC, BD retain their size, the mass of the aforementioned solid is not increased, nor decreased, but only the oblique *fibers* AB, CD are shortened, the obliqueness of the prism ABDC necessarily decreases and approaches the erectness of AGHC; consequently the acute angle BAC will be increased, as is GAC, and thence the weight R is drawn upward.

And all this speculation is based on that well known [or: worn-out] proposition of EUCLID, that two prisms ABDC and AGHC, upon the same base AC, between two parallel planes are constituted as equal to each other and conversely. From which it follows that the above mentioned equal prisms are not equally long, or equally thick; since that one ABDC is more oblique, longer and tighter than the less oblique AGHC by the amount the longer sides AB, CD are shortened and the more the width of the prism is increased. Let us now see whether the reasoning of these famous men agrees with the principles assumed and with experimentation. When the *fibers* of the prism AB, CD are shortened and coincide with AG, CH, then the fibrous prisms are necessarily thickened, otherwise they do not fill the space. Therefore, the *fibers* of the muscle become thicker, which is against their hypothesis. [*Argument 1*]

Secondly, all *fibers* in a *straight muscle* shorten parallel to each other. Therefore, with no penetration of material being given, they [the muscles] must be inflated and thickened, which they [the authors] likewise deny. [*Argument 2*]

Thirdly, in the intercostal muscles, the ribs are near to each other, and all the *fibers* are shortened at the same time, their interstices cannot be made larger since the obliquity of the *fibers* is increased. Therefore the entire mass of the *muscle* is diminished, which they deny. [*Argument 3*]

Finally, what is most powerful in this affair is the mechanism through which, by means of a mediating instrument, the force of the muscle moves the resting [object]. Further, the nature and composition of the muscle, or of the rhomboidal instrument, seems most unsuited for the lifting of the weight R. This can clearly, demonstratively be easily proved through those things, which should be set forth one after another; but, lest the teaching order be disturbed, it will suffice to accomplish the matter in imagined experiments.[85]

Let two equal straight lines, AC and BD, Fig. 6, Tab. I, be assumed and let these be brought together with several equal threads AB, CD etc., and let the end of the rod A be attached to the fixed nail in E, and the weight R be suspended to the extremity D. You will first see that in the destroyed rhomboidal figure ABDG, the rod BD is united and leads contact of the line AC, so that from these is made a unique straight line AC, DR perpendicular to the horizontal.

And if the large number of intercepted cords and the thickness shall have hindered the contact of the rods, a rhomboid arises narrow and lengthened, Fig. 7, Tab. I, whose diameter ADF runs in oblique motion toward a place perpendicular to the horizontal. It occurs in the same way, if the *fibers* AB, CD are solid, but flexible, like the twigs of trees; but in this case the rhomboid will keep a larger size. Let us see now, whether by shortening the cords AB, CD or by drawing them upwards, or by moistening them, these follow the lines together with the weight R appended. And let us observe, Fig. 5, Tab. I, besides, as the adhesion and union of the rods BD and AC and the inclination of the entire rhomboid is obstructed as is fitting, that the rod BD is retained by transverse ties or by possible pulling transversely at X and Z; and then when the rods have been contracted, BD approaches AC in a motion [still being] equidistant; nor will the cords around the center A towards AG ever be lifted as long as the rod BD is drawn down by the weight R. Therefore, by the medium of the *simple rhomboidal muscle*, the moving power of the *fibres* will not be able to raise the resistance R. [*Argument 4*]

Yet, in truth, in some cases the proposition can be verified that if the *fibers* were attached to a firm *bone* EAC, Fig. 8, Tab. I, and the side of rhomboid BD shall be kept in the smooth and slippery channel LF carved in a column, then it is even possible by the contraction of the *fibres* AB, GH, CD, the *tendon* BD is drawn upwards with the appended weight R. But this hypothesis has no place among animals in whom such simple *muscles* of rhomboidal shape are not found, whose *tendon* or moveable side BD runs in a smooth channel. Wherefore it must be concluded, such *simple muscles* are not to be found in nature, nor do they act in such a way as those famous Authors think. But such action can take place only in some *muscles composed* of many *rhomboidals*, as we have set forth in this place; indeed it is not true in those *simple muscles* which constitute one single rhomboid about which the famous Authors speak in words or portray in figures.

Borelli, in what I have called his Argument 1, stated that fibers during contraction become thicker, and that this was against the hypothesis of the anonymous opponent. Stensen, in his Supposition 4, held that the width remained the same during contraction, but Stensen deduced in the Main Theorem, the *Propositio*, that in any muscle there will be a swelling during contraction, i.e., increased thickness [*crassitudo*]. Thus, there is no real weight in Borelli's Argument 1 against Stensen.

There is no disagreement at all between what I call Borelli's Argument 2 and Stensen's Proposition.

Borelli's Argument 3, if anything, is in support of the position of

[85] [*sufficiet sensatis experimentis negotium conficere.*]

Stensen and Swammerdam, saying that muscles can contract even in a very restricted space.

In Argument 4, Borelli (in an imagined experiment) found the unipennate muscle unable to raise a load R, unless supplied with an external force at X and Z. Alternatively, the muscle needed one tendon to be fixed, and the other tendon to be retained in a smooth and slippery groove, as illustrated in Borelli's Fig. 8, Tab I. Because mechanical principles made the construction unfit to raise a load, Borelli concluded that such single muscles are not normally seen.

This is an interesting example of reasoning. It is evident that Borelli's Fig. 5, Tab. I is analogous with Stensen's model. Because of line-asymmetry, any force produced by the motor fibers will lead to a force tending to rotate the parallelogram of flesh of any unipennate muscle, unless balanced by a counterforce at X and Z, or unless the whole structure is stabilized by bone along A C. This is both true and original, but Borelli forgot to look to the consequences in reality of his own considerations. Several such muscles exist. Stensen had pointed out examples, such as the chewing muscles, and one of the strongest muscles of the human body, the deep head of the quadriceps muscle. This muscle is fixed to bone with a pennation angle at one end; at the other end it is fixed in the patella, which moves in a slippery groove almost as required (see figure on page vi).

Thus, an imagined experiment, not any observation, in this crucial case led to the strongest argument in science, a counter proof. While Stensen had focused on the structure of muscles in order to build a system, Borelli evidently focused on a system to imagine a structure: Borelli's own concept of the muscle contraction was built on a principle similar to that of Croone's theory, namely, that of bladder expansion. Borelli added that muscles consist of numerous minute vesicles, *machinulæ rhomboidales*, described in his Proposition 115 as "so small that their length does not exceed 1/20 of a finger breadth." Otherwise the emphasis in the 457 propositions of Borelli's monumental work lies in considerations on the mechanics of the entire body in man and animal.[86]

6. Conflict of Paradigms

TOWARDS THE END of the seventeenth century, there was clearly a conflict of paradigms on the mechanics of muscular contraction. In 1685 Godfred Bidloo of Amsterdam reproduced Stensen's scheme without comment or source (Fig 15). Different ideas were illustrated in 1694 all in one plate (Fig. 16) from the dissertation by Johannes Gottsched[87] of Königsberg in East Prussia. Gottsched presented in his paragraph XI a short, fair descrip-

[86] Cf. P. Maquet, *Iatrophysics to biomechanics.* Some of Borelli's calculations were evaluated in 1873 by Samuel Haughton, *Principles of animal mechanics*, pp. 73–74.

[87] Gottsched's thesis from 1694 was reprinted by Haller in *Disputationes anatomicarum*, vol. 3, pp. 359–410. Göttingen 1748.

