

ON THE ACTION OF BI-ARTICULAR MUSCLES, A REVIEW

by

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SUMMARY

In various multi-joint movements where an animal is in contact with his environment, the interaction with the environment may constrain the control of joint moments and joint displacements. If the hand or foot has to exert an external force on the ground or on an object, the joint moments necessary to control the direction of this force are to be judged as independent from the joint displacements required in the same task. The moments required to control this force may even be opposite to the direction of the joint displacement at one of the joints. It is shown that bi-articular muscles can provide a unique solution to this type of conflict. These muscles are able to change the distribution of net moments and joint power over the joints that are crossed allowing the mono-articular muscles to contribute to positive power irrespectively of the required net moments in the joints crossed by these muscles. This results in a considerably more efficient utilisation of the work capacity of the mono-articular muscles than what would be possible with mono-articular muscles only. The mechanical reasoning where these concepts are based on is explained with help of a few simplified examples and their recent identification is placed in a context of ideas of the pioneers in this field of physiology and functional morphology.

KEY WORDS: two-joint muscles, antagonists, motor control

INTRODUCTION

Over the past 20 centuries, many scientists have speculated about the actions of muscles who pass over more than one joint. This is especially true for the muscles in the human extremities who pass over two joints such as the long heads of biceps and triceps, the rectus femoris, gastrocnemius and hamstring muscles. In the century between 1850 and 1950 a large number of studies have been published in which it was convincingly argued and even demonstrated that these bi-articular muscles can perform unique actions which can not be performed by two mono-articular muscles crossing over the same two joints. It is striking, however, that little of this knowledge has been incorporated in contemporary textbooks on (functional) morphology or kinesiology. In most textbooks the bi-articular muscles are classified according to the location of their line of action relative to the joint axes

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of rotation. The hamstring muscles, for example, are classified as hip extensors and knee flexors. With this classification it is difficult to imagine that the hamstrings can support knee extension in a movement where the hip- and knee joints are simultaneously extended as for example occurs in standing from a chair and in jumping. Such paradoxical actions, however, have already been explained and demonstrated with models at the begin of this century (*e.g.* LOMBARD, 1903; BAEYER, 1922; K. FISCHER, 1927). The fact that this type of knowledge has not entered into textbooks may have to do with the rather abstract mechanical reasoning necessary to understand such actions (*e.g.* MOLBECH, 1966). Although Galen (1131-201 AD) early on argued that one should study the actions of muscles in relation to the action of the whole animal (a statement repeated by many others (*e.g.* O. FISCHER, 1902; K. FISCHER, 1927; FENN, 1938; BERNSTEIN, 1967)), it seems as if most zoologists and kinesiologists tend to relate muscle actions only to the joint displacements which are required in a movement. A vertical jump for example requires the extension of hip- and knee joints and thus the hip- and knee extensors are expected to be active.

Inverse dynamical analyses of a number of human movements (see next sections) have shown that the actual intermuscular coordination is much more complicated while especially the bi-articular muscles show activity patterns which seem to have no relation with the required displacements in the joints that are crossed.

The purpose of this review is to explain the unique role of the bi-articular muscles in such multi-joint movements. After a short overview of the main results of pioneers in this field, some attention is paid to mechanical expressions and definitions which should facilitate the reader to understand the reasoning used in the explanation of these old and new concepts.

PROPOSED ACTIONS

In his *De usu partium*, Galen (131-201 AD) was most likely the first who explicitly paid attention to the existence of bi-articular muscles. With respect to the action of the rectus femoris muscle he remarks" when it is tensed, it naturally not only draws up the tibia toward itself, but also flexes the femur, ..." (*De usu partium* II p. 373, translation: MAY, 1968). Although no unique function is described, Galen strongly supports the opinion of many scientists throughout the centuries that "Nature created nothing without purpose" (Aristotle, 384-322 BC, *De incessu animalium*, p. 704). The unique actions which were proposed since that time can be summarized into the following categories:

A. *Coupling of Joint Movements*

Since BORELLI (1685) showed that the maximal knee flexion force is influenced by the hip joint angle, many authors stressed the fact that bi-articular muscles may couple the movements in both joints that are crossed (HUNTER, 1977; CLELAND, 1867; HUETER, 1869; FICK, 1879; LANGER, 1879; HERING, 1879; O. FISCHER, 1902; LOMBARD, 1903; BAEYER, 1921; K. FISCHER, 1927; FENN, 1938; ELFTMAN, 1939a; MARKEE, 1955; LANDSMEER, 1961; WENTINK, 1978; WINTER, 1984; GREGOIRE *et al.*, 1984; HOGAN, 1985; INGEN SCHENAU *et al.*, 1987; BOBBERT & INGEN SCHENAU, 1988; WELLS, 1988; WEEREN, 1989). This effect is visualised in fig. 1. Imagine that the knee is extended by activation of the knee extensors and that the gastrocnemius simply acts

