Bulletin of Mathematical Biology, Vol. 41, pp. 791–802
Pergamon Press Ltd. 1979. Printed in Great Britain
© Society for Mathematical Biology
0007-4985/79/1201-0791 $02.00/0

A SIMPLE ANATOMICAL MODEL OF MUSCLE, AND THE EFFECTS OF INTERNAL PRESSURE

■ B. HEUKELOM, A. VAN DER STELT and P. C. DIEGENBACH
Zoological Laboratory,
44 Plantage Doklaan,
Amsterdam, Netherlands

The purpose of this study is to investigate the relationship between the structure of muscle and its function, especially with regard to the influence of the internal pressure when a muscle contracts. A model is constructed based on the anatomy of muscle. For different shapes of muscle, but of equal volume, the muscle features (i.e. force exerted etc.) are computed after every contraction step. A function for the internal pressure is also calculated. The internal pressure influences the structure of the muscle which also depends in a certain way upon the function of the muscle.

1. Introduction. In their paper, Gans and Bock (1965) present a series of statements concerning the relationship between the architecture (i.e. arrangement of muscle fibers and manner of attachment) of a muscle and its function (i.e. force exerted on a load and contraction distance). For example it is suggested that a muscle with long fibers has a long contraction distance, while a muscle of equal volume with short fibers develops greater force, but over a shorter contraction distance.

The present analysis attempts to describe some aspects of the relationship between the architecture of a muscle and its function in the living animal. As in the field of engineering (see Rashevsky, 1965), a theoretical–anatomical model of the muscle is constructed. The features of the "parts" (i.e. the single muscle fibers) are obtained by simplifying the results of physiological experiments of Hill (Hill, 1970). The length–tension curve of a single muscle fiber is used to determine the functional features of this model of a muscle with a particular architecture. Attention is also paid to the influence of the internal pressure.

What is the architecture of a muscle and how does this structure enable the muscle to function in the living animal? Muscle activity (the manner in which muscle converts chemical energy into developed work) can be described using a number of physiological parameters which are distinct, but not independent of each other. The most fundamental are: (1) the total work of muscle; (2) the magnitude of the contraction force exerted by the active muscle fibers; (3) the area over which a particular force is exerted; (4) the distance over which contraction forces are allowed to work; (5) the duration and repetition of the activity; and (6) the contraction velocity.

Gans and Bock (1965) write that "...it would be interesting to speculate upon the effects of internal pressure upon the efficiency of the muscle". Van der Stelt (1968) also suggests that the effects of the internal pressure can not be neglected and are related to the deformation of the muscle during contraction. Not all the chemical energy is transformed into work. A part of the chemical energy is needed for the deformation itself, for heat, or for mass displacement in muscle and for the generation of elastic stretch in connective tissue as in, for example, the fascia around the muscle fibers. If a muscle fiber is shortening, the form of the muscle changes as well as the angles of attachment of the individual fibers. For example, the initial, resting, state may occur when all the muscle fibers of a parallel-fibered muscle are straight and unstretched. When such a muscle shortens, the outer fibers bulge and then it is possible that the forces exerted by the outer fibers are only partly used for the production of muscle traction (i.e. force perpendicular to the tendon-plates parallel to the length of the muscle). As a result of the other component of the force exerted by the outer fibers the inner fibers are put under pressure. This internal pressure induces an outward directed force on the tendon plates of the muscle in a direction opposite to that of the muscle traction. Hence the internal pressure can influence the efficiency of the conversion of chemical energy into external work. The value of the internal pressure depends on the structure of the muscle and its activity, but, in turn, the geometrical structure of the muscle can be influenced by the internal pressure.

The internal pressure might be important in a different way. Using Scherrer's definition of fatigue (see Monod, 1973) "Physiological fatigue is a decrease of activity in a living system, related only to the working of its system, occurring in spite of a constant flow of the adequate stimulus and disappearing after rest", it can be postulated that as the internal pressure increases, it squeezes the blood vessels which supply oxygen-rich blood to the muscle thereby depriving the muscle of its oxygen and fatiguing it. The internal pressure depends upon the developed force and Monod (1973) shows a relationship between the exerted force (precentage of maximum force) and the work which can be continued without exhaustion.

