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BRINGING MUSCLES INTO FOCUS; THE FIRST TWO MILLENNIA

ANTIQUITY AND THE HELLENISTIC AGE

In the development of thought about the bodies of men and animals there came a time when the age-old acceptance of undifferentiated body-substance, the biblical 'flesh of rams' or the meat on which Homeric heroes feasted, gave place to a realisation that it consisted of individual muscles. How early did this happen and when was the function of these muscles as instruments of movement realised? With these questions our story naturally begins.[1]

The Hippocratic collection of writings on medicine and its philosophy, by a number of writers of his school as well as perhaps by Hippocrates of Cos himself, was put together before the end of the third century B.C. and includes works of the two previous centuries, some indeed containing ideas from still earlier times.[2] There is thus no such thing as a single system of thought to be found in them; the different treatises of the Corpus, some sixty in number all told, represent several different, and even opposing, schools. Three of them have been attributed by some distinguished scholars to the great physician of Cos himself,[3] and eight more are considered to date from his time (460 to 380 B.C.).[4] The only certainly pre-Hippocratic one is the 'Sevens', a prognostic text which implies the humoral theory of disease and the doctrine of critical days.[5]

In these Greek writings the tendons (which were confused with nerves) were endowed with the power of causing movement. In fact the same word

[1] In what follows I have had the advantage of the advice of Dr G. H. Lloyd of King's College, Cambridge. We owe to Bastholm (1) an excellent history of muscle physiology which has also been of much assistance.

[2] Singer & Underwood (1).

[3] E.g. by W. H. S. Jones (1), 'Prognosis', 'Regimen in Acute Diseases' and 'Epidemics' I and III.

[4] 'Sacred Disease', 'Airs, Waters and Places', 'Diet', 'Head Wounds', 'Ancient Medicine', 'Nutriment', 'The Art' and 'Breaths'. The last three of these, though containing the earliest Greek mention of the pulse, were not from the Coan school itself.

[5] It may go back to the 6th cent. B.C. On the whole Corpus see conveniently Sarton (1) vol. 1, pp. 96 ff.; Castiglioni (1) pp. 151 ff. The substance of the famous 'Oath' may also be of the 6th cent. B.C.

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neuron was used indiscriminately for both, just as *phlebes* was used indifferently for the veins and the arteries.[1] Thus: 'The bones give a body support, straightness and form; the nerves [tendons] give the power of bending, contraction and extension; the flesh and the skin bind the whole together and confer arrangement on it; the blood-vessels spread throughout the body, supply breath and flux and initiate movement.'[2] The last phrase of this sentence introduces the theory of *pneuma*, destined to have such influence in succeeding centuries. It was the main subject of one of the Hippocratic treatises already mentioned, the 'Breaths', certainly of the later fifth century B.C., but it is also important in another of the early works, the 'Sacred Disease' (epilepsy). There was certainly a connection here with the pre-Socratic philosophers, especially Diogenes of Apollonia (d. *ca.* 428 B.C.) who greatly emphasised the pre-eminence of the element Air in all Nature. He believed that the blood was everywhere accompanied by air (*pneuma*) in the vessels, and that sleep occurred when the air was driven down to the chest and abdomen.[3] Empedocles (d. *ca.* 430 B.C.) also associated blood and air very closely in his theory of respiration,[4] but Diogenes was probably more indebted to Anaximenes (d. *ca.* 494 B.C.), who had seen in air the source of all the other elements and the substrate of all change.[5] *Pneuma* is also prominent in the 'Nature of Man',[6] another Hippocratic treatise, probably written by Polybus of Cos, about the beginning of the fourth century B.C., reputedly Hippocrates' son-in-law and successor as head of the Coan school.[7]

Polybus' book is the main source for the other basic biological idea of the Hippocratic writers, the humoral theory. This no doubt originated in a sense from the concept of Anaximander (fl. 560 B.C.) and Empedocles that all matter was composed of four 'roots' (elements) – fire and water; earth and air.[8] These are pairs of opposites, and Empedocles added two 'original causes', love (*philia*)and hate (*neikos*), or forces of attraction and repulsion, to explain their combination and splitting apart.[9] But the development of medical theories was complicated. While the 'Nature of Man' certainly expounds four humours, blood, yellow bile, black bile and phlegm, there are

[1] It is interesting that in ancient Chinese writings the word *chin* bore just the same ambiguity as *neuron*. For an account of the Chinese equivalent to the Hippocratic Corpus see Needham & Lu (1).

[2] 'On the Nature of the Bones', tr. Littré (1) IX, p. 183; eng. auct.

[3] Freeman (1) pp. 279 ff., (2) pp. 87 ff.

[4] Freeman (1) p. 195. It is interesting that Empedocles visualised a blood–air interface advancing and retreating within vessels and pores, closely similar to what goes on (as we know today) in the tracheal respiration of insects. It was in connection with this that Empedocles used his famous demonstration of the wine-pipette.

[5] Freeman (1) pp. 65 ff.

[6] Filliozat (1) p. 189.

[7] Sarton (1) vol. 1, p. 120.

[8] Freeman (1) pp. 56, 181.

[9] Freeman (1) pp. 172 ff., (2) pp. 51 ff.; Leicester (1).

traces of a two-humour system (bile and phlegm only) in earlier books such as the 'Airs, Waters and Places' and the 'Sacred Disease'.[1] Moreover the physicians were sometimes very critical of the adoption of any ideas from the philosophers. The whole polemic of the 'Ancient Medicine' is directed against this, and Empedocles is even mentioned by name in it.[2] That did not prevent the doctors from borrowing from natural philosophy of course, and the 'Nature of Man' seems rather like a deliberate attempt to synthesise the idea of four humours with that of the four elements.

Similar notions originated in the much earlier Vedic writings of India from the fourteenth century B.C. onwards, as Filliozat has shown.[3] The physiological ideas contained in them were elaborated and systematised in the Ayurvedic Corpus, especially the *Suśruta-samhita*[4] and the *Caraka-samhita*.[5] Here we find the living body considered as composed of the 'elements' air (*vāyu*), fire (*tejas*), water (*ap*) and earth (*prthivī*).[6] Even in the earliest texts breath or *prāṇa* (with a role closely comparable to that of *pneuma*) was divided into five or seven varieties, distinguished, when they came to be defined, by the parts of the body they served.[7] One of these, *vyāna*, ran through all the limbs and explained their movement.[8]

The later Hippocratic writers pictured all the parts of the body as composed of four humours.[9] These were: blood, hot and wet (corresponding to air); yellow bile or *chole*, hot and dry (corresponding to fire); black bile or *melanchole*,[10] cold and dry (corresponding to earth); and phlegm or saliva, cold and wet (corresponding to water). These humours were afterwards considered to be characteristic of the liver, gall-bladder, spleen and lungs respectively.[11] Health depended on the right balance (*krasis*) between these four. Of course the thought of the Hippocratic schools was not in reality as clear-cut as this. There are many different humoral theories in the Corpus.[12] That in the 'Nature of Man' is closest to the scheme just outlined, and unlike some other authors who derived three of the humours from blood,

[1] As also in the 'Affections' and 'Diseases I', books of the Cnidian school.

[2] Para. 20, tr. Adams (1) vol. 1, p. 175.

[3] Filliozat (1) pp. 46 ff.

[4] Datable between the 2nd cent. B.C. and the 2nd cent. A.D., in its present form by the 7th cent. A.D.

[5] Datable between the 1st cent. B.C. and the 3rd cent. A.D., in its present form by the 8th cent. A.D.

[6] Filliozat (1) pp. 20 ff.

[7] Filliozat (1) pp. 141 ff. Completing the circuit of the Old World *pneuma* and *prāṇa* had a close equivalent in Chinese culture, *ch'i*, of immense significance in all ancient and medieval East Asian biology and medicine (see J. Needham (1) vol. 2).

[8] Filliozat (1) p. 23.

[9] Cf. Leicester (1); Jevons (1).

[10] According to Jevons, this idea was probably derived from the observation of the lower part of a blood clot.

[11] Cf. Singer (1); Singer & Underwood (1).

[12] This shows itself even in secondary and propaedeutic sources. Singer (1) p. 8 has fire associated with blood and air with yellow bile; Singer & Underwood (1) p. 46, reverse this.

