

TENDON ACTION OF TWO-JOINT MUSCLES: TRANSFER OF MECHANICAL ENERGY BETWEEN JOINTS DURING JUMPING, LANDING, AND RUNNING*

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Abstract—The amount of mechanical energy transferred by two-joint muscles between leg joints during squat vertical jumps, during landings after jumping down from a height of 0.5 m, and during jogging were evaluated experimentally. The experiments were conducted on five healthy subjects (body height, 1.68–1.86 m; and mass, 64–82 kg). The coordinates of the markers on the body and the ground reactions were recorded by optical methods and a force platform, respectively. By solving the inverse problem of dynamics for the two-dimensional, four-link model of a leg with eight muscles, the power developed by the joint (net muscular) moments and the power developed by each muscle were determined. The energy transferred by two-joint muscles from and to each joint was determined as a result of the time integration of the difference between the power developed at the joint by the joint moment, and the total power of the muscles serving a given joint. It was shown that during a squat vertical jump and in the push-off phase during running, the two-joint muscles (rectus femoris and gastrocnemius) transfer mechanical energy from the proximal joints of the leg to the distal ones. At landing and in the shock-absorbing phase during running, the two-joint muscles transfer energy from the distal to proximal joints. The maximum amount of energy transferred from the proximal joints to distal ones was equal to 178.6 ± 45.7 J ($97.1 \pm 27.2\%$ of the work done by the joint moment at the hip joint) at the squat vertical jump. The maximum amount of energy transferred from the distal to proximal joints was equal to 18.6 ± 4.2 J ($38.5 \pm 36.4\%$ of work done by the joint moment at the ankle joint) at landing. The conclusion was made that the one-joint muscles of the proximal links compensate for the deficiency in work production of the distal one-joint muscles by the distribution of mechanical energy between joints through the two-joint muscles. During the push-off phase, the muscles of the proximal links help to extend the distal joints by transferring to them a part of the generated mechanical energy. During the shock-absorbing phase, the muscles of the proximal links help the distal muscles to dissipate the mechanical energy of the body.

INTRODUCTION

The functions of two-joint muscles during locomotion remain unclear. Recently, one such function, the transportation of mechanical energy between joints, has been widely discussed (Bobbert and van Ingen Schenau, 1988; Bobbert *et al.*, 1986, 1987; van Ingen Schenau, 1989; van Ingen Schenau *et al.*, 1985, 1990; Pandey and Zajac, 1991; Pandey *et al.*, 1990; Wells, 1988). According to one research group (van Ingen Schenau *et al.*, 1985, 1990; Bobbert and van Ingen Schenau, 1988), during vertical jumps the transfer of mechanical energy from proximal to distal joints of

the lower extremities occurs because of the unique action of two-joint muscles. However, Pandey *et al.* (1990), and Pandey and Zajac (1991) have shown that during a vertical jump, energy generated by muscles was directed in the opposite direction, from distal links to proximal ones. In our opinion, the different results obtained by the two research groups are a consequence of different definitions of 'transfer of mechanical energy'.

Our understanding of mechanical energy transfer by two-joint muscles can be explained using the following example (see also van Ingen Schenau *et al.*, 1990). Assume that in one of the phases of a movement, the hip joint is extended as a result of the positive work done by the hip extensor muscles. If the two-joint rectus femoris muscle contracts isometrically, i.e. its length does not change, then additional mechanical work can be done at the knee joint because of the rectus femoris muscle, which does not do mechanical work itself. In this case, one can say that part of the energy generated by the hip extensors appears as mechanical work at the knee joint; i.e. the energy was 'transferred' from the hip to knee joints by the rectus femoris muscle. This action of two-joint muscles was described many years ago (Cleland, 1867; Fick, 1879; Lombard, 1903), and was called 'tendon (tendinous, ligamentous) action' of two-joint muscles (for review see van Ingen Schenau *et al.*, 1990).

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Tendon action of two-joint muscles was usually studied by using indirect experimental data (Elftman, 1940; Fenn, 1938; van Ingen-Schenau *et al.*, 1985; Morrison, 1970), mathematical simulation (Alexander, 1989; van Ingen-Schenau *et al.*, 1990; Pandey *et al.*, 1990), or observation of a physical model of a human lower extremity during jumping (Bobbert *et al.*, 1987). For instance, van Ingen-Schenau *et al.* (1985) reported that the maximum power developed at the ankle joint during a squat vertical jump was 6 times higher than that developed in one-joint plantar flexion of the foot. Their conclusion was that part of the extra power came from the more proximal joints through two-joint muscles. In another study (Bobbert *et al.*, 1987), the jump height of a physical model of the leg was shown to increase when the thigh and foot were connected by a non-stretchable thread simulating the gastrocnemius. However, at present, the question as to whether or not the tendon action of two-joint muscles occurs in human movements remains open.

The aim of this study was to estimate experimentally the function of two-joint muscles in the lower extremities of humans, with respect to the transfer of mechanical energy between joints during locomotion.

METHODOLOGY

The transfer of mechanical energy by two-joint muscles between joints of the lower extremities was estimated during vertical jumping from a deep squatting position, landing after jumping down from a height of 0.5 m, and during jogging.

