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The role of the biarticular hamstrings and gastrocnemius muscles in closed chain lower limb extension

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Abstract

The role of the biarticular muscles is a topic that has received considerable attention however their function is not well understood. In this paper, we argue that an analysis that is based upon considering the effect of the biarticular muscles on the segments that they span (rather than their effect on joint rotations) can be illuminating. We demonstrate that this understanding is predicated on a consideration of the relative sizes of the moment arms of a biarticular muscle about the two joints that it crosses. The weight of the previous literature suggests that the moment arms of both the biarticular hamstrings and gastrocnemius are smaller at the knee than at the hip or ankle (respectively). This in turn leads to the conclusion that both biarticular hamstrings and gastrocnemius are extensors of the lower limb. We show that the existence of these biarticular structures lends a degree of flexibility to the motor control strategies available for lower limb extension. In particular, the role of the gastrocnemius and biarticular hamstrings in permitting a large involvement of the quadriceps musculature in closed chain lower limb extension may be more important than is typically portrayed. Finally, the analysis presented in this paper demonstrates the importance of considering the effects of muscles on the body as a whole, not just on the joints they span.

Keywords

musculoskeletal modelling; segment-based approach; moment arm; quadriceps

Introduction

The study of muscular functional anatomy is concerned with understanding the role of individual muscle elements (both individually and in concert with other muscle elements) in creating and resisting movement of the musculoskeletal system. Typically, the musculoskeletal system is conceived as a system of rigid segments that are connected by joints that act as hinges between the segments. The functional anatomy of a muscle element is then described in terms of the inter-segmental joint moments that the muscle tends to create about the “joint hinge”. The bulk of the biomechanics literature has adopted this “joint-based” conception of musculoskeletal function, and biomechanical analyses of motion are described and solved based upon considerations of joint moments and muscle moments.

Recently we have argued [1–5] that it may be more appropriate to utilize a “segment-based” approach to the description and analysis of musculoskeletal function. A segment-based biomechanical analysis is based upon considering the rotation effect that muscle elements, ligaments and joint reaction forces exert upon the segments they span. This approach has the potential to provide an insight as to musculoskeletal function which is in part precluded by joint-based approaches. A key reason for this is that joint-based approaches often do not explicitly include all of the forces that act upon the segments. For instance, it is common that the rotational effects of the joint reaction forces are not explicitly described – instead their effects are implicitly captured by the assumption of the “joint hinge”. Thus, in a joint-based approach, some of the detail as to how the forces created by the muscles create movement is lost. This limitation may be particularly important when considering some of the more complex architecture of the musculoskeletal system. For example, the reaction force between the patella and femur has a strong rotation effect on the femur [5], however this is not included in a standard joint-based approach.

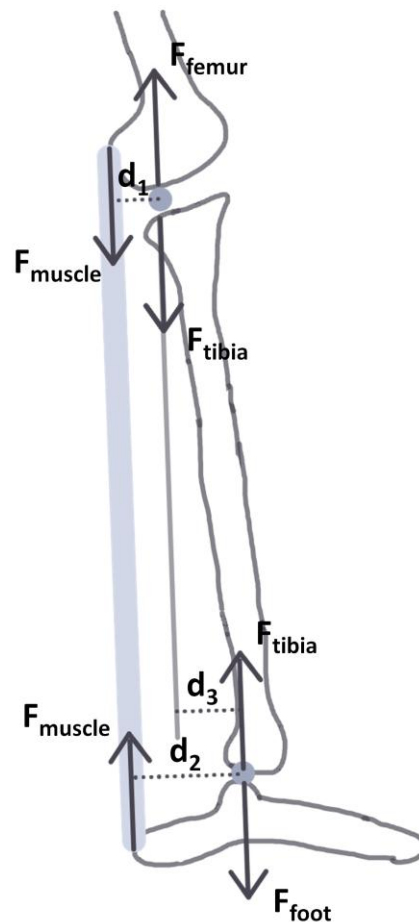
The role of the biarticular muscles of the lower limb is not well understood, and there have been a number of theories advanced to explain their purpose [6–11] (these are described later in more detail). However, as we will show in this article, the use of a segment-based approach to analyze the function of the biarticular muscles can provide further detail as to their role. In particular, in this paper we will use a segment-based approach to analyze the role of the biarticular hamstrings and gastrocnemius during closed kinetic chain lower limb extension (CKE). This choice has been made due to the major role that these biarticular muscles are thought to play in these activities [12,13].

