

Proposed Mechanism of Force Generation in Striated Muscle

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Recordings of the change in tension in striated muscle after a sudden alteration of the length have made it possible to suggest how the force between the thick and thin muscle filaments may be generated.

ONE approach to the elucidation of the kinetics of movement of the "cross-bridges" which are widely assumed to generate the relative force between the thick and thin filaments during contraction of a striated muscle fibre is to record and analyse the transient response of stimulated muscle to a sudden change either of tension or of length. Considerable progress has been made in this way by Podolsky and his colleagues¹⁻³ who recorded the time course of shortening after a sudden reduction in load. Similar responses have been recorded repeatedly in this laboratory but have not been published because we did not succeed in making the tension change sharply enough to distinguish the component of length change that is truly synchronous with the tension change from that which lags behind the tension change. We therefore turned⁴ to the inverse type of experiment, in which the length of the fibre is suddenly altered (by $\pm 0.1-1.5\%$) and the time course of the resulting tension change is recorded. The results have led to some fairly definite suggestions about the way in which the cross-bridges may actually produce the force between the thick and thin filaments.

All the experiments were carried out on isolated fibres from the semitendinosus muscle of the frog *Rana temporaria*, at $0^{\circ}-4^{\circ}$ C. Length changes, complete in less than 1 ms, were produced by means of a servo system⁵, and tension was recorded with a capacitance gauge⁶. Compliance in the apparatus itself is small enough to be completely disregarded; precautions were taken to reduce the compliance in the tendon attachments to a minimum, and in some of the experiments it was eliminated altogether by using the "spot-follower" device⁵, which continuously measures the length of a middle segment of the fibre.

Responses to Stepwise Length Change

The general time course of tension in these experiments is shown in Fig. 1. This article is concerned only with the changes that occur simultaneously with the length change itself and during the first few milliseconds after it. As has already been briefly reported⁴, these changes are of the kind shown in Fig. 2: the tension undergoes a relatively large alteration simultaneously with the step change of length, but recovers quickly towards a level closer to that which existed before the step. The final recovery to the original tension which has been seen by many earlier investigators⁷⁻⁹ takes

place on an altogether slower time scale. The early changes seen in Fig. 2 have only come to light through the improved time resolution of present-day apparatus.

The behaviour shown in Fig. 2 suggests the presence of two structural elements in series. One of these would be an elastic element whose length is altered simultaneously with the change of length that is applied to the whole fibre, thus producing the large initial change of tension. The other would be an element with viscous as well as elastic properties, whose length readjusts itself during the period of a few milliseconds immediately after the length change, as a result of the change in tension. As this readjustment proceeds, the imposed length change comes to be shared between the two structures, giving a tension intermediate between the values immediately before and immediately after the length change. At the time of our first note⁴ about this quick initial tension recovery, we thought it likely that the recovery took place by sliding, with movement of the cross-bridges, but that the instantaneous elasticity was mostly in the filaments themselves. Since then we have measured these responses in fibres stretched so as to reduce the amount of overlap between thick and thin filaments. We found¹⁰ that the responses to a given absolute length change were altered only by a reduction in the scale of the tension changes, which varied in direct proportion to the amount of overlap and therefore also to the number of cross-bridges capable of contributing to tension. On these grounds we now believe that the instantaneous elasticity (or at least the greater part of it) resides in the cross-bridges themselves, as well as the structure responsible for the tension recovery.

The relations between length change and tension are illustrated in Fig. 3. The curve T_1 shows the extreme tension reached during the step change of length. It is somewhat non-linear, becoming stiffer with increasing tension as is commonly found in biological materials. This curve is the best experimental approach that we have to the instantaneous elasticity of the fibre, but it is clear from records such as viii-x in Fig. 2 that the tension drop in the larger shortening steps is cut down because the quick recovery has progressed