Experiment

The experiments involved a total of five male subjects (ranging from 1.68 to 1.86 m in body height, and from 64 to 82 kg in body mass). They performed all of the tasks on a special track fitted with a built-in force platform (PD 3-A, VISTI, former U.S.S.R.). The platform was used for recording the longitudinal and vertical projections of the resultant vector of the ground reaction forces, and the coordinates of its application. Reflective markers were attached to five joints (metatarsophalangeal, ankle, knee, hip, and shoulder joints), and were illuminated during the experiments by pulse stroboscopes at frequencies of 50 Hz (for vertical jump and landing) and 100 Hz (for jogging). The markers were filmed on photoplates (size 13 × 18 cm) of photogrammetric cameras (UMK-10, Carl Zeiss Jena, former G.D.R.); the filming was synchronized with the ground reaction recordings. The marker coordinates on the photoplates were digitized with a precision of 1 μ m by the semiautomatic stereocomparator 'Stekometer' (Carl Zeiss Jena, former G.D.R.). Some of the experiments were conducted using the optoelectronic motion registration system 'Selspot' (Selcom, Sweden). The LEDs of this system were attached to the same joints. The LEDs coordinates were recorded at a frequency of 104 Hz.

Vertical jumps were performed by three subjects instructed to jump as high as possible from the maximally deep squatting position (heels did not touch the ground) without arm swing. Jumps down were performed by three subjects from a height of 0.5 m. The subjects were instructed to hold their hands behind their backs and land 'softly' by bending their legs, and to 'fix' the final landing posture of the body. During jogging, the subjects (two persons) were instructed to land on the toe first.

Mathematical model

For the computations, we used a two-dimensional mathematical musculoskeletal model of a leg consisting of four links (foot, shank, thigh, and pelvis) and eight muscles (tibialis anterior, soleus, gastrocnemius, hamstrings, vastus femoris, rectus femoris, iliacus, and gluteus maximus). The motions were analysed in the sagittal plane. It was assumed that the angular motion of the pelvis corresponded to the motion of the trunk. From known motion (coordinates of the joints and ground reactions), the model makes it possible to determine the net moments at the joints, and to estimate the force developed by each muscle (for more details see Zatsiorskii and Prilutskii, 1989). Each of the aforementioned eight muscles was an 'equivalent' muscle simulating the action of all the muscles with similar functions. For instance, the moment developed by the tibialis anterior at the ankle joint for foot dorsal flexion corresponds to the total moment of all the foot dorsal flexors.

The algorithm for determining the muscular forces was based on the 'principle of superposition' of two motor programs: reciprocal activation of the muscles and co-activation of the muscle antagonists (Feldman, 1979). To eliminate redundancy in the musculoskeletal model, the following assumptions were made (Zatsiorskii and Prilutskii, 1989):

- (1) The net moments at the joints are known.
- (2) For each (*j*th) degree of freedom, the values of the coefficient $R_j(t)$ [$0 \leq R_j(t) \leq 1$] depending on time (*t*) and characterizing the relation between the degree of use of the two motor programs (program of reciprocal activation of the muscles and program of co-activation of the muscle antagonists) are known. For $R_j(t)=0$, only the program of reciprocal activation of the muscles is used. For $R_j(t)=1$, only the program of co-activation of the muscle antagonists is used. For all other values of $R_j(t)$, both programs are used jointly.
- (3) The tensions of all agonists serving each joint, and located on the proximal link of two links forming this joint, are equal.

Expressions for calculating muscular forces from a known movement and coefficients $R_j(t)$, were described in (Zatsiorskii and Prilutskii, 1989). The coefficients $R_j(t)$ can be determined experimentally. In this study, the coefficients $R_j(t)$ were unknown, and they were assumed to be equal to zero (see discussion of this assumption later in this section). This

assumption meant that none of the one-joint antagonists of the musculoskeletal model of the lower extremity were active. In this case, force F_{ij} of the i th agonist serving the j th joint could be obtained from the expression

$$F_{ij}(t) = A_{ij} [M_j(t) - \sum_{q=1}^{n_j} M_j^{qm}(t)] / \sum_{q=1}^{n_j} d_{qj}(t) A_{qj}, \quad (1)$$

where j is number of the joint ($j=1$ is the ankle; $j=2$ is the knee; $j=3$ is the hip); t is the time; $M_j(t)$ is the moment at the j th joint; $\sum M_j^{qm}(t)$ is the arbitrary designation of the sum of the moments induced by the action of the two-joint muscles serving two joints, including the given one, and determined by calculations for the preceding joint; n_j is the number of agonists serving the j th joint and located on the proximal link; A_{qj} is the physiological cross-sectional area of the q th agonist serving the j th joint and located on the proximal link; $d_{qj}(t)$ is the moment arm of the q th agonist serving the j th joint and located on the proximal link.

From formula (1) one can calculate the forces of all muscles of the model of the lower extremity used in this study. Let us clarify how this can be done. Let the moments at each joint cause extension. The extension moment at the ankle is created by two agonists, the one-joint soleus and the two-joint gastrocnemius muscles. In the first step using formula (1), the forces of these two muscles are calculated. Here $\sum M_j^{qm}(t) = 0$. Next, one calculates the moment produced by the gastrocnemius muscle about the knee joint. Let us subtract this moment [$\sum M_j^{qm}(t)$; see formula (1)] from the joint moment at the knee joint. The difference obtained corresponds to the moment created by the muscles located on the thigh (the proximal link of two links forming the knee joint); that is, the one-joint vastus and two-joint rectus femoris. Then the calculations are similar to those in the first step. It is necessary to note that this algorithm leads to an absence of co-activation of two antagonistic two-joint muscles serving two of the same joints. In the model considered here, these muscles are the rectus femoris and the hamstrings. If the extension moment at the knee joint is higher than the gastrocnemius moment at the knee joint, activity of the hamstrings is not predicted by the model.

Let us discuss some assumptions of the model. The assumption that all one-joint antagonists of the model are not active does not agree with the real situation. It is a well-known fact that antagonists' activity is observed in different forms of locomotion: in running (Elliott and Blanksby, 1979), jumping (Bobbert and van Ingen Schenau, 1988), and cycling (van Ingen Schenau, 1989). Nevertheless, we think it is possible to assume that the one-joint antagonists are not active, for two reasons. First of all, it is natural to suppose that in those phases of movement where high values of joint moments are observed (for example, during the support period of locomotion), the muscle activity (force) of one-joint antagonists is much less than that

of the agonists. Otherwise, the moments at joints could not be high enough. Therefore, the errors in estimating the forces exerted by the agonists, caused by the assumption that one-joint antagonists are inactive, are likely not very large for support periods.