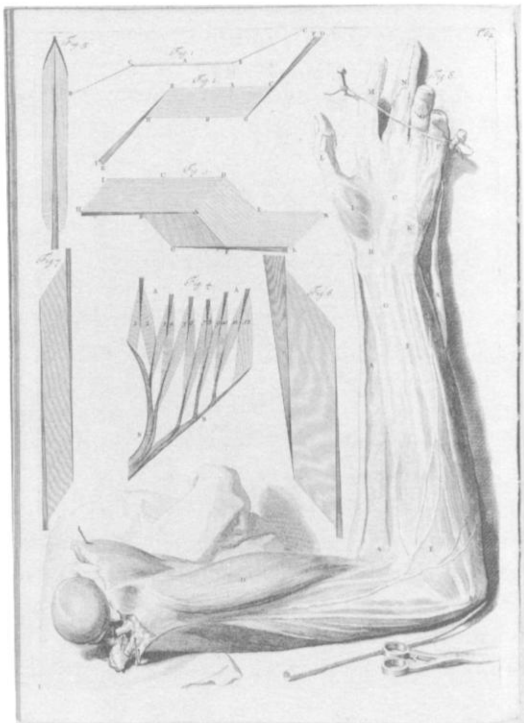

FIGURE 15. **Plate from Godfred Bidloo (1649–1713)** ***Anatomia humani corporis,*** **Amsterdam 1685.**

tion of the structure of Stensen's geometrical model, but like Mayow he concluded that the model did not work without accession of new material.

A clear misinterpretation of Stensen's muscular structure is found in an essay on medicine of 1678 by the French author F. Bernier.[88]

Several of the geometrical figures from *Elementorum myologiæ specimen* are included in a highly artistic plate in Godfred Bidloo's *Anatomia humani corporis,* Amsterdam 1685.[89]

6.1 Johann Bernoulli: 1694

In 1694 the mathematician Johann Bernoulli (1667–1748) presented at Basel his inauguration dissertation, *De motu musculorum,*[90] in which he praised Borelli's work and elaborated mathematically the curve following which the muscle is expanded. In paragraph III, Bernoulli discussed Stensen's work:

Steno in his Specimen of Myology is of the opinion that the Muscle is contracted without the accession of new material, undoubtedly only through the change in

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88 Quoted from a facsimile p. 387 in Schiller and Théodoridès, fig. 3, p. 156.

89 Reproduced in Harald Moe, *Deu anatomiske Billedkunst i Renassanceu og Barokken,* Rhodos, Copenhagen 1994, p. 175.

90 Translation by M.E.C. from Opera Omnia, pp. 99–100.

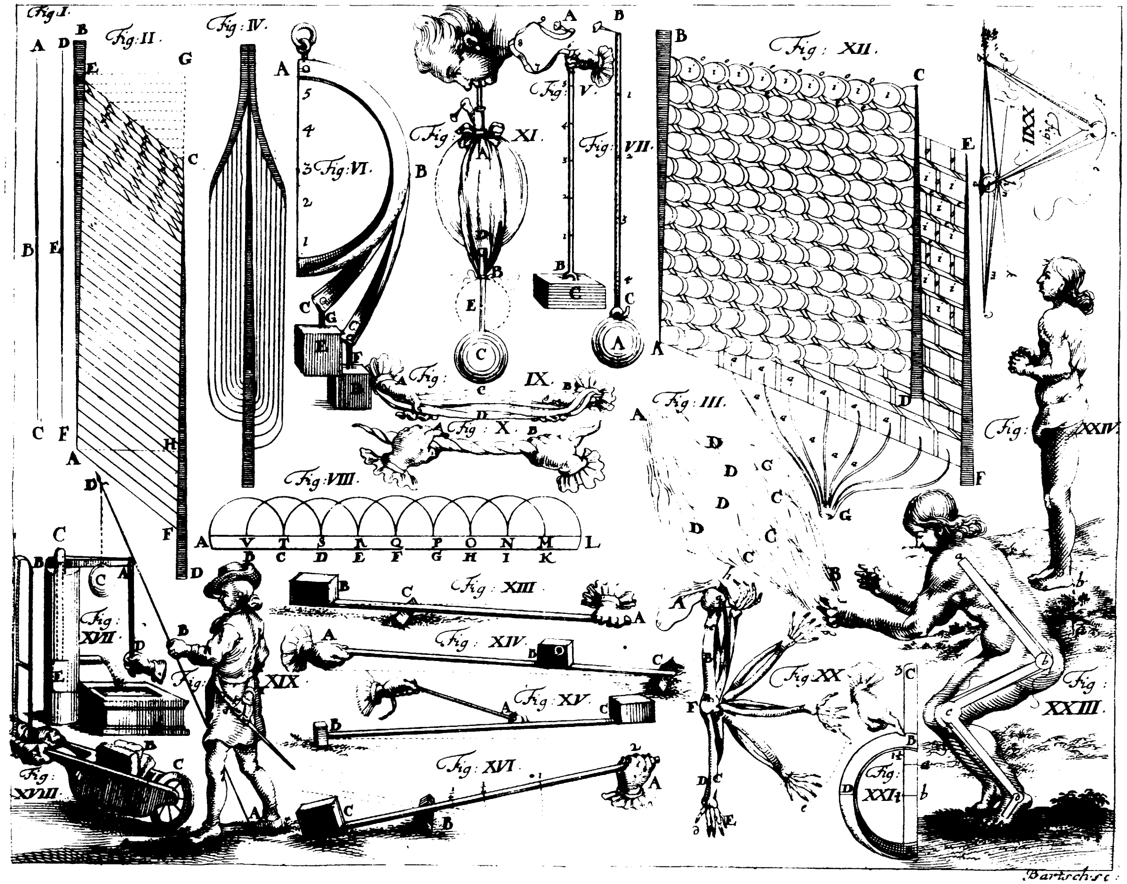

FIGURE 16. Conflicting paradigms on muscle mechanics towards the end of the seventeenth century from the dissertation by J. Gottsched, Königsberg 1694. Figs. I and II show Stensen's unipennate arrangement. Fig. III, Mayow's description of the muscle structure. Fig. IV is close to Stensen's Tabula II, Fig. II showing the structure of the biceps brachii muscle. However, in Gottsched's version there is a tendon connection all along the muscle. In Fig. XI a person blows into a bladder, the bottom of which can lift a load from the ground. This is the experiment of Wilkins applied by Croone. Fig. XII shows the *machinulae rhomboideales*—the so-called globular structure of muscles with numerous small tubes leading spiritus animalis to the small muscle chambers. Figs. XIV–XXIV show mechanical principles of motion according to Borelli. DNLSM.

the shape in moving from an oblique angled parallelogram to a right angled one. This opinion is utterly ridiculous and should be considered a sheer jest of the ingenious Author. For even beyond the fact that the contraction of the right angled Muscle cannot be explained in this way, unless the interpenetration of the bodies is established, it is impossible to conceive whence the Muscle is moved and the nature of the prime mover, or that the well worn Axiom "Everything that moves is moved by something else" can be defended by reason. . . . By many other arguments, moreover, concerning which Borelli and Mayow should be consulted, the Stenonian theory is overturned. I think that the men who have disclosed it to be caused by a certain inflation have touched upon the true cause of the contraction of the muscles. Among them the chief is Willis and the two Men mentioned above, who all agree that a swelling arises in the Muscles which distends the fibers so that they lose in length what they gain in width.

It is interesting that Bernoulli referred to the Aristotelian concept of movement, *Omne quod movetur, movetur ab alio*, as a hindrance to the acceptance of Stensen's theory. The same point of view was expressed as late as 1761 by Guichard Joseph Duverney (1648–1730) in the posthumous *Oeuvres Anatomique.*[91]

Johann Bernoulli's influence as a mathematician was immense. Before he settled in his home town, Basel, he spent several years in the Netherlands as a professor at Groningen. In the Netherlands he became acquainted with Hermann Boerhaave, the influential professor at Leiden.