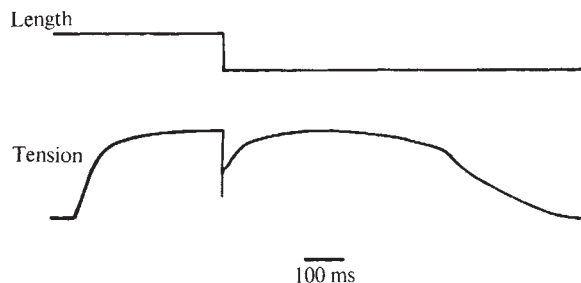
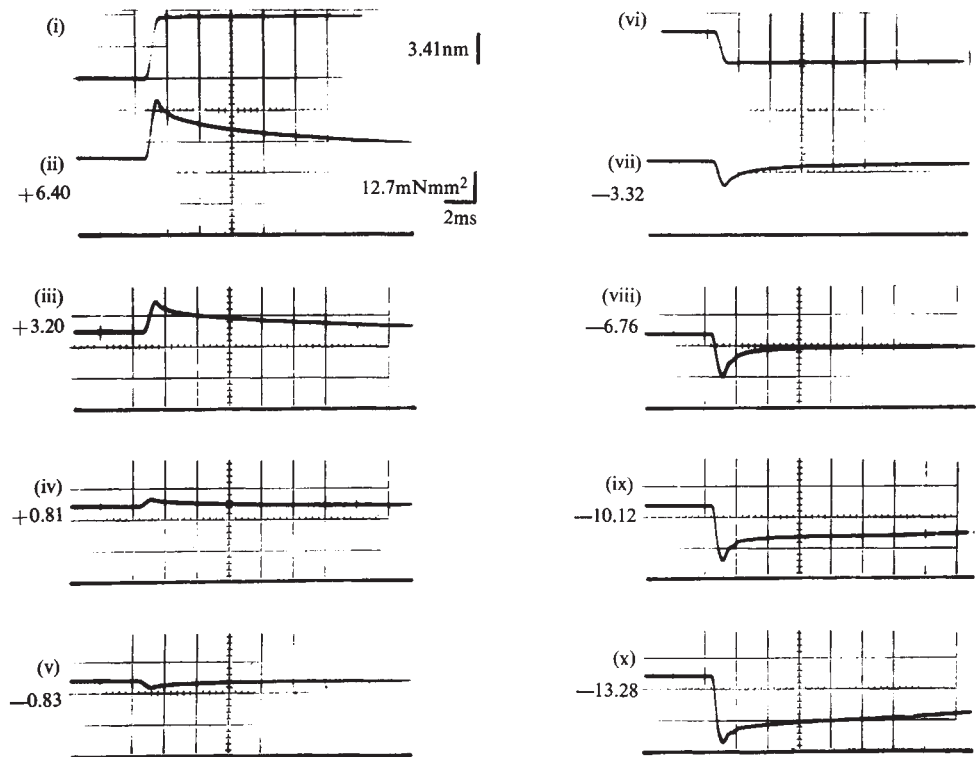


Fig. 1 Isometric tetanus of an isolated muscle fibre (frog, 4° C), with an imposed shortening step. This article is concerned with the tension changes during, and in the first few milliseconds after, the length step; these are shown on a fast time scale in Fig. 2.

Fig. 2 Transient changes in tension exerted by stimulated muscle fibre when suddenly stretched (ii-iv) or shortened (v, vii-x); same experiment as Fig. 1, which shows the whole of the contraction during which record ix was taken. (i) and (vi): records of length change during tension records (ii) and (vii) respectively. The number by each tension record shows the amount of the length change per half-sarcomere, in nm.



to an appreciable extent before the length change is complete. The true curve of the instantaneous elasticity is therefore less curved on the shortening side than the curve of T_1 in Fig. 3; it is even possible that it is practically straight, as indicated by the broken line.

In contrast to this straightforward behaviour of the instantaneous elasticity, the quick tension recovery is highly non-linear both in its extent and in its speed. The line T_2 in Fig. 3 shows the level approached at the end of the quick phase of recovery; for moderate amounts of shortening it has the unusual feature of being concave downwards, reflecting the fact that after a small length step the tension returns practically to its previous level (Fig. 2, iv, v). As regards the time course, it is evident from Fig. 2 that the early tension recovery is much more rapid in releases than in stretches, and that its speed varies continuously over a wide range with the size of the length step. The recovery is not exponential, but an estimate of the dominant rate constant can be obtained and is plotted against the size of the stretch or release in Fig. 4; it is roughly fitted by a curve of the form

$$r = \frac{r_0}{2(1 + \exp - \alpha y)} \quad (1)$$

All these features can be given at least a qualitative explanation if we assume that the force on a cross-bridge influences the length changes in that cross-bridge in the way that is assumed by Eyring and others^{11,12} in their theory of the visco-elastic behaviour of high molecular weight polymers. The treatment presented in the following paragraphs is meant only to indicate the way in which these features would emerge from such a theory; a more complete treatment will be needed in order to test whether it is fully consistent with the data.

