THE FUNCTION OF MUSCLES IN LOCOMOTION

HERBERT ELFTMAN

From the Department of Zoology, Columbia University, New York City

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The analysis of the forces involved and of the energy transfers which take place in walking, presented in the previous paper, serves to concentrate attention on the dominant rôle which muscles play in locomotion. Not only do the muscles provide forces which modulate the other forces present so as to ensure the desired trajectory of the body, but they also govern the fluctuations in energy, occasioned by the changes in kinetic and potential energy of the body. This involves the alternate acceptance and release of energy by the muscles of the leg, the process going through two complete cycles during each double step.

In order to obtain further information concerning the function of muscles and to investigate some of the factors which influence their efficiency, it is necessary to recast in terms of muscle units the data obtained in the form of resultant muscle torques on parts of the leg. This could be done and a unique solution obtained, if the muscles with which we are concerned in all cases passed over only one joint. Although the vasti and many of the muscles around the hip-joint satisfy this requirement, such important muscles as the hamstrings, rectus femoris and gastrocnemius traverse two joints. No unique solution is possible for such a system with the data at hand, but the limiting conditions can be found by a consideration of a system composed entirely of one-joint muscles and of one consisting of a single muscle passing over the three joints.

Torques of one-joint muscles. If only one-joint muscles were present, their torques would be those which are plotted in figure 1. The torque exerted on the foot by the muscle which crosses the ankle would be the total torque on the foot, previously determined. The muscle would exert an equal and opposite torque on the shank; the soleus, for instance, provides a negative torque on the foot and a positive one on the shank. Knowing the torque of the ankle muscle on the shank and the total torque on the shank, we can compute the torque of the knee muscle. The torque of the muscle which passes over the hip-joint is already known from the muscle torque on the trunk.

The one-joint muscles would be present in pairs of flexors and extensors, unless the line of action shifted over the axis of the joint. If both members of the pair were acting simultaneously, the curve plotted would be the algebraic sum of their torques. The alternation between flexor and extensor action may be followed from figure 1. It is noticeable that the extensors are more important at the ankle and knee, the converse being true at the hip.

Energy transfer of one-joint muscles. Although the torques exerted by a one-joint muscle on the members to which it is attached are equal in magnitude, but of opposite sign, no such simple relationship holds for the rate at which energy is transferred between the muscle and the two members. This depends on the torque and on the angular velocity of the member. It may best be illustrated by the ankle muscle during the later portion of the period of contact of the foot with the ground. The torque of the muscle on the shank at this time is opposed to the angular velocity of the shank. In consequence work is done on the muscle, as indicated by

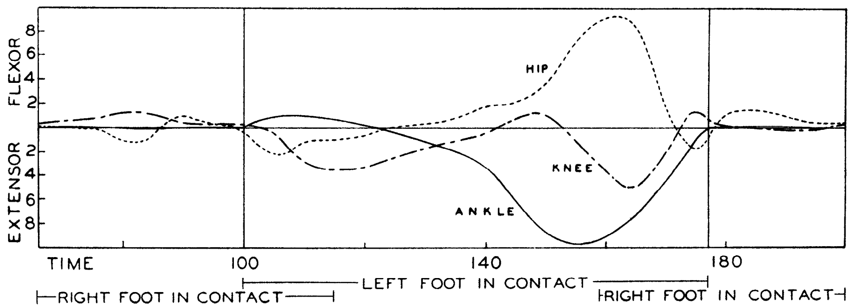

Fig. 1. Torque in kg.m. of one-joint muscles

the dashed line in figure 2. The torque on the foot is of the same sign as the angular velocity of the foot, the rate at which it is doing work being shown by the dash-dot line. The algebraic sum of these two rates represents the rate at which energy is exchanged by the muscle tissue. Energy is at first received, later work is done. The difference between the energy absorbed by the muscle tissue and the total work done by the shank on the muscle represents energy transmitted by the muscle from its origin to its insertion. This transmission may be referred to as "tendon action." It involves the presence of tension in the muscle but neither reception nor expenditure of energy by the muscle tissue, except for the production and maintenance of tension.