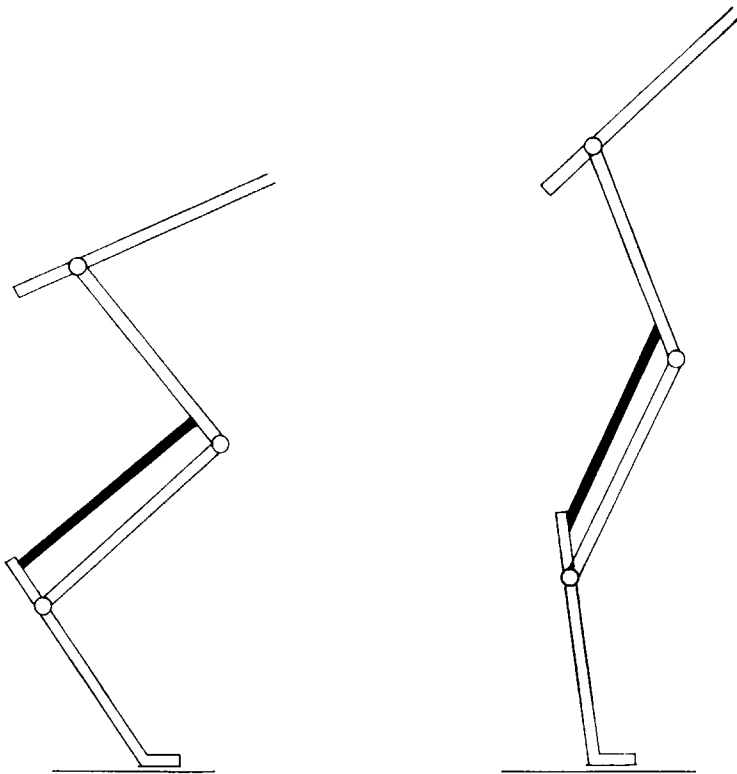


Fig. 1. A bi-articular muscle can couple the movements in the joints that are crossed. If the knee is extended the gastrocnemius can, for example, couple this knee extension to plantar flexion. This can easily be imagined if the gastrocnemius were a stiff tendon but this coupling effect is also present if the gastrocnemius is an active muscle.

as a stiff tendon. Since the origin of the gastrocnemius is displaced, the insertion will be displaced as well. This means that the extension of the knee will also cause a plantar flexion. This effect, which is also present when the gastrocnemius is an active muscle, was defined by CLELAND (1867) as a "ligamentous action" of bi-articular muscles. Since most animals have bi-articular muscles at both sides of the upper and lower leg, it is not difficult to imagine that these muscles can couple the movements in the hip to the movements in the knee and the movements in the knee to those in the ankle. These couplings make it possible to control distal joints with long tendons while the bulk of the muscle mass which delivers the necessary force and work can be located close to the trunk (CLELAND, 1867; FICK, 1879; BAYER, 1921). The mono-articular parts of the gluteus maximus can thus support plantar flexion (LANGER, 1879). In this way the moments of inertia of the most distal segments can be kept small (BAYER, 1921).

B. *Transport of Energy*

A number of authors have expressed the effects of the coupling between joints in energetic terms. Since proximally located mono-articular muscles may support the movements of distally located joints which are not crossed by these mono-articular muscles, one can speak of a transport of energy since for example the work done in plantar flexion can (partially) be delivered by knee- and even by hip extensor muscles. In contemporary mechanical approaches such as used in inverse dynamical analyses (ELFTMAN, 1939b; see next section) this can be expressed in well defined parameters such as net joint powers (INGEN SCHENAU *et al.*, 1987; BOBBERT & INGEN SCHENAU, 1988; INGEN SCHENAU & CAVANAGH, 1990). Recently, however, we discovered that, albeit in more ambiguous terms, this transport of energy concept was presented already more than a century ago. CLELAND (1867) argued that bi-articular muscles "... convey from one joint to another the effects of the actions of other muscles." and thus make it possible to apply the total amount of muscle power in an extremity in that (or those) joint(s) where it can be used in the most effective way (CLELAND, 1867). This concept, expressed in contemporary parameters such as net joint moments and joint powers will further be elaborated below on the basis of recent developments.

C. *Decreased Contraction Velocity*

In the "concurrent movements" (FENN, 1938) where for example the hip- and knee joints are simultaneously extended or flexed, the

displacements of the origin and insertion of the bi-articular muscles are in more or less the same direction. This means that the shortening velocities of these muscles can be considerably smaller than those of their mono-articular agonists. This phenomenon has been stressed by many authors (CLELAND, 1867; DUCHENNE, 1867; FICK, 1879; FENN, 1938; GREGOIRE *et al.*, 1984; BOBBERT *et al.*, 1988). Due to the force-velocity characteristics of muscle fibres this low contraction velocity allows relatively high muscle forces of bi-articular muscles in concurrent movements relative to the forces in the mono-articular muscles (BOBBERT *et al.*, 1987a, b).

A number of authors have proposed actions in addition to those mentioned above. DUCHENNE (1867), MARKEE *et al.*, (1955) and BARATTA *et al.*, (1988) for example discussed the possible role of bi-articular muscles in joint stabilization. This, however, is not to be judged as a unique action which can not be performed by mono-articular muscles. Moreover, it can not be excluded that these hypotheses have been proposed on the basis of observations that bi-articular muscles are often co-activated with their mono-articular antagonists at one of the joints (*e.g.* the knee extensors and gastrocnemius in the example of fig. 1). As will be explained below, these paradoxical co-activations are highly functional and do not necessarily point at a need for joint stabilization. Others have argued that bi-articular muscles are activated whenever their action is consistent with the moments required at the joints at which they act (CAPOZZO, 1976; WELLS & EVANS, 1987; WELLS, 1988). This reasoning, however, is based on a circular argument since the moments as measured in their analyses are in part determined by the actions of bi-articular muscles.

JOINT MOMENTS AND JOINT POWER

Recently we identified an indispensable action of bi-articular muscles in the control of external forces in multi-joint movements (INGEN SCHENAU, 1989a,b; GIELEN *et al.*, 1990; INGEN SCHENAU *et al.*, 1990). These new insights may facilitate the understanding why the coupling actions as described above are extremely important in most animal movements. Moreover they can shed new light on the design of the extremities of different animals. The explanation of these concepts, however, requires some knowledge of the nature of expressions like "net joint moment" and "net joint power".