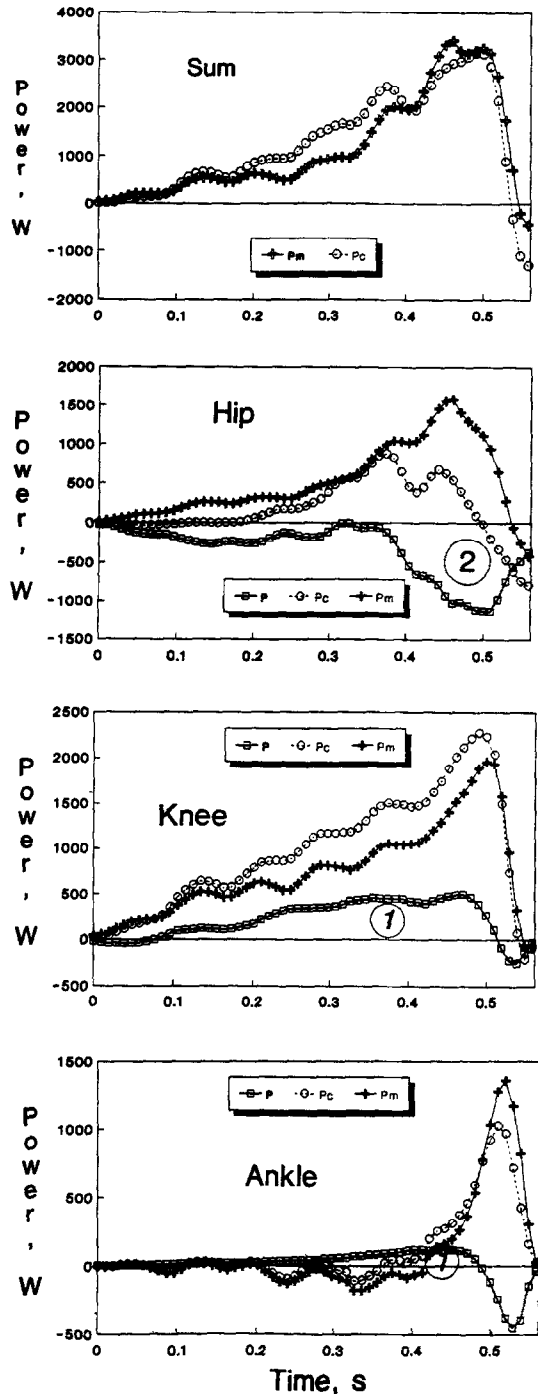


Fig. 1. Power developed by the joint moment (P^j), total power developed by the muscles serving the joint (P^m), and difference between them (P) for three joints of two legs during a squat vertical jump. The marks enclosed in circles on graphs P denote the number of the variant of energy transfer by two-joint muscles (Table 1). Subject being tested: B.P.

As can be seen later, a transfer of mechanical energy through two-joint muscles is observed mainly in the support period (Figs 1-3). Secondly, the assumption regarding the reciprocal character of muscle activity makes it possible to get rather explicit results, i.e. the lowest estimates of the muscle forces. If, in fact, the

one-joint antagonists are active, then the real forces of the agonists may be higher, but not lower than those predicted by the model. From this it follows, in particular, that power and work of the separate mus-

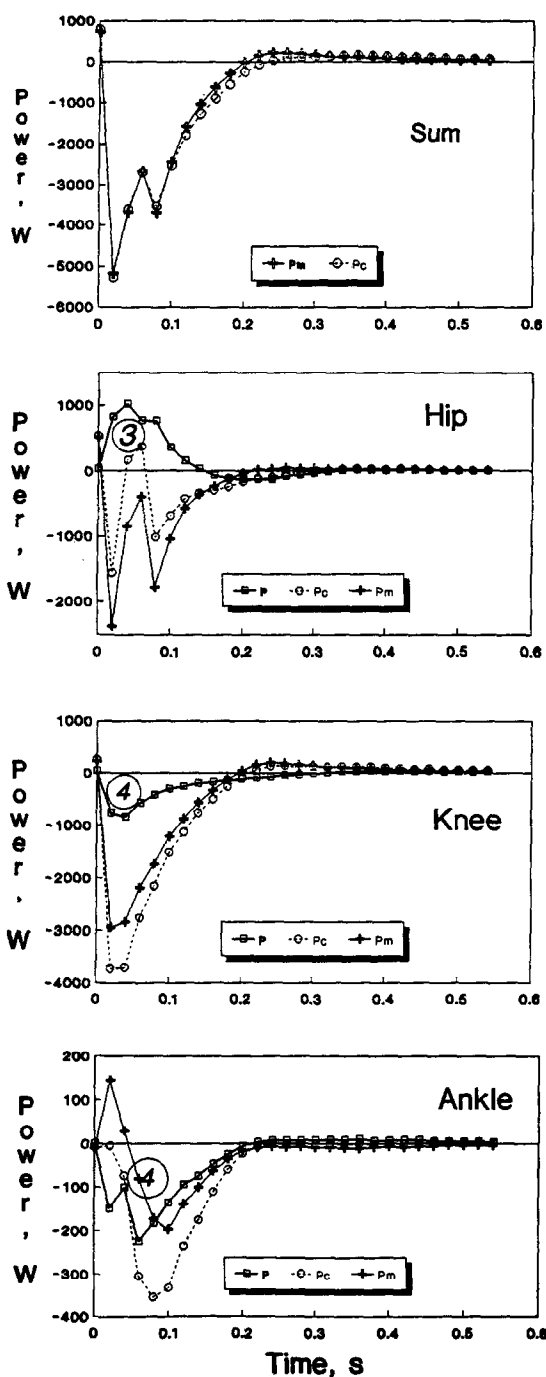


Fig. 2. Power developed by the joint moment (P^c), total power developed by the muscles serving the joint (P^m), and difference between them (P) for three joints of the left leg during landing. The marks enclosed in circles on graphs P denote the number of the variant of energy transfer by two-joint muscles (Table 1). Subject being tested: O.B.