The joint contact forces caused by a biarticular muscle rotate the intermediate segment spanned by the muscle

In a remarkably insightful paper [14] that appears to have largely passed unnoticed by the biomechanics community (with zero citations as measured by standard databases 20 years after publication), Zatsiorsky and Latash described the mechanism by which biarticular muscles create rotations of the segments which they span. Their work is a great illustration of the benefits of employing a segment-based analysis. In particular, the effect of a biarticular muscle can only be properly characterized by considering the joint reaction forces that it creates. As the simplified segment-based analysis in Figure 1 shows, a biarticular muscle creates a rotation of all three segments it spans. The proximal and distal segments are

rotated by the couples created by the line of action of the muscle force in combination with the joint reaction force that it creates. The intermediate segment is rotated solely by the joint reaction forces created by the biarticular muscle.

Figure 1. Rotation of body segments by a biarticular muscle [14] (in this case the action of gastrocnemius is illustrated).



Notes: The thick, light grey line indicates the gastrocnemius muscle, and the grey circles indicate the centres of rotation of the joints. The black arrows indicate the forces created by tension in the muscle where F_{muscle} is the magnitude of the force directly exerted by the muscle, F_{femur} is the joint reaction force acting on the femur, F_{tibia} is the reaction force acting on the tibia, F_{foot} is the reaction force acting on the foot, and $F_{\text{muscle}} = F_{\text{femur}} = F_{\text{tibia}} = F_{\text{foot}}$. The dotted lines d_1 and d_2 indicate the moment arms of gastrocnemius about the knee and ankle joints respectively. The moment arm of the couple created by the joint reaction forces acting on the tibia (d_3) can be seen to be equal to $d_2 - d_1$.

Based upon a consideration of Figure 1, it is apparent that the direction of rotation of the intermediate segment spanned by a biarticular muscle is dependent on the relative size of its moment arms about each joint that it spans. For instance in Figure 1, the moment arm (d_2) of the biarticular muscle about the distal joint is greater than the moment arm (d_1) about the proximal joint. The moment arm of the joint reaction forces on the intermediate segment ($d_3 = d_2 - d_1$, see Figure 1 and Zatsiorsky and Latash [14]) thus causes a counter-clockwise rotation of the segment.

In this paper, we will define an extension moment to be one that rotates a lower limb segment in a direction that is consistent with a lower limb extension. So for instance, in Figure 1 a counter-clockwise rotation of the intermediate segment (the tibial segment) would be defined to be extension and a clockwise rotation to be flexion. In this figure the (illustrated) moment arm of the gastrocnemius is smaller at the superior joint (representing the knee) than at the inferior joint (ankle) which would suggest that the gastrocnemius creates an extension of the tibial segment. However, if the moment arm at the knee was greater than at the ankle then the gastrocnemius would create a flexion of the tibial segment. It is therefore clear that in order to understand the function of the biarticular muscles (and in particular their effect on the intermediate segments that they span) that it is necessary to compare the moment arms of the muscles at the joints they span. One aspect of this paper is therefore to review the previous literature that has quantified the moment arms of two important biarticular muscle groups of the lower limb (the biarticular hamstrings and gastrocnemius) in order to characterise their function in terms of their effects on the intermediate segments they span, and then in turn to propose a fundamental description as to the role of the biarticular muscles that is precluded by a joint-based approach.

The biarticular hamstrings and gastrocnemius are predominantly lower limb extensors

There is a large body of literature that has attempted to quantify the moment arms of the musculature of the lower limb. Interestingly, and probably reflecting the dominance of the joint-based paradigm, a minority of these have evaluated the moment arms of biarticular muscles at both joints that they cross. In addition, the measured moment arm is dependent upon the method used to quantify it [15–17]. Thus to the casual reader of the literature it is not straightforward to ascertain the relative sizes of the biarticular hamstrings' moment arms at the hip and knee, or the gastrocnemius' moment arms at the knee and ankle. This is reflected by confusion as to the relative sizes of these moment arms within the literature. For instance, the moment arm of gastrocnemius has been suggested to be both larger at the knee than the ankle [18] and conversely larger at the ankle than the knee [12,19].