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Polybus considered all four independent and 'congenital'. Although the association with organs is late, it does occur in the Cnidian 'Diseases IV', but in this case the four humours include water instead of black bile, and the associations are all different, blood connected with the heart (not the liver), yellow bile with the liver, water with the spleen and phlegm with the head rather than the lungs. In the thought of Aristotle (384 to 322 B.C.) all substances were made of primary matter and on this matter different forms could be reversibly impressed.[1] The fundamental properties or 'qualities' were hotness, coldness, moisture and dryness; and by combining these in pairs the four elements (fire, air, earth and water) were obtained.[2] The relation between the qualities, the elements (or roots) and the humours is illustrated in fig. 1.

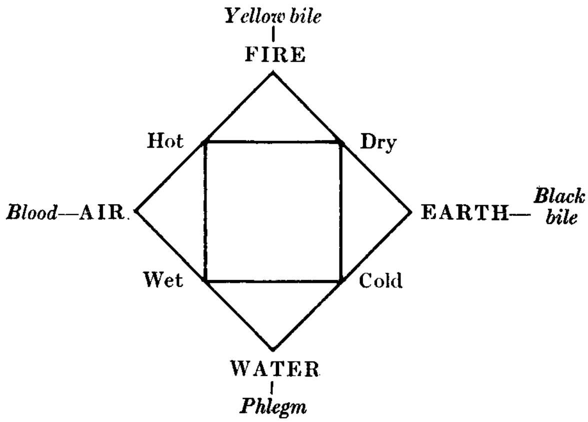

Fig. 1. The relationship, according to Aristotle, between the Qualities, the Elements and the Humours. (Singer & Underwood (1).)

The roles attributed to the *pneuma* and the humours in one presentation (the 'Sacred Disease') can be seen in the two quotations following.

For when a person draws in breath by the mouth and nostrils, the breath (*pneuma*) goes first to the brain, then the greater part of it to the internal cavity, and part to the lungs and part to the blood-vessels, and from them it is distributed to the other parts of the body along the blood-vessels; and whatever passes to the stomach cools it and does nothing more. But the air which goes into the lungs and the blood-vessels is of use (to the body) by entering the brain and its ventricles, and thus it imparts sensibility and motion to all the members; so that when the blood-vessels are excluded from the air by the phlegm and do not receive it, the man loses his speech and intellect, and the hands become powerless and are contracted, the blood stopping and not being diffused as was its wont...[3]

[1] Hence the philosophical sanction for all Hellenistic and mediaeval alchemy.
[2] *De Partibus Animalium*, 646a 14 ff., tr. Ogle (1).
[3] *De Morbo Sacro*, tr. Littré (1) VI, p. 373; eng. Adams (1) vol. 2, p. 850, mod. auct.

Again:

It is the brain which is the messenger to the understanding. For when man draws the breath (*pneuma*) into himself, it passes first to the brain, and thus the air is distributed to the rest of the body, leaving in the brain its acme, and whatever has sense and understanding. For if it passed first to the body and last to the brain, then having lost in the flesh and veins the judgment, it would be hot, and not at all pure, but mixed with the humidity from the fleshy parts and the blood, so as to be no longer pure.[1]

The idea of a metabolic activity of the flesh is well pictured in this quotation: 'The flesh draws upon both the stomach and the environment; it is clear that the whole body breathes in and breathes out. The little blood-vessels warmed by being overcharged with blood raise up the hot (or burnt) material and excrete it immediately: as yellow bile if the fatty element predominates; as black bile if blood predominates.'[2]

The protection afforded by the flesh against extremes of heat and cold was regarded as one of its main functions, since changes in temperature were believed to have serious effects on the balance of the humours. In the Hippocratic treatise 'On Diseases' we find:

When these humours (bile and phlegm) are set in movement and moistened, the individual, whether drunk or not, is seized with shivers; the side, which naturally is the part of the body most deprived of flesh, and which, far from having anything inside which supports it, is adjacent to a cavity, the side, we say, particularly feels the cold...the flesh which is at the side and the venules draw themselves together and contract, and what there is of bile and of phlegm in the flesh itself or in the venules of the flesh is, largely or totally, secreted inwards towards the warmth, because towards the outside the flesh is compact. These (the bile and phlegm)...cause intense pain, become warmed up, and by the heat attract to themselves bile and phlegm out of the veins and the neighbouring flesh.[3]

It is perhaps curious that the 'contraction of the flesh' due to cold, here described, was not thought of in the context of muscular motion. Muscle twitching and convulsions were also commented upon, but put down to movement in the blood vessels, transmitted to the muscles.

For Aristotle, the flesh was characterised by its divisibility in any direction, unlike the tendons and blood-vessels, but particularly by being the most important organ of the sense of touch. 'An animal [he says] is by our definition something that has sensibility, and chief of all the primary sensibility, which is that of Touch; and it is the flesh, or analogous substance, which is the organ of this sense.'[4] He regarded the sinews as responsible for motion, as we read:

[1] *De Morbo Sacro*, tr. Adams (1) vol. 2, p. 856.
[2] *Epidemiorum*, tr. Littré (1) v, p. 323, eng. auct.
[3] *De Morbis*, tr. Littré (1) vi, p. 193, eng. auct.
[4] *De Partibus Animalium*, 653b 23 ff., tr. W. Ogle (1).

The movements of animals may be compared with those of automatic puppets which are set going on the occasion of a tiny movement; the levers are released, and strike the twisted strings against one another...Animals have parts of a similar kind, their organs, the sinewy tendons to wit and the bones; the bones are like the wooden levers in the automaton, and the iron; the tendons are like the strings, for when these are tightened or released movement begins.[1]

Aristotle gave the 'more honourable part' to the heart rather than to the brain,[2] and communication with the rest of the body he regarded as due to the vessels full of blood containing *pneuma.*

Now experience shows us that animals do both possess connatural[3] spirit (*pneuma*) and derive power from it...And this spirit appears to stand to the soul-centre or original in a relation analogous to that between the point in a joint which moves, and (that which is) unmoved. Now since this centre is for some animals in the heart, in the rest in a part analogous with the heart, we further see the reason for the connatural spirit being situate where it actually is found...We see that it is well disposed to excite movement and to exert power; and the functions of movement are thrusting and pulling. Accordingly the organ of movement must be capable of expanding and contracting; and this is precisely the characteristic of spirit. It contracts and expands naturally and so is able to pull and to thrust from one and the same cause, exhibiting gravity compared with the fiery element, and levity compared with the opposites of fire.[4]

It is in the work of Herophilus of the Alexandrian school (early third century B.C.) that we find, as Bastholm rightly says, the first hint of the responsibility of the muscles for movement, and the first attempt to distinguish between the various cord-like organs which had all been classed together under the name of *neura.*[5] This work is known to us only through the writings of Galen, Rufus of Ephesus and one or two other later writers The following extracts illustrate these points.

Herophilus assigns the motive power of the body to the nerves [or sinews], the arteries and the muscles.[6]

We shall consider again whether twitching is something that affects only the muscles as Herophilus thought or whether it affects the skin and arteries too...[7]

If one believes Herophilus there are nerves of voluntary movement which arise from the brain and the dorsal marrow [medulla], others which are inserted some from one bone to another [ligaments], some from one muscle to another [aponeuroses], and finally others which attach (them to) the joints [tendons].[8]

[1] *De Motu Animalium*, 701b 1 ff., tr. A. S. L. Farquharson (1). Some idea of the automatic puppet theatres of the Hellenistic age can be gained from Beck (1).
[2] Because it was more central to the body (*De Partibus Animalium*, 665b 19 ff.).
[3] Innate or congenital.
[4] *De Motu Animalium*, tr. A. S. L. Farquharson (1) 703a 9 ff.
[5] See the study of Dobson (1).
[6] Galen, *De Historia Philosophica* (Pseudo-Galen), tr. Kühn (1) XIX, p. 318; eng. Wright.
[7] Galen, *De Tremore, Palpitatione, Convulsione et Rigore*, tr. Kühn (1) VII, p. 594; eng. Wright.
[8] Rufus of Ephesus, *Opera*, tr. Daremberg & Ruelle (1) p. 185, eng. auct.

