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The patella: A mechanical determinant of coordination during vertical jumping

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Highlights

- The geometry of the patellar mechanism changes as the knee extends

- A femoral to tibial pattern of moment production is seen during vertical jumping

- The changing geometry of the patella can explain 93% of the variance in the pattern

- Mechanical considerations are important in the organisation of movement

Highlights

Article

The patella: A mechanical determinant of coordination during vertical jumping

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Abstract

The patella is traditionally understood to be a "joint spacer" that increases the moment arm of the patellar tendon. This characterisation is unsatisfactory as it fails to explain the more interesting characteristics of the patella: 1) that the changing pivot point of the patella causes the ratio of quadriceps to patellar tendon force to almost double as the knee flexes; 2) that the patellar tendon exerts an anteriorly directed force on the tibia when the knee is extended but this switches to a posterior draw as the knee flexes; and 3) that the presence of the patella allows the quadriceps to exert different moments on the femur and tibia. Here, I use a simple, model of the geometry of the knee to calculate the changes in the effective moment arms of the quadriceps on the femur and tibia as the knee extends during vertical jumping. These effective moment arms are then contrasted with the actual changes in moments seen during a vertical jump. This analysis demonstrates that the changing geometry of the knee alone can explain 93% ($p < 0.05$) of the variance in the characteristic femoral to tibial pattern of moment production during jumping – suggesting that the mechanics of the patella have a crucial influence on the coordination of jumping. These results lend support to the contention that mechanical considerations play a pivotal role in the control of movement by creating a stronger imperative towards a particular movement solution than might be suggested by the large degree of redundancy in the neuromuscular system. This idea is consistent with dynamic systems theories of motor control, i.e. the mechanical structure of the musculoskeletal system itself is important in the organisation of movement (so called mechanical intelligence).

Introduction

The presence of the patella in the human lower limb is normally explained by reference to its action as a "joint spacer" – that is that the existence of the patella increases the moment arm of the quadriceps muscle group about the tibiofemoral joint (Amis and Farahmand, 1996; Gwinner et al., 2016; Kaufer, 1971; Vanlerberghe et al., 2018). However this rationale, although true, is somewhat unsatisfactory as it fails to explain three of the most interesting characteristics of the functional anatomy of patellofemoral joint (Cleather et al., 2014; Regnault et al., 2017; Soo Im et al., 2015). This is particularly surprising as these aspects of the anatomy of the patellofemoral joint have been clearly described in literature dating back at least 40 years (and that is described below). In this article, I draw on our previous work (Cleather et al., 2014) in order to show how these characteristics may contribute to the motor control movement.

The first characteristic of the patellofemoral joint which is not explained by the proposition that the patella is a joint spacer is the fact that the patella acts as a lever. Furthermore, as the patella tilts and translates relative to its articular surface on the trochlea, the position of the pivot point on the posterior surface of the patella changes as the tibiofemoral joint flexes (Bishop and Denham, 1977; Buff et al., 1988; Gill and O'Connor, 1996; Huberti et al., 1984; van Eijden et al., 1986), which in turn produces a changing relationship between the tension in the quadriceps and patellar tendons (this has been well established in both experimental (Bishop and Denham, 1977; Buff et al., 1988; Huberti et al., 1984) and in silico work (Gill and O'Connor, 1996; van Eijden et al., 1986)). The nature of this change is profound: at or near full extension the tension in quadriceps and patellar tendons is approximately equal, whereas at around 120° of tibiofemoral flexion the tension in the quadriceps tendon is almost double that of the patellar tendon (Mason et al., 2008).

The second interesting characteristic of the patellofemoral joint is that the changing position of the patella results in a change in the orientation of the patellar tendon relative to the tibia, and that this relationship is again mediated by the degree of tibiofemoral joint flexion (DeFrate et al., 2007; Herzog and Read, 1993; Varadarajan et al., 2010). Again, the effect of this change is profound: when the knee is more extended the line of the patellar tendon is orientated anteriorly relative to the tibia and tends to load the anterior cruciate ligament, however, this angle decreases approximately linearly with tibiofemoral flexion such that the direction of pull of the tendon switches to a posterior orientation that loads the posterior cruciate ligament at a tibiofemoral angle somewhere between 60° and 90°.