Table 1 summarises some of the moment arms of the biarticular hamstrings that have been reported in the literature. There is a fairly clear trend that suggests that the moment arms at the hip are greater than at the knee. Certainly, this is a relationship which has been assumed in musculoskeletal modelling studies of the human lower limb (see for example van Soest et al. [12]). Equally there is evidence that the same relationship is evident in apes [20], felines [21], the hare [22], the cheetah [23] and the greyhound [24]. (It is worth noting at this juncture that there is some conflicting evidence regarding semitendinosus which is sometimes reported as having a greater moment arm at the knee than the hip [20,25]. If so, this might

The biarticular extensors of the lower limb

suggest a fundamentally different function compared to the other muscles of the hamstring group.)

1 Table 1. Moment arms (mm) of the biarticular hamstrings at the hip and knee joints.

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Study	Hip Range	Comments	Knee Range	Comments
Nemeth & Ohlsen [27]	Mean = 61	MA increases up to 35° of hip flexion and then decreases		
Visser et al. [28]	66 – 94†α	MA increases with increasing hip flexion	11†α	
Herzog & Read [37]				
Biceps Femoris			14 – 27‡α	Variation in relationship between hamstring MA and knee flexion angle for individual hamstring muscles, but average hamstring MA increases until around 100-120° of knee flexion and then decreases slightly
Semitendinosus			-4 – 74‡α	
Semimembranosus			13 – 28‡α	
Wretenberg et al. [38]				
Biceps Femoris			20 – 23‡	Semitendinosus and semimembranosus MAs increase with knee flexion up to 60°
Semitendinosus			29 – 39‡	
Semimembranosus			23 – 30‡	
Buford et al. [39]				
Biceps Femoris			12 – 31†β	MA first increases then decreases with increasing knee flexion in all hamstring muscles, but knee flexion angle of maximum MA varies
Semitendinosus			22 – 48†β	
Semimembranosus			13 – 37†β	
Kellis & Baltzopoulos [40]			24 – 28‡	
Arnold et al. [26]				

Semitendinosus	39 – 72†β	MA first increases then decreases with increasing hip flexion	36 – 49†β	MA first increases then decreases with increasing knee flexion
Semimembranosus	33 – 57†β		33 – 39†β	

† MA determined by tendon excursion method

‡ MA determined by geometric considerations

α Values calculated from regression equations presented in the paper (and where appropriate, reported subject parameters)

β Values estimated from graphical depiction of results in the paper

Table 2. Moment arms (mm) of gastrocnemius at the knee and ankle joints.

Study	Knee Range	Comments	Ankle Range	Comments
Visser et al. [28]	12 – 18†α	• MA decreases with knee flexion		
Rugg et al. [41]			‡	• MA increases with plantar flexion
Klein et al. [42]			53†	
Wretenberg et al. [38]	39 – 42‡			
Buford et al. [39]	16 – 35†β	• MA increases and then decreases with increasing knee flexion		
Maganaris et al. [43]			44 – 70‡	• MA increases with plantar flexion • MA is greater during isometric contraction than when relaxed
Maganaris et al. [15]			42 – 70†‡	• MA increases with plantar flexion • TE and COR methods yield similar values when muscle is relaxed • MA is greater during contraction for COR method only
Maganaris et al. [44]			49 – 60‡	

Magnusson et al. [45]	51‡	
Rosager et al. [46]	55 – 58‡	
Maganaris [47]	51 – 70†	• MA increases with plantar flexion
Maganaris [48]	49 – 63†	• MA increases with plantar flexion
Maganaris [16]	43 – 70†‡	• MA increases with plantar flexion • COR method yields greater MA than TE method • MA is greater during contraction for COR method only
Morse et al. [49]	52‡	
Maganaris et al. [50]	47 – 61‡	
Morse et al. [51]	46†	
Lee & Piazza [52]	31 – 42†	• Sprinters have shorter MAs than non-sprinters
Fath et al. [17]	35 – 57†‡	• MA increases with plantar flexion • COR method yields greater MA than TE method
Karamanidis et al. [53]	42†	
Kongsgaard et al. [54]	43‡	
McCullough et al. [55]	53†	
Baxter et al. [56]	52 – 59‡	• Sprinters have shorter MAs than non-sprinters • No significant differences in MA between contracted and at rest conditions
Hashizume et al. [57]	35 – 56‡	• MA increases with plantar flexion • MA is smaller if measured in 3D than