In another place Galen says:

And here I blame Praxagoras[1] and Herophilus, the former for calling tremor an affection of the arteries, and the latter for trying to show that it originates in the nervous system. Praxagoras was far from the truth, and Herophilus was mistaken in referring the affection of the faculty to the instruments. For he knew that the nervous system, not the arterial, is subordinate to voluntary motions; but since it is not the body of the nerve itself which causes their motion, this being but an instrument, and the moving cause the power which passes through the nerve, here I blame him for not distinguishing power and instrument...Now in the case of dead bodies, neither muscles nor nerves are subject to any such affections as Herophilus and Praxagoras suppose, but all their motion ceases when the soul departs, muscles and nerves being but its instruments; so it is not the property of either muscle or nerve to produce motion, but only of soul.[2]

But since we know from Galen himself that Herophilus 'placed the dominant principle of the "soul" in the ventricles of the brain'[3] he was not really open to much criticism; all the less so indeed if he was really trying to say that there may be some conditions of uncontrollable tremor due to faults in the conducting nerve-channels rather than the voluntary activity of the 'soul'. Herophilus distinguished between arteries and veins (noting the great difference in thickness of their walls), and realised that the arteries contained blood. He investigated the pulse, and put it down to contraction of the arteries (resulting from a stimulus from the heart) followed by elastic return.[4]

Erasistratus, a younger contemporary of Herophilus, went further and distinctly recognised the muscles as organs of contraction.[5] He made further elaboration of the *pneuma* theory, postulating two kinds both coming from the air. This air, passing through the lungs and pulmonary veins, was drawn into the left ventricle of the heart during diastole; there a particular *pneuma* (the *pneuma zootikē* or *spiritus vitalis*), was formed from it. This vital spirit was pumped during systole to other parts of the body by way of the arteries; Erasistratus considered that the arteries contained no blood, the latter travelling only in the veins. When the *spiritus vitalis* reached the brain it was changed into a second kind, the *pneuma psychikē* or *spiritus animalis*.[6] 'Erasistratus says that the animal spirit comes from the head, the vital from the heart.'[7] The *spiritus animalis* was thus distributed through the (hollow tubular) nerves to the muscles, and here for the first time we find a theory of the mechanism of contraction, one which was to

[1] Praxagoras of Cos, fl. 340 to 320 B.C., physician and anatomist (cf. Sarton (1) vol. 1, p. 146).
[2] Galen, *De Tremore*..., tr. Kühn (1) VII, p. 605, eng. Dobson (1).
[3] Galen, tr. Kühn (1) XIX, p. 315; cf. Dobson (2).
[4] Dobson (1). [5] Dobson (2).
[6] 'He wrote accurately', said Galen, 'about the brain's four ventricles' (Kühn (1) v, p. 602).
[7] Galen, *De Hippocratis et Platonis, Placitis* II, tr. Kühn (1) v, p. 281, eng. Wright.

have influence centuries later.[1] 'Erasistratus says that the muscles, if they are filled with *pneuma*, increase in breadth but diminish in length, and for this reason are contracted.'[2]

Erasistratus is credited with the discovery of the bicuspid and tricuspid valves and seems to have considered the heart as a unidirectional pump.[3]

The heart, when it is dilated, is filled by the inrush into a vacuum; but the arteries when they are filled, are dilated; and they are filled by the *pneuma* sent from the heart. Both must occur at the same time, the dilation and filling, but he thinks that the one is the cause of the other, in the heart the dilation, and in the arteries the filling, as is observable elsewhere. A blacksmith's bellows are filled because they are dilated; sacks, wineskins and so on are dilated because they are filled.[4]

This distinction between active dilatation and passive expansion (with the implicit corollaries of positive contraction and mere elasticity respectively) was one of considerable insight. Some uncertainty remains whether Erasistratus was the first discoverer of the cardiac valves, for the Hippocratic book 'On the Heart' displays some knowledge of them; this however is now considered on linguistic grounds to be post-Aristotelian and therefore very little, if at all, anterior to the time of Erasistratus.[5] In any case he glimpsed the function of the valves though he thought that they prevented the regurgitation of *pneuma* rather than blood.

Rufus of Ephesus (early second century B.C.) was outstanding for his isolation of muscles by dissection. Erasistratus had regarded the muscles, like other organs, as built up by an aggregation of fine particles of blood around the *triplokia* (or *vasa triplicia*) – a basal fibre structure of nerves (or sinews), veins and arteries.[6] Rufus now recognised muscle as a tissue built on a particular pattern with a specific function – that of voluntary movement.

The muscle is a firm and dense body, not simple but resulting from an interlacing of nerves, veins and arteries, not deprived of sensibility; it is the organ of voluntary movement.[7]

The flesh is the solidified part which, in the viscera, is found between the vessels; it is at the same time a sort of tissue and a kind of packing between the network of the vessels so that there should be no spaces between them; then there is the flesh of the muscles, fibrous and resistant; and finally the coagulum which forms in wounds and is found in the cavities of the bones.[8]

[1] E.g. in the ideas of Descartes and Borelli, considered on pp. 14 & 23 below.
[2] Galen, *De Locis Affectis*, tr. Kühn (1) VIII, p. 429, eng. Wright. Cf. IV, p. 707.
[3] Wilson (1); Dobson (1); cf. Galen (Kühn (1) V, pp. 166, 206, 548 ff.).
[4] Galen, *De Differentia Pulsum*, tr. Kühn (1) VIII, p. 703, eng. Wright; cf. V, p. 562.
[5] Abel (1).
[6] Galen, tr. Kühn (1) II, p. 96, III, p. 538, XIV, p. 697.
[7] Rufus of Ephesus (attrib.), 'On the Anatomy of the Parts of the Body', in *Opera*, tr. Daremberg & Ruelle (1) p. 184, eng. auct.
[8] Rufus of Ephesus, 'On the Names of the Parts of the Body' in *Opera*, tr. Daremberg & Ruelle (1) p. 164, eng. auct.

We come now to Galen (129 to 201 A.D.), the writer of the greatest works of Western antiquity on animal anatomy and physiology. For Galen true muscles were to be defined as organs of voluntary movement, and the heart, uterus, oesophagus, etc. were classed as muscle-like. He made it clear that a muscle has only two possibilities – contraction and relaxation; the latter he regarded as a purely passive movement brought about by the contraction of the antagonist. '...The natural activity of the muscles consists in contracting and withdrawing upon themselves, and lengthening and relaxation takes place when the antagonist muscles pull and draw towards themselves.'[1] The possibility for an organ like the tongue to move in several directions depended on the presence of several different muscles.[2] Galen also performed experiments to show the effect upon movement of cutting off the muscle from communication with the spinal cord.[3] Although he was clear that the muscle mass had the power of movement he believed that tendon also took an active part.[4]

Galen's detailed dissections of muscles went far beyond anything that had gone before, and 'myology' was placed by him on a permanently scientific basis. Even though his dissections were made mostly on animals rather than on the human body his descriptions read strangely like those in a modern anatomical handbook. This may be illustrated by quoting a little of his account of the extrinsic muscles of the tongue.[5]

Should you wish to dissect all the tongue muscles separately in the body of a dead animal, as I am about to describe for you, then you must, I say, commence by reflecting the skin over the neck and the lower portion of the mandible. Next remove the muscle which is called the 'muscular carpet' [*M. platysma myoides*]... When you have reflected it you will see the peculiar muscle of the mandible, which is the one that is tendinous in its middle portion [*M. digastricus*], and simultaneously with it there will appear firstly the muscle of the tongue that is called the 'transversely directed' one [*M. mylohyoidens*], whether you like to call it one muscle with two parts, or else two muscles associated closely and united with one another...Then pass on to the 'oblique' muscle [*M. hyoglossus* with *M. chondroglossus*] which in apes has its source and origin on the lower rib [greater *cornu*] of the bone which resembles the letter Λ [lambda] of the Greek script [the hyoid bone], one on either side of the neck...

And so on at length. No other contemporary civilisation carried anatomy to the height attained by the indefatigable Pergamene physician. After all, the

[1] 'On Muscular Movements' in 'Oeuvres anatomiques, physiologiques et medicales', tr. Daremberg, II, p. 334, eng. auct.

[2] Ibid. II, ch. IV and V. [3] Ibid. II, p. 323. [4] Ibid. II, p. 327.