6.2 Hermann Boerhaave

In 1710 Hermann Boerhaave (1668–1738) published a new edition of Borelli's *De motu animalium*, to which Bernoulli wrote an addendum: *Meditationes mathematicæ de motu musculorum*, on the curve according to which the muscle expands: *de naturæ curvæ secundum quam fibra motrix expanditur.* Boerhaave, clearly under the influence of Bernoulli, described his view of Stensen's contraction theory in a lecture, no. 415 in the posthumous edition published in 1743 with notes and comments by Haller:[92]

All muscle fibers form oblique parallelograms with two tendons. Hence, in a contraction of the muscle, the fibers are drawn towards the beginning, the angles are changed, the figures become shorter, more like rectangles, and decrease as much in length as they increase in width. So this most brilliant man [Stensen] thought that, by these phenomena, he had sufficiently proved what they indicated—the contracted muscle becomes shorter and more swollen. In truth he had not paid attention to another theorem from mathematics, from which we teach that among parallelograms the rectangle includes the greatest area, when any figure of them have equal interchangeable lines. Therefore the greater space is contained within the same perimeter. . . . For if he had been mindful of this

[91] "*Stenon* attribue le raccourcissement des muscles au seul changement de figure des angles des fibres, sans le secours d'aucune nouvelle matière. Cette hypothèse est incompatible avec une loi de la nature, sçavoir qu'un corps qui est en repos, ne peut recevoir du changement par lui-même, & qu'il sera toujours privé de mouvement, s'il ne reçoit du changement par quelque chose qui soit hors de lui, qui le mette en mouvement." Vol. 1, p. 491.

[92] P. 430. Translated by M.E.C.

well known theorem, he would easily have seen, according to the proper hypothesis, that when the parallelogram becomes shorter, it is the result of the new material which fills in the increasing area.

Boerhaave presented Stensen's theory in a way different from that in which it was originally delineated, but similar to the way Mayow—to whom the lecture made no reference—and Bernoulli had done. According to Mayow, Bernoulli, and Boerhaave, the muscle fibers of the parallelogram do not shorten, but they are inflated causing an increased pennation angle. Boerhaave regretted that Stensen had not accounted for the volume increase resulting from his own modification of Stensen's model.

6.3 Albrecht von Haller: 1762

Mayow, Borelli, Bernoulli, and Boerhaave's misrepresentation and misinterpretation of Stensen's theory went almost unchanged into the *Elementa physiologiæ corporis humani*, published in 1762, a work of tremendous importance by the great Swiss compiler of physiology, Albrecht von Haller (1708–1777), who had studied with Boerhaave at Leiden and with Bernoulli at Basel. In the section, *Rhombi Stenoniani*,[93] Haller, with a reference to Borelli's Proposition V, wrote:

This theory pertains to the muscles even to this day. Yet it is very simple. The illustrious man says, he thinks any muscle is made up of two tendons and of fleshy fibers which form oblique angles with tendons at both sides in every kind of animal. . . . This structure is not true. It is rare to be offered muscles of this kind, whose fibers make oblique angles with a tendon on both sides. Most often they make very acute angles with a tendon. . . . Nor does the illustrious Steno furnish a provision of fluid matter, which according to his hypothesis should be poured into the space of the fibers, unless he wishes them to become empty. For while the rhombuses change into quadrates, at the same time their areas are enlarged and become more capacious. Therefore it is necessary to replenish the rhombuses.

Finally in 1779 the curator of the Pisa Academy of Science, Angelo Fabroni (1732–1803), in his biography of Stensen, once again repeated the erroneous representation of Stensen's geometry of muscular contraction:[94]

One marvels that Steno rejected the best known theorem in geometry, the impossibility of an oblique-angled parallelogram's changing into a rectangle without receiving new material with which the greater part of the space is filled.

6.4 Summary of Arguments Rejecting Stensen's Theory

The arguments against Stensen's muscle theory can be summed up:

1. Mayow in 1674 wrote that Stensen's parallelogram with shortened

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[93] Vol. IV, Lib. XI. *Motus animalis*, § XXIII, pp. 549–50. Translated by M.E.C. Same verdict in Haller's *Bibliotheca anatomica*, vol. 1, p. 493. . . . Intumescentiam musculi simplicissime explicari posse sibi persuasit, si rhomboidea fibrarum strata in rectangula quadrangula mutarentur (quod quidem fieri nequit, nisi plurima materies eam auctam aream repleat).

[94] *Vitæ Italorum*, vol. 3, pp. 24–25.

muscle fibers and unchanged volume could not make muscles hard and swollen in contraction. Moreover, Stensen's model did not agree with the concept that muscle volume increases in contraction. With that in mind, Mayow "improved" Stensen's model, so that the muscle fibers did not shorten. With an increased pennation angle during contraction, the area of the parallelogram of flesh increased; or in a three-dimensional structure, the volume of the muscle increased.

2. Borelli in 1680 discarded the "rhomboid instrument," that is, the unipennate structure, based on imagined experiments, because he thought such structure would be unable to lift a load. Borelli questioned the anatomical foundation: "Such single muscles are not seen normally."
3. Bernoulli in 1694 took up Mayow's misrepresentation and altogether discarded Stensen's theory because it disregarded the Aristotelian rule, that any movement must be caused by an external force. This argument was repeated by Duverney, published in 1761.
4. In Boerhaave's interpretation printed in 1743, Stensen's model was again misrepresented as similar to Mayow's "improved" version. Thereafter Boerhaave criticized Stensen, for making no provision for the necessary volume expansion.
5. Haller in 1762 and Fabroni in 1779 repeated the erroneous representation of the geometry. Like Borelli, Haller questioned the anatomical background.

Thus, Stensen's theory was refuted, and disappeared because of repeated claims of one or several of the following four errors: that the theory did not fit with the concept of volume expansion of muscles in contraction; that it did not obey the Aristotelian rule of movement; errors in geometry; errors in the anatomical background. As remarked recently by the researcher in muscular mechanics, Peter A. Huijing, it is indeed remarkable that so many eminent scientists deliberately overlooked the fact that Stensen had said[95] that the muscle *fiber length* is shortened in muscle contraction.

7. New Interpretations

STENSEN'S THEORY on muscular contraction was dealt with separately by Gosch, Maar, Bastholm, and Scherz.

7.1 C.C.A. Gosch: 1873

Stensen's works, not only that on muscle theory, had been neglected by scholars for about a century when in 1873 C.C.A. Gosch (1832–1913) reviewed Stensen's scientific work, including an extensive analysis of

[95] See p. 201.

Stensen's muscle theory and its reception.[96] Immediately, Gosch was able to discard the first three of the four objections recorded in the literature. But,

the correct objection is that one also emphasized by Haller, that muscles can not in fact according to their structure be reduced to such a normal figure. This became beyond doubt, when the microscopic examination of tissues, hardly started at the time of Steno, evolved. Although Steno's views from the beginning attracted much attention, and were adopted by many, they enjoyed only a brief life in science. He had become fascinated by an ingenious idea whose correctness he lacked the means sufficiently to verify. Nevertheless, there was a correct thought behind the idea, and, considering that he was only twenty-nine years old at the time, one should consider the mistake permissible.

So far Gosch in his fascinating analysis of the literature, which is basic to this study.

7.2 Vilhelm Maar: 1910

In 1910 Vilhelm Maar (1871–1940) edited the collected scientific works of Stensen for publication in their original language. The annotated two volume edition, the *Opera philosophica,* has become the basis for the study of Stensen's work. In his analysis of the *Elements of Myology,* Maar[97] came to the same conclusion as Gosch, that something was wrong in the structural background of Stensen's theory of muscle contraction:

When in spite of much diligence and the most careful proofs he still did not arrive at a correct result, this was due to the following errors. Firstly his starting-point was a wrong conception of the course of the muscular fibres. As has already been mentioned he thought that every muscular fibre at either end passed into a tendinous fibre, and he furthermore was of opinion that the course of the muscular, as well as that of the tendinous fibre were each of them rectilinear, forming an angle at the two places, where the muscular fibre became a tendinous one, neither of which suppositions have proved to agree with the actual facts. Secondly, he did not pay attention to the fact that every separate muscular fibre, when shortened by contraction, must needs become thicker, and that this in its turn must act on the whole figure of the muscle during the contraction.