Assumptions

The key assumptions that have to be made are (1) that the movement by which a cross-bridge performs work during the period while it is attached takes place in a small number of steps, from one to the next of a series of stable positions with progressively lower potential energy, and (2) that there is a virtually instantaneous elasticity within each cross-bridge

allowing it to shift from one of these stable positions to the next without a simultaneous displacement of the whole thick and thin filaments relative to one another.

These assumptions could be incorporated into some of the mechanisms that have been proposed for the action of the cross-bridges, for example, that of Davies¹³, in which each cross-bridge shortens by folding at a number of points, or that of H. E. Huxley¹⁴, in which the head of the myosin molecule (H , Fig. 5) rotates relative to the thin filament, acting as a lever which pulls the thick filament along by a link AB which is also part of the myosin molecule. Our assumptions fit very conveniently on to H. E. Huxley's proposals, and we shall discuss them on this basis in the way illustrated in Fig. 5. The features shown there which are additional to H. E.

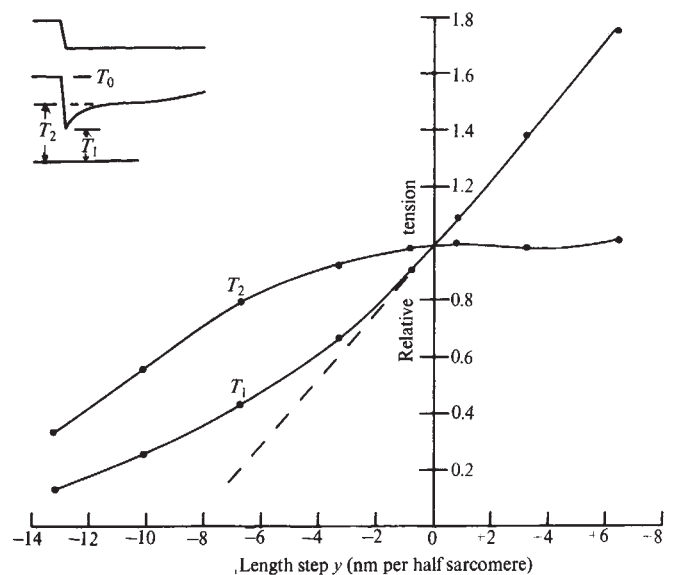


Fig. 3 T_1 , Extreme tension reached during step, and T_2 , tension approached during quick recovery phase, plotted against amount of sudden stretch (positive) or release (negative). Broken line: extrapolation of the part of the T_1 curve which refers to stretches and small releases. From records in Fig. 2.

Huxley's scheme are as follows. (1) The link AB is not inextensible as in H. E. Huxley's proposal but contains the instantaneous elasticity which shows up as curve T_1 (Fig. 3). (2) The head has a small number s of combining sites (M_1, M_2 and so on, in Fig. 5), each of which is capable of combining reversibly with a corresponding site (A_1, A_2 and so on) on an actin molecule in the thin filament. A single $M-A$ attachment allows variation of θ (rotation in the plane of the diagram of Fig. 5) without hindrance, but no other degree of freedom of the myosin head relative to the actin molecule. (3) The affinity between these myosin and actin sites is smallest for M_1A_1 , larger for M_2A_2 and so on. (4) The sites are placed so that the myosin head has $(s-1)$ stable positions, each of which allows two consecutive M and A sites to be attached simultaneously. (5) When the myosin head is in its $(s-1)$ th stable position it can be detached from the thin filament by a process involving the hydrolysis of ATP.

On this basis the quick tension recovery is due to the tendency for the myosin head to rotate to positions of lower potential energy, while the fact that the recovery occurs at a finite speed is a manifestation of the rate constant for movement of the system from one of the stable positions to the next.

Potential Energy Diagram of a Cross-bridge

Curves i-iv in Fig. 6 show the potential energy diagrams for individual attachment sites (M_1A_1, M_2A_2 and so on) on a single cross-bridge. Each contains a flat-bottomed well extending over the range of myosin head positions where that particular attachment can exist. Curve v is the sum of curves i-iv, and therefore gives the total potential energy of the cross-bridge (in the absence of force in the link AB); it consists of a series of steps, separated by narrow troughs at the positions where two of the links are attached simultaneously. The depth of each trough will depend on the shapes, and on the exact positions, of the sides of the potential wells that contribute to it; it is assumed in Fig. 6 that these are such that the quantities E_1 and E_2 (v, Fig. 6) are the same for each of the troughs.