[5] In ch. 7 of book 10 of his work 'On Anatomical Procedures' (Duckworth, Lyons & Towers (1) pp. 56 ff.). Only the first eight and a half books of this survived in Greek and were in recent years retranslated by Singer (2); the remaining six and a half came down only through the Arabic, whence they were put into German by Max Simon and English by W. L. H. Duckworth, hence the above-mentioned publication. It is of interest that John Caius printed a revised Greek text of the first portion at Basel in 1544.

morphological description of muscles was an indispensable preliminary to the analysis of the contractile function of muscle. In later times it would be necessary, for example, to distinguish between red and white muscles, smooth and striated muscles, etc., and biochemists would want to select equal and opposite anatomical pairs of muscles.

A fundamental change which Galen made in the physiological scheme of Erasistratus was his demonstration that the arteries contain not air (*pneuma*) but blood. There has been much debate on Galen's conception of the *pneuma* theory; one interpretation may be described thus.[1] Air taken in by the lungs goes to the left ventricle where it plays its part both in maintaining the innate heat (essential for life as Galen emphasised) and in providing 'refreshing cooling' lest the heart should become overheated. Most of the air returns to the lungs and is expired with some waste substances. Galen regarded the *pneuma psychikē* or *spiritus animalis* as an exhalation of the blood produced under the influence of the innate heat. He believed that waves of dilation passed through the walls of the arteries causing the sucking in of blood from the veins, and of air both from the heart and from the exterior through the pores of the skin. The gently maintained heat in the arteries produced in the brain blood rich in *spiritus animalis*; the latter passed to the muscles along the nerves.

These Galenic conceptions were destined to hold the field in Western Europe with no alternative and little criticism for the next 1300 years. Further research on minor Latin writers, and especially on Byzantine and Arabic contributions (to say nothing of cultures further east), may well discover some interesting developments, but by and large the influence of Galen in the field of muscle contraction as in other realms of physiology and medicine reigned unchallenged until the Renaissance.

THE RENAISSANCE AND THE SEVENTEENTH CENTURY

In what has so far been considered we may discern, running through the whole, four threads of enquiry. First, the identification of the functional motile tissue – whether muscle itself or tendon. Secondly, the function of the flesh, apart from the problem of movement – its protective action, its sensitivity to touch and its metabolism (which on primitive views was bound up with the humoral theory). Thirdly the important matter of the inciting influence reaching the effective motor organ (whether muscle or tendon) and the channel (whether the blood-vessels or the nerves) by which the influence travelled; this was the province of the *pneuma* theory. Fourthly the problem of the morphology of the muscle tissue gradually descried, in so far as this could be studied through fine dissection without

[1] That of Wilson (1); see also Bastholm (1) pp. 87 ff.

the aid of the simplest microscope. Just raising its head, as we see in the work of Erasistratus, was the ambition to explain the mechanism by which the muscle shortened.

The ideas of Aristotle concerning the four qualities and elements, combined with the earlier Hippocratic concept of humours, were used by physicians throughout the middle ages; before their gradual abandonment in the seventeenth century, however, some new concepts had been added to them. It is worth while to mention these since, as will be seen, they clearly influenced the theories of contraction elaborated by seventeenth-century workers.

Aristotle taught that under the influence of the sun two vapours were emitted from the earth, one *anathumiasis* moist, the other hot, dry and smoky.[1] If these vapours were imprisoned in the earth, the former gave rise to the metals, while the latter gave rise to the *fossiles* or refractory minerals.[2] In later times alchemists identified the moist vapour with mercury, the dry with sulphur. Paracelsus (1493 to 1541) considered all matter to be ultimately composed of the four Aristotelian elements, but immediately of the *tria prima*, salt, sulphur and mercury. These identifications were not to be taken literally but as abstractions of qualities: the salt embodied the principle of incombustibility and non-volatility; the mercury the principle of fusibility and volatility; the sulphur the principle in virtue of which substances take fire.[3] Important for us is the paper by Debus (1) in which is described Paracelsus' concept of a 'Sal nitric food'. In the *Liber azoth*, besides the idea of a vital fire or sulphur, there is the theory of a nitrous salt or saltpetre, having amongst other functions that of an aerial nutriment for the muscles. In the century succeeding the death of Paracelsus many workers were concerned with the Sal nitric from an alchemical and often mystical point of view. In the sixteen seventies we shall come again upon the nitro-aërial particles, this time in Mayow's interpretation of his experiments on muscle.

The influence of these ideas on the writings of Thomas Willis and of John Mayow on muscle contraction will be discernible later. An interesting passage in Willis' work 'Of Feavers' (1684) reads as follows:

> The mass of the Blood, by the opinion of the Antients, was thought to consist of four humours, to wit, Blood, Phlegm, Choler and Melancholy...This opinion, though it flourished from the time of Galen, in the Schools of Physicians, yet in our Age, in which the Circular motion of the Blood, and other affections of it were made known, before not understood, it began to be a little suspected...because these sort of humours do not constitute the blood, but what are so called (except the Blood) are only the recrements of the blood, which ought to be continually

[1] *Meteorologica*, 341 b 6 ff., tr. H. D. P. Lee (1) p. 29. [2] Eichholz (1).

[3] These ideas can be studied in detail in the books of Pagel (1), Debus (2), Sherwood Taylor (1), Holmyard (1) and Leicester (2).

separated from it: For in truth the Blood is an only humour; not one thing about the viscera, and another in the habit of the body...and wheresoever it is carried through all the parts of the body it is still the same...But as these humours commonly so called, are made out of the other Principles, viz. Choler out of Salt and Sulphur, with an admixture of Spirit and Water; and Melancholy out of the same with an addition of Earth; and as the blood is immediately forged out of these kind of principles, and is wont to be resolved sensibly into the same, I thought best...to bring into use these celebrated Principles of the Chymists, for the unfolding of the Nature of the Blood and its affections.[1]

In a later variant 'acid' and 'alkali' were taken as two fundamental and opposing principles of matter, 'a duality replacing the Aristotelian quartet.'[2] Such theories were held by Franciscus Sylvius (working at Leiden from 1658 to 1672), an influential figure in the application of chemistry to biological processes. He made a study of the nature of salts, realising that they resulted from a union of acid and base. Since potassium carbonate was the commonest alkali available, acid–alkali neutralisation, effervescence and fermentation became amalgamated to virtually a single concept in Sylvius' theories. It is clear, as we shall see, that these ideas influenced Borelli in the picture he made of the mechanism of muscle contraction in the sixteen seventies. The ebullient acid–alkali concept was refuted both by Robert Boyle[3] and by Boerhaave in the early eighteenth century, though as Jevons has pointed out, something of it remained in the latter's ideas of acescence and alkescence, characteristic of plants and animals respectively. From the middle of the seventeenth century atomistic chemistry took over more and more, as witness the words of Boyle (1) concluding the 'Sceptical Chymist' (1679): 'For by that (the former part of my discourse) I hope, you are satisfied, that the Arguments, brought by Chymists to prove that all Bodies consist of either Three Principles, or Five, are far from being so strong as those that I have employed to prove, that there is not any certain and Determinate number of such Principles or Elements to be met with Universally in all mixt Bodies.'

In returning to the muscle story we may mention first Vesalius, whose great work *De Humani Corporis Fabrica* was published in 1543. His ideas of the fine structure of muscle are shown in the following quotation.

But if nature had simply divided the nerve and tendon in this way, and had not stuffed the spaces in between, the interstices of the fibres, with a soft substance that provided for the fibres' body some kind of structure and a secure foundation, the muscles could not preserve these fibres unbroken and unharmed for even the shortest period of time. Now 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

[1] T. Willis, 'Of Feavers', tr. S. Pordage (1). [2] Jevons (1). [3] Boas (1) p. 154.