Maar's overall rating of the *Elements of Myology* was that, in spite of being a work which Stensen himself seemed to have valued highly, it is "perhaps, now considered the weakest in his writings."

As for the two objections mentioned by Maar, the first one contains two parts: Maar correctly objected to Stensen's idea of one continuing fiber with a flesh-part in the middle and two tendon-parts at each end.

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[96] *Udsigt . . .* Gosch, p. 204, mentioned one supporter of Stensen: "Against Mayow's criticism, Steno was defended by, among others, Joannes Diego in a thesis *De motu musculari* (Montpellier 1710), in which Diego emphasized that Steno just had intended to show that the swelling of the contracted muscle could be explained without access of new material, but otherwise that he had had no intention to decide on the causality for contraction." I have not been able to study Diego (Joannes) Perpiniancensis, *De motu musculari,* B.N. Thèses Montpellier, 4,023, T.2653 5A.

[97] Maar, *Life and works of Nicolaus Steno.* Introduction to OPH vol. 1, p. XVIII.

The second half of the first question, on the pennation angle, is to be addressed in the final section. The second objection is identical with what I have called Argument 1 of Borelli.

None of Maar's objections are critical to the theory, and they were not built on any new measurements, but on a different judgment. Maar's judgment is less qualified than Stensen's, since it was not based on observations and did not result in any alternative model.

One finds an example of Danish wit relevant to the substance of this discussion in humorist Storm P.'s words[98] that it requires a high moral standard to sell elastic material by the yard. To make models of muscular structure and to discuss them bear a sort of resemblance, which Stensen realized: "I admit that the tissues of the flesh are so extremely delicate that it is not possible to determine with any certainty the relation [of the lateral surfaces] to the transverse plane." (See page 103.)

Maar concluded that Stensen had not arrived at "a correct result." It needs hindsight to say that this statement of Maar was incorrect, but no hindsight to assert that Maar's statement was poorly founded. Recent technological developments in soft tissue imaging techniques make *in vivo* morphometry of muscles possible, but even current muscle models used for experimental study, are basically founded on measurements *post mortem* in the anatomical dissection room (Fig. 17).

7.3 Eyvind Bastholm: 1950

Maar had placed Stensen's muscle work in relation to Stensen's other works; Eyvind Bastholm (1904–1989) placed it in relation to the development of muscle physiology in his excellent thesis "The history of muscle physiology" at Copenhagen University in 1950. Bastholm further established that Stensen's theory was "anything but well received," mainly because his opponents "quite overlooked the fact that Steno was in no way interested in discussing the question of the ultimate cause of contraction." Bastholm repeated Maar's criticism of the structure behind the model, saying in particular that Stensen "overlooked the circumstance that muscle naturally becomes thicker when each muscle fiber becomes shorter, which of course it does during contraction."[99] Again we meet Borelli's first objection, which will be dealt with later. Bastholm, nevertheless, conveys the clear impression that *Elements of Myology*, played an important role in the history of muscle physiology.

7.4 Gustav Scherz: 1957[100]

When the handwritten, original manuscript of *Elements of Myology* used by the printer was offered for sale, Gustav Scherz (1895–1971)

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[98] Robert Storm Petersen (1882–1949).

[99] Bastholm, p. 158. Maar's reservation against Stensen's theory on muscular action had been quoted in 1939 by Axel Hansen, p. LV, a work of considerable importance in the Danish Stensen literature.

[100] The Austrian-born, Danish Redemptorist Gustav Scherz, *Dr. Sc. & Th. & Th. h.c.*, has left his mark on all aspects of Stensen research with outstanding editions of Stensen's

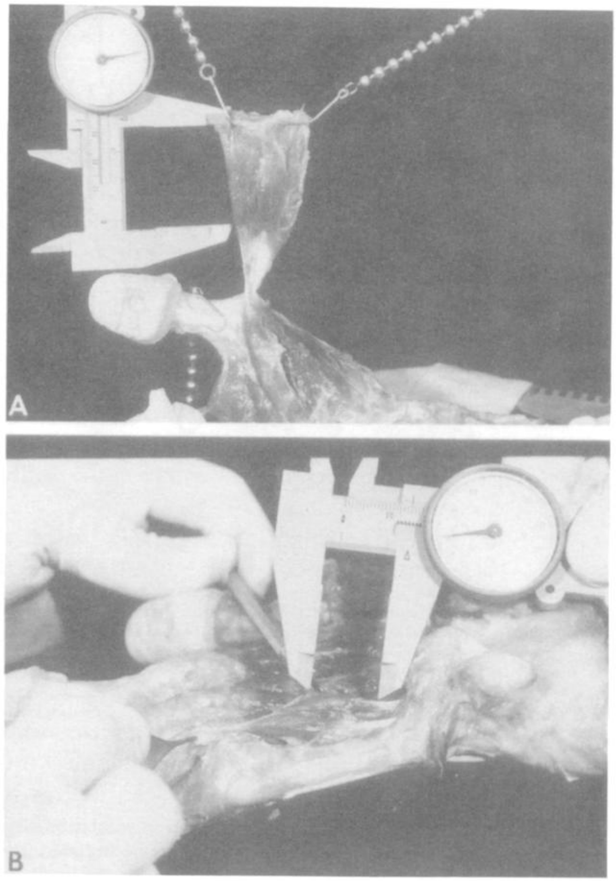

FIGURE 17. **Techniques for dissection of muscles. From the study by Linscheid and coworkers 1991. The publishers of *Clinical anatomy*, Wiley-Liss, Inc., by permission.**

arranged for Dr. H.C. Hagedorn (1888–1971) to buy the manuscript and donate it to the Royal Library in Copenhagen on the occasion of the 25th anniversary in 1957 of the Steno Memorial Hospital in Gentofte, Denmark, a hospital devoted to research and care of patients with diabetes mellitus.

Scherz has stressed the stimulating influence of the scientific environment in the *Academia del Cimento* of Florence on Stensen's work.[101] He emphasized also the conflict between Borelli and Stensen, suggesting that several of the disputes referred to in the letter to Thévenot must have

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theological works, the correspondence, and an English translation of the geological works. Father Scherz also edited an annotated selection of Stensen's works in German translation, *Pionier der Wissenschaften*, and wrote numerous scholarly and popular articles, recovering from libraries and archives in two continents Stensen's student notes, his first dissertation, and numerous letters. Scherz's two-volume Stensen-biography in German was completed posthumously by Harriet M. Hansen, M.A.

[101] *Danmarks Stensen manuskript.*

been with Borelli. Fittingly, Scherz characterized the *Elements of Myology* as Stensen's most controversial work.

7.5 Other Reviews

In the third of his lectures on the history of physiology, "Borelli and the influence of the new physics" published at Cambridge in 1901, Michael Foster wrote that "Stensen had come very near to a true conception of the structure of muscle." In the following paragraph Foster touched upon the substance of the controversy between Borelli and Stensen:[102] "It is true that he [Borelli] refutes Stensen's mathematical mechanical conceptions of the arrangement of the fibers, replacing them by conceptions of his own; but this is a matter of little moment." This sentence leaves no doubt to me that Foster did not acknowledge the validity either of Stensen's, or Borelli's *mathematical* conceptions on muscular contraction, but unfortunately Foster did not explain how he had come to this insight.