2. Construction of a First Model of Muscle. A simple model of the muscle would be two parallel tendonplates, with perpendicular arranged muscle

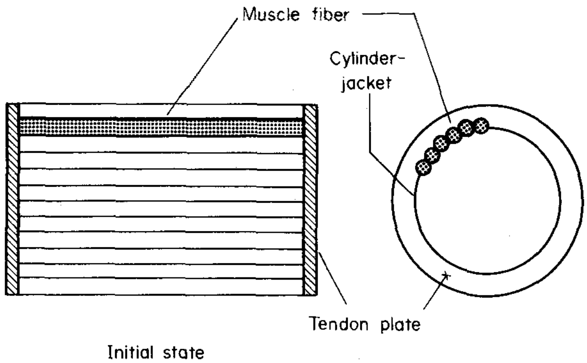

Figure 1. Simple muscle model, two parallel tendonplates with perpendicular arranged muscle fibers

fibers between them which contracts when stimulated. A fascia (mainly connective tissue) encloses these fibers. It is assumed that the muscle fibers are straight in the initial state and will be arranged as shown in Figure 1. The conditions of this model must represent "biological reality". There are obligatory conditions, such as the fact that a liquid muscle mass is not compressible. On the other hand, a choice can be made about the inclusion of some assumed features of the model. For example the tension–time curve is not essential to this model.

Obligatory conditions. (1) The liquid contained in muscle fibers is not compressible hence the volume of the muscle is constant.

(2) The muscle fibers are attached at the tendonplates and the location of attachment does not change during contraction or afterwards.

Assumptions. (a) The fascia (or perimysium) which encloses the muscle fibers has a structure such that each bulging which is caused by shortening of the distance between the tendonplates during contraction can be approximated by an arc of a circle. It is not claimed that this relation is more realistic than any other form function that describes the bulging of the muscle fibers. The justification of this assumption is only that it facilitates the computations without making great errors, as long as the deformation of muscle mass is not large. Catenary or parabolic functions may be used as well, as long as it is realised that the use of specific form functions can only really be justified if more of the structure of the collagenous muscle skeleton is known.

(b) The tendonplates are circular and stiff. They will not bend and they resist stress and pressure.

(c) All muscle fibers have identical properties (except for their location) and contract simultaneously.

(d) The internal pressure does not affect the contractility of the muscle fibers.

(e) According to the results of experiments by Hill (1970) we propose a linear tension–length relation for muscle fibers in contraction at the lengths considered here. Supposing that the shortening is slow enough, the tension of the muscle fiber will depend only on the length of the fiber. At the initial distance between the tendon plates D we will assume the tension $T_{D,0}$ to be 5000 gram cm^2, and the tension to be zero if the contraction coefficient $n_{max}=0.65$ (i.e. below lengths of 65% of the intial length of the fiber, see Hill, 1970). Hence the tension–length relation for one muscle fiber is

$$T_{D,n}=T_{D,0}(n_c-n_{max})/(1-n_{max}), \tag{1}$$

where n_c is the actual contraction coefficient, D_n/D.

(f) No intercellular space is assumed.

Considerations. If in contraction the muscle fibers shorten against some load, work is done. As noted in the introduction, only a part of the force can be used for the production of muscle traction. Contraction of the bulged outer fibers will produce an internal pressure in the muscle and in effect counteracts muscle traction. The total work thus done can be divided between work done in producing muscle traction and work done on the muscle itself in holding the parts together, producing internal pressure and tension in the tendon plates. The internal work done on the muscle in contraction can be considered as wasteful but it is real work and it may even be essential for muscle function since it makes the muscle tissue in contraction stiff in comparison to the flaccid muscle mass in the noncontracted state. A flaccid muscle would for instance be incompatible with the supposed action of a pinnate muscle as considered in the second muscle model.

In our model both amounts of work can be estimated. The total amount of work may be derived from the product of force produced by the muscle fibers and the computed amount of shortening of curved fibers. The amount of work done in traction is the product of the force vector in the direction of traction and the amount of decrease of the distance between the tendon plates in the same direction. The difference between the two quantities of work can be accounted for as work done on the muscle and can be related to the internal pressure.