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. Yet your picture will be nearer the truth in proportion as you imagine more and closer packed rushes or channels thrust through the cheese and not only stretched along the sides of the cheese.[1]

Vesalius abandoned the idea of flesh as the organ of sensation, deciding from his own observations that this faculty is seated in the skin. As Michael Foster (1) showed in his famous lectures, Vesalius saw clearly that contractile power resides in the actual muscle substance:

Muscle therefore, which is the instrument of voluntary movement..., is composed of the substance of the ligament or tendon divided into a great number of fibres and of flesh containing and embracing these fibres. It also receives branches of arteries, veins and nerves, and by reason of the presence of the nerves is never destitute of animal spirits so long as the animal is sound and well. Now I do not regard this flesh as merely a foundation or basis, as it were a bed or support by which the fibres and the above-mentioned divisions of the nerve are held together. Nor do I with Plato and Aristotle (who did not at all understand the nature of muscle) attribute to the flesh so slight a duty as to serve, after the fashion of fat or grease or some sort of clothing, the purpose of lessening the effects of heat in summer and of cold in winter. On the contrary I am persuaded that the flesh of muscles, which is different from everything else in the whole body, is the chief agent, by aid of which (the nerves, the messengers of the animal spirits not being wanting) the muscle becomes thicker, shortens and gathers itself together, and so draws to itself and moves the part to which it is attached, and by help of which it again relaxes and extends, and so lets go again the part which it had so drawn.[2]

Continuing the work of Vesalius, Fallopius (1523 to 1562) was keenly interested in fibrous tissue in connection with movement. Bastholm remarks that it was he who first enunciated the functional significance of the fibre: 'These...things are to be observed, as I have said, in every part that moves itself, and they cannot exist unless the part itself has fibres, and indeed internally fleshy fibres. For...motion requires a fibrous nature in the actual body that is moved; since (experience shows) whatever moves itself does so by contraction or extension.'[3]

Fabricius ab Aquapendente (1537 to 1619), pupil of Fallopius and teacher of William Harvey, carried out fine dissections of muscles, and he also emphasised the difference between their fibrous nature and that of other organs. Although Fabricius does write of the contractile function of the flesh he yet feels obliged, on account of its softness and weakness, to lay the main duty on the tendons:

So the twofold nature of the tendon was called for by the twofold use that was proposed, so that it was constructed in one part unitary, alone and compact, in

[1] Edition of 1543, p. 220, tr. Wright. The analogy with cheese and cheese-making played a considerable part in ancient and mediaeval biological speculation (see J. Needham (2), passim), as Vesalius was no doubt well aware.

[2] Foster (1) pp. 69–70.

[3] *Opera omnia*, vol. I, p. 94, tr. Wright.

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the other split into fibres and divided. For where it appears unitary and compact and cartilaginous, there it is stronger and employs this opportune strength in lifting and moving bones; for this reason the tendon almost alone has always been recognised as the mover of bones. But where it is seen to be split into fibres and divided, there it is softer and more suitable for the bringing about of contraction; this happens more in the belly and the middle and even the beginning of the muscle, where contraction is required to a greater degree.[1]

It is interesting to notice that William Harvey in his notes[2] and lectures[3] on muscle returns to the view that the contractile material is flesh and not tendon or sinew. He remained entirely under the influence of the Aristotelian *pneuma* as the causation of movement.

This is not the place to discuss the whole upsurge of science in the seventeenth century. The new chemistry, typified by Boyle and Mayow, as well as the old, influenced the thought of those concerned with muscle function in this period; the science of mechanics as founded by Galileo and the mathematics of Descartes and Newton sent out their inspiration; in physiology Harvey's demonstration of the circulation of the blood had profound effects, disposing in the end (though not at once) of the ancient ideas of the distribution of nutrient substances and spirits by ebb and flow in the veins and arteries.[4]

Descartes was a mathematician and philosopher – no physiologist; but he applied himself to the explanation of the working of the whole body as a machine. 'We must admit' wrote Foster (1) 'that he did succeed in showing it was possible to apply to the interpretation not only of the physical but also of the psychical phenomena of the animal body, the same method which was making such astounding progress when applied to the phenomena of the material world.' Descartes still used the concept of animal spirits, but he treated them as a very subtle fluid amenable to physical laws; he also postulated that the rational soul was something added to and independent of bodily mechanisms, including that of the brain. His ideas (1646 to 1647) with regard to muscular movement can be illustrated as follows:

Now according as these spirits enter thus into the concavities of the brain, they pass thence into the pores of the substance, and from these pores into the nerves; where according as they enter or even only as they tend to enter more or less into the one rather than into the others, they have the power to change the shape of

[1] *Opera omnia anatomica et physiologica*, p. 404, tr. Wright.
[2] *De Motu Locali Animalium*. Ed. and tr. Whitteridge (1).
[3] *The Anatomical Lectures of William Harvey*. Ed. and tr. Whittridge (2).
[4] Galen had admitted such a tidal flow in part, but expressed himself obscurely on the motions of the blood, hence some misrepresentation of his beliefs by modern historians of science. Fleming (1, 2) has attempted to rectify the matter. Galen's assumptions of pores in the intraventricular septum of the heart, and of a partial ineffectiveness of the mitral valve, are not in dispute however.

the muscles in which these nerves are inserted, and by this means to make all the limbs move. Just as you can have seen in the grottoes and foundations in the gardens of our kings, that the same single force by which the water moves, coming out from its source, is enough to move diverse machines and even to make them play instruments or to pronounce words according to the different disposition of the tubes which conduct it.[1]

And truly one can well compare the nerves of the machine which I describe with the tubes of the machines of these fountains, its muscles and its tendons with the other diverse engines and springs which serve to move them, and its animal spirits with the water which puts them in motion, of which the heart is the source and the concavities of the brain the reservoir. Further, the respiration and other such actions, which are natural and usual to it, and which depend on the course of the spirits, are like the movements of a clock or mill, which the ordinary course of the water can render continuous.

For the single cause of all the movement of the limbs is that some muscles shorten and that some muscles lengthen...; the single cause that makes a muscle shorten rather than its antagonist is that there comes a certain amount (it may be little) more spirit from the brain to it than to the other. Not that the spirits that come immediately from the brain suffice alone to move the muscles, but they determine the other spirits which are already in these two muscles to come out very promptly from one of them and to pass into the other; by means of which the one which they leave becomes longer and limper; and the one which they enter, being promptly inflated by them, shortens and pulls on the limb to which it is attached. This is easy to imagine provided one realises that only very little of the animal spirits comes continually from the brain towards each muscle. There is always a quantity of other spirits enclosed in the same muscle which move about there very quickly, sometimes swirling round only in the place where they are (when they do not find passages open for their exit) and sometimes flowing into the antagonist muscle, according as there are little openings in each of the muscles, by which the spirits can flow from one to the other, and which are so disposed that, when the spirits which come from the brain towards one of them have even little more force than those which go towards the other, they open all the entrances by which the spirits of the other muscle can pass into this one, and close at the same time all those by which the spirits of this muscle can pass into the other. Thus all the spirits contained before in these two muscles are assembled in one of them very quickly and thus inflate and shorten it, while the other lengthens and relaxes.[2]

In the intellectual climate which had thus been created, much observation, experiment and cogitation were expended during the latter half of the century, by several contemporaries, on the mechanism of muscle contraction. We may next consider therefore the work of Croone, Borelli, Willis, Stensen and Mayow.

[1] Once again we see the influence of mechanical simulacra of life on physiological thinking (cf. p. 6 above). This occurred in other civilisations also (see J. Needham (1) II, p. 53 ff.).

Chapuis (1) describes the 'hydraulic gardens' of the 17th cent. and their automatic puppet-plays.

[2] 'Oeuvres', ed. Cousin, p. 347, eng. auct.

William Croone's first work on muscular movement, *De ratione motus musculorum*, was published anonymously in 1664. From experiments on nerve section Croone deduced that something (for which he still used the word spirit) necessary for contraction of the muscle, passed along the nerve from the brain. In his mind the word had a new connotation, reminiscent of the interpretation used by Descartes: 'As often therefore as I say the Animal Spirits, I mean the most subtle, active and highly volatile liquor of the nerves, in the same way as we speak of spirit of wine or salt...those spirits in the nerve called Animal, are nothing else than a rectified and enriched juice of this kind.'[1] He pictured the muscle as containing countless tendinous fibres, which were loosely arranged in the belly of the muscle (where more abundant flesh occupied the spaces), but joined together at each end to form a rope-like structure. The following paragraphs describe his point of view.

What, I ask, is more likely than that the force is carried with this liquor or rather, that this liquor itself, or animal spirits of the fibres, is struck out from the branchlets of the nerves by some impulse? If this be so it will also be highly probable that from the mixture of this liquor or spirit with the spirits of the blood there occurs continuously a great agitation of all the spirituous particles which are present in the vital juice of the whole muscle, as when spirit of wine is mixed with the spirit of human blood. For I have stated above that all parts of living things are swollen with a certain vivifying and spirituous liquor;...and no one is such a novice in chemistry as not to know how great a commotion and agitation of the particles is accustomed to occur from different liquors mixed with each other, as may be discerned in the example just mentioned, and also in common water with oil of vitriol or butter of antimony dissolved with spirit of nitre and in an almost infinite number of other cases of this kind.