In 1926 John F. Fulton in a monograph *Muscular contraction*[103] wrote that Stensen "laid the foundation of Muscular Mechanics as we know it now." A comprehensive subject review[104] on muscle contraction theories in the seventeenth century is that of Leonard G. Wilson of Minneapolis, formerly a student and collaborator of Fulton at Yale.[105] Another inspiration for my present study has been the pioneering work by the physician and Italian translator of *Elements of Myology*, Marco Marzollo.[106]

The seventeenth century was the golden age of Danish medicine and natural science studded with names like Ole Worm, the Bartholins–Caspar, Thomas, Caspar Jr., and Erasmus–Simon Paulli, Ole Borch, Ole Rømer, and Niels Stensen,[107] the last considered to be Denmark's greatest biologist.[108] Most historical studies assert that Stensen first discovered the motor fiber and he estimated that muscle and not tendon is active in contraction, but most focus principally on other achievements in his research. Few writers refer to Stensen's geometrical description of muscular contraction–"a trial of the reader's patience" was in fact my own comment not long ago.[109] It is, therefore, without malice that I note that Stensen's mathematical approach to muscular contraction was described as "not quite satisfactory" in one of the volumes of the edition celebrating Copenhagen University's fifth centenary in 1979;[110] and that recent biog-

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102 *Lectures*, p. 72.
103 Pp. 16–17.
104 Wilson, *William Croone's theory of muscular contraction.*
105 Fulton edited and translated *Selected readings in the history of physiology*, the second edition completed by Wilson, with excerpts from works on muscles by Galen, Croone, Swammerdam, Steno, Willis, Glisson, and Borelli, pp. 201-222.
106 *Anatomie e fisiologia del musculo nell'opere di Niccolò Stenone.*
107 Petersen, *Bartholinerne og Kredsen om dem.*
108 Krogh, p. 44.
109 Kardel, *A specimen of observations upon muscles*, note 31, p. 131.
110 *Københavns Universitet.* Vol. 12, p. 129.

raphies characterized Stensen's geometrical considerations on muscle fibers as incorrect[111] and "une fausse piste."[112]

8. Reappraisal

AN OPPORTUNITY appeared in 1986. Having completed work on an annotated edition of the 1712 English translation of *De musculis*, I lectured on Stensen to the History of Medicine Club of the Mayo Clinic at Rochester, Minnesota. After the lecture Professor Ronald L. Linscheid, drew my attention to works by his group and to those of another group of orthopedic surgeons and investigators. Two investigations,[113] both published in 1981, demonstrated close similarity in the architecture of anatomical muscle preparations in the human with that of Stensen's illustrations from 1667, as they are reproduced by Bastholm in 1950. While intending to improve methods of orthopedic tendon transfers through anatomical dissections, these investigators had rediscovered Stensen's finding of the pennation angle between muscle fibers and tendon, and an almost equal muscle fiber length in each individual muscle (Fig. 18). We easily agreed on the desirability of a translation of Stensen's text.

Following an invitation, I spent part of the winter of 1989 as a visiting scientist at the Orthopedic Biomechanics Laboratory of the Mayo Clinic, dividing my attention between Marianne Alenius's new Danish translation of *Elements of Myology*: "Prøve på en elementær muskellære eller: Beskrivelse af musklen," and what Professor Kai-Nan An and Dr. Kenton R. Kaufman taught me about muscle modeling. It took me eight days to learn that the Mayo Clinic investigators were presently working on computer models similar to those that Stensen analyzed geometrically 322 years earlier, and that the new models were based on rediscoveries of anatomical structures illustrated in Stensen's works. Two months later I presented to fellows and staff members the final report of my stay with a draft of an English translation of *Elements of Myology*, prepared together with Sister M. Emmanuel Collins. Upon receiving the following memo from the director of the laboratory, Edmund Y.S. Chao, I understood that they somehow agreed with me:

> In an era of non-stop leapfrogging of scientific and technological developments as well as rapid obsolescence of knowledge, it is truly amazing that a 17th-Century development by Stensen, although not recognized by contemporary and later scientists, can retain such a long and enduring life span. Indeed, only the truth of Nature is immortal.

Later that year I received inspiring criticism from referees before obtaining the final acceptance of a historical review of Stensen's myology by the editors of the *Journal of Biomechanics* in 1990. In order that the scientific com-

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[111] Moe, *Niels Stensen—en billedbiografi*, p. 100.
[112] C.G. Ahlström, G. Regnéll, and P. Ekström, *Nicolas Sténon, anatomiste, naturaliste, et son cheminement vers l'église catholique*, p. 26.
[113] Brand et al. 1981; An et al. 1981.

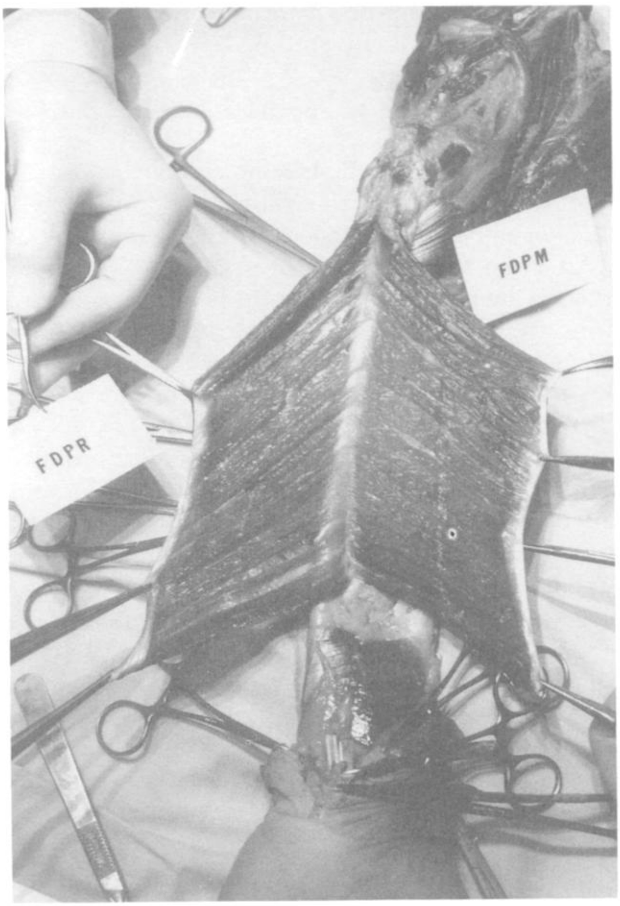

FIGURE 18. Rediscovery of the unipennate structure of flexor digitorum profundus muscle. From Brand et al. 1981. The publishers of *J Hand Surg*, Mosby-Year Book, Inc., by permission. Compare with Placentinus 1627 (Fig. 2).

munity may make its own judgment of the case, Stensen's texts are now made available in full in English translations completed by Paul Maquet. With much overlapping, recent studies evaluating the unipennate actuator are classified as anatomical, as dealing with mechanics, or as model simulation studies.

8.1 Anatomy of Muscular Action

Ten anatomical studies published after 1980 by seven groups of investigators confirm the structural foundation upon which Stensen built his theory and model: that *the unipennate arrangement is the commonplace structure in skeletal muscles of mammals* and also in other animals, e.g., in the chela of crabs and lobsters.[114] This knowledge has been useful in orthopedic tendon transfer operations.

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114 Other studies show the adaptation of the unipennate arrangement of skeletal

Anatomical studies, computer model simulations, and biomechanical and historical review articles dealing with the unipennate actuator. Studies that recognize Stensen's contribution are marked with an asterisk [*].

Anatomical studies			
Beritoff	1925	Hindlimb	Frog
Kolb	1937	Anterior tibial	Man
Rollhäuser and Wendt	1955	Gastrocnemius	Cat
* Brand et al.	1981	Hand	Man
* An et al.	1981	Elbow	Man
Wickiewicz et al.	1983	Lower limb	Man
Cooney et al.	1984	Thumb	Man
Huijing	1984	Gastrocnemius	Man
Lieber and Blevins	1989	Hindlimb	Rabbit
Heslinga and Huijing	1990	Gastrocnemius	Rat
Friedrich and Brand	1990	Lower limb	Man
* Linscheid et al.	1991	Hand	Man
Spoor et al.	1992	Gastrocnemius	Man
Lieber et al.	1992	Arm	Man
Overview studies			
Pfuhl	1937	Biomechanics	
Benninghoff and Rollhäuser	1952	Biomechanics	
Gans and Bock	1965	Biomechanics	
Alexander	1968	Biomechanics	
* Otten	1988	Biomechanics	
Zajac	1989	Biomechanics	
* Kardel	1990, 1991	Historical	
* Huijing	1991	Biomechanics	
Kaufman et al.	1991	Biomechanics	
Model simulations			
Huijing and Woittiez	1984, 1985	Gastrocnemius	Rat
Woittiez et al.	1984	Gastrocnemius	Rat
* Otten	1985, 1988	Hindlimb	Cat
* Kaufman et al.	1989	Same data as Woittiez et al.	
An et al.	1989	Elbow	Man
Hoy et al.	1990	Lower limb	Man
Mai and Lieber	1990	Hindlimb	Frog
Pandy et al.	1990	Lower body	Man
Pandy and Zajac	1991	Lower body	Man
* Zuurbier and Huijing	1992	Hindlimb	Rat
* Van Leeuwen and Spoor	1992	Gastrocnemius	Man

8.2 Mechanics of Muscular Action

Several theoretical studies review the mechanics of muscular action with emphasis on the unipennate structure. In particular the study of Gans and Bock has stressed the theoretical advantage of the unipennate structure in relation to a low intramuscular pressure build-up. An illustration given by Gans and Bock (Fig. 19) is similar to that of Stensen. One

muscle in immobilization atrophy by Cardenas et al. 1977, and in growth by Heslinga and Huijing 1990.