The uppermost curves of figure 2 give the total rate at which the leg muscle tissue does work, is worked on, and transmits energy by "tendon action." The relatively large amount of energy handled by transmission while the foot is on the ground is noteworthy. The fact that some muscles are receiving energy while others are doing work is also significant. With muscles differently attached this antagonism of effort would be unnecessary.

The efficiency of a system of one-joint muscles is limited by the fact that tension must be maintained in at least three separate muscles at all

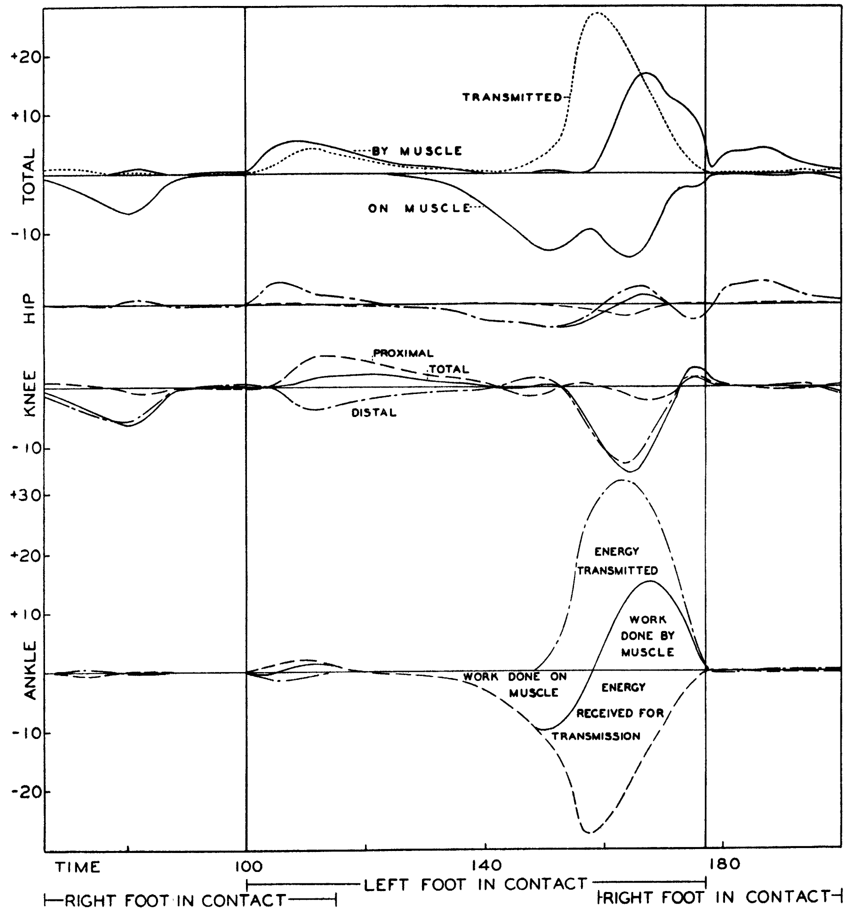

Fig. 2. Rate at which work is done by one-joint muscles in kg.m./sec. Proximal end of muscle, dashed line; distal end, dash-dot. The algebraic sum of these, giving the rate at which energy is released or received by the muscle tissue, is shown by a continuous line. Uppermost series of curves gives totals for entire leg musculature of rate of work done on muscle tissue, by muscle tissue, and transmitted.

times. The one-joint muscles do not function with a minimum amount of energy exchange, since some of the muscles receive energy while others are doing work.

A single three-joint muscle. From a consideration of a system of one-joint muscles we shall go to the other extreme, discussing the situation which would be present if all the muscles traversed the hip-, knee- and ankle-joints. The characteristics of such a system may be obtained from those of the system of one-joint muscles in a manner illustrated in figure 3. The two positions of the leg chosen for illustration are phases 84 and 164 of the series. About the axis of each of the joints an arc of a circle is described, its position with respect to the leg depending on whether the muscle torque about the joint is flexor or extensor. The radii of the arcs are proportional to the torques of the one-joint muscles at the moment under consideration, the radius about the joint around which the torque is greatest being arbitrarily drawn of constant length.