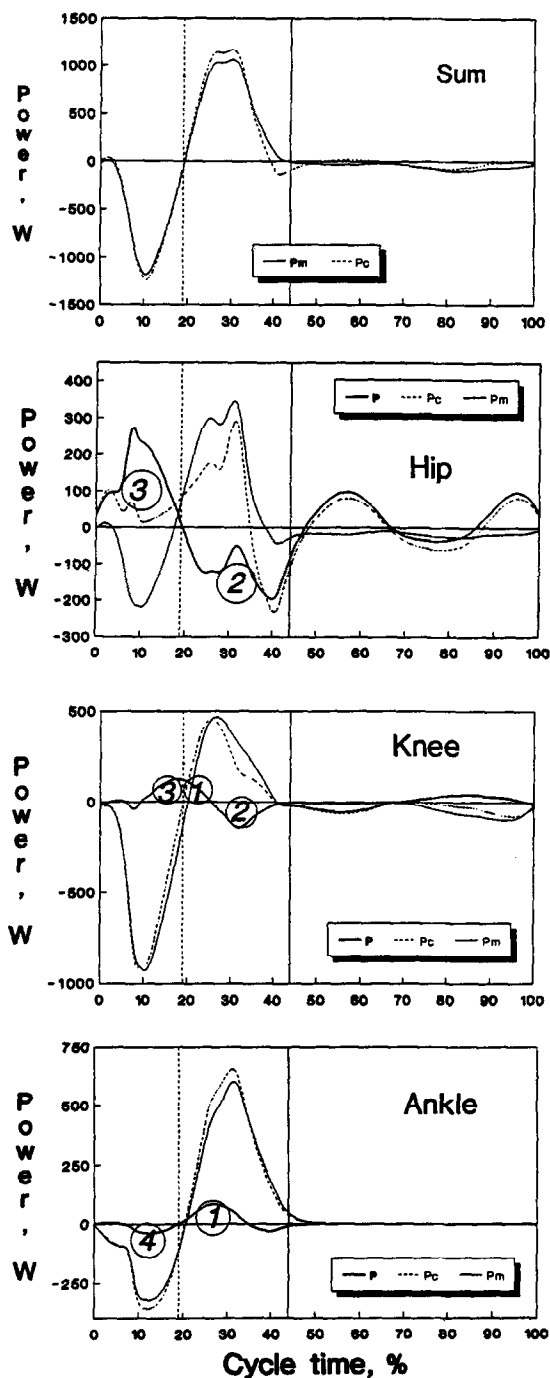


Fig. 3. Power developed by the joint moment (P^c), total power developed by the muscles serving the joint (P^m), and difference between them (P) for three joints of the left leg during running. The vertical dash line separates the shock-absorbing and push-off phases. The speed of running is 1.57 m s^{-1} . The marks enclosed in circles on graphs P denote the number of the variant of energy transfer by two-joint muscles (Table 1). Subject being tested: B.P.

cles predicted by the model are also the lowest estimates of the real values. Thus, it can be stated that the real values of the energy transferred through two-joint muscles during human locomotion are not less than those estimated in this study (Table 2).

Let us discuss the assumption concerning the equal tension of agonists. Amis *et al.* (1980) used this assumption to determine the forces of separate muscles during some strenuous isometric actions. This assumption follows from the principle of 'nonindividualized' control of muscle activity (Gelfand and Tsetlin, 1966) which was proposed on the basis of numerous physiological experiments. According to this principle, a central nervous command is identical for all agonists of a joint (Feldman, 1979). Therefore, the differences in the muscle forces will be determined by the intrinsic biochemical properties and architecture of the muscle, and mechanical conditions under which the muscle is functioning, that is, the current relative muscle length and velocity. The mechanical conditions under which one-joint agonists function are similar. However, this is not true for two-joint muscles because their length and velocity depend on the angles of two adjacent joints. Among the parameters of the internal structure responsible for the exertion of muscle force, muscle fiber composition (Henneman *et al.*, 1965) and the physiological cross-sectional area (Ikai and Fukunaga, 1970) deserve some attention. However, our model takes into account only the influence of the physiological cross-sectional area on the muscle force. Thus, the assumption of the equal tension of agonists at each joint during multi-joint movements is not fully substantiated from the theoretical point of view. However, a comparison of muscle forces computed using the model, and the IEMG of the corresponding muscles during walking

(Zatsiorskii and Prilutskii, 1989) showed that errors were relatively small. Consequently, the model can be used for the computation of muscle forces.