Sheehan [58]	47 – 56‡	<p>when measured in 2D</p> <ul style="list-style-type: none"> • MA increases when moving from dorsi-flexed to neutral but then drops slightly during plantar flexion from neutral • Measured in 3D and scaled (calculation in 2D was greater but not presented here)
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† MA determined by tendon excursion method

‡ MA determined by geometric considerations

α Values calculated from regression equations presented in the paper (and where appropriate, reported subject parameters)

β Values estimated from graphical depiction of results in the paper

There is a large amount of literature considering the moment arms of gastrocnemius, some of which is summarised in Table 2. Much of this work has been motivated by an interest in the moment arm of the Achilles tendon. Similar to the hamstrings, most studies do not report the moment arm of gastrocnemius at both joints that it spans. Despite this, there is still a clear trend for the moment arm at the ankle to be greater than that at the knee. Again, this has been assumed in musculoskeletal modelling studies [12,19] and is replicated in the animal kingdom [20,22–25].

The relative sizes of these moment arms suggest that the effect of the hamstrings is to cause an extension of the femur, and the effect of the gastrocnemius is to cause an extension of the tibia (see Figure 1). As we have seen, there is a fairly large weight of literature that suggests that this is a consistent function that is also evident in many animal models. Thus we can summarize the following: the hamstrings extend the pelvis and femoral segments and flex the tibial segment; whereas, gastrocnemius flexes the femoral segment and extends the tibial and foot segments (Table 3).

Table 3. A summary of the rotation effects of the biarticular muscles.

Muscle	Rotation effect on:		
	Proximal segment	Intermediate segment	Distal segment
Biarticular hamstrings	Extension	Extension	Flexion
Gastrocnemius	Flexion	Extension	Extension

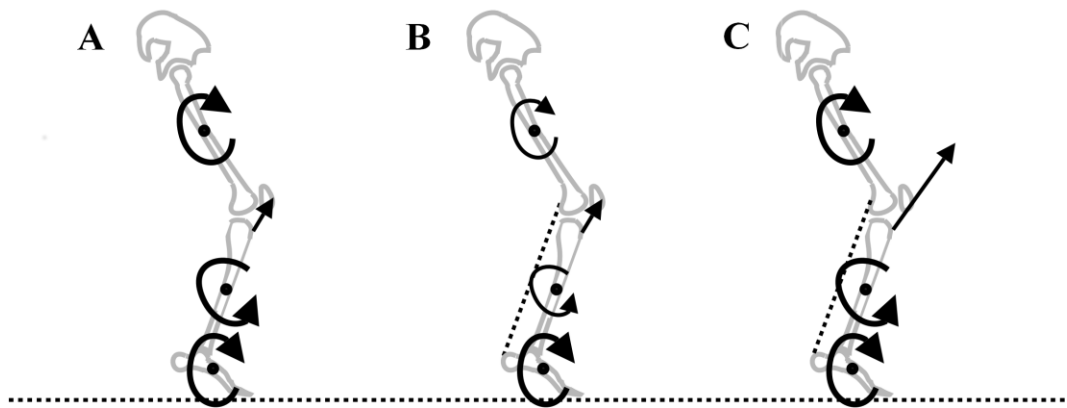
Force in the biarticular hamstrings and gastrocnemius requires that the quadriceps play a greater role in CKE

In order to understand the mechanism by which the biarticular muscles provide an advantage we consider an athlete performing a vertical jump. We will only consider the propulsive part of the movement – that is from the point that the athlete has flexed their lower limb to prepare for the extension phase (the propulsive phase of the vertical jump is a common CKE task). In addition we will ignore the upper body, and consider it simply as a point mass sitting atop of the pelvis. In order to execute the vertical jump the athlete must extend the pelvis, femoral, tibial and foot segments. Our analysis will consider how the musculature of the lower limb can create an extension of all of these segments, by considering each in turn. It should be emphasized that in the analysis below it is assumed that the moment required to rotate each segment is known – the analysis then considers how this moment can be achieved by the relative activity of the musculature of the lower limb. Equally, the case when the limb is activated by purely monoarticular muscles is contrasted with the situation when there are also biarticular muscles.