Computation. In the conditions for the first model we did not mention any constraints limiting the many forms possible for this model. We want to investigate the influence of one form factor, i.e. the length of the muscle fiber considering only a family of cylindrical muscles with the same volume to test the statement that muscles with the same volume will have the same output of work under comparable conditions. The computation on several forms of this family of first models will be executed in steps, accounting for a number n of consecutive small shortenings (Figure 2). Other steps in the computation are accounting for the differences between a number j of muscle cylinder jackets concentrically arranged (Figures 1 and 3). The initial state occurs when the muscle fibers are straight and not stretched. Let the volume of the muscles to be tested be V cm^3 and the tendonplates area be a variable which determines D, and the radius be r, then the total number of muscle fibers will be equal to

$$N = V/\pi r^2 D. \tag{2}$$

In the computations r is set equal to 0.005 cm and $V = 3$ cm^3.

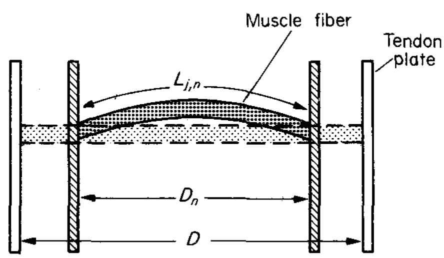

Figure 2. Shortening from D_0 to D_n causes the muscle fiber to shorten to $L_{j,n}$

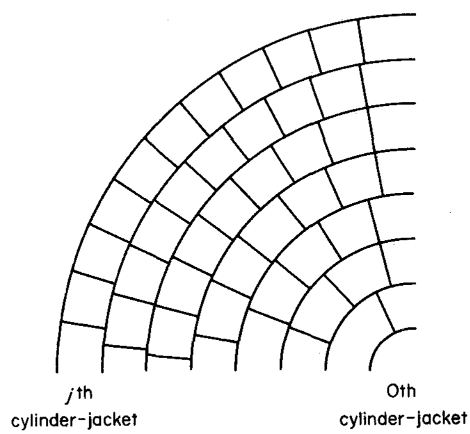

Figure 3. Diagrammatical cross section of muscle, considered as consisting of concentrically arranged cylinder jackets of muscle fibers

We will consider the muscle as consisting of concentrically arranged cylinder jackets of muscle fibers (Figure 3). The number of muscle fibers in the j-th cylinder jacket is

$$Z_j = \pi/\arcsin\left(\frac{1}{2_j}\right). \tag{3}$$

The total number of cylinder jackets is N_j.

The decrease in the distance between the tendonplates in each step of a length d is taken as 1 % of D, so

$$D_n = D - n \cdot d,$$

and the force developed by one muscle fiber after n steps would be

$$F_{D,n} = T_{D,0}\pi r^2 (n_c - n_{\max})/(1 - n_{\max}), \tag{4}$$

where $n_c = D_n/D$.

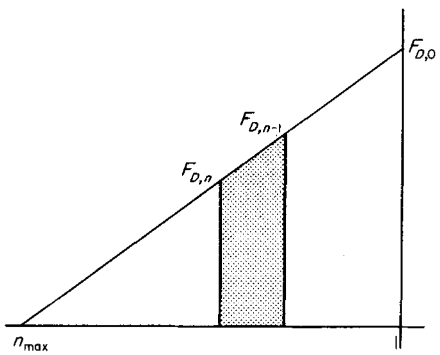

Figure 4. Length–force relation for our single muscle fiber. Dotted area: The amount of work done in shortening of a single muscle fiber during one step contraction

This equation should hold if no bulging of muscle fibers occurred. However since the length of the muscle fibers along the arc $L_{j,n}$ (Figure 2) will be greater, this equation will have to be adapted where the length $L_{j,n}$ is the length along the muscle fiber in the jth jacket after n steps of shortening. So the force developed will be

$$F_{L_{j,n}} = T_{D,0}\pi r^2 \left(\frac{\frac{L_{j,n}}{D} - n_{\max}}{1 - n_{\max}} \right) \text{gram}. \tag{5}$$