Moreover, since it has been shown already that all the motions of the spirits in the parts of a muscle are contained in certain spaces, and in addition, that these spaces are broader and more definite where the belly of the muscle is...I say that the agitation of the spirits which is made by the different liquors within the heaving membranes of the muscle necessarily impels them with a great effort through straight lines towards A and C (the ends of the muscle). And since, in the intervals or spaces, they always strike against the smaller ends, they turn back on themselves and are accumulated in greater quantity around the middle or belly of the muscle...and hence the muscle begins to swell.[2]

It is interesting that Croone carried out an experiment from which he drew support for this hypothesis. He showed that when a weight of 7 pounds was hung at the bottom of an empty bladder, and water was poured into it, the weight was raised.

Just about this time the Danish anatomist Nicholas Stensen was actively working on muscle structure and movement. In 1664 he published *De musculis et glandulis observationum specimen* and three years later *Ele-*

[1] W. Croone (1), tr. Wilson (2). [2] Ibid.

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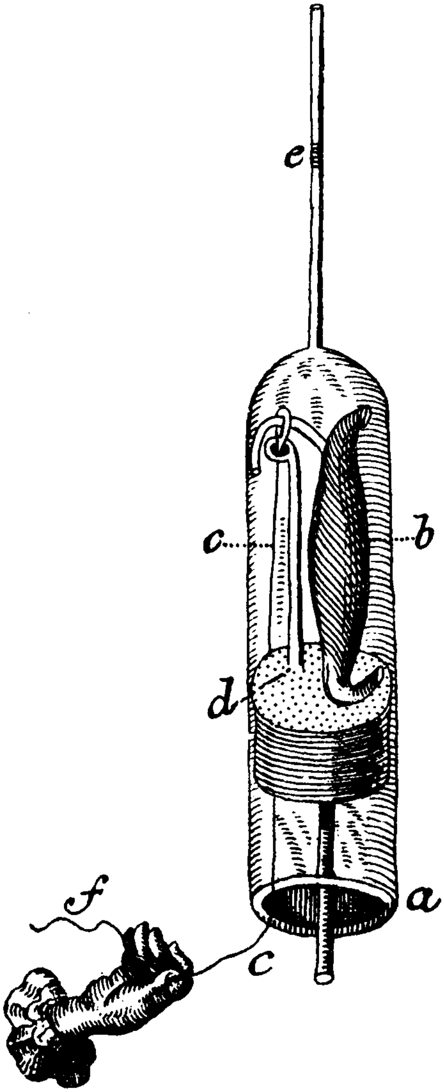

Fig. 2. Swammerdam's experiment (see text).

mentorum myologiae specimen seu musculi descriptio geometrica.[1] He described how the heart and other muscles contain no parenchyma but are composed of motor fibres which may be dissected into most minute fibrils. The fibres run from one tendon to the other and the middle parts are of a

[1] Ed. Maar (1).

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different nature, soft and broad, making up the fleshy part of the muscle.[1] So striking are his descriptions that some commentators (e.g. Foster (1) and Wilson (2)) have felt that they strongly suggest he had made microscopic observations. Walter Charleton (1) a few years earlier had said 'The flesh is of such a nature as to yield easily to the *pneuma* coming in,'[2] and Stensen too was clear that the fleshy part of the fibres alone, and not the tendinous part, was concerned in contraction. Stensen's assertion that the heart is a muscle with the same structure and function as other muscles was a very important contribution, since it undermined the ancient idea of the heart as the source of vital heat; even Harvey had laid emphasis on 'innate heat' in the blood of the heart as the prime cause of distension in diastole.[3]

Up to this time it was tacitly assumed that the contracted muscle, hard to the touch and appearing swollen, had increased in volume. Charleton[4] however, in 1658, had expressed the view that its breadth increased as its length diminished and so the volume was unchanged. Stensen (2), in his book of 1667, expounded a complicated geometrical theory which would allow of contraction without change in volume. This depended on the representation of the fleshy part of the muscle as forming a parallelepiped with oblique angles, and of the tendons at each end as forming rectangular prisms.

Wilson suggests that Stenson emphasised this constancy in volume knowing of the experiments of his friend Jan Swammerdam, made about 1663 but published only some sixty years later. Swammerdam[5] placed a frog's muscle, still attached to its nerve, in a tube drawn out at one end to a capillary containing a drop of water (fig. 2). The nerve was attached to a wire which passed out through a fine hole in the stopper of the tube. Movement of the wire caused irritation of the nerve and contraction of the muscle, but the bubble in the capillary scarcely moved – indeed it fell rather than rose. Then Francis Glisson, in his work *De ventriculo* published in 1677, described[6] another experiment to prove that there was no increase in volume on contraction. In this case a strong muscular man inserted his arm into a large tube filled with water and carefully sealed except for a small glass side-tube; contraction of the muscles even led to a slight fall of water in this tube. This experiment has often been attributed to Glisson himself, but he made no claim to it. As Hierons & Meyer (1) have pointed out, it was described in the Register of the Royal Society as carried out by Dr Jonathan Goddard in 1669 (see fig. 3), though it was not published until 1756 in Birch's *History of the Royal Society*.[7]

[1] Foster (1) p. 71. [2] Tr. Wright.
[3] E.g. the 'Second Essay to Riolan', tr. Franklin (1).
[4] See Portal (1) III, p. 86. [5] Swammerdam (1) p. 127. [6] Glisson (1) p. 167.
[7] Fig. 3 shows the diagram which appears in Goddard's original paper – a slightly different version from that in the Royal Society's Register Book.

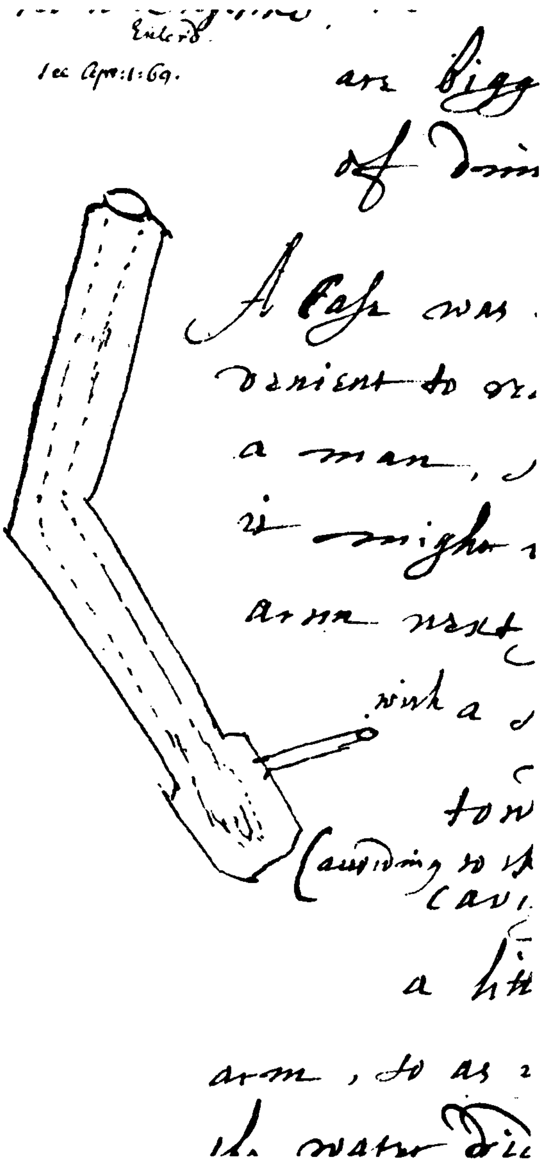

Fig. 3. Dr Goddard's experiment (see text).

In his later work Stenson expresses caution about the muscle fluids:

Concerning the fluids of muscle our knowledge is so uncertain as to be non-existent...Many people talk of the animal spirits, the more subtle part of the blood, the juice of the nerves – but these are mere words expressing nothing. Those who would continue further would introduce salty and sulphureous parts, or those analogous to spirit of wine; which may be true perhaps, but are neither certain nor sufficiently distinct. Just as the substance of this fluid is unknown to us, similarly its movements are uncertain; seeing that it has not yet been established definitely, either by arguments or experiments, whence it comes, by what means it proceeds or whither, once departing, it is received.[1]

In his later publication (1675) Croone (2) was much influenced by Stensen. He had now elaborated a theory which would permit the operation of the mechanism already proposed, but would not involve increase in volume of the muscle as a whole. With reference to his previous publication he writes:

An Objection rose, That we did not see any such conspicuous swelling in the belly of a muscle; to answer which, and explicate the hypothesis more clearly, I made this farther addition.