Extension of the foot segment can be achieved by activity of either the monoarticular ankle extensors (e.g. soleus) or the biarticular gastrocnemius. The use of either monoarticular or biarticular musculature to extend the foot segment will in turn create an extension of the tibial segment. The magnitude of the extension moment exerted on the tibial segment by the monoarticular muscles will be equal to the extension moment exerted on the foot segment

(this is a well known property of the monoarticular muscles). However, the magnitude of the extension moment exerted on the tibial segment by gastrocnemius will be less than it exerts on the foot segment (Figures 2A and 2B). This is a direct consequence of the fact that the moment arm of gastrocnemius on the tibial segment is the difference between its moment arm at the ankle and knee (as described earlier). Thus recruitment of the gastrocnemius to extend the foot results in a smaller extension moment being applied to the tibial segment than would be applied if only monoarticular muscles fulfilled this role.

Figure 2. The role of gastrocnemius in CKE.



Notes: Figure 2A depicts an extension of the lower limb by monoarticular muscles alone. Now, assuming the same moment must be exerted on each segment, Figure 2B shows that if gastrocnemius is recruited (and as the sum of the moments exerted by gastrocnemius and the monoarticular ankle extensors on the foot must be the same as in Figure 2A) then the net moment exerted on the tibial and femoral segments is reduced (as gastrocnemius will exert less of a rotation effect on the tibial segment than the monoarticular ankle extensors, and as gastrocnemius will exert a flexion moment on the femoral segment). Figure 2C shows that an increased recruitment of the quadriceps musculature can compensate for these reduced moments such that the required (original) moments are exerted on each segment.

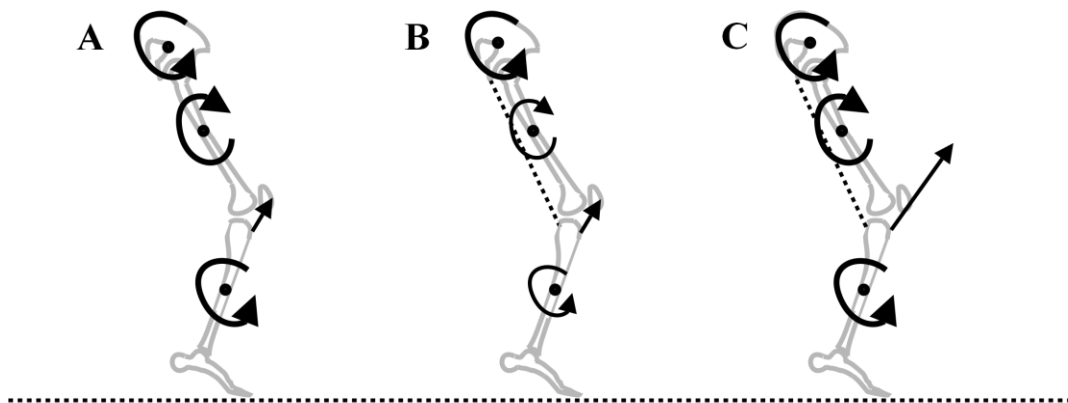
The fact that recruitment of the gastrocnemius results in a smaller extension moment being applied to the tibial segment by the ankle extensors means that, if there is a requirement for a given extension moment to be applied to the tibia, then the reduced contribution of the mono- and biarticular extensors of the ankle must be compensated for by other musculature. For the tibial segment this implies a need for an increased moment applied to the tibia by the patellar tendon. That is, that the presence of the gastrocnemius results in an increased imperative for force in the quadriceps to extend the tibial segment (Figure 2C). Of course, force in the gastrocnemius also imposes an undesirable flexion moment upon the femoral segment. However, the increased force in the quadriceps musculature (to provide the compensatory extension of the tibia) will in turn create an increased extension moment upon the femoral

segment (Figure 2C). The resultant effect of these competing moments will be determined by the relative moment arms of the gastrocnemius and the extensor mechanism of the quadriceps.