The total potential energy of an attached cross-bridge contains also the potential energy of stretching the elastic link AB . The latter term is shown in curve vi, and the total in curve vii.

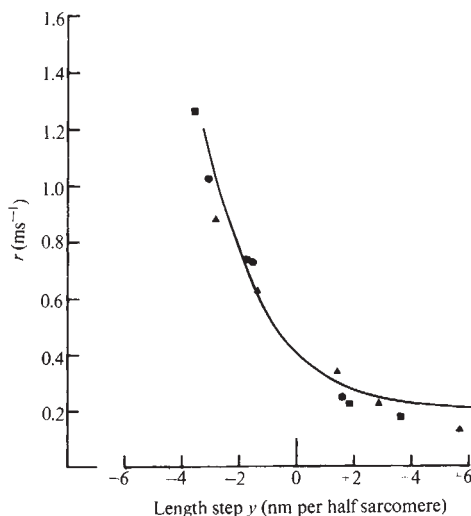


Fig. 4 Rate constant r of quick recovery phase following a length step of magnitude y (positive for stretch). Estimated as $(\ln 3)/t_{1/3}$ where $t_{1/3}$ is the time for recovery from T_1 to $(2T_2 + T_1)/3$ (see Fig. 3). From three experiments using the "spot-follower" device; temperature 4°C . The curve is $r = 0.2(1 + \exp -0.5 y)$.

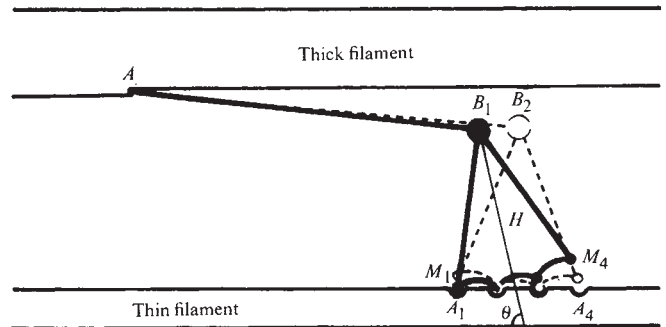


Fig. 5 Diagram showing assumed cross-bridge properties. The myosin head H is connected to the thick filament by a link AB containing the undamped elasticity which shows up as T_1 (Fig. 3) in the whole fibre. Full line shows head in position where M_1A_1 and M_2A_2 attachments are made; broken lines show position where M_2A_2 and M_3A_3 attachments are made.

Responses Expected Theoretically

In the mathematical section at the end of this article, we derive equations describing the response of a system of this kind to a step change of length. The system treated there is simplified by assuming that only two stable positions are available to each attached cross-bridge. The corresponding potential energy diagram is sketched in Fig. 7. This shows that B_2 , the activation energy for transfer of a bridge from position 1 to position 2, contains a term W which depends on the force in the link AB , being increased by a stretch and reduced by a release. B_1 , however, the activation energy for the reverse transfer, contains no such term and is independent of the force. It is this asymmetry which enables the theory to account for the way in which the rate constant of the quick tension recovery varies with the direction and magnitude of the length step: the theoretical result is expressed in equation (12) which is identical in form with equation (1), already shown (Fig. 4) to represent adequately the experimental data. The theory also leads to equation (16) for the tension level approached at the end of the quick recovery phase; this is plotted in Fig. 8 which is seen to reproduce the main features of the experimental T_2 curve in Fig. 3.

The two striking features of the quick tension recovery are thus accounted for by this theory. The numerical values used in obtaining this degree of agreement are: $E_1 - E_2$, the potential energy difference between the stable positions of attachment of a cross-bridge, is equal to $4 kT$; h , the travel of point B between its two stable positions, is 8 nm ; K , the stiffness of the link AB , is $2.5 \times 10^{-4} \text{ N m}^{-1}$.

The following considerations show, however, that the assumption that the cross-bridge movement takes place in a single step is probably not correct.

Isometric force and number of bridges. Equations (4) and (7) show that the isometric force per attached cross-bridge is $(E_1 - E_2)/h$; with the values mentioned in the last section this amounts to $2.0 \times 10^{-12} \text{ N}$. To reach a total force of $3 \times 10^5 \text{ N m}^{-2}$, such as real fibres produce, would therefore need 1.5×10^{17} attached bridges m^{-2} in each half-sarcomere. This is about 1.5 times greater than the number of myosin molecules present. The discrepancy would be greater if the number of cross-bridges were equal to the number of projections on the thick filaments detected by low-angle X-ray diffraction since this appears to be about half the number of myosin molecules¹⁵, and greater still if a substantial proportion of the cross-bridges were unattached during isometric contraction. (It is conceivable that each of the two heads on a myosin molecule should be counted separately; this would be appropriate only if the instantaneous elasticity existed within each of the heads, allowing them to shift independently.)