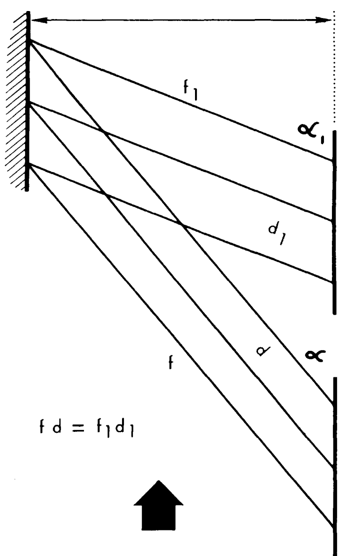

Fig. 6. Diagram demonstrating that an evenly pinnate muscle will not develop any internal pressure during contraction unless the distance between attachment surfaces shortens

FIGURE 19. Model description from Gans and Bock 1965. The publishers of *Ergebn Anat EntwGesch*, Springer Verlag, by permission.

should, therefore, be able to test Stensen's model in typical muscles, expecting only small and uniform increases in intra-muscular pressure during contraction, unless other factors dominate that pressure. In 1988 Otten mentioned intramuscular pressure as among the unsolved problems of muscle physiology, mainly because "nonhomogeneous recruitment of subvolumes of muscle is very hard to model,"[115] a question recently elaborated by Van Leeuwen and Spoor, see below. Astonishingly, Stensen dealt with the same type of problem: "There remains another problem no less momentous and not yet solved: namely, in what does the movement of the fluid in a muscle differ when this contracts, from the movement of the fluid in the same muscle when this is at rest, uncontracted? Is its quantity changed or does it remain the same? . . . Does the fluid move because the solid part contracts, or does the contraction of the solid part proceed from the movement of the fluid?"

The figure of Gans and Bock from 1965 obviously demonstrates the thickening of each motor fiber during contraction within Stensen's model, thus answering those authors, who like Borelli 1680, Maar 1910 and Bastholm 1950, could not find such thickening of the motor fiber during contraction in Stensen's model.

In an investigative review, Otten carried out an arithmetical computation analogous to Stensen's geometrical deduction, and thereby analogous

[115] Otten 1988, p. 119.

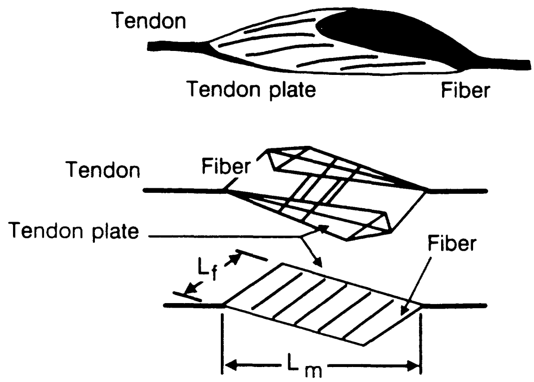

FIGURE 20. **Recent muscle model by Woittiez et al. Compare with Stensen (Fig. 5). Computer generated and observed data of length-tension diagram in action and relaxation were compared. The publisher of *J Morphol*, Alan R. Liss, Inc., by permission.**

to Euclid's proposition XI. 29, p. 243. Otten concluded: *The volume of a pinnate muscle does not change when shortening, if the distance between the planes of insertion of its fibers is kept constant.*[116]

8.3 Model Simulation of Muscular Action

Only the calculating capacity of modern computers could lift the reflections on time-related changes of structure in animal movement into a scientific theory with predictive power. At least eleven studies from six centers located in the Netherlands and the U.S.A., have employed muscle models identical with, or closely approximate to, Stensen's muscle model, as exemplified by Fig. 20. The value of these models has been demonstrated at first hand by a convincing match between predicted and observed data on the length-tension relation during action and relaxation in several compound muscles in three species: rat, cat, and man.

A study by Pandy and coworkers in 1990 deserves attention because it provides a connection of contemporary physiology to science of the past: "The human body is modeled as a four-segment, planar, articulated linkage, with adjacent links joined together by frictionless revolutes. Driving the skeletal system are eight musculotendon actuators, each muscle modeled as a three-element, lumped-parameter entity, in series with tendon. Tendon is assumed to be elastic" (Fig. 21). Pandy et al. built-up their model of the human body by components strikingly similar to structures described by Borelli in his Plate IV and VI (Fig. 22). As of the actuator, the only difference is the elasticity of the tendons in the modern model compared to rigid tendons in Stensen's model.

Thus, after three-hundred years the ideas of Stensen and Borelli, the two contenders who ignored each other in their writings, are united into an almost Cartesian human machine by Zajac, Hoy, and Pandy of Stanford University and affiliated institutions. Pandy and his colleagues have

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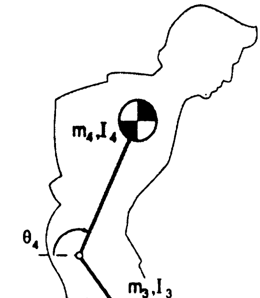
[116] Otten 1988, appendix E, p. 123.



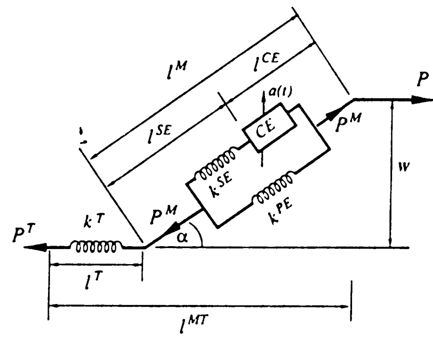


Fig. 3. Schematic representation of the musculotendon model. Note that: $l^{MT} = l^T + l^M \cos\alpha$; $l^M = l^{SE} + l^{CE}$; $l_0^M \sin\alpha_0 = l^M \sin\alpha = W = \text{const.}$; $P^T = P^M \cos\alpha$; where l^{MT} is the length of the musculotendon actuator, l^M and l^T are the lengths of muscle and tendon respectively; l^{SE} and l^{CE} are the lengths of the series-elastic and contractile elements; P^M and P^T are muscle and tendon forces; α is the pennation angle of muscle; k^T is tendon stiffness; k^{SE} and k^{PE} are the stiffness of the series-elastic (SE) and parallel-elastic (PE) elements; CE and MT denote the contractile element and musculotendon actuator respectively; W (a constant) represents muscle thickness; l_0^M, α_0 are the fiber length and pennation angle at which peak isometric force is developed; and $a(t)$ designates activation of the contractile element.

Fig. 2. Schematic representation of the four-segment model for the vertical jump. m_1, m_2, m_3, m_4 are the lumped masses of the foot, shank, thigh, and HAT (head, arms, and trunk) respectively; I_1, I_2, I_3, I_4 are the mass moments of inertia of the foot, shank, thigh, and HAT respectively. Body-segmental parameters are specified in Appendix 1.