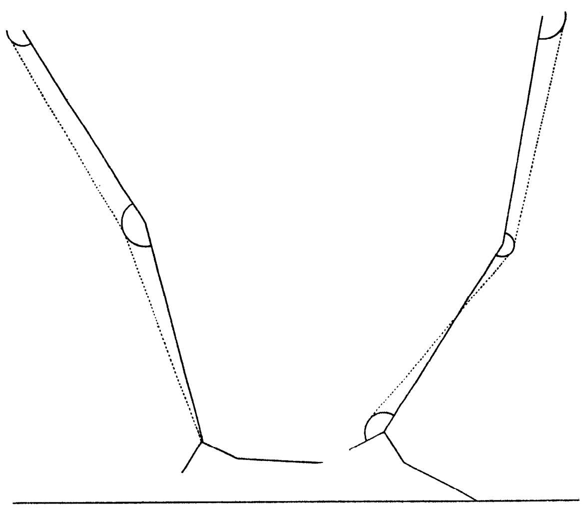

Fig. 3. Diagram of a three-joint muscle capable of performing the functions of all the leg muscles. Phase 84 at left, phase 164 at right.

The radius of the arc consequently represents the lever arm of muscles which are tangent to the arc. Since the torque of the muscle is the product of tension and lever arm, the effect obtained by increasing or decreasing the radii of the arcs, provided their relative proportions are maintained, is to decrease or increase the requisite tension in the muscle. The one-joint muscles would be represented on this scheme by lines tangent to the arcs and attached to the two adjacent members. Such a line may be tangent to the arc at only one point, the muscle then being indicated by a straight line, or the muscle may follow the arc, as if it were a frictionless pulley. The arcs may consequently be taken to represent one-joint muscles.

Any muscle which is so placed as to be tangent to the arcs described will provide the proper torque about the joints. It is consequently possible, in theory, to have a single muscle attached only to the trunk and the foot which will provide all of the muscle torques necessary and take care of all the energy changes. Such a muscle would have the same tension throughout its length, the torques at the various joints depending on the lever arms. In the three-joint muscle illustrated, the lever arm is arbitrarily held to a constant value at the joint about which the torque is greatest, this being the knee-joint at phase 84 and the hip-joint at phase 164. The tension in the muscle would consequently vary, its instantaneous value being shown by the lowermost curve in figure 4, for a muscle with a con-

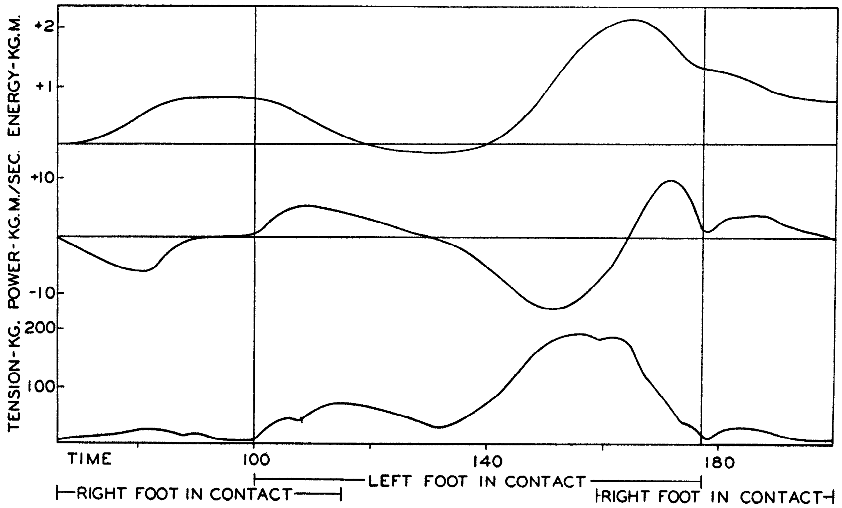

Fig. 4. Characteristics of a three-joint muscle with a constant lever arm of 5 cm. at the joint about which it produces maximum torque. Lower curve: tension in kg. Middle curve: power in kg.m./sec. Upper curve: integrated energy exchange of muscle due to external forces, in kg.m.

stant maximum lever arm of 5 cm. This value for the lever arm was chosen because it lies within the range of the maximum lever arms of the major leg muscles.