I supposed each carnous fibre as AE to consist of an infinite number of very small globules, or little bladders, which for explication sake I here express as so many little triangles, e.g. four in this fibre, ALB, BMC, CLD, DOE, all opening into one another at the points A, B, C, D, E.

I did not only suppose, but endeavoured to prove, that from the artery of each particular muscle, the nourishing Juice of the muscle was thrown out and extravasated to run at large among the Carnous Fibres, and insinuating itself by the constant pulse of the heart was driven on, and after mixing with another liquor it meets with between the Fibres in the Muscles, came to be strain'd through the coat of each globule or little bladder into the cavity of it: And likewise, that 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 mixed together as I said, enter into each little Bladder, and by these constant agitations, ebullition or effervescence...keeps these Globules or small vesicles always distended.

Croone then went on to calculate that the distension of four little bladders would be as effective in raising the weight from F to E as distension of one great one, AKE, and that 'if instead of four little bladders in a fibre we substitute 4000 that fibre shall raise the Weight in the space EF with 1/4000 part of the swelling; and so, of 1/400000 etc.' (See fig. 4*a*.)

Croone was also influenced by Leeuwenhoek's account of the appearance of muscle fibres under his microscope, as he emphasises in the concluding paragraph of this paper (see fig. 4*b*).

It is true that in 1674 Leeuwenhoek[2] wrote of the smallest muscle elements as composed of 'conjoyned globules'. But in 1682 (the first to

[1] Stensen (2) tr. Wilson (2).

[2] Leeuwenhoek (1) I, p. 111. Letter to Mr N. Oldenburgh.

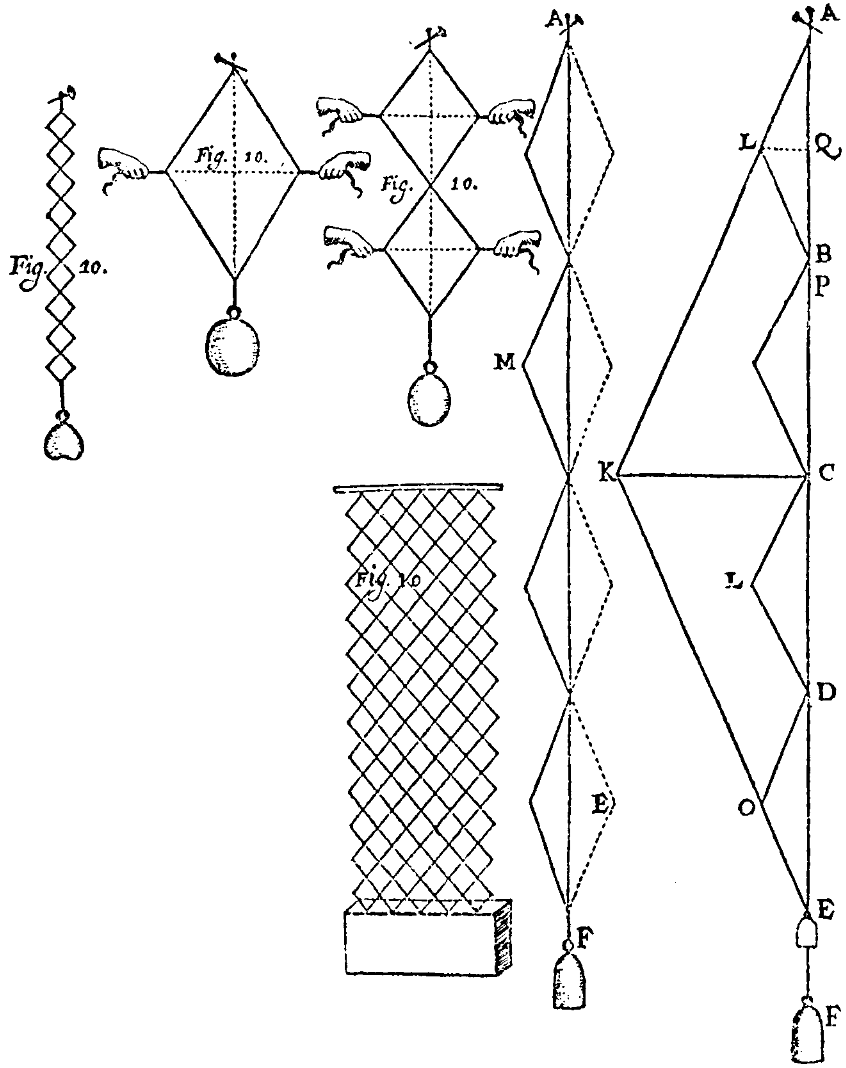

Fig. 4*a*. Diagram illustrating the lectures of William Croone, after *Philosophical Collections* (Royal Society) ed. Robert Hooke, 1680. This figure follows the words of Croone: 'as if we shall suppose four little bladders only for Example's sake each of them being distended from Q to L, shall all together raise the weight F to E, as well as one great swelling C to K'.

describe the transverse striations of the skeletal muscle fibre) he said:[1] 'The case now is that I often imagined that I could distinctly see that the fleshy fibres of which the greater part of a muscle consists were composed of globules.' He then described the very thin muscle fibres (he estimated one

Theſe and ſeveral other Particulars I did endeavour to make out at large in thoſe Lectures; yet only in the way of an *Hypotheſis*, not as if I did preſume to beleive I had found out the true Secret of *Animal Motion*, when I am almoſt perſuaded, no Man ever did or will be able to explicate either this or any other *Phænomenon* in Nature's true way and method: But becauſe I reckon ſuch Speculations among the beſt Entertainments of our Mind, I may chance to collect and publiſh ſometime or other what I then ſaid, and have lately try'd about it. And I am the more willing, Firſt, becauſe 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, and them, becauſe a ſheet or two, and two or three ſchemes, of that long expected Work of *Borelli*, *de Motu Animalium*, having been ſent to the *Royal Society*, I find there ſome Schemes for explicating Muſcular Motion, the very ſame with thoſe I make uſe of, and the ſame Experiment of the Bladder applied in another Scheme to this occaſion likewiſe: How he has explain'd or manag'd them, as yet I know not, but his uſing them, has made me have a better opinion of this Thought than elſe I ſhould ever have had;

Fig. 4*b*. Part of a page from Croone's paper in Hooke's *Philosophical Collections*, 1680.

million to the square inch) in which 'rings and wrinkles' became apparent, giving the appearance of globules. He went on:

Since I observed this I have been able to make out why our fingers, arms and legs, nay our entire body cannot lie stretched out straight, when reposing, but must be slightly bent...I also conceived the reasons of the movements, the stretching and the shortening of our muscles, that is to say, that when a muscle is stretched the fibres that constitute the muscles show no wrinkles or rings, but when a muscle is not stretched, but contracted and thick, each flesh-fibre is full of rings and wrinkles.

[1] Leeuwenhoek (1) III, p. 385 ff. Letter to the Royal Society of London, addressed to Mr R. Hooke.

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Fig. 5[1] pl. gives one of his drawings of a fibre from fish muscle, together with his description of it. From his observations he calculated that such a fibre might contain some 3000 filaments; 'who can tell', he wrote, 'whether each of these filaments may not be enclosed in its proper membrane and contain within it an incredible number of still smaller filaments?'