Estimation of the amount of energy transferred between joints by two-joint muscles

To estimate the amount of energy transferred by two-joint muscles between joints, let us consider the equality

$$P_j(t) = P_j^c(t) - \sum_j P^m(t), \quad j = 1, 2, 3 \quad (2)$$

as the fundamental one (see also Morrison, 1970), where subscript j is the number of the leg joint, t is the time, $P_j^c(t)$ is the power developed by the joint moment at the j th joint, and $\sum_j P^m(t)$ is the arbitrary designation of the sum of the powers developed by all the muscles serving the j th joint. Within the framework of the considered musculoskeletal model, and with the assumption that all the muscles serving the j th joint are one-joint muscles, the difference (2) equals zero. However, if among the muscles serving the j th joint there are two-joint muscles, the difference (2) is not necessarily equal to zero. Here, the variable $P_j(t)$ [see formula (2)] is essentially the rate at which the energy is transferred to or from a given joint through two-joint muscles. In such a case, energy can be transferred in five major ways (Table 1). In fact, if the total power of muscles serving a given joint and the power of moment at the joint have the same sign, and the difference (2), i.e. power $P_j(t)$, has a positive sign, then this means that an extra amount of mechanical energy comes to the joint (variants 1 and 3, Table 1). This energy can come only through two-joint muscles from adjacent joints. If the power $P_j(t)$ is negative, i.e. the power of moment at the joint is smaller than the total power of muscles serving a given joint, energy is

Table 1. Variants of mechanical energy transfer by the two-joint muscles

Variant No.	$P_j(t)$	$P_j^c(t)$	$\sum_j P^m(t)$	Direction and rate of energy transfer through the two-joint muscles	Functions of the muscles serving the j th joint
1	>0	>0	≥ 0	To the j th joint at a rate of $ P_j(t) $ from the side of the $(j-1)$ th and/or $(j+1)$ th joints	Generate energy at a rate of $ P_j^c(t) - P_j(t) $
2	<0	≥ 0	>0	From the j th joint at a rate of $- P_j(t) $ to the $(j-1)$ th and/or $(j+1)$ th joints	Generate energy at a rate of $ P_j^c(t) + P_j(t) $
3	>0	≤ 0	<0	To the j th joint at a rate of $ P_j(t) $ from the side of the $(j-1)$ th and/or $(j+1)$ th joints	Absorb energy at a rate of $-[P_j^c(t) + P_j(t)]$
4	<0	<0	≤ 0	From the j th joint at a rate of $- P_j(t) $ to the $(j-1)$ th and/or $(j+1)$ th joints	Absorb energy at a rate of $-[P_j^c(t) - P_j(t)]$
5	$=0$	≥ 0 <0	≥ 0 <0	(a) Energy is not transferred through two-joint muscles. (b) Energy is delivered to the j th joint at a rate of $ P_j(t) $ [e.g., from the side of the $(j+1)$ th joint] and transferred from it at a rate of $- P_j(t) $ [e.g., to the $(j-1)$ th joint]	Generate energy at a rate of $ P_j^c(t) $ or absorb energy at a rate of $- P_j^c(t) $

transferred from this joint to the adjacent joints through two-joint muscles (variants 2 and 4, Table 1). Thus, knowing the power $P_j(t)$, one can judge the direction and rate of mechanical energy transfer through two-joint muscles, while the time integral of power $P_j(t)$ gives the amount of energy transferred.

Computations

Computations were performed on the SM-1420 computer using specially developed programs. The computations were used to obtain the values of the powers developed by the ankle, knee, and hip joint moments (as the product of the joint moment and the angular velocity at the joint), and the power developed by each of the eight muscles of the model (as the product of the force of the muscle and the rate of change of its length). Changes in muscle lengths during motion were calculated from the joint angles using the empirical regression equations (Aruin *et al.*, 1988). The velocities were calculated with the numerical differentiation procedure based on the moving-average approximation of discrete values of the function by the least-squares method. The value $\sum_j P^{jm}(t)$ [see formula (2)] for each joint was computed as an algebraic sum of the powers developed by all the muscles serving a given joint. For instance, the total power of the muscles acting relative to the knee joint is equal to the sum of the powers developed by the gastrocnemius, vastus femoris, and rectus femoris (or hamstrings).

RESULTS

Direction of energy transfer through two-joint muscles

Figures 1–3 present the typical curves of powers $P_j^c(t)$, $\sum_j P^{jm}(t)$, and $P_j(t)$ [see formula (2)] in the cases of squat vertical jumps, landing, and jogging.

Jump. During squat vertical jumps the powers of the joint moments and total powers developed by the muscles acting relative to each of the joints have a positive sign (Fig. 1). During the major part of the push-off phase the sign of the power $P_j(t)$ for the ankle and knee joint is positive. This result corresponds to the first variant (denoted by the mark enclosed in a circle in Fig. 1) of energy transfer by two-joint muscles (see Table 1). In the hip joint the sign of the power $P_j(t)$ is negative (the second variant). Thus, mechanical energy is transferred by two-joint muscles from the hip to knee and from the knee to ankle, i.e., from proximal to distal joints.

Landing. During landing, the reverse takes place (Fig. 2). The powers developed by joint moments and the total powers of the muscles in the joints are essentially negative. The sign of the powers $P_j(t)$ is negative in the knee and ankle joints, which corresponds to the fourth variant of energy transfer by two-joint muscles (Table 1). In the hip joint, the sign of the power $P_j(t)$ is positive (third variant). Thus, mechanical energy is transferred by two-joint muscles from

the ankle to the knee and from the knee to the hip, i.e. from distal to proximal joints.