Most joints in the extremities, predominantly, allow only rotations to occur. This means that most muscle actions (which are translatory movements) first are transformed into joint rotations. Most tasks,

however, require a translation of hand or foot relative to the trunk or the translation of the trunk relative to the foot, which requires a further transformation of joint rotation into these task specific translations. Since muscle contractions cannot directly be related to the required task specific translations, we have to apply some mechanics which describes these transformations. The transformation of muscle shortening into the required displacements of hand or foot is described by goniometrical relations of which the exact structure is not essential for this paper. To describe the transformation of muscle force to external force, some notion about the relations between muscle forces and joint moments and between joint moments and external forces is inevitable, however. If muscle forces and their lever arms are known, the first relation will not give much problems. For example the muscles outlined in fig. 2 will lead to a net moment in the knee according to

$$M_k = F_{vas} \cdot a + F_{rf} \cdot a - F_{ha} \cdot b$$

This net moment is positive (extending) if the contribution of the rf and vas muscles is larger than that of the ha muscles and negative (flexing) in the opposite case. With the same addition of the products of muscle forces and their lever arms the net moment in the hip joint can be calculated.

The relation between external forces and these net joint moments is much less common coin. Since the proper understanding of this relation is crucial for the remaining part of this paper, this needs to be discussed in some details. The reader should realise that there is a causal relation between the net forces and moments in the joints, the angular and translational accelerations of the segments and the external forces (gravity, ground reaction force etc.). This relation can be deduced by means of a so called inverse dynamical analysis. In this analysis, which was introduced by ELFTMAN (1939b), Newtonian equations of motion are used to calculate the net force and net moments in the joints. The body is approximated as a system of linked rigid segments connected by the joints. Using cinematographic methods (film or automatic opto-electronic systems), the (angular) accelerations are calculated. Equations for translational and angular motion are applied to each segment and the number of equations for each segment is sufficient to calculate the unknown net force and net moment in each joint provided that the external forces are known. The expression "inverse" is used to indicate that the analysis uses the result of the movement and its effect on the environment (*e.g.* the ground reaction force) to calculate the responsible net moments. For the explanation of the concepts to be discussed below it is not necessary to discuss the details of this analysis. It is sufficient to realise

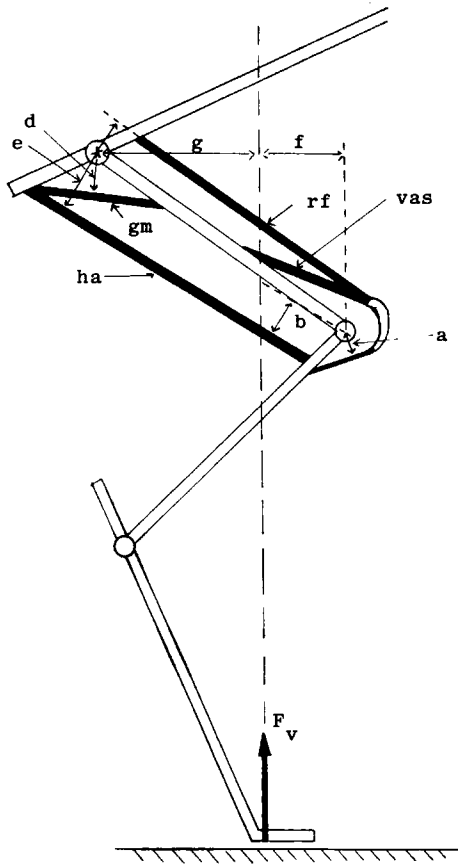


Fig. 2. Example to demonstrate the relation between muscle forces and net joint moments and between net joint moments and the external force F_v (see text).

that this relation between net joint moments and external forces is always present. This means that the realisation of an external force of certain direction and magnitude always requires the control of a distinct combination of net moments. In slow and static movements and ignoring the influence of gravity one can approximate these moments directly from the magnitude and direction of the external force. For the example of fig. 2 this can be performed by multiplying the magnitude of the ground reaction force with the smallest distance between its line of action and the location of the center of rotation of the joint. For the knee and hip joints this leads to

$$M_k = F_v \cdot f \text{ and } M_h = F_v \cdot g$$

respectively. The sign of the moments can be found by realising that it should be opposite to the effect of F_v if this force would not be opposed by these moments. In the example of fig. 2 this means an extending moment in both the hip and the knee. The important point which should be realised after this short discussion of net joint moments is that in the actual order of cause and effect one can state that this combination of moments is necessary to realise the magnitude and direction of F_v . Any other combination of joint moments will result in an other magnitude and/or direction of F_v . It should be emphasized, however, that these moments were calculated here using a highly simplified approach. In fast movements the actual moments may deviate considerably since the moments are also responsible for the segmental accelerations. This, however, does not prevent the formulation of a general statement that the control of an external force always requires a particular combination of net moments in the joints.