The great physiological work of Alfonso Borelli, *De motu animalium*, was published posthumously in 1680–1. There is no doubt that Borelli knew of Croone's earlier work,[2] and Wilson considers that Borelli, like Croone, but not perhaps knowing of Croone's later work, had set out to find a way in which inflation might bring about contraction without increase in volume of the muscle; 'in muscles, by diligent inspection, the volume does not seem to be increased, for the length of the muscle is instead contracted and shortened, and indeed the breadth and thickness do not seem to be increased but retain the same measurement'.[3] Borelli's picture of muscle structure is very similar to that elaborated by Croone, the fibres in the muscle consisting of chains of rhombs of inextensible material, collapsed in the resting muscle but capable of inflation so that they become 'shortened, hardened and swollen'. Borelli also pictures the nerve fibre as tense with spirits or *succus nerveus*, coming from the brain; thus any disturbance could cause exudation of a few drops into the fleshy mass of the muscle, and lead to a violent chemical reaction between the nerve juice and the blood in the muscle. He describes the latter as saline, the former as abounding in alkaline salts. 'Salty fluids and acid liquors mixed with saline liquors of another kind; namely fixed or alkaline, excite boiling and effervescence.' 'Thus they can excite heat and boiling nearly instantaneously in the fibres or spongy tubules of the muscles, or their interstices, whence inflation, hardness and contraction of the muscles follow.'[4]

Still another contemporary of Croone contributing to the contraction problem was Thomas Willis (1621 to 1675). He was an outstanding anatomist of that time, especially concerned with the brain and nervous system and first adumbrated his theory in *De Cerebri Anatome* in 1664. The following quotation from *De Motu Musculorum* (published in 1670) shows his point of view to be rather similar to that of Croone in *De ratione motus musculorum*:[5]

Therefore as to muscular motion in general, we shall conclude after this manner... that the animal Spirits being brought from the head by the passage of nerves to every muscle and (as it is very likely) received from the membranaceous fibrils, are carried by their passage into the tendinous fibres, and there they are plentifully laid up in fit Store-houses; which Spirits, as they are naturally nimble and

[1] Leeuwenhoek (2) II, pt. 3, p. 113.
[2] Wilson (2).
[3] Vol. II, p. 27, tr. Wilson (2).
[4] Vol. II, p. 64, tr. Wilson (2).
[5] For an interesting appraisal of the mutual influence of workers concerned with muscle see Hierons & Meyer (1).

elastick, wherever they may, and are permitted, expanding themselves, leap into the fleshy fibres; then the force being finished, presently sinking down, they slide back into the Tendons, and so vicissively. But whilst the same animal spirits, at the instinct given for the performing of motion, do leap out of the tendinous fibres into the fleshy, they meet there with active particles of another nature supplied from the blood, and presently they grow mutually hot; so that by the strife and agitation of both the fleshy fibres, for that they are lax and porous, are stuffed up and driven into wrinkling, from all which being at once wrinkled and shrivelled up, the contraction of the whole muscle proceeds; the contraction being finished, the sincere or clear spirits, which reside or are assuaged, go back for the most part into the tendinous fibres, the other particles being left within the flesh; the loss or wasting of these the blood supplies, as the nerves do those.

If it be demanded, of what nature, to wit whether spiritous, saline, as may be believed, or of any other disposition, the animal spirits, derived from the Brain into the Muscles, may be; and then whether the other Latex, immediately carried to them from the blood, is sulphureous or nitrous. Concerning these, because it appears not to the sense, we shall pronounce nothing rashly or positively.[1]

The mention by Willis of 'Latex sulphurous or nitrous' brings us to the key work of John Mayow in 1674, on the substance in the air responsible for both combustion and respiration – his nitro-aërial particles. In 1660 Robert Boyle[2] was doing experiments which demonstrated the necessity of air for combustion. Robert Hooke[3] continued such experiments and, besides confirming the general principle that combustible substances would only burn in the presence of air, showed that certain of them, e.g. charcoal and sulphur, would burn if heated with nitre in absence of air. He concluded, in accord with the commonly accepted view of that time, that inherent in air is a substance resembling (or even identical with) saltpetre. Mayow now applied these ideas to the living organism and showed that when a small animal was confined in air over water, its respiration was accompanied by a diminution in volume of the air. He was also interested in muscle and wrote 'It is probable that this aerial salt is altogether necessary for every movement of the muscle.'

The nitro-aerial particles, he stated, seemed 'in a high degree to fit the character of animal spirits'. He pictured them as transmitted by means of respiration from the air to the mass of the blood and thence to the brain; here the nitro-aerial spirit was separated from the blood and stored, to be despatched when the need arose via the nerves to the muscles. For contraction, interaction of these particles with another kind was necessary – particles 'of a saline–sulphureous quality' carried to the muscle in the blood:

I think, namely, that sulphureous and saline particles brought to the highest volatility in the mass of the blood by its continuous fermentation...and most

[1] Willis (2), tr. Pordage (1). [2] McKie (1).

[3] Hooke (1); and Birch (1) for the description of Hooke's experiments before the Royal Society.

intimately joined together, are separated from the blood by the action of the muscular parenchyma and stored up in the motor parts for setting up their contraction. For we may note that no small loss of fat takes place in the more violent exercises, and that it almost wholly disappears in long-continued hard work; while yet, on the other hand, animals indulging in ease and free from hard work become very obese, and fat is deposited on their muscles in quite sufficient abundance. Whence we may gather that the sulphureous particles of the blood, of which the fat is formed, have some share in the production of muscular contraction.[1]

The effervescent reaction taking place, with generation of heat, between the two sorts of particle was of a very special nature; he wrote:

> So that for effecting the contraction of the muscles there is required an excitement of the elastic particles, of a kind that can be accomplished instantaneously and without any sort of coagulation. And indeed I do not know if there be in the nature of things any other such fermentation but the singular case of the effervescence of nitro-aerial and saline-sulphureous particles, which mutually, as their nature is, excite themselves to a rapid motion. We must therefore conclude that it is from that that muscular contraction proceeds.[2]

He also pictured that supply of nitro-aerial particles was essential for the proper fluidity, fermentation and motion of the blood. (A difficulty arises here since it is not made clear what prevented interaction in the blood of the two kinds of particle.)

From examination of muscle boiled for some time, Mayow concluded that parallel, fleshy fibres were inserted obliquely into the tendons and that a great number of fibrils ran transversely to the fibres, joining them together. Contraction was ascribed to these fibrils, the fleshy fibres acting as a filter to remove the saline-sulphureous particles from the blood. The contraction itself he believed was due to contortion of the fibrils 'caused by nitro-aerial particles set in motion and even pretty intensely warmed in the motor parts'. He gave the analogy of a 'very fine music string' held above a lighted candle; this contraction also was put down to 'nitro-aerial particles bursting out of the flame of the lamp'.[3]

Mayow died in 1679 at the age of thirty-six. His work was fundamental to the ideas concerning utilisation in contraction of that part of the air which we now know as oxygen; of great interest too is his observation of the actual using-up of a body constituent in the process.[4] But his contribution was ignored by his contemporaries and forgotten for more than a hundred years, only being noticed again after the rise and fall of the phlogiston theory and the recognition of oxygen.[5]

[1] Alembic Club Reprint No. 17, ch. 3.
[2] Alembic Club Reprint No. 17, ch. 4.
[3] Alembic Club Reprints No. 17, chs. 2 and 6.
[4] For an account of the development of concepts of respiration in the 17th cent. see Wilson (3).
[5] Cf. Bastholm (1) p. 209.

During the 150 years intervening between the work of Vesalius and of Mayow we can see the gradual realisation of the primary role of the muscles in contraction and of the importance of their fibrous structure for this function. The idea of the bringing of animal spirits to the muscles by way of the nerves came to be very generally held, though the nature of these spirits and that of the change caused by their arrival in the muscle allowed of diverse speculations. During this period Francis Glisson (1597 to 1677) introduced the conception of intrinsic irritability in tissues, and this property was intensively studied with particular regard to muscle by Albrecht von Haller in the middle of the next century. About that time too interest in electrophysiology was to arise. To these themes we shall return later on.[1]

After the late years of the seventeenth century little change took place for a long time in the ideas of the mechanism of muscle contraction, though we should mention the variants of the main idea, such as that inspired by Newton, in which the *succus nerveus* was replaced by a nerve 'aether' transmitting oscillations.[1]

The century and a half succeeding the work of Boyle in 1660 was a time of great chemical advances. Workers on muscle during the late eighteenth century and the nineteenth century were much occupied with the application of this chemical knowledge to the living organism: oxidation reactions, analyses of tissues, the fate of nutrients, catalytic processes and so on. During these times the *succus nerveus* came to be forgotten, and new types of chemical theorisation (more sophisticated but just as speculative as their predecessors) held the field. Theories of contraction from about 1850 also owed much to improvements in microscopy.[2]

[1] Ch. 13. [2] Ch. 7.