The fact should be stressed that the three-joint muscle considered here is only one of a family of such possible muscles. The disposition of the muscle is determined by the signs and relative magnitudes of the torques about the various joints. The absolute magnitudes of the lever arms and the tension in the muscle are related only by the requirement that their product shall equal the torque. In the example given, the lever arms are subjected to the condition that the maximum lever arm remains constant, the variations in tension being thus determined.

Properties of the three-joint muscle. It is a common property of all muscles not encountering frictional resistance in their course that the tension must be the same throughout the length of the muscle. A possible advantage of a three-joint muscle over a system of one-joint muscles is that the former would need to maintain tension in only one muscle instead of in three. The values of the tension in the muscle, given in figure 4, are for a muscle with a constant maximum lever arm of 5 cm. Since this value for the lever arm is near the maximum of the actual leg muscles, the area under the tension curve, measuring tension-time, may be considered as an approximate minimum for the muscles concerned in this particular double step.

The rate at which the muscle tissue of the three-joint muscle exchanges energy is shown by the middle curve of figure 4. This is equal to the algebraic sum of the rates of all the leg muscles, obtained by a consideration of their energy exchange with the separate parts of the leg and with the trunk, or by the analysis of one-joint muscles. It is the curve which would be obtained by adding the two curves at the top of figure 2 for the total work done on and by one-joint muscles. All of the muscle tissue is either receiving or liberating energy at the same time; different muscle masses are not working against each other.

The energy exchange goes through two cycles in the course of a double step. Energy is received during the later part of the swing and work is then done in approximately equal quantity. Energy is again received, followed by the doing of work as the heel rises and during the early portion of the swing. The time between the maximum rate of reception of energy and the maximum rate of doing work is 0.26 sec. for the first cycle and 0.20 sec. for the second cycle in this particular step.

The total energy exchange of the muscle mediated by external forces can be obtained from the power curve by integration. It is plotted in kilogram meters as the uppermost curve of figure 4. That this curve does not reach the base line at the conclusion of the double step is due to the fact that the subject slowed down slightly, as is evident from the recorded velocities. If the velocities and positions of all parts of the body were identical at the end of the step and at the beginning, except for forward movement of the entire body, the energy curve would terminate on the base line.

Combination of two-joint and one-joint muscles. A three-joint muscle of the type considered does not enter into the actual construction of the leg. It would be exceedingly difficult to provide, in the body, the changeable lever arms demanded. This is especially true when they swing across the axis of the limb. That such a system is not entirely preposterous, however, is indicated by muscles such as the gracilis, which exerts either a positive or a negative torque on the trunk, depending on the position of the thigh. Another difficulty encountered by a leg containing only one three-joint muscle would be that the advantage in walking would be more than offset by the inability of such a muscle to allow individuated movements of separate parts of the leg, so necessary under other circumstances.

A compromise is effected by having a combination of two-joint and one-joint muscles (disregarding the presence of the lower ankle-joint and the transverse tarsal joint in classifying the muscles). The two-joint muscles retain many of the advantages of the three-joint muscle and, in combination with the one-joint muscles, render the system adaptable to varying requirements. Among the advantages retained in part by muscles passing over two joints are the maintenance of tension in less muscle tissue and a reduction of the necessity of having some muscles release energy while others are receiving it. There is also the possibility in muscles which pass over more than one joint of placing the muscle tissue closer to the trunk. This reduces the moment of inertia for swinging the leg about the hip-joint, while increasing it for rotation about the ankle. Since it is the forward swing about the hip-joint which occurs with the greater velocity, this arrangement is advantageous.