Using the same model of linked segments as discussed above but now in an application where power equations are deduced for each segment, one can prove (after summation of these equations) that the muscle power, which can be used to move the segments and against opposing forces from the environment, equals the sum of the joint powers (ALESINSKY, 1986; INGEN SCHENAU & CAVANAGH, 1990). These joint powers are defined as the products of net joint moments and joint angular velocities. If the net moment in a joint equals M and the joint angular velocity is ω , the joint power equals $P = M\omega$. If M and ω have opposite signs, this power is negative. It should be emphasized that joint power mostly does not equal the power liberated in the muscles that cross that particular joint. Moreover, negative joint power does not necessarily mean that mechanical power is degraded into heat. Apart from the possibility that power is temporally stored in elastic components of muscle tendon complexes which oppose the joint movement, it can be shown that bi-articular muscles can transport power between joints in such a way that negative power of one joint appears computationally as positive power in the other joint that is crossed. Imagine for example that the *ham* muscles in fig. 2 are not active and all other muscles are activated but the *rf* stronger than the *gm* leading to a large net extending moment in the knee but a small negative and thus flexing moment at the hip. This combination of net moments which results in a reaction force which is more backwards directed (and thus an action force more forward directed) is present at the onset of the downstroke in cycling (the pedal is pushed in a forward/downward direction). In this phase of the cycling movement both joints are extended. This means that the joint power in the knee joint is positive but it is negative in the hip. Power delivered by the

concentrically contracting gluteus maximus does not appear as positive hip joint power but it is said to be transported from hip to knee through the ligamentous action of the *rf* muscle. Since all muscles shorten in this phase of the cycling stroke (INGEN SCHENAU, 1989a), no mechanical power is converted into heat by eccentric muscle actions; the total amount of available mechanical power being equal to the sum of the powers in all joints. The same type of transport of energy is present in the example illustrated by fig. 1. Even in the case that the gastrocnemius is a passive tendon, one would find a positive joint power in the ankle since the net ankle moment will be positive (the direction of plantar flexion) and the ankle is plantar flexed. Clearly this power can not be delivered by this tendon (apart from re-utilisation of elastic energy) but is transported from the knee to the ankle. The knee joint power would be higher if this opposing gastrocnemius were not present (at the same power output of the knee extensors) since the gastrocnemius decreases the net moment in the knee. These examples may have sufficiently illustrated the rather hypothetical nature of these net joint moments and net joint powers in order to follow the reasoning which is used in the next section.

THE CONTROL OF POSITION AND FORCE

It was argued above that the fact that we can mainly rotate in our joints leads to two types of transformations (fig. 3).

- I . The transformation of muscle displacement into joint rotation and of joint rotation into the required displacement of hand or foot or that of the trunk relative to the foot.
- II. The transformation of muscle force into joint moments and of joint moments into the direction and magnitude of the required external force.

The main topic of this paper concerns the observation that these transformations of position (I; the displacements and rotations) and those of force (II) are to a large extent independent. This is visualized in fig. 4. Imagine a subject sitting at a table who has to displace an object over the table in the indicated directions. On a horizontal table, the displacements require a force on the object in the direction of the displacements. An inverse dynamical analysis would show that for the task of fig. 4a. the subject needs to apply a net flexing moment in the shoulder and a net flexing moment in the elbow. (In the simplified approach mentioned above one might say that the reaction force tends to extend the shoulder and the elbow joint which means that the action requires net flexing moments in both joints). From fig. 4a. it can be observed, however, that if the object is displaced, the task requires a

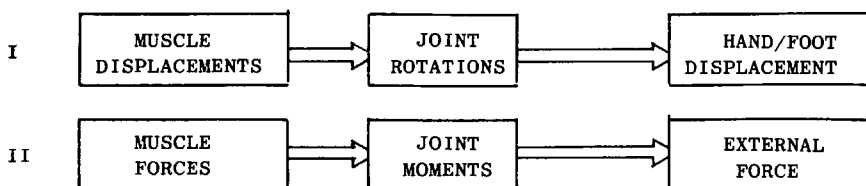


Fig. 3. In most movement tasks we need two transformations: one of position and one of force. These two transformations often lead to conflicting requirements with respect to muscle actions.

flexion in the shoulder but an extension in the elbow. This means that the sign of the necessary net moment in the elbow (which is in the direction of flexion) is opposite to the sign of the required joint displacement. When expressed in mathematical terminology, this is associated with the fact that the transformation matrices (the Jacobian and its transpose) which describe the relations between hand displacement and joint displacements and external force and joint moments, is in general not symmetric (GIELEN *et al.*, 1990). As we have seen above the net joint moments and the joint rotations determine the joint work and its derivative: joint power. The opposite signs of moment and displacement at the elbow means that negative work is done at the elbow joint. If the elbow extension were to contribute to the external work on the object, the net elbow joint moment would have to be positive (extending). However, an extending elbow moment (combined with a flexing shoulder moment) would result in an external force on the object which would be directed much more upwards (in the plane of fig. 4). This means that a conflict exists at the elbow between the net moment necessary to control the direction of the external force and the moment necessary to contribute to positive work. If the arm would be equipped with mono-articular muscles only the only possible way to perform the task would be that the shoulder flexors deliver considerably more work than the work done on the object while the difference is converted into heat in the eccentrically contracting elbow flexors. Activation of the elbow extensors would be useless since the flexors would have to reduce the net moment to the required net flexing moment. So all work done by concentrically contracting elbow extensors would then also be converted into heat. These conflicting requirements with respect to the net moment at the elbow would lead to a waste of energy and also to a situation where muscle(s) who are in the position to shorten and to contribute to positive work, have to remain passive.