Jogging. In jogging (Fig. 3), during the first half of the support period (shock-absorbing phase) the behavior of the powers $P_j^c(t)$, $\sum_j P^{jm}(t)$, and $P_j(t)$ is very similar to those during landing (Fig. 2). Thus, as a result of the action of two-joint muscles, mechanical energy is transferred from the ankle to knee and from the knee to hip [see the marks enclosed in circles on the graphs of power $P_j(t)$ in Fig. 3]. During the second half of the support period (push-off phase) the powers $P_j^c(t)$, $\sum_j P^{jm}(t)$, and $P_j(t)$ vary similarly to those of the vertical jump (Figs 1 and 3). This result means that

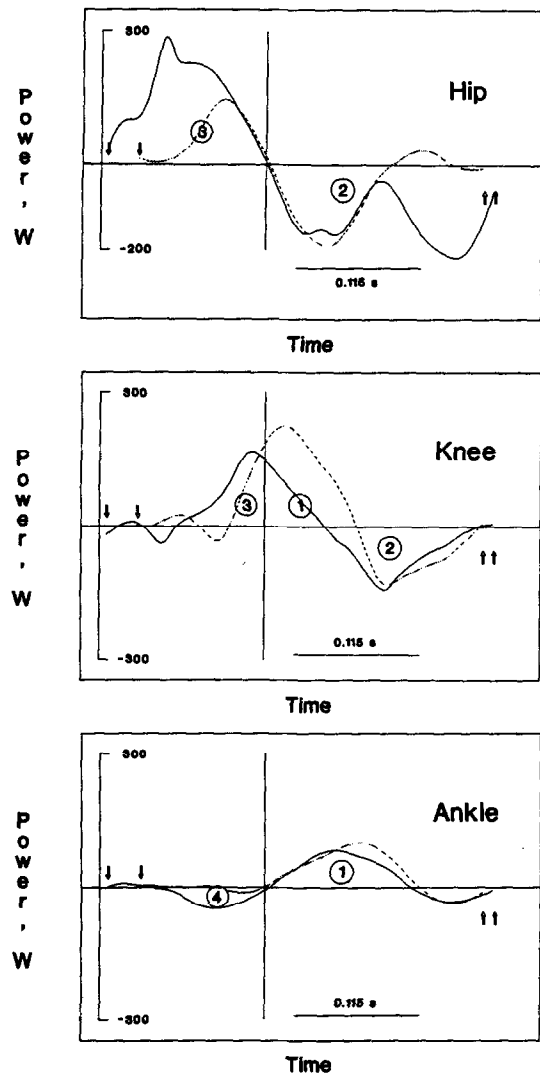


Fig. 4. Power $P [= P^c - \sum P^{jm}]$ [see formula (2)] for three joints of the left leg during the support period in running. The solid lines show the results of tests conducted on B.P.; the dotted lines show the results of tests conducted on N.M. The solid vertical line separates the shock-absorbing and push-off phases. The small arrows show the instants of the beginning and the end of ground contact. The marks enclosed in circles on graphs P denote the number of the variant of energy transfer by two-joint muscles (Table 1).

two-joint muscles transfer energy from the hip to knee and from the knee to ankle.

However, in jogging, certain peculiar features can be distinguished. Whereas for the ankle and hip joint during the shock-absorbing and push-off phases the marks on the graphs of power $P_j(t)$ coincide with the corresponding marks for landing and jumping (Figs 1–3), no such coincidence takes place for the knee joint. Let us review this situation in more detail.

Figure 4 shows the power $P_j(t)$ in the support period for each leg joint of the two running subjects. In the shock-absorbing phase, energy is transferred from the ankle to the knee (marks 4 and 3 for the ankle and knee joints, respectively). At the same time, energy comes to the hip from the knee (mark 3 for the hip joint). Thus, energy is not only delivered to the knee, but also transferred from the knee to the hip joint.

During the first half of the push-off phase, mechanical energy is transferred from the hip to the knee (marks 2 and 1 for the hip and knee joints, respectively, Fig. 4). At the same time, energy is transferred from the knee to the ankle (mark 1 for the ankle joint, Fig. 4). During the second half of the push-off phase, energy is transferred from the knee to the ankle (marks 2 and 1 for the knee and ankle joints, respectively, Fig. 4). Thus, within the push-off phase in running, the knee joint obtains energy from the hip joint and then in turn transfers energy to the ankle joint.

The results presented in Figs 1–4 show that during ground locomotion of humans, two-joint muscles exhibit tendon action. This action manifests itself in the shock-absorbing phase as the transfer of mechanical energy from the distal joints of the extremities to the proximal ones, and in the push-off phase as the transfer of mechanical energy from the proximal to the distal joints.

Within the framework of the musculoskeletal model used in the present study, this energy transfer may be accomplished by the following two-joint muscles: the gastrocnemius (from the ankle to the knee or from the knee to the ankle), and the rectus femoris (from the knee to the hip or from the hip to the knee (see the diagrams shown in Fig. 5).

Amount of energy transferred by two-joint muscles between joints

Table 2 presents the amounts of mechanical energy transferred between the joints by the gastrocnemius and rectus femoris during the observed locomotion. These amounts were obtained by integrating powers $P_j(t)$ (Figs 1–4). On average, the mechanical energy transferred by two-joint muscles from the proximal joints to the distal ones ranges from 17.3 ± 9.1 J in running ($26.7 \pm 12.6\%$ of the work done by the joint moment at the hip joint in the push-off phase), to 178.6 ± 45.7 J ($97.1 \pm 27.2\%$) in the case of squat vertical jump. The latter value means, in particular, that the energy generated by the hip extensor muscles is used in approximately equal amounts for extension at the hip joint and for extension at the distal joints (knee

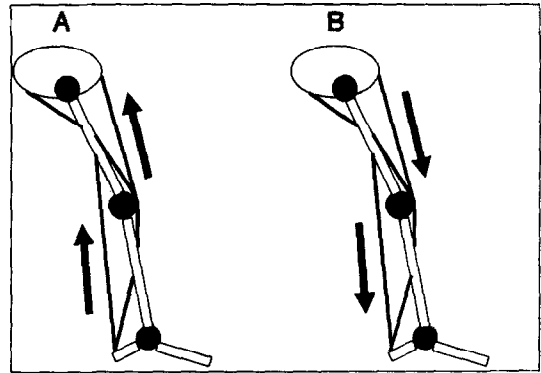


Fig. 5. Diagram illustrating transfer of mechanical energy by two-joint muscles of a leg: (A) shock-absorbing phase; (B) push-off phase.

and ankle) (Tables 1 and 2). The energy transferred by two-joint muscles from the distal joints to the proximal ones ranges from 1.5 ± 1.6 J ($1.4 \pm 1.4\%$ of the work done by the joint moment at the ankle joint) in the shock-absorbing phase in running, to 18.6 ± 4.2 J ($38.5 \pm 36.4\%$) in landing (Table 2).