Work per attached cross-bridge. An upper limit to the external work done by the fibre per cross-bridge attachment will be given by the integral in equation (17), between the

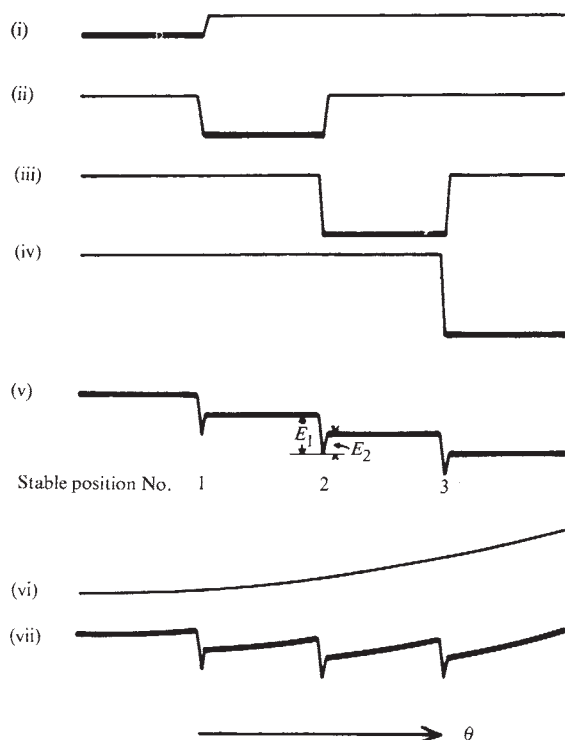


Fig. 6 Potential diagrams relating to the system illustrated in Fig. 5. i-iv, Diagrams for individual attachments M_1A_1 , M_2A_2 , M_3A_3 , M_4A_4 respectively; in each the thick line corresponds to the range of θ within which the corresponding M and A sites are attached; v, sum of i-iv, giving potential energy of a system composed only of a myosin head and a thin filament; vi, potential energy due to stretching the elastic link AB ; vii, total potential energy.

isometric point $y=0$ and the point ($y=-12.0$ nm) where $\varphi_2=0$. With the adopted values of α and h , this is $3.8 kT$. This result is only about half the value which can be calculated as follows from the actual performance of frog muscle. Work can be as much as 40% of (work + initial heat)¹⁶, and the latter quantity is about 11 kcalories/mol⁻¹ of phosphorylcreatine split¹⁷, giving the work term as 4.4 kcalories/mol⁻¹. This is equal to $7.3 kT$ per molecule, which will represent the work per cycle of attachment and detachment of a cross-bridge if it is assumed that the cycle is coupled (presumably through ATP) to the hydrolysis of one molecule of phosphorylcreatine.

Probable number of stable positions. The quantitative treatment just presented has thus led to low values for the force and work per cross-bridge. It is just possible that revised values for α and for the number of cross-bridges will resolve these discrepancies, but it seems to us more likely that it will be necessary to assume that the cross-bridge movement takes place not in a single step but in two or perhaps more. This would lead to proportional increases in the calculated force and work, but the expected time course and extent of the quick tension recovery, which are already in good agreement with the experimental results, would not be much altered if each step has the same height $E_1 - E_2$ as has already been assumed and the value of h is reduced so as to keep the same total range of travel. Fig. 5 is drawn for the case where the number of steps is 2 (3 stable positions and 4 points of attachment), which at present seems the most probable number.

Relation to Earlier Theories

The idea of applying Eyring's theory of polymers to muscle is not new. A comprehensive theory of muscle was developed by Polissar¹⁸, in which the shortening of links in actomyosin chains was influenced in this way by the load, but this theory lost its relevance when it became clear that major changes of length take place by sliding, not folding, of the filaments.