As an interesting aside, the extensor apparatus of the quadriceps does not function as a monoarticular muscle. We have recently shown that with increasing knee flexion, the moment exerted upon the femoral segment by force in the quadriceps is greater than the moment exerted on the tibial segment by the same force [5]. This consequently suggests that an increased use of the quadriceps to extend the tibial segment at deeper knee flexion angles results in an even greater extension of the femoral segment, which will in turn provide a greater ability to compensate for the flexion moment imposed by gastrocnemius on the femoral segment.

A similar argument can be advanced to understand the role of the biarticular hamstrings in lower limb extension (Figure 3). If the biarticular hamstrings are preferentially recruited (instead of the glutes) to extend the pelvis then a smaller extension moment is applied to the femoral segment. This must be compensated by an increased extension moment applied by the quadriceps, which will in turn offset the flexion penalty that the biarticular hamstrings impose upon the tibial segment.

Figure 3. The role of the biarticular hamstrings in CKE.



Notes: Figure 3A depicts an extension of the lower limb by monoarticular muscles alone. Now, assuming the same moment must be exerted on each segment, Figure 3B shows that if the biarticular hamstrings are recruited (and as the sum of the moments exerted by the biarticular hamstrings and the monoarticular hip extensors on the pelvis must be the same as in Figure 3A) then the net moment exerted on the femoral and tibial segments is reduced (as the biarticular hamstrings will exert less of a rotation effect on the femoral segment than the monoarticular hip extensors, and as the biarticular hamstrings will exert a flexion moment on the tibial segment). Figure 3C shows that an increased recruitment of the quadriceps musculature can compensate for these reduced moments such that the required (original) moments are exerted on each segment.

Thus we can see that the presence of the biarticular muscles requires a greater use of the musculature of the thigh (specifically the quadriceps, but also the hamstrings) in creating extension in CKE activities. The biarticular musculature of the posterior aspect of the lower limb therefore grants a flexibility to the motor control strategies available to the lower limb - requiring the use of the quadriceps to be increased in CKE tasks. For instance, if the lower limb was only actuated by monoarticular extensors and given a defined extension requirement of the tibia, then the activity of the monoarticular knee extensors would be tightly linked to the activity of the monoarticular ankle extensors (and vice versa). This is because the monoarticular ankle extensors would be the only potential rotators of the ankle, and thus their contribution to the rotation of the tibia would be fixed by the requirements of foot rotation. The only remaining extensors of the tibia would then be the monoarticular knee extensors, which would provide the remainder of the extension moment. In this case therefore, the activity of quadriceps is constrained by the need for the monoarticular ankle extensors to rotate the foot. Thus the presence of the biarticular muscles requires a greater relative involvement of the quadriceps by reducing the constraint provided by the need for the monoarticular extensors of the ankle and hip to rotate the foot and pelvis respectively.

Changes in moment arms with joint flexion and extension

So far the analysis we have presented is based upon the assumption that the moment arms of the biarticular muscles considered remain constant. However, the data presented in Tables 1 and 2 clearly demonstrates that this is not the case – there is a relationship between the moment arm of a muscle about a joint and the flexion/extension angle of the given joint. It is important therefore to consider how this relationship might affect the function of the biarticular muscles with respect to the ideas presented above.

The data presented in Table 1 suggests that the moment arm of the biarticular hamstrings about the hip joint firstly increases as the hip is flexed from a neutral position. The data of Arnold et al. [26] and Nemeth and Ohlson [27] then suggest that from about 35-50° of hip flexion the moment arm then decreases with increasing hip flexion, whereas the data of Visser et al. [28] suggests that the moment arm continues to increase up to 80° of hip flexion (it should be noted that the methodology of Visser is based upon the assumption that the relationship between moment arm and joint angle can be described by a linear equation and so a curvilinear relationship would not be captured by their methodology). Similarly, the data in Table 1 suggests that the moment arm of the biarticular hamstrings about the knee, also increases then decreases with increasing knee flexion angle, although there is quite a lot of variation in the angle at which the turning point occurs. What is most important to note for the biarticular hamstrings is that for the majority of the research presented the ranges of the moment arms at the hip and knee show little overlap. That is, that the lower end of the hip moment arm range is generally greater than the higher end of the knee moment arm range. This would suggest that the biarticular hamstrings consistently act as extensors of the femur, although the strength of this effect may vary with hip and knee flexion. For instance, if the hip is in a neutral position, but the knee is flexed to around 80° the moment arms at the hip and knee may be quite similar (the data of Arnold and colleagues [26] which compared moment arms at both knee and hip may even indicate that the moment arm of semitendinosus at the knee is greater than at the hip in this position). It is unlikely that the limb would exhibit this posture in typical CKE activities where the knee and hip are both flexed. However, this may be a pattern that is useful in gait. For instance, at toe off the hip is