DISCUSSION

Musculoskeletal model and its potential influence on the obtained results

The adequacy of the musculoskeletal model used in the present study can be verified by a comparison of the total power of all muscles of the lower extremity, and the total power of the joint moments at all joints of the lower extremity. If the model is adequate, these two characteristics must be equal. Results of such comparisons for the three forms of locomotion are shown in Figs 1–3 (the top curves). It is clearly seen that there is good accordance between the total muscle power and the total power of joint moments of the lower extremities, although differences between the two curves depicting the squat vertical jump (Fig. 1) are significantly larger than those of landing (Fig. 2) and running (Fig. 3). This result can be explained by the fact that considerably larger magnitudes of motion were observed in joints during the squat vertical jumps. For example, during the support periods, the angle at the knee joint changed from 28° to 175° for jumping, from 96° to 163° for landing, and from 128° to 156° for running. The moment arms and muscle elongations necessary for computing the muscle power were determined by the joint angles using the empirical regression equations (Aruin *et al.*, 1988). According to Aruin *et al.* (1988), the use of these equations is recommended for the ranges of flexion of the ankle, 80 – 150° ; the knee, 70 – 180° ; and the hip, 40 – 220° . Apparently, during the vertical jumps, joint angles exceeded these ranges, and this leads to errors in the muscle moment arms, elongations, velocities, and hence, powers. Nevertheless, the results of the

Table 2. Amounts of mechanical energy transferred by two-joint muscles between various joints of a leg during different forms of locomotion

Locomotion	Joint	ETV	TMTE	DET	Energy (mean \pm S.D.)	
					J	Percentage of $ W^p + W^n $
Squat vertical jump ($n=3$)	Hip	2	RF	From hip to knee	178.6 \pm 45.7	97.1 \pm 27.2
	Knee	1	RF	To knee from hip	125.6 \pm 21.5	23.7 \pm 3.4
	Ankle	1	GA	To ankle from knee	18.1 \pm 5.0	22.8 \pm 5.1
Landing ($n=3$)	Hip	3	RF	To hip from knee	60.7 \pm 28.0	53.2 \pm 38.0
	Knee	4	RF	From knee to hip	49.1 \pm 48.2	15.1 \pm 11.3
	Ankle	4	GA	From ankle to knee	18.6 \pm 4.2	38.5 \pm 36.4
Jogging, speed 1.78 \pm 0.09 ms ⁻¹ , ($n=2$)	Hip	3	RF	To hip from knee	16.0 \pm 10.9	24.6 \pm 15.6
	Knee	3	GA	To knee from ankle	5.6 \pm 1.8	4.2 \pm 0.9
	Ankle	4	GA	From ankle to knee	1.5 \pm 1.6	1.4 \pm 1.4
	Hip	2	RF	From hip to knee	17.3 \pm 9.1	26.7 \pm 12.6
	Ankle	1	GA	To ankle from knee	7.9 \pm 1.0	7.4 \pm 1.3
(1) Shock-absorbing phase	Knee (first half of push-off phase)	1	RE	To knee from hip	7.9 \pm 6.4	6.3 \pm 5.1
	Knee (second half of push-off phase)	2	GA	From knee to ankle	10.9 \pm 0.2	8.4 \pm 1.3

Notes: ETV is the energy transfer variant (see Table 1); TMTE is the two-joint muscle transferring energy; DET is the direction of energy transfer; W^p is positive work done by a net moment at a given joint during the support phase in jumping or landing, or during the shock-absorbing phase in running if variants 3 and 4 of energy transfer are observed (Fig. 3), or the push-off phase in running if variants 1 and 2 of energy transfer are observed (Fig. 3) [W^p is numerically equal to the areas under the curves of the powers P^c with positive values (Figs 1–3)]; W^n is negative work done by a net moment at a given joint during the support phase in jumping or landing, or during the shock-absorbing phase in running if variants 3 and 4 of energy transfer are observed (Fig. 3) and the push-off phase in running if variants 1 and 2 of energy transfer are observed (Fig. 3) [W^n is numerically equal to the areas under the curves of the powers P^c with negative values (Figs 1–3)]; GA is the gastrocnemius muscle; RF is the rectus femoris muscle; n is the number of subjects being tested.

The amounts of energy (in J) transferred by two-joint muscles are numerically equal to the areas under the curves of the powers P with indicated energy transfer variants (see Figs 1–4). Computations of amounts of transferred energy were performed for two legs at jumping and landing and for one leg at running (jogging).

comparison of the total muscle power and total power of the joint moments make it possible to conclude that these characteristics are clearly in agreement, and so the model is sufficiently adequate.

The model used in this study could not predict simultaneous force production of the rectus femoris and hamstrings muscles. However, these muscles show co-activation during human movements: running (Elliott and Blanksby, 1979), jumping (Bobbert and van Ingen Schenau, 1988), and cycling (van Ingen Schenau, 1989). In these cases, hamstrings could transfer mechanical energy from the knee joint to the hip joint during push-off phases [see also van Ingen Schenau *et al.*, 1990, Fig. 41.6] and in the opposite direction during shock-absorbing phases. Thus, it should be taken into account that the amount of transferred energy through the rectus femoris (Table 2) is an overestimate, and that the hamstrings can transfer a certain amount of energy between the knee and hip joints in the opposite direction than energy transferred through the rectus femoris muscle. However, according to Pandy *et al.* (1990) and Pandy and Zajac (1991), the hamstrings do not play an essential role in the increase of the segments' energy or angular velocity at joints during the push-off phase. Therefore, we

think it is possible to ignore transferred energy by this muscle for the first rough estimate. The most important function of hamstring muscles as two-joint muscles may be the control of the direction of an external force during leg extension (van Ingen Schenau, 1989).