The proposal that the sliding movement is generated by the tendency of attachments between the filaments to move through a series of a few positions of progressively lower potential energy was made many years ago by H. H. Weber¹⁹, who also pointed out that in this case the rate constants for shifting from one position to another would be affected by the force on the attachment. He discussed this idea purely on the basis of a translational movement of the thick relative to the thin filament, with a site rigidly fixed to one of the filaments transferring itself from one to the next of the sites on the other filament to which it could be attached. It is difficult to visualize a mechanism of this kind operating over the rather large distances—several nanometres—that the transient responses show to be involved, but the difficulty disappears if there is an elastic structure allowing one of the attachment sites to undergo substantial displacements relative to the filament to which it belongs.

On the kinetic side, the scheme discussed here combines the advantages of the proposals made by A. F. Huxley²⁰ in 1957 and by Podolsky *et al.*³. In each of these schemes the production of force was assumed to occur as an immediate consequence of the formation of a myosin-actin link. In A. F. Huxley's scheme, attachment was assumed to be the main rate-limiting factor in steady shortening, while detachment after the performance of work by a cross-bridge was relatively rapid; with these assumptions it is possible to fit A. V. Hill's relations between load, speed and heat production but not the transient responses discussed here. Podolsky *et al.* reversed the assumptions about the rate constants, making attachment rapid and breakage rate-limiting; in this way they were able to fit many aspects of transient responses but, as they recognized, not the thermal data. With appropriate rate constants for the initial attachment and final detachment of each cross-bridge, the present scheme can probably account for the force-velocity and thermal relationships in the same way as A. F. Huxley's 1957 scheme, while the rapid transfer between stable positions of the myosin head produces transient responses not unlike those which, on the theory of Podolsky *et al.*, result from the rapid formation of new attachments. The present proposal is able to combine the successful aspects of both of these theories because it subdivides the force-generating event into distinct stages, one for attachment and others for stretching the cross-bridge, the latter being much more rapid than the former. This separation also removes another difficulty that both of the earlier theories would very likely have met in a fully quantitative treatment. They assumed that tension is already present in the cross-bridge when it attaches to the thin filament; thermal motion would so seldom bring the cross-bridge to such a large deflexion that it might be impossible to account in that way for the rapidity of contraction that some real muscles achieve.

Mathematical Section

Equations will be derived for the extent and time-course of the quick tension recovery to be expected from a system

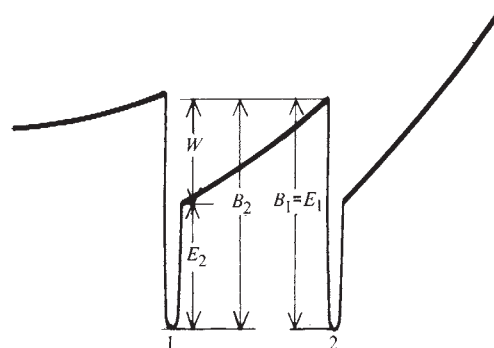


Fig. 7 Potential energy diagram equivalent to Fig. 6 (vii) but referring to the simplified system with only two stable positions.

similar to that shown in Fig. 5 but with only two instead of three stable positions of the myosin head relative to the thin filament. The following additional simplifying assumptions are also made. (1) Actual detachment and re-attachment of cross-bridges are slow enough to be disregarded. (2) Filaments themselves are completely rigid. (3) Filaments undergo no sliding movements except when the total length of the fibre is being altered. (4) The elasticity of the link *AB* obeys Hooke's law. (5) The link *AB* is capable of exerting negative as well as positive tensions. (6) In the isometric steady state, every attached cross-bridge spends equal amounts of time in each of the two available positions (this cannot be strictly true in real muscle because the spacings along the thick and thin filaments are not in any simple ratio, so the relative positions of the myosin and actin molecules must vary from one cross-bridge to another). (7) The time taken in transferring from one to the other of the two positions is negligible.

The following notation will be used; n_1 : fraction of attached bridges in position 1; $n_2 (=1-n_1)$: fraction of attached bridges in position 2; y : displacement of thick relative to thin filament when fibre is stretched or shortened (zero in isometric state before the applied length change; positive for stretch); y_0 : extension of elastic link *AB* when bridge is midway between positions 1 and 2 (equal to amount of sudden sliding movement needed to bring tension to zero from the isometric state); h : increase in length of *AB* when bridge shifts from position 1 to position 2; K : stiffness of link *AB* (assumed to obey Hooke's law); F_1 : tension in *AB* when bridge is in position 1; F_2 : tension in *AB* when bridge is in position 2; ϕ : time average of F_1 and F_2 .