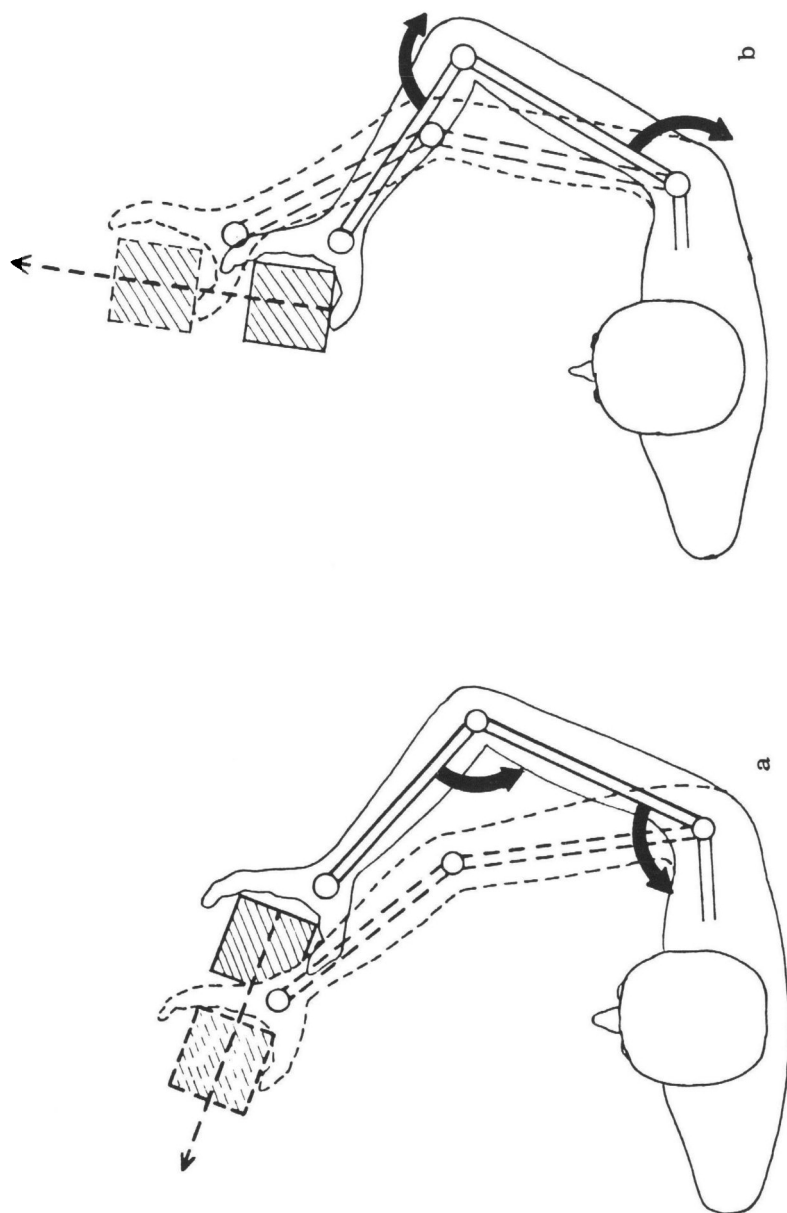


Fig. 4. The force necessary for the displacement of an object requires a particular combination of net moments in the joints. These moments are often not related to the displacements in the joints. In the example of the left hand side, the task requires a net flexing moment in the elbow while the elbow is extended. The same type of conflict is present in the shoulder joint in the task on the right hand side.

A comparable conflict is present at the shoulder joint in the task of fig. 4b. Now, the required moment in the elbow joint is in the same direction as the elbow joint displacement but at the shoulder the task requires an extending moment while the shoulder is flexed. Again this task would be associated with a considerable internal waste of energy if the arm contained only mono-articular muscles. One can calculate that these type of conflicts are only absent if the line of action of the external force runs between both joints. Clearly this is the case in a limited part of workspace which is smaller the more the elbow is in an extended position at the onset of the task. It should be noted, however, that the most important point is not the occurrence of such a conflict at one of the joints but the different requirements for the control of force and position which are to be judge as independent from each other. This statement can be imagined if the same tasks of fig. 4 with respect to the required displacements would have to be performed while other external forces such as gravity and friction vary (*e.g.* a non-horizontal table). Clearly, these varying forces will require a varying force exerted by the subject and thus a varying distribution of net moments in the joints at the same required joint displacements.

CO-ACTIVATION OF ANTAGONISTS

These different requirements for the control of force and position were originally identified in an inverse dynamical analysis of cycling (INGEN SCHENAU, 1989a). This analysis included the registration of the activity of different mono- and bi-articular leg muscles by means of surface electromyography (emg). The activity patterns appeared to point at a certain coordination between mono- and bi-articular muscles aimed at a unique solution of the above mentioned conflict. In the first part of the downstroke in cycling we observed a strong co-activation of antagonists at the hip joint: the mono-articular gluteus maximus and the bi-articular rectus femoris muscles. During the second part of the downstroke the mono-articular vasti appeared to be co-activated with their antagonistically acting hamstrings. Especially this last co-activation has often been described and judged as uneconomical (ANDREWS, 1987; GREGOR *et al.*, 1985; SUZUKI *et al.*, 1982). However, when placed in the light of the above mentioned conflict, these paradoxical co-activations appear to be highly functional. This is explained with help of fig. 5. At the onset of the downstroke cyclists appear to direct the force on the pedal in a slightly forward direction while during the downstroke the direction is changed from slightly forward to slightly backwards. Though the actual experiments were based on a complete inverse dynamical analysis, it is attempted here