In the study of Bobbert *et al.* (1986), the mechanical energy transfer rate from the knee to the ankle through the gastrocnemius during a vertical one-leg jump just after a preliminary counter movement was computed. This characteristic was determined as the product of the moment developed by the gastrocnemius at the knee joint and the angular extension velocity of the knee joint. Since the length of the gastrocnemius, as reported by Bobbert *et al.* (1986), decreased at the push-off phase, one can consider that all energy which came to the proximal end of the gastrocnemius (from the knee) was transferred to its distal end (to the ankle). In this case, the rate of energy transfer computed by Bobbert *et al.* (1986) is equivalent to the power $P(t)$ computed in this study using formula (2) for the ankle joint. A comparison of both of these powers shows their qualitative agreement: a sharp increase from the onset of the second half up to the beginning of the last quarter of the push-off phase (peak power), then a sharp decrease. Maximal values

of energy transfer rates through the gastrocnemius equal about 15–20% of the maximum power of moment at the ankle joint in both cases.

It can be seen from Table 2 that the amount of energy transferred from one joint, for example the hip, to an adjacent joint, for example the knee, and the amount of energy that comes to the second joint (the knee) through the same two-joint muscle are not equal (Table 2, jump, hip and knee joints; landing, hip and knee joints; running, shock-absorbing phase, knee and ankle joints; and push-off phase, hip and knee joints). This difference in energy might be caused by mechanical work done by the two-joint muscle during the transfer of energy. For example, during jumping, the rectus femoris muscle might perform negative work (Pandy and Zajac, 1991). In this case, part of the energy being transferred from the hip joint is dissipated in the rectus femoris, and less energy comes to the knee joint (Table 2, hip and knee joints). During landing, for example, the rectus femoris might perform positive work that increases the amount of energy that comes to the hip joint (Table 2, hip and knee joints).

Functional significance of tendon action of two-joint muscles

We think that the disclosed mechanism of energy transfer by two-joint muscles is of great functional importance. The muscles located on the proximal links of the lower extremity have considerably larger volumes than those of the muscles of the distal links. This is due to longer fibers and relatively short tendons (Alexander and Ker, 1990), and large cross-sectional areas (Schumacher and Wolff, 1966) of the proximal muscles. Such a distribution of muscle volume along the leg reduces its moment of inertia relative to the 'suspension point', the hip joint. This allows the leg to move with a lower consumption of energy. Moreover, the lower inertia of the leg makes it possible to reduce the time delay between the delivery of a command from the CNS, and the response to this command, expressed as a motion. However, such a distribution of muscle volume poses certain problems for the interaction between the leg and the ground. Because of the relatively small volume of the distal muscles, dissipating mechanical energy of the body (doing negative work) during the shock-absorbing phase, and accelerating the body (doing positive work) during the push-off phase is limited. This limitation is because the amount of work a muscle can do is proportional its volume. The proximal muscles are more suited to performing mechanical work (Alexander and Ker, 1990). The mechanism of the tendon action of two-joint muscles as observed in our research makes it possible to circumvent the aforementioned problems of the distal muscles by distributing mechanical energy between distal and proximal joints.

For instance, in the shock-absorbing phase when touch-down is performed by the toes, the ground reaction force tends to flex the ankle joint [Fig. 5(A)]. This flexion is countered by the ankle extensor mus-

cles which, contracting eccentrically (shown by the negative power in the ankle joint, see Figs 2 and 3, shock-absorbing phase), do negative work; i.e. they absorb (dissipate) the mechanical energy of the body. Acting as a ligament, the gastrocnemius causes additional flexion of the knee (the fourth variant of energy transfer, Table 1) under the influence of the ankle flexion. Knee flexion is countered by the knee extensor muscles which, contracting eccentrically (the power in the knee joint is negative, Figs 2 and 3, shock-absorbing phase), dissipate the mechanical energy which was partly transferred to the knee from the ankle (variant 3, Table 1). The knee extensor muscles also dissipate the mechanical energy related to flexion at the knee joint under the ground reaction force. Acting as a ligament, the rectus femoris causes an additional flexion at the hip joint (variant 4, Table 1) under the action of knee flexion. Hip flexion is countered by the hip extensor muscles which, contracting eccentrically (Figs 2 and 3, shock-absorbing phase), dissipate mechanical energy, part of which was transferred to the hip from the knee (variant 3, Table 1). Thus, because of the tendon action of two-joint muscles, the muscles of the proximal links help distal muscles to dissipate the mechanical energy of the body during the shock-absorbing phase.

In the case of the push-off phase because of two-joint muscles, the muscles of the proximal links of the leg help to extend the distal joints by transferring to them part of the generated mechanical energy [Fig. 5(B)]. For instance, extension of the hip by the action of the hip extensor muscles doing positive work (power in the hip joint is positive, see Figs 1 and 3, push-off phase), assists in extending the knee joint (second variant of energy transfer, Table 1). The additional energy comes to the knee from the hip joint through the rectus femoris which acts as a ligament (variant 1, Table 1). Extension in the knee joint by the action of the knee extensor muscles performing positive work (Figs 1 and 3, push-off phase) contributes to foot plantar flexion. The additional energy comes to the ankle from the knee through the gastrocnemius muscle which acts as a ligament (variant 1, Table 1).

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