From these definitions,

$$F_1 = K(y + y_0 - h/2) \text{ and } F_2 = K(y + y_0 + h/2) \quad (2)$$

and the time average of tension is

$$\phi = \frac{n_1 F_1 + n_2 F_2}{K(y + y_0 - h/2 + hn_2)} \quad (3)$$

In the isometric state, $y=0$ and $n_2=1/2$, and this equation reduces to the expression for the isometric force per attached cross-bridge

$$\phi_0 = Ky_0 \quad (4)$$

The rate constants k_+ for transfer from position 1 to position 2, and k_- for transfer from 2 to 1, are governed by the energy barriers $B_2 (=E_2 + W)$ and $B_1 (=E_1)$ respectively (Fig. 7). W is the work done in stretching *AB* when the bridge transfers from position 1 to position 2, and is given by

$$W = h \frac{F_1 + F_2}{2} = Kh(y + y_0) \quad (5)$$

from equations (2).

Assuming the k s proportional to $\exp -B/kT$, we have

$$k_+ = k_- \exp (B_1 - B_2)/kT = k_- \exp (E_1 - E_2 - W)/kT = k_- \exp (E_1 - E_2 - Kh(y + y_0))/kT \quad (6)$$

where k_- is constant since B_1 is a fixed quantity independent of the tension in *AB*.

In the isometric state we have assumed $n_1 = n_2$, so $k_+ = k_-$; also $y=0$ since y is defined as a length change from the isometric state. It then follows from (6) that

$$E_1 - E_2 = Kh y_0 \quad (7)$$

and (6) becomes

$$k_+ = k_- \exp -y.Kh/kT \quad (8)$$

In the experiments we are considering, y is suddenly altered by imposing a length change on the muscle fibre, and is sub-

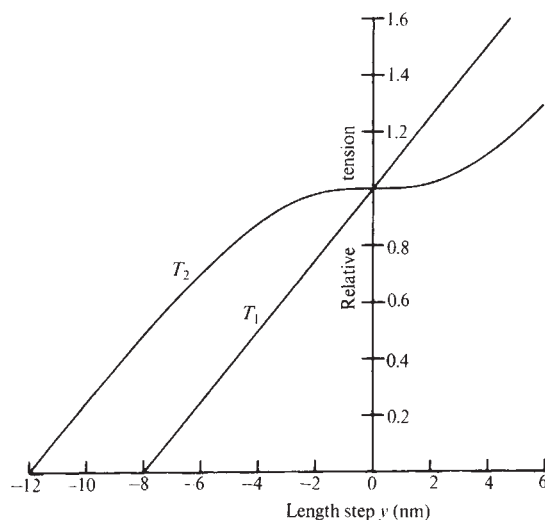


Fig. 8 Curves of T_1 and T_2 calculated from the simplified system, plotted on same scales as the experimental values in Fig. 3. T_2 curve: Equation (15) with $E_1 - E_2 = 4 kT$, $1/\alpha = 2$ nm, $h = 8$ nm.

sequently held constant. The transfer of myosin heads from one position to the other is then governed by the equation

$$\frac{dn_2}{dt} = k_+ n_1 - k_- n_2 = k_+ - (k_+ + k_-) n_2 \quad (9)$$

This equation represents an exponential approach, with rate constant r given by

$$r = k_+ + k_- \quad (10)$$

towards an equilibrium where

$$n_2 = k_+ / (k_+ + k_-) \quad (11)$$

Substituting from (8) into (10) we have

$$r = k_- (1 + \exp -y.Kh/kT) \quad (12)$$

This has the same form as equation (1), and the equations become identical, giving approximate agreement with the experimental results in Fig. 4, if we take

$$Kh = \alpha kT \quad (13)$$

Equation (8) can therefore be written

$$k_+ = k_- \exp -\alpha y \quad (14)$$

and (11) becomes

$$n_2 = \frac{1}{2} \left(1 + \tanh \frac{\alpha y}{2} \right) \quad (15)$$

The tension ϕ_2 at the end of the quick recovery (corresponding to T_2 in the whole fibre) is obtained by combining (3), (13) and (15) to give

$$\phi_2 = \frac{\alpha kT}{h} \left(y_0 + y - \frac{h}{2} \tanh \frac{\alpha y}{2} \right) \quad (16)$$

The work done during shortening at a low enough speed so that n_2 always has its equilibrium value would be obtained by integrating (16):

$$\int \phi_2 dy = kT \left(\frac{\alpha y}{h} \left(y_0 + \frac{y}{2} \right) - \ln \cosh \frac{\alpha y}{2} \right) \quad (17)$$

To match the points in Fig. 4, α is taken as $5 \times 10^8 \text{ m}^{-1}$, the value used for the curve in that figure. $(E_1 - E_2)$ is shown by equations (7) and (13) to be equal to $\alpha y_0 kT$. From Fig. 3 (broken line), y_0 is about 8 nm, giving $E_1 - E_2 = 4 kT$. h has to be chosen to give the right shape for the curve of T_2 against y (equation 15). A value $4/\alpha$, or 8 nm, is used in Fig. 8; lower values give a less inflected curve and higher values give a curve with a region of negative slope.