It is possible to ascertain which of the two-joint muscles actually present in the body would be in proper position for the exertion of torque by referring to figure 3. In the first illustration, of phase 84, the hamstrings would be properly placed, while at phase 164 the rectus femoris is correctly located. Neither of these muscles, however, has the proper ratio of lever arms about the hip- and knee-joints to exert the torques alone. At phase 84, the long head of the biceps, representing the hamstrings, has a lever arm of 6.7 cm. about the hip-joint and 3.4 cm. about the knee. It would be necessary to supplement its action by either a one-joint flexor of the knee or by a one-joint flexor of the hip. The third possibility, of concurrent action by the gastrocnemius, is acceptable for the knee but not for the ankle.

At phase 164 the rectus femoris has a lever arm of 3.9 cm. at the hip-joint and 4.4 cm. at the knee. It could be supplemented by a one-joint flexor at the hip-joint, leaving only the ankle-joint which the soleus could provide for amply. If the gastrocnemius were in action, the torque of the rectus about the knee-joint could be increased, necessitating less one-joint flexor action at the hip-joint.

These two illustrations indicate both the possibilities and the difficulties of extending the analysis which we have made of one-joint and three-joint muscle systems so as to include two-joint muscles. Such a variety of possible combinations is afforded that no unique solution can be found for such a system. Its efficiency must lie between that of the two limiting cases: a system consisting of one-joint muscles and one containing only one three-joint muscle.

As far as the exertion of torque is concerned, the intervals during which any one of the two-joint muscles present in the leg might be profitably employed may be determined from figure 1. In the later portion of the swing, which occupies the first part of the graph, the knee torque is flexor and the hip torque extensor; this condition is satisfied by the hamstrings and by the gracilis. Both torques then become flexor, which is true for the sartorius. As the foot touches the ground, the hamstrings and gracilis

TIME	70	80	90	100	110	120	130	140	150	160	170	180	190	200
L_{57}	+5	−2	0	+6	+104	+17	−113	−337	−852	−887	−432	+8	+6	+5
L_{35}	−55	−138	−39	−19	+295	+330	+166	+44	−97	+369	+221	−16	+11	−29
L_{13}	−9	−128	+86	+41	−94	−45	+37	+173	+406	+899	+190	+121	+102	+49
$L_{57} \cdot \dot{\varnothing}_7$	+26	−10	0	−12	−59	0	0	0	+196	+3011	+2230	−28	+14	+26
$L_{75} \cdot \dot{\varnothing}_5$	−30	+8	0	+10	+122	+13	−62	−290	−1162	−2502	−873	+10	−7	−20
Ankle muscle	−4	−2	0	−2	+63	+13	−62	−290	−966	+509	+1357	−18	+7	+6
$L_{35} \cdot \dot{\varnothing}_5$	−276	−586	0	+33	−348	−224	−91	−38	+132	−1040	−446	+19	+13	−119
$L_{53} \cdot \dot{\varnothing}_3$	+70	−55	−11	−10	+549	+442	+212	+66	−90	−18	−177	+26	−31	+34
Knee muscle	−206	−641	−11	+23	+201	+218	+121	+28	+42	−1058	−623	+45	−18	−85
$L_{13} \cdot \dot{\varnothing}_3$	−11	+51	−23	−20	+175	+61	−47	−260	−377	+42	+152	+199	+289	+58
$L_{31} \cdot \dot{\varnothing}_1$	−1	+7	−1	−4	+10	−7	+5	+12	−12	−135	−29	+12	+14	+3
Hip muscle	−12	+58	−24	−24	+185	+54	−42	−248	−389	−93	+123	+211	+303	+61
Total+	0	+58	0	+23	+449	+285	+121	+28	+42	+509	+1480	+256	+310	+67
Total−	−222	−643	−35	−26	0	0	−104	−538	−1355	−1151	−623	−18	−18	−85
"Tendon"	96	8	0	20	407	231	96	50	286	2544	902	10	20	57
Integrated energy	+5.0	+49.6	+80.6	+79.9	+40.7	−0.9	−14.7	+4.1	+95.6	+201.4	+185.3	+127.9	+90.8	+77.2
Tension	11.0	27.6	19.2	8.2	59.0	66.0	33.2	67.4	170.4	179.8	86.4	24.2	20.4	9.8