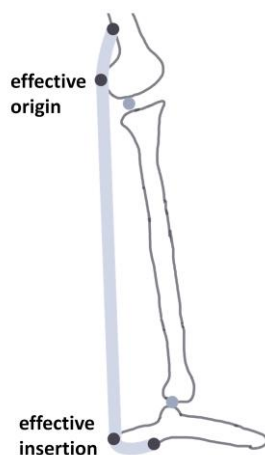
extended with the knee flexed, and the femur segment is rotating in the flexion direction (as defined in this paper).

The data presented in Table 2 demonstrates a similar pattern for the gastrocnemius. In particular, there is again little overlap between the ranges of the values for the moment arms of gastrocnemius at the knee and ankle (with the moment arm at the knee being consistently smaller than at the ankle). There are some discrepancies in the literature as to the dependence of the moment arm at the knee on knee flexion angle, but a fairly consistent trend that suggests that the moment arm at the ankle increases with ankle plantar flexion. Similar to the biarticular hamstrings, this then indicates that gastrocnemius is also a consistent extensor of the tibia, but that the strength of this effect is dependent on joint position. For instance, the effect may be weaker with the knee flexed and the ankle dorsiflexed. This pattern is consistent with some common CKE activities – for example, when ascending out of a squatted position (where the limb will have this posture), there is more rotation of the femur than the tibia [5].

Limitations

It should be noted that the analysis in this paper is based upon the assumption that the biarticular muscles can be represented as straight line elements between origin and insertion, and that the joint reaction forces at the proximal and distal ends of the intermediate segment are therefore parallel. This analysis therefore does not entirely encapsulate the behaviour of biarticular muscles that wrap around bony, muscular or other soft tissue structures. Despite this, this simple model still has utility in understanding the function of biarticular muscles. For instance, the muscle might wrap around structures that are functionally part of either the proximal or distal segment, but not connect with the intermediate segment. In this case, provided the moment arms have been calculated based upon the effective origins and insertions of the muscle (that is the points at which the muscle finally loses contact with the proximal or distal segment respectively) then the analysis presented here is entirely valid as the effective line of action of the muscle is straight (Figure 4).

Figure 4. Wrapping of a biarticular muscle around musculoskeletal structures.



Contrasting joint-based and segment-based analyses

We have characterized the biarticular hamstrings and gastrocnemius as lower limb extensors. For instance, the biarticular hamstrings are extensors of the pelvis and femur, and flexors of the tibia (however, the flexion effect on the tibia can be off-set by increased recruitment of the quadriceps). This is a somewhat different interpretation as to the function of this musculature as compared to a joint-based analysis. In particular, a joint-based analysis would characterize the biarticular hamstrings as extensors of the hip and flexors of the knee. This gives a more ambiguous picture of their function – it is less clear whether they predominantly serve as lower limb extensors or flexors in CKE.