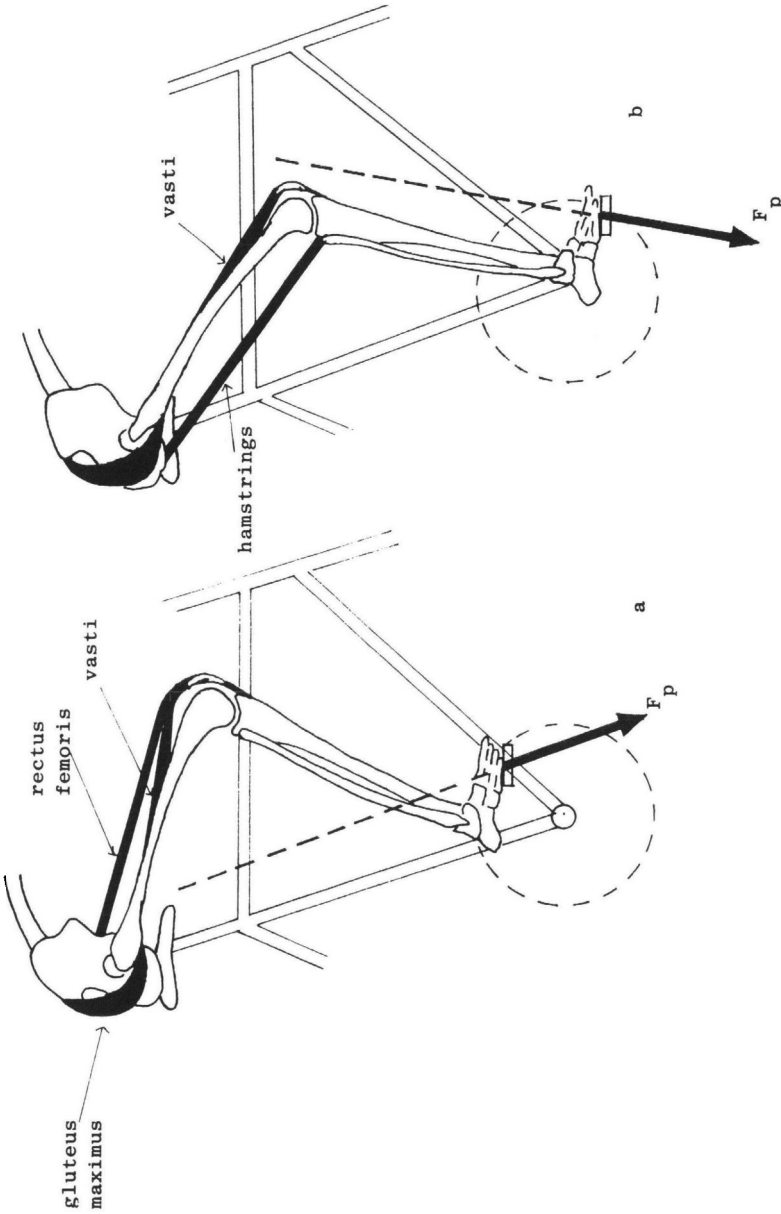


Fig. 5. The control of the direction of the force F_p on the pedal during cycling requires a combination of a low moment at the hip and a large knee extending moment at the onset of the downstroke and a large hip extending moment combined with a negative (and thus flexing) moment at the knee in the second part of the downstroke. Since the hip and knee are extended throughout the downstroke, the mono-articular hip extensors and knee extensors can contribute to positive work. Through co-activation of their bi-articular antagonists, their work output is transported to other joints in such a way that the required net moments can be warranted.

(for didactic reasons) to use the simplified reasoning explained above in order to facilitate the imaging of the consequences of this change in direction to a broad audience. At the onset of the downstroke the line of action of the pedal force runs far behind the knee and points more or less into the direction of the hip joint. This means that the control of this force requires a small moment at the hip and a large extending moment at the knee. If we had only mono-articular muscles this would have to be realised by the activation of the knee extensors only. If mono-articular hip extensors would be activated as well, the hip joint would be an extending moment and the direction of the force on the pedal would be more vertical. This more vertical force would be less effective since the pedal can only be displaced in a forward-downward direction in this phase. What actually occurs is an activation of not only the knee extensors but also the mono-articular gluteus maximus. The net moment at the hip, however, is kept small (or even negative) through co-activation of the gluteus maximus by the bi-articular rectus femoris. As explained with help of fig. 2 the power delivered by the gluteus maximus is now transported to the knee and appears computationally as an increase of the knee joint power through the tendinous action of the rectus femoris. Later on, during the second part of the downstroke, the line of action of the pedal force runs far in front of the hip and even in front of the knee in a phase where both hip and knee are still extended. This direction requires a large extending moment at the hip but a flexing moment at the knee. As explained for the arm tasks of fig. 4 this means that there is a conflict at the knee with respect to the moment necessary to control the direction of the pedal force and the moment which would be necessary to contribute to positive knee joint power. If the knee moment would be extending in this phase, the direction of the pedal force would be forward-downward which is almost at right angles to the direction of displacement of the pedal which means that F_p would hardly be able to do work on the pedal. Again: with mono-articular muscles only, the task of fig. 5b would require the activation of hip extensors and knee flexors and the de-activation of the knee extensors. While the powerful knee extensors who are still in the position to shorten would have to be passively shortened, the eccentrically contracting knee flexors would convert part of the mechanical power delivered by the hip extensors into heat. With the bi-articular hamstrings, these problems can efficiently be avoided, however. Through activation of the hamstrings, the mono-articular vasti are enabled to contribute to positive work despite the fact that the result of this co-activation has to be a net flexing moment. As explained above, the work done by the vasti is now transported to the hip and appears there as hip joint