In each step of contraction the total work, W'_n, done by the muscle (in the case of the straight fiber), can be estimated by the decrease of capacity of each muscle fiber to do work and is the product of the decrease in length $(L_{j,n-1} - L_{j,n})$ and its force developed $F_{L_{j,n}}$ (see Figure 4):

$$W'_n = \sum_{j=0}^{N_j} Z_j (L_{j,n-1} - L_{j,n}) F_{L_{j,n}} \text{ gram cm.} \tag{6}$$

To compute the actual work done in displacing an actual load, we have to calculate the length of arc $L_{j,n}$ (see Figure 2) of the circle caused by bulging of muscle fibers of every cylinder jacket at the nth step of contraction under the restraint of constant volume. Since the length of the arc $L_{j,n}$ is completely determined by the assumption of the constancy of muscle volume and only dependent on the distance between the tendonplates, it can be calculated for every step. Total external work W_n done by the muscle during the nth step is, then,

$$W_n = \sum_{j=0}^{N_j} Z_j (D_{n-1} - D_n) F_{L_{j,n}} \cos\alpha \text{ gram cm,} \tag{7}$$

where (see Figure 5)

$$\alpha = 2 \arctan(k/0.5D_n), \tag{8}$$

and k is a measure of transverse displacement by bulging.

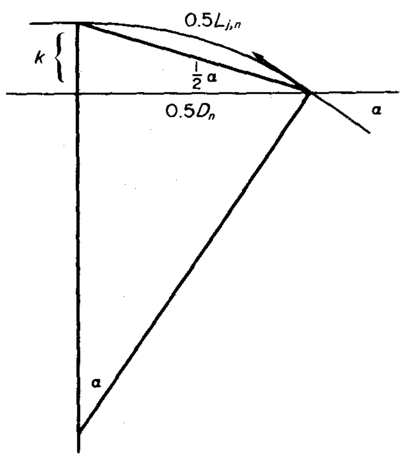

Figure 5. The tension vector of muscle fiber L_{jn} should be multiplied by the cosine of the angle between the fiber and the direction of the displacement. The maximum amount of transverse displacement by bulging is k

An estimated mean value, P_n, (because an exact calculation will be too complicated in this model) of the internal pressure after n steps, is computed as follows: we assume that chemical energy is only converted into energy needed for the displacement of the load (external work) and energy needed for the deformation of the muscle itself. As a consequence of this assumption the energy needed for the deformation in the nth step is $W'_n - W_n$. The mean contribution to the internal pressure is then $(W'_n - W_n)/(d \cdot V/D)$, because the pressure is uniform along the muscle fibers and tendonplates and inward directed. The total internal pressure ("sum of contributions") after n steps is

$$P_n = \sum_{i=1}^{n} \frac{W'_i - W_i}{d(V/D)} \text{gram cm}^{-2}, \tag{9}$$

where (V/D) is the tendonplate area.

This pressure is perpendicular to the tendonplates and diminishes the force which can be developed by the whole muscle. At every step of 1% contraction, the internal pressure (gram cm^{-2}), the exerted tension on a load (gram cm^{-2}) and the work done from the beginning of the contraction (gram cm) can be computed. In Table I the percentage of shortening is given ($=n$), at which external work is no longer produced. For that step is also given: (1) percentage of the total work done in muscle traction; (b) the force still exerted by muscle (gram); and (c) the total work done after stimulation (gram cm). Figure 6 shows the relationship between the internal pressure and exerted tension on behalf of the muscle function (percentage), versus the shortening of the distance between the tendon plates.

Though the formulation of this model is clearly in conformity with the principles for the arrangement of muscle fibers in a "parallel-fibered muscle" as given by Gans and Bock (1965) real muscle is not likely to have a structure as described in this model.

3. The Pinnate Muscle. Most muscles are more or less pinnate depending on the decrease of the angle between the tendonplates and the muscle fibers. In the first model only one mode of deformation by shortening of the muscle fibers was possible by a decrease of the distance between the tendonplates. Most muscles are more or less pinnate and have more degrees of freedom for a deformation. To get a simple model of pinnate muscle only the angle between the muscle fibers and the tendonplates in the first model has to be changed. The other conditions and assumptions hold for this model in the same way. There is a difference, however,