FIGURE 21. Except for elasticity of the tendons, the actuator of Pandy et al. (1990), upper right, is identical with Stensen's muscle model. Based on this actuator Pandy et al. built-up a two-dimensional model of a person jumping from the squat position. The publisher of *J Biomech,* Pergamon Press, by permission.

compared computational solutions with experimental results of maximum-height squat jumping in man. They report that the model reproduced the major features from the pressure distribution underneath the feet to overall jump height.

We have thus reached a time when mathematics can calculate the limits of human physical performance. Perhaps it is less spectacular than when Leonardo described the range of the extremities by encircling the human body, but most certainly these recent studies are a fulfillment of Stensen's commitment to make the study of muscles part of mathematics.

Apparently biomechanics is in the throes of a protracted revolution. Scientists of the seventeenth century established the fundamental laws of physics based on observations of the celestial bodies and the free fall of bodies on earth. The voluntary control and the structural complexities have required modern technologies to handle the algorithms needed to analyze animal movement. Attempts based on muscle models to predict and analyze the effect of architectural features of the muscles on the distribution of forces and muscular coordination strategies, were carried out

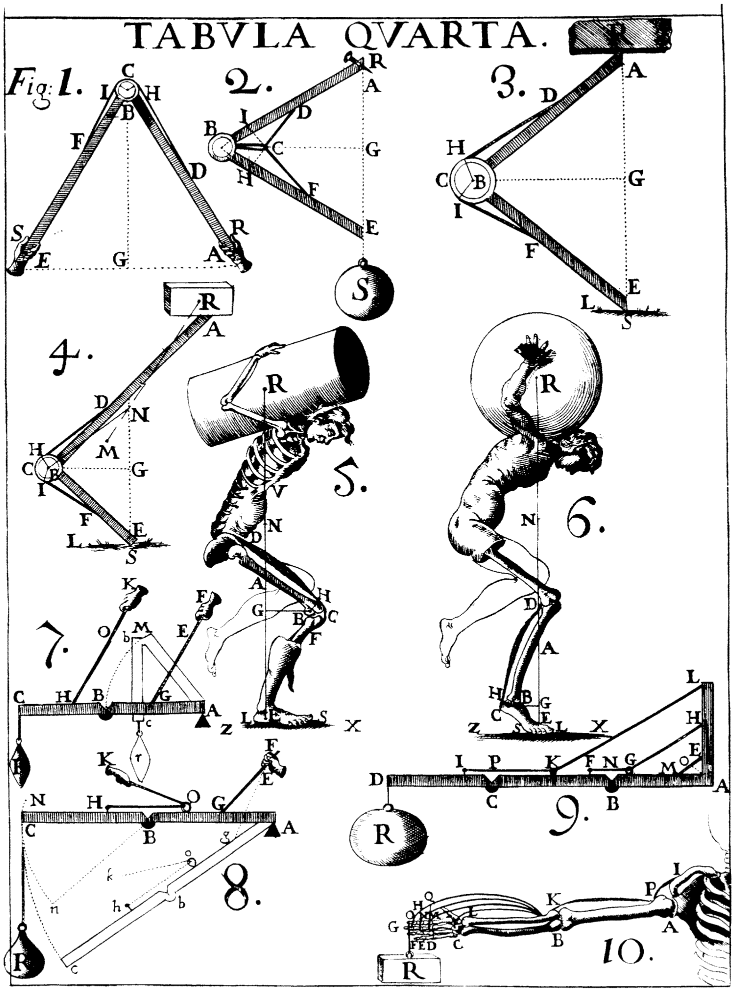


FIGURE 22. **Plate from Borelli *De motu animalium* 1680. DNLSM. Compare with Pandy et al. 1990 (Fig. 21).**

in 1989 by An and his colleagues for the upper extremities and in 1991 by Pandy and Zajac 1991 for the lower extremities in man, and in 1990 by Mai and Lieber for the frog and by Heslinga and Huijing for the rat. This area of research is rapidly expanding, because its results are applicable to sport and exercise physiology as well as in protecting laborers from occupational disorders in the locomotor system. A complete human "musculom," able to simulate human movement on computer, may well be on its way constructed by biomechanical investigators almost at the same time as the human "genom" is being revealed by their biochemical counterpart.

In 1991 Simonsen applied an elaborate computer system to process data from multiple sensors, electromyographic recordings, and high speed cine films of gait experiments in man. Such recordings enable the appropriate empirical control of the predictive power of model simulations to avoid Cartesian-style mistakes from deductions. From experiments in the rat gastrocnemius reported in 1992 by Zuurbier and Huijing, it is further established that empirical control *is* essential to current work with muscle models. By in vivo morphometry during muscular activity these authors describe slight anomalies compared with the parallelepiped muscle model: neither the length of aponeurosis nor the perpendicular distance between aponeuroses in Zuurbier and Huijing's set-up remained constant throughout muscular contraction. In particular, variable elasticity of both the tendons and the aponeuroses is important to animal motion.

8.4 Integration

Most recently Van Leeuwen and Spoor combined biomechanical analysis, model simulation, and anatomical dissection of the gastrocnemius muscle in man. From analysis they found that most models of muscular architecture, although useful for reasons of simplicity, violate fundamental laws of mechanics at some point. Van Leeuwen and Spoor derived mechanical stable solutions for muscle architecture by equating the pressure developed by curved muscle fibers with the pressure under the curved tendinous sheet. Their model (Fig. 23) predicted details of the curved muscular architecture, which the authors verified in anatomical examinations. Thereby, this study from the University of Leiden has extended Stensen's model and theory developed in the same university 329 years earlier, and the report was published by the Royal Society in London 324 years after the society first printed a review of the model.

Altogether, anatomical studies, model simulation studies, and bio-

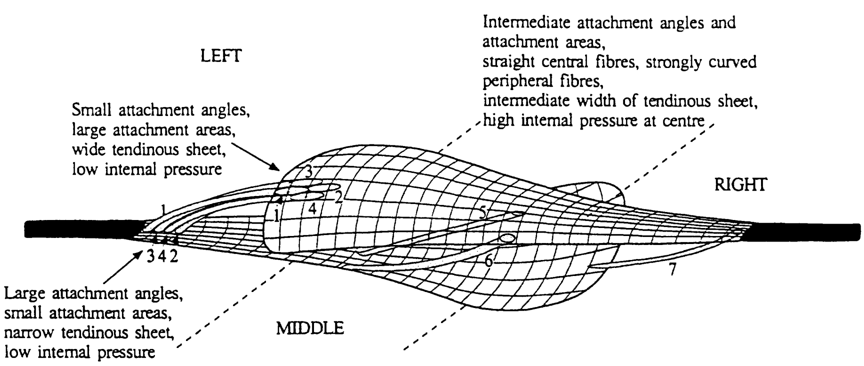


Diagram of a unipennate muscle with in-line tendons (black). The upper tendinous sheet is made transparent for muscle-fibre bundles. Only a few muscle-fibre bundles (numbered 1 to 7) are shown (stippled). Muscle-fibre bundle attachment areas are shown also (heavily stippled). Muscle-fibre bundles 3 and 4 are positioned between bundles 1 and 2 at the lower tendinous sheet so as to obtain an optimal filling of the muscle belly. The central muscle-fibre bundle 5 is straight, whereas the peripheral bundle 6 is strongly curved (this is not very clear owing to the chosen viewpoint).

FIGURE 23. Mechanically stable muscle model from the study of Van Leeuwen and Spoor, 1992. The publisher of the *Phil Trans*, the Royal Society, London, by permission.

mechanical overview studies have recognized Stensen's pioneering contribution to the study of structure and modeling of muscular architecture, emphasizing the key role of the unipennate structure in the mechanics of compound muscles and, indeed, of his dictum of the necessity of mathematics for the study of animal movement.

9. Theses and Conclusion

I.