Explanation of table. The torque of a muscle is indicated by L, the subscripts referring to the members of the body to which it is attached, the foot being 7, the shank 5, the thigh 3 and the trunk 1. The notation L_{57} consequently stands for the torque of a one-joint muscle connecting the shank and the foot, as it acts on the foot. The torque of the same muscle, as it acts on the shank would be L_{75}. The activity of the muscle as it acts on the foot is $L_{57} \cdot \dot{\varnothing}_7$, in which $\dot{\varnothing}_7$ is the angular velocity of the foot, given in the table accompanying the previous paper. The algebraic sum of the activities of the muscle on both members to which it is attached gives the work done by (+) or on (−) the muscle tissue. The resulting sums for the three muscles are totalled separately for the muscles that are doing work at the moment and those upon which work is being done. When a muscle is doing work upon one of the members to which it is attached and is worked upon by the other, the rate at which energy is transmitted from one member to the other by "tendon action" is given by the smaller of the two values for the activity of the muscle on the two members. These rates have been totalled for the three muscles without regard to sign.

The rate at which energy is exchanged by the three-joint muscle tissue is the algebraic sum of the rates of work done by and on the three one-joint muscles; it is not listed separately. The result of integrating this curve is given. The tension of the three-joint muscle described in the text is obtained by dividing the largest torque of a one-joint muscle for each instant by five.

would momentarily be advantageous. Almost immediately both torques become extensor and so continue for a third of the period of contact. There is no two-joint muscle which has this action. The condition could be met by a combined action of the hamstrings and the rectus femoris, since the former have their longer lever arm on the trunk and the latter on the shank. The hip-joint torque then becomes flexor while that of the knee remains extensor, affording congenial conditions for the rectus femoris. This continues almost until the foot leaves the ground, except for a brief interval during which the knee-joint torque is flexor. During this interval both the sartorius and the gracilis, the origin of which now lies in front of the hip-joint, could act. Just before the foot leaves the ground the hamstrings are again in correct position, followed, during the swing, by the rectus femoris.

The gastrocnemius is placed for advantageous torque exertion during the brief intervals in which the knee-joint torque is flexor, while the foot is in contact with the ground. This occurs once as the foot is about to leave the ground and once about 0.2 sec. earlier.

Discussion. The present investigation has resulted in definite information concerning the rôle which muscles play in a normal activity, that of walking, and has disclosed some of the factors which are important in a consideration of muscular efficiency. Instead of estimating the work done by the muscles from considerations of changes in kinetic and potential energy of the body, the actual torques exerted by the muscles on the various segments of the leg were determined and the rate at which they did work was calculated. Muscles participate in energy exchange by receiving energy; by dissipating energy; by doing work; and by transmitting energy by "tendon action."

For a full consideration of the efficiency of muscles many factors additional to those treated in this paper would have to be included. Among these are the cost of the maintenance of tension; the extent to which the production of tension is due to external forces; the extent to which energy is required for overcoming frictional resistance and in non-elastic deformation; and the limitations placed upon muscles by the necessity of nervous coördination. The dissipation of energy by muscles emerges as a factor of double interest. Not only is it important because it limits the extent of possible energy storage; it is indispensable when the body must lose energy, as in deceleration.

SUMMARY

1. Muscles function in locomotion by 1, exerting torques which coöperate with the other forces present in determining the movements of the body; 2, regulating energy exchange, by transmitting, absorbing, releasing and dissipating energy.

2. The exertion of torque, without movement, and the transmission of energy by "tendon action" involve the doing of no physical work by the muscle tissue. They do involve the production of tension and its maintenance.

3. The total energy received by the muscles of the leg is equal to the total amount of work which they do in the course of a double step, pro-

vided that the initial condition of the body is duplicated at the end of the step.

4. A single muscle passing over the hip-, knee- and ankle-joints would be able to perform efficiently all the functions of the leg muscles in walking. Such a muscle, however, would present structural difficulties and would not be adaptable to individuated movements. The actual system of one-joint and two-joint muscles represents a compromise between the efficiency of the three-joint muscle and the adaptability of those passing over only one joint.

5. The ability to dissipate energy, regrettable as it may seem during the maintenance of regular movement, is as necessary a function of muscle as any other, since it makes deceleration possible.