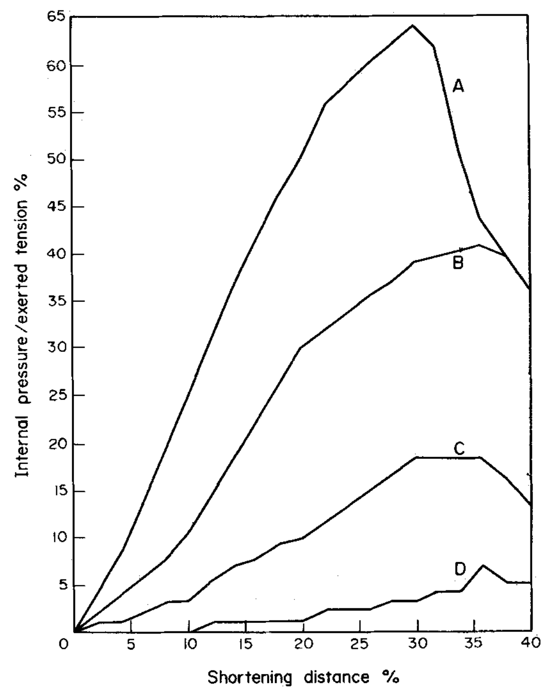

Figure 6. The relationship between the internal pressure and exerted tension in behalf of the muscle function (muscle traction) versus the shortening of the distance between the tendonplates. (A) tendonplate area is $2\,cm^2$, (B) $1.5\,cm^2$, (C) $1\,cm^2$, (D) $0.5\,cm^2$.

TABLE I

Results of Computations on Model I. Two Parallel Tendonplates with Perpendicular Arranged Muscle Fibers

D (cm)	Percentage of shortening ($=n$)	Percentage total work in muscle traction	Force on tendon plates (gram)	Total work done (gram cm)
6	36	100	40	2633
3	36	94	709	2478
2	28	71	1500	1814
1.5	18	57	1820	1151

concerning the internal pressure. The internal pressure developed in the first model is a consequence of the muscle action, depending on the possibility of shortening of the distance between the tendon plates. In this second model the internal pressure prevents the distance between the tendonplates from shortening too much and, in this way the muscle can exert a force in the direction of V (see Figure 7).

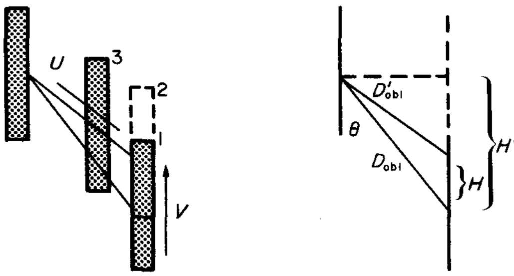

Figure 7. The transformation in steps is indicated by the vectors U and V. From the initial state the tendonplate is lifted over the distance H

Computation on a model of the pinnate muscle. The deformation of a pinnate muscle in contraction is described through three consecutive steps to facilitate computations. The initial state (first step) is defined by the area of the tendonplates and the angle between the fibers and the tendonplates. Therefore the number of muscle fibers is

$$\frac{\text{Tendonplate area}}{\pi r^2/\sin\theta}. \tag{10}$$

In the second step the tendonplates move parallel to each other until the length of the muscle fibers becomes a certain percentage of the original length (see Figure 7). In this step there is no internal pressure, because the outer fibers do not bulge. The work done in the direction of V and the new angle between the muscle fibers and the tendonplates are calculated. We need the following variables (Figure 7):

$$H' = \sqrt{D_{\text{obl}}^2 - (D_{\text{obl}}\sin\theta)^2}, \tag{11}$$

and

$$H = \sqrt{D_{\text{obl}}'^2 - (D_{\text{obl}}'\sin\theta)^2 - H'}.$$

In the third step the muscle contracts in the direction of U until the internal pressure becomes equal to the tension developed by the muscle fibers in the direction of $U.\sin\theta$. In Table II the first number represents the percentage of the shortening of the muscle fibers in the second step. The second number is the percentage of contraction in the third step (n) and Table II also shows (a) the new angle between the tendonplate and fibers (degrees), (b) the work done in producing muscle traction (gram cm), and (c) the internal pressure to the tendonplates (gram cm^{-2}).