power. Since the lever arms of the hamstrings are larger at the hip than at the knee (LOMBARD, 1903; K. FISCHER, 1927) the hamstrings will hardly show phases of eccentric actions in these types of concurrent movements, where both joints are simultaneously extended. The same is true for the rectus femoris since here the lever arm at the knee is larger than that at the hip. More reliable data on muscle lengths as a function of hip and knee joint angles will be necessary to be able to determine to what extent eccentric actions can completely be avoided in these types of leg extension. It should be emphasized, however, that the major advantage of these paradoxical co-activation of antagonists is not only the prevention of energy consuming eccentric actions but to a much larger extent the utilisation of the shortening capacity of the mono-articular muscles. Without bi-articular muscles the hip extensors would hardly be able to contribute to external work in the cycling phase of fig. 5a while the vasti would have to be de-activated in the last phase of the downstroke. This means that CLELAND (1867) was right when he said that bi-articular muscles make it possible to utilise the total amount of muscle power by transporting this power to the joints where it can be most effectively applied to meet the specific task demands.

The examples have shown that the intermuscular coordination is much more complicated than what might intuitively follow from the classification of muscles (activate extensors in an extension abductors in an abduction etc.). Apart from "walking" in space, most tasks require a contact with the environment and the control of magnitude and direction of one (or more) external force(s). The question now arises to what extent the versatile system of mono- and bi-articular muscles is always used in the way as it was found for experienced cyclists.

To a certain extent one might follow Aristotle's believe in Nature as Spinoza (1632-1677) did when he said "In nature there is nothing contingent, but all things are determined from the necessity of the devine nature to exist and act in a certain manner". (*Ethics*, Part I, prop. 29; translation W. H. White). From the standpoint of a biomechanist, it would indeed be surprising if we would find that this efficient coordination between mono- and bi-articular muscles would not be found in other movements and other animals as well. Recently, it was found that in an arm task comparable to that of fig. 4a, one observes a co-activation of the bi-articular part of the biceps and the mono-articular part of the triceps while the mono-articular elbow flexors are not activated (GIELEN *et al.*, 1990). This of course fits well in the explanation of co-activation of a mono-articular agonist and its bi-articular antagonist as described for cycling. At present, static ex-

periments are performed where subjects have to exert forces of different directions on a force plate in a position as outlined for cycling (fig. 5). The experiments show that directions with a forward component always show an activation of the rectus femoris with little or no activity of the hamstrings while in those with a backward component the opposite activation occurs. In the literature on muscle activity patterns of walking, running and jumping cats, it can be observed that especially the bi-articular muscles show a task dependent behavior while the mono-articular muscles seem to act as simple force and/or work generators (*e.g.* HOFFER *et al.*, 1987a,b; PERRET & CABELGUEN, 1980; SPECTOR *et al.*, 1980; WALMSLEY *et al.*, 1978). This all might be judged as experimental evidence in favor of a general hypothesis concerning the coordination between mono- and bi-articular muscles as outlined for cycling. Based on this hypothesis some possible implications for the functional morphology of the extremities are discussed.

POSSIBLE IMPLICATIONS

The actions of mono- and bi-articular muscles as explained in this paper may facilitate the understanding of certain aspects of the design of the extremities of different animals. Since the extremities of most animals contain three major segments, there are three sets of mono-articular antagonists and two sets of bi-articular antagonists necessary to be able to control all directions of an external force in a sagittal plane in the efficient way as explained above (fig. 6). During concurrent leg extensions, muscles 7 and 9 can transport power from proximal to distal joints while the transport can take place in opposite direction through activation of muscles 10 and 8. It will not be difficult to realise that a reaction force in the direction of F_3 will require a net extending moment in the hip, a flexing moment in the knee and a plantar flexing moment in the ankle. This requires the activation of the mono-articular muscles 1 and 6 and if the system makes optimal use of the shortening capacity of mono-articular muscles, nr. 3 will be activated as well. To warrant the correct distribution of net moments over the joints the bi-articular nrs. 8 and 9 will also be activated. Since the extending moment in the hip will have to be relatively large while the knee joint moment has to be flexing, the nr. 8 bi-articular muscle has to be well developed if this movement is important for the animal. In most quadrupes the line between the point of force application on the foot and the animal's centre of gravity will point in more forwards direction (like F_3) than what is the case in men (more like F_2). This means that in running, sprinting and jumping, quadrupes will need a reaction force with a line of action which often runs in front of the

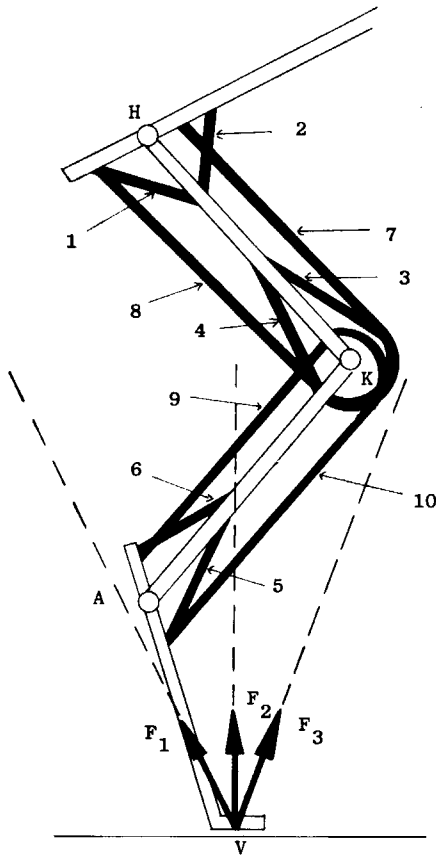


Fig. 6. Possible design of a hindlimb with three joints (H: hip, K: knee and A: ankle) equipped with mono- and bi-articular muscles which should be able to exert an external force on the environment in various directions while the leg is extended. The indicated force vectors are reaction forces.

knee. This may explain why the hamstrings often belong to the hind limb muscles with the largest cross sectional area. A leg extension with a reaction force like F_1 , requires a combination of a flexing moment in the hip, an extending moment in the knee and a dorsi-flexion moment in the ankle. This can be achieved by activation of three mono-articular mrs. 1, 3 and 6 (still coupled to the joint displacements) and the bi-articular mrs. 7 and 10. If the distance AV is small it will, however, hardly occur that the line of action runs behind the ankle joint. This is most likely the reason that nr. 10 is not present in humans.