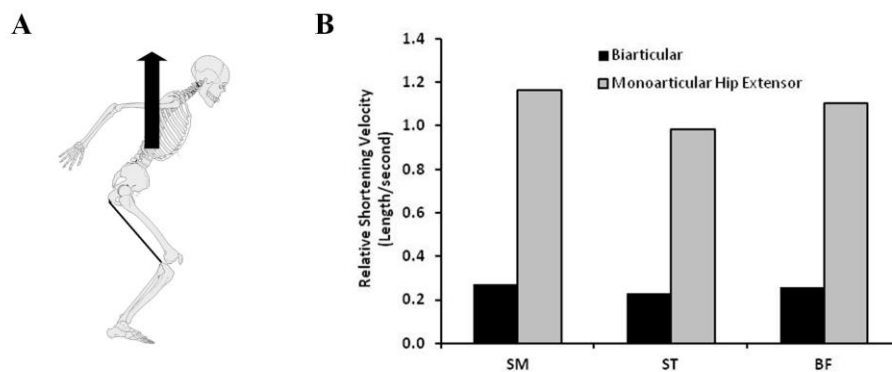
A number of possible reasons for the presence of biarticular muscles have been proposed (generally based upon joint-based considerations), although there are three that have a sound mechanical basis, and which we will now consider in turn. The first explanation is that the biarticular muscles allow the transfer of power from proximal to distal joints [6–8,29]. For instance, a joint-based analysis of the action of gastrocnemius would suggest that work done extending the knee can be expressed as ankle extension. This transfer of power has a number of advantages. Firstly, it means that musculature can be kept closer to the trunk and the extremities can have a lower mass making them easier to accelerate [30]. Secondly, the transfer of power between the joints allows the timing of full extension to be optimised (for instance, in vertical jumping allowing the knee to reach full extension at the point that the foot leaves the floor) [31]. Finally, activation of the biarticular muscles to transfer power between the joints allows the direction of the external force vector to be controlled in a way that is not possible if the limb is solely powered by monoarticular muscles [29–33]. A segment-based analysis is consistent with these ideas - as the moment arms of both hamstrings and gastrocnemius are smaller at the knee, the effect of both muscles is to allow increased activity of the monoarticular knee extensors (which arguably does allow musculature to be kept closer to the trunk). This could be characterized as a transfer of the power generated by the quadriceps to both the hip and ankle, which in turn allows the extension of the knee and the direction of the external force vector expressed at the foot to be optimised.

The second explanation is that they enhance the stability of the musculoskeletal system [9]. Specifically, their presence permits a co-contraction of the musculature around joints arguably without penalty. This explanation is in accord with the analysis presented here. For instance, force in the gastrocnemius causes a necessity for greater quadriceps recruitment to extend the tibial segment (as we have seen). The flexion moment imposed upon the femoral segment by force in gastrocnemius is ameliorated by the activity of the quadriceps. Hence there is co-contraction of the musculature crossing the knee (and thus greater stability).

The third idea is that they reduce the need for as great a length change of the muscles (i.e. a lesser degree of shortening) during many activities, resulting in lower contraction velocities and allowing the muscles to produce higher forces [10,11] with a greater efficiency of contraction [34]. For instance, Figure 5 suggests that the velocity of contraction of the biarticular hamstrings during vertical jumping is approximately a quarter of the value required if they were monoarticular. If this result is interpreted in terms of the previously reported force-velocity relationship of muscle [35] it suggests that the biarticular muscles can

express approximately three times the force of their monoarticular analogue. This advantage is again commensurate with the depiction of biarticular muscle function presented here (although it should be noted that a minimal length change in a biarticular muscle still requires length changes in other muscles). The results presented here suggest that higher forces in the biarticular muscles as a result of slower contraction velocities allow a greater recruitment of the quadriceps muscles. This picture of lower limb extension function is commensurate with the great capability that the quadriceps muscle group has for creating extension moments, both in terms of its size and its structure.

Figure 5. Relative shortening velocity of biarticular muscles during vertical jumping and their hypothetical monoarticular analogues.



Notes: SM=semimembranosus; ST=semitendinosus; BF=biceps femoris (long head); the biarticular hamstrings muscle group is indicated by the solid line in Figure 5A. The analysis here is based upon the musculoskeletal geometry of the Klein Horsman et al. [36] data set and the moment arms of Arnold et al. [26] for a jump of 0.2 s in duration.

Conclusions

In this article we have shown how a segment-based analysis of the biarticular hamstrings and gastrocnemius leads to a refined picture as to their function in CKE. In particular, we have advanced the novel proposition that the role of this musculature is to grant flexibility to the motor control strategy, requiring a greater involvement of the quadriceps musculature in extension of the lower limb. As we have shown in this paper, without the biarticular muscles the involvement of the quadriceps would be constrained by the rotation requirements of other segments. This observation is in accord with previous literature that has demonstrated that the biarticular muscles permit a greater involvement of the quadriceps in CKE activities. This adaptation is advantageous to many CKE tasks in permitting the large proximal muscle groups to play a greater role without sacrificing the ability to control the external forces expressed by the limb. We have also demonstrated the importance of an understanding of the

relative sizes of the moment arms of the biarticular muscles and suggest that future anatomical studies should seek to quantify this in a range of muscles and species.

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