TABLE II
Results of Computations on Model II (pinnate muscle)

Percent shortening in 2nd and 3rd step	Final angle (degrees)	Work done (gram cm)	Internal pressure (gram cm^{-2})	Initial angle (degrees)
4–30	10.3	2657	1	10
12–23	11.3	2762	1	10
20–14	12.4	2734	1	10
4–25	31.1	2269	106	30
12–20	34.3	2198	58	30
20–15	38.5	2118	22	30

Tendonplate area is 1 cm^2, volume muscle is 3 cm^3, the initial angle is 10 and 30 degrees respectively.

4. Discussion. Using this simple model, peculiarities of the architecture of a specific muscle cannot be discerned. To do this, the specific features of the muscle fibers themselves (i.e. length, kind of fibers) must be known. This model gives only a general view of the relationship between muscle architecture and muscle function. Looking at the influence of the internal pressure the following statements may be made:

(1) The internal pressure caused by mass displacement in the muscle during contraction will influence the performance of the muscle. For example (see Table I), if the tendon plates are large compared to the fiber length (2 cm, volume is 3 cm^3), the shortening of the distance between the tendonplates must not be larger than approximately 10–20% of the initial distance between the tendonplates. In this case the muscle still exerts a great external force although the proportion between the work done and loss of ability to do work is less. A shortening of 40% is possible if the tendonplates are relatively small. Figure 6 shows the proportion between the internal pressure and the exerted tension for the production of muscle traction. From this figure it is clear, that the shape of muscle influences strongly the extent of internal pressure.

(2) The mass displacement will influence the energy conversion; the more the outer fibers bulge, the less efficient the conversion will be. When the outer fibers bulge, the tendonplate of the muscle will push in the direction opposite of the force exerted by the whole muscle on a load. This could be advantageous to the muscle: in relaxation phases if a series of repetitive quick contractions are needed. Hence the existence of internal pressure is not a theoretical loss (*contra* Gans and Bock, 1965).

(3) The internal pressure perpendicular to the tendonplates will be small in pinnate muscle if the angle between the muscle fibers and the tendonplate is small (see Table II). The work done is greater if the angle is small and the influence of the differences in contraction rate upon the work is nil. It seems to be advantageous to use a pinnate muscle if a force is needed over a long time period, because the internal pressure is very small, hence the blood vessels will not be squeezed.

(4) The amount of the tension in the connective tissue (fascia) around the muscle will be dependent upon the relationship between the direction of the tension and the direction of the contraction force. It is also possible that the connective tissue determines how muscle fits the available space, for the muscle must perform its required function in a living organism.

LITERATURE

Bendall, J. R. 1974. *Molecules and Movement*. Heinemann: London.

Benninghof, A. and H. Rollhauser. 1952. "Zur inneren Mechanik des gefiederten Muskels." *Plugers Arch.*, **254**, 527–548.

Briskey, E. J., R. G. Gassens and B. B. Marsh. Eds. 1970. *The Physiology and Biochemistry of Muscle*. Wisconsin: The University Wisconsin Press.

Gans, C. and W. J. Bock. 1965. "The functional significance of muscle architecture." *Ergebn. Anat. EntwGesch.*, **38**, 110–142.

Carlson, F. D. and D. R. Wilkie. 1974. *Muscle Physiology*. Prentice Hall.

Hill, A. V. 1938. "The heat of shortening and the dynamic constants of muscle." *Proc. R. Soc. B.*, **126**, 136–195.

———. 1970. *First and Last Experiments in Muscle Mechanics*. Cambridge: Cambridge University Press.

Jewell, B. R. and D. R. Wilkie. 1960. "The mechanical properties of relaxing muscle." *J. Physiol.*, **152**, 30, 47.

Monod, H. 1973. "How muscles are used in the body." In *The Structure and Function of Muscle*. Ed. G. H. Bourne. Academic Press.

Rashevsky, N. 1975. "Models and mathematical principles." In *Theoretical and Mathematical Biology*. Eds. T. H. Waterman and H. J. Morowitz. New York: Blaisdell.

Rosen, R. 1967. *Optimality Principles in Biology*. London: Butherwords.

Stelt, A. van der. 1968. *Spiermechanica Bij Vissen*. Amsterdam: Veen.

RECEIVED 7-12-77
REVISED 7-13-78