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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.

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.

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.

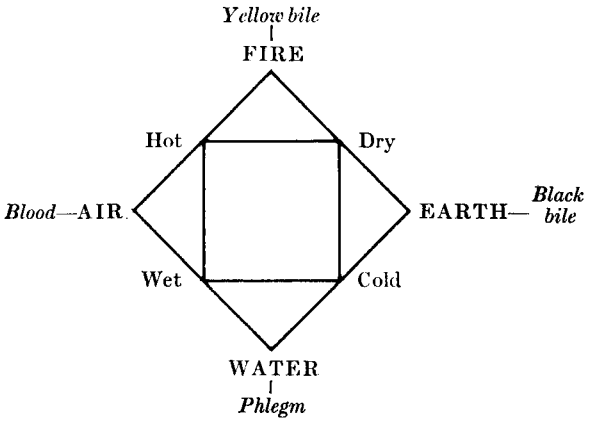

Fig. 1. The relationship, according to Aristotle, between the Qualities, the Elements and the Humours. (Singer & Underwood (1).)

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*, 701 b 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*, 665 b 19 ff.).
[3] Innate or congenital.
[4] *De Motu Animalium*, tr. A. S. L. Farquharson (1) 703 a 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.