If the reaction force runs in front of the hip and ankle joint and behind the knee joint (like F_2), one needs extending moments in hip and knee and a plantar flexing moment in the ankle. In this situation one may observe a co-activation of the bi-articular muscles at both sides of the segments. This seems paradoxical since, when expressed in the transport of power terminology, power seems to run around as by an endless chain from hip to knee and vice versa and from knee to ankle and vice versa (LOMBARD, 1903). However, for frogs and men it has been found that the lever arms of hamstrings and rectus femoris are such that both muscles shorten in such concurrent movements (LOMBARD, 1903; K. FISCHER, 1927). This means that co-activation of these two muscles will result in an increase of net joint power of both the hip- and the knee joints. The same effect seems to take place between knee and ankle which led Lombard to the statement: "if the muscles on the front of the lower leg of man crossed over the knee as they do in the frog, how he would break the records" (LOMBARD, 1903). It might be interesting to investigate to what extent the locations of origin and insertion and the lever arms of bi-articular muscles might be associated with the prevention of uneconomical eccentric actions (on the level of contractile elements) in the most essential movements of the various animals.

Active Muscles or Passive Tendons

It is known that in many quadrupeds (such as the horse) the more distal bi- or poly-articular muscles contain little or no muscle fibres. As explained above, the tendinous action of bi-articular muscles make it possible to locate the most powerful (and bulky) muscles close to the trunk. By applying tendons, the distal segments can be build very slender without the weight of muscle. The relatively low moments of inertia associated with these slender segments allow large rotational accelerations which are important for running at relatively low metabolic cost. A disadvantage of the application of tendons in comparison to muscle-tendon complexes, of course, is the absence of the possibility for length adjustments of the bi-articular muscles. This limits the versatility of the system. Animals with predominantly tendinous bi- (or poly-) articular muscles will thus show much more stereotyped movements than animals which can change the length of these muscles. (CLELAND, 1867; LANGER, 1879).

Motor Control

Possibly due to the strong focus on the position detection characteristics of muscle spindles in lengthening muscles which came into use

since Sherrington published his series of papers (*e.g.* SHERRINGTON, 1909), most theories on organisational principles in motor control are focussed on the joint displacements required in different tasks. This, for example, is true for most servo control theories such as the well known equilibrium point hypotheses (*e.g.* FELDMAN, 1986; BIZZI *et al.*, 1982). In these theories the necessity to control the distribution of net moments over the joints is not explicitly accounted for (INGEN SCHENAU, 1989b,c). The position taken here is that these skilled movements are learned on the basis of multi-modal sources of information used for a gradual adaptation of neuronal networks along the lines as for example demonstrated by Hopfield in his simulations of neural networks (HOPFIELD, 1984). For innate movements one can imagine that the architecture of these networks (or pattern generators) is determined genetically. Though sensory (or visual) information may considerably affect the output of such networks (*e.g.* BERKINBLIT *et al.*, 1986) it has been shown that animals can move reasonably well without sensory information (TAUB & BERMAN, 1968; LOEB, 1984) which can be judged as further evidence against servo control theories (INGEN SCHENAU *et al.*, 1990). In the light of the different roles of mono- and bi-articular muscles as shown above, it will be interesting to investigate to what extent the (learning to) control of mono- and bi-articular muscles might be based on different processes (INGEN SCHENAU, 1989b).

FUTURE DIRECTIONS

This review was mainly focussed on one particular category of poly-articular muscles located in the hindleg. Many other types of poly-articular muscles are not discussed such as for example the flexors and extensors of the fingers which produce movement in one direction in all the joints over which they pass (CLELAND, 1867). The main aim of this review, however, was to show how the interaction of the moving animal with its environment may constrain the requirements for the control of joint moments and joint displacements and how co-activations of mono- and bi-articular muscles can help to deal with these constraints. This, of course, is also true for the foreleg. Both inverse as well as direct dynamics (simulations) will be used in the near future in order to validate the hypothesis concerning the actions of bi-articular muscles. Inverse dynamical analyses will be necessary to investigate if the coordination between mono- and bi-articular muscles as predicted on the basis of fig. 6 will hold for different animal actions. Direct dynamics will be necessary in order to predict an optimal leg design for different tasks. For example with respect to the op-

timal lever arms of the mono- and especially the bi-articular muscles but also for more complicated problems such as the background(s) for the variety in segmental lengths (foot, lower leg and thigh). There seems to be a tendency in nature that quadrupeds which can be qualified as good jumpers and sprinters such as the carnivores have rather long thighs and lower legs relative to the length of the metatarsus and poly-articular muscles with substantial muscle bellies while the typical long distance runners like antilopes have relative long slender metatarsi and more tendinous poly-articular muscles along the distal segments. Computer simulations of actions performed by extremities equipped with reliable muscle models (including intrinsic properties of active and passive components) will be one of the most powerful tools in the near future to relate such differences in morphology to function.

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