With a few adjustments, Stensen's geometrical theory of muscular contraction, conceived during anatomical examinations at Leiden in 1663, first published in 1664 at Copenhagen, discussed with French scientists in 1665 at Paris and later that year with British scientists at Montpellier, and formulated in a formal, geometrical treatise at Florence in 1667, has found its place in science through studies published after 1980 by fulfilling what is in general required from a scientific theory: (1) that it describe a great number of observations without arbitrary assumptions; (2) that it permit prediction of new observations; and (3) that it qualify for falsification. Perhaps the latter qualification has been slightly overemphasized in the past.

II.

The respect for a scientific authorship suffers when a primary work, like the *Elements of Myology*, is persistently met with skepticism. Its reappraisal invites one to a general reassessment of Stensen's methods in science.

III.

The *Elements of Myology* followed the author's description of the neural basis of motor control in his "Lecture on the Anatomy of the Brain" from Paris. Both treatises were prompted by the posthumous publication of Descartes's *Traité de l'homme.* They were pioneering clashes with scientific reasoning based on unconfirmed assumptions—with theories in biology based on the action of arbitrary forces. Moreover, the explicit emphasis on what is *not* known concerning a matter described makes these works unique in contemporary scientific writing.

IV.

The strategy used by Stensen for working with a scientific model: (1) defining the structure and a time sequence; (2) geometrical deductions; (3) control of the predictions by new observations enabling hidden structures and properties to be recorded or adjustments of the model to be made, is applied in today's elaborate computer modeling of muscular action.

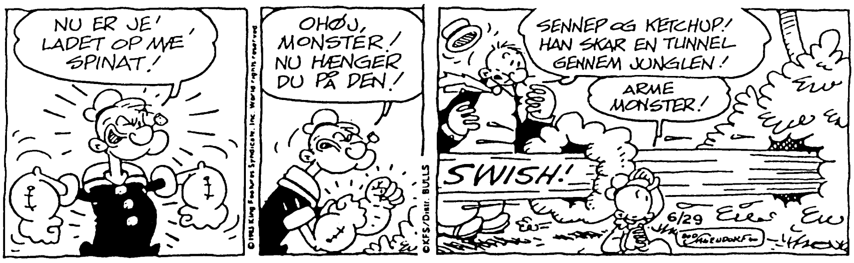


FIGURE 24. **But the myth lives on that something is pumped into the muscles to make them swell and contract. Popeye the Sailor by Bud Sagendorf. Reprinted with permission by King Features Syndicate/Distr. Bulls.**

V.

Modes and structures by which scientific ideas are formulated and evaluated in the *Elements of Myology*, and in its reception in science, do not contradict the sources of knowledge described as "Conjectures and Refutations" by Karl R. Popper, who said, *Science must begin with myths, and*

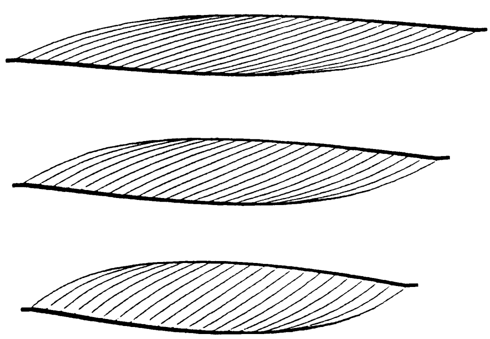


FIGURE 25. **Almost like Stensen's muscle model, beautiful but mechanically unstable: Otten's computer-generated illustration of unipennate gastrocnemius muscle in contraction from 1988. The publisher of *Exerc sport sci rev*, McGraw-Hill, Inc., by permission. For the purpose of the re-issue of *Elements of Myology*, E. Otten comments on the modeling functional architecture of skeletal muscles in the 1990s:**

During dissection of skeletal muscles, one cannot help wondering what the fiber arrangement and tendinous divisions mean in terms of muscle function. A model of functional architecture of skeletal muscles should contain some representation of muscle elements, such as fibers, tendinous sheets, etc. The question is to what refinement one should go. There is a simple rule of thumb here: The anatomical detail in the model should always be justifiable in terms of the required functional detail.

Presently, there are a number of good architectural models of skeletal muscles. The future in modelling may lie in two directions: (1) it is useful to have an atlas of types of muscle architecture and their associated functional properties (such as width, shape of length force curves, shape of force-velocity curves and internal pressure). (2) in order to study particular examples of muscle architecture, such as the peculiar serial fiber arrangement in some muscles, it is useful to have a nodal points model in which one can define any type of elastic element between the nodes. These elastic elements would then be pieces of muscle fiber and parts of tendinous sheets. The initial positions of the nodes should also be chosen freely, so that any shape of muscle can be simulated. Dynamic force production would then be dependent on the movement of the nodes in space, which depend on the dynamic balance of the elastic elements attached to the nodes. In this way, using fast computers, it is possible to understand the intricacies of complex muscle architecture in terms of muscle function.

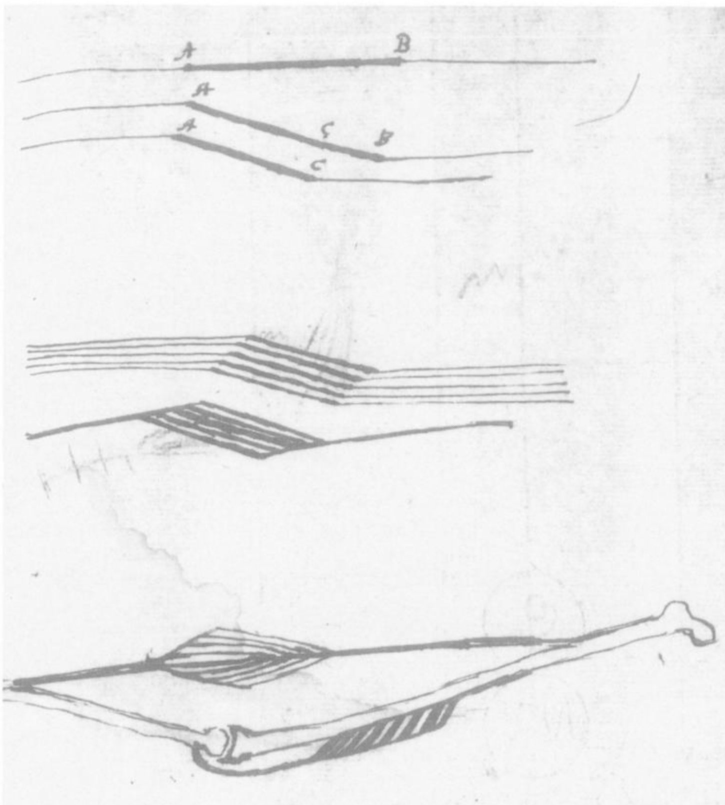
with the criticism of myths.[117] Ensuing comparisons may transform a myth into a scientific theory.

I have been asked repeatedly, what then is Stensen's theory all about? After several years I am now ready to answer. Niels Stensen's geometrical theory of muscular action *tells how* muscles make a swelling mainly at one surface in iso-volemic contraction, the way we see them do when we show muscle; not, in the manner of Popeye the Sailor's barrel-shaped arms, in which case spinach serves as an equivalent to the animal spirits of the ancient myths (Fig. 24). How this happens is that fibers of unipennate muscles *do not follow the surface* of the spindle-shaped muscle, but *do cross over* between opposite, approximately parallel, tendon plates (Fig. 25). It seems almost too simple to be true, but behind that knowledge appear far-reaching possibilities to explain the movement of muscles.

[117] Popper, *Conjectures and refutations*, p. 50.

Nicolaus Stenonius

Portrait of Niels Stensen as scientist to the Court of the Grand Duke of Tuscany. Unsigned, attributed to the Court painter Jan Sustermans. Uffizi Gallery, Florence.



Ink-drawing, probably by Stensen, of muscles around the knee. From a loose leaf in the volume containing Stensen's CHAOS-manuscript, the manuscript to *De solido intra solidum* and other manuscripts by Stensen. Bibiotheca Nazionale Centrale, Florence.