Generation of Tension

The tension changes observed in the first few milliseconds after suddenly changing the length of an active muscle fibre suggest the following mechanism for the generation of tension or shortening by the cross-bridges. Each cross-bridge has three stable positions with progressively lower potential energies, in steps of about 4 times kT , separated by about 4 nm of travel. Transfer from one of these positions to the next is made possible, without simultaneous displacement of the whole filaments through an equally large distance, by the presence of elasticity associated with each individual cross-bridge. The tension generated in this way in the elastic element will show up as such if the muscle length is held constant, or will help to make the filaments slide past each other if shortening is permitted.

A simplified theoretical treatment is given; a more complete treatment will be presented later.

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How Dextrous was Neanderthal Man?

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Results of multivariate statistical analyses indicate that the bones of the hand of Neanderthal man were metrically and morphologically unique and that he may not have been as dextrous as living *Homo sapiens*.

THE postcranial skeleton of Neanderthal man has been studied less intensively than his skull. This is to be regretted because any serious attempt to re-assess the phylogenetic status of the Neanderthals must be based on their total morphological pattern¹ and not solely on evidence of cranial variation. In an attempt to rectify this situation I have made a detailed study of as many as possible of the Neanderthal hand bones listed by Vallois and Movius². Measurements were taken on these bones and on comparative samples of European Upper Palaeolithic, Mesolithic and modern hand bones. These measurements and indices calculated from them were then submitted to discriminant function (canonical variate) analyses and Mahalanobis's D^2 tests³. This article presents some of the conclusions drawn from this investigation⁴.

Thumb

(1) The metacarpal seems to have been neither relatively nor absolutely short, as earlier workers had suggested^{5,6}, and it was instead the great transverse width of the head, a feature which had also aroused comment^{7,8}, which proved to be the most important dimension. This observation may be correlated with a very noticeable anatomical feature, a flange which runs up the distal half of the radial side of the shaft (Fig. 1). Into this was inserted opponens pollicis muscle, clearly large and powerful in Neanderthal man⁹, a suggestion which is

in keeping with recent theories on the role of this muscle as an abductor of the thumb in a firm grip¹⁰. Associated with this flange is a marked depression⁸ diagonally opposite, from which arose the first metacarpal head of the first dorsal interosseous, another "power" muscle.

Other unusual features of the Neanderthal thumb metacarpal include an asymmetry in the transverse curvature of the head and the presence in several specimens of a condyloid rather than a saddle-shaped proximal articular surface. The asymmetry has been noted in some non-human primate genera^{11,12} and may reflect difficulties in opposing the thumb to the other digits. The condyloid articular surface, clearly visible in the specimen from La Chapelle-aux-Saints⁵ but only partly developed in those from Kiik-Koba⁹ and La Ferrassie

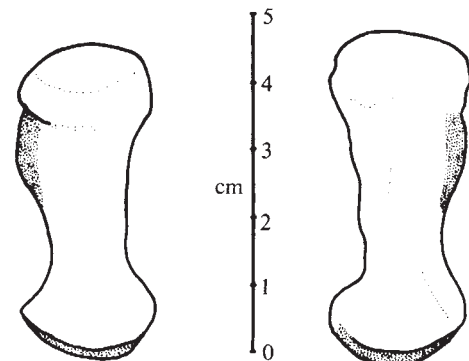


Fig. 1 Palmar aspect of Neanderthal thumb metacarpals. The principal features are: (1) the radially projecting ridge (stippled) into which was inserted opponens pollicis muscle; (2) the asymmetry of the curve of the distal articular surface; and (3) the narrow waist at the proximal end of the shaft, formed on the ulnar side by the impression for the origin of the first metacarpal head of the first dorsal interosseous muscle. Both specimens belonged to male Neanderthals. Tracings were made from photographs of casts.