The final characteristic of the patellofemoral joint which is of relevance to this discussion is the fact that the presence of the patella means that the vastus muscle group cannot be considered as a simple monoarticular muscle. For most monoarticular muscles it is common to assume that they exert equal and opposite moments on the two segments to which they attach – this is a reasonable assumption based upon a "joint based" analysis (i.e. considering that a muscle creates a moment about a joint that is equal to the product of the muscle's moment arm about the centre of rotation of the joint it spans and the tension in the muscle (Cleather and Bull, 2012)) and Newton's third law. However, because the patellar tendon attaches to the patella rather than directly to the femur, such an assumption does not hold for vastus (although it is often still employed (Arnold et al., 2010; Correa et al., 2011; Ogihara et al., 2009)). Instead, in order to understand the effect of tension in vastus it is more appropriate to employ a segment based analysis where the effect of a muscle on a segment is calculated by considering the rotation effect of all the individual forces that act on the segment (Cleather and Bull, 2012; Zatsiorsky and Latash, 1993). In our previous work we used a simple two dimensional, segment based, geometrical model of the lower limb to show

that the presence of the patella means that tension in the vastus muscle group can produce quite different rotation effects on the femur and tibia (Cleather et al., 2014). Again, this is a profound difference that means that the function of vastus is fundamentally distinct from other monoarticular muscles.

When considered together, the combination of these three characteristics mean that the effect of tension in the vastus muscle group is highly dependent on the tibiofemoral knee flexion angle. In our previous work, we showed that when the tibiofemoral joint is more flexed that tension in vastus tends to preferentially exert a rotational effect on the femur, whereas when the joint is more extended tension in vastus creates rotation of both femur and tibia (Figure 1; Cleather et al., 2014). This is qualitatively easy to understand from the above discussion. For instance, when the tibiofemoral joint is flexed to an angle of between 60° and 90° the orientation of the patella is close to parallel to the longitudinal axis of the tibia, meaning that its ability to provide a rotation moment to the tibia is diminished. At the same time, in this position a greater amount of tension in the quadriceps tendon is required to produce a given amount of tension in the patellar tendon than when the tibiofemoral joint is near full extension. This in turn means that the rotation of the tibia will be relatively weaker (as the muscular force that acts on the tibia is impressed by the patellar tendon) than the rotation of the femur (which is rotated by the force in the quadriceps tendon).

In our previous work (Cleather et al., 2014) we speculated that the variation in the rotation effect of vastus which is created by the presence of the patella is consistent with the characteristic proximal to distal pattern of movement found in many lower limb extension activities. The primary purpose of this study was therefore to test this idea within one of the most fundamental lower limb extension activities – the vertical jump. I hypothesized that the geometry of the patella would be significant in explaining the variance in the moments

exerted on the femur and tibia. The most viable alternative to this hypothesis is that the distinctive pattern of moments is principally created by the central nervous system in precisely controlling the activation of the individual muscle units. The secondary purpose of the study was to extend our previous model to include the rectus femoris muscle within the same analysis.

Methods

This study is essentially a geometrical study of the patella mechanism. Firstly, a simple two dimensional musculoskeletal model of the knee extensor mechanism is used to evaluate the effective moment arms of tension in the vastus and rectus femoris muscle groups, following the example of our previous work (Cleather et al., 2014) based upon purely geometrical assumptions. The change in these effective moment arms is then compared with the actual pattern of moment production seen in vertical jumping (in particular during the propulsive phase) in order to evaluate the influence of the patella on coordination during jumping.

Model Description

The model used in this study is extended from a model that we have presented previously (Cleather et al., 2014). The model is posed only in the sagittal plane and consists of pelvis, femur, tibia and patella segments. The tibia is fixed in the global frame, and the knee is flexed by rotating the femur around the tibia in 5° intervals. There are no external forces acting on the system and the only forces that act on each segment are those that arise due to 1N of tension in either the vastus or rectus femoris muscle groups (the effect of vastus and rectus femoris are calculated separately). For the purposes of this model we consider it acceptable to model the vastus with just one line element as our interest is only in the

geometry of the saggital plane. The muscle-tendon forces and the ligament and joint reaction forces that oppose the forces in vastus or rectus femoris (Figure 2) are calculated based upon the assumption that in each position each segment is in force and moment equilibrium (this is a valid assumption as we are simply interested in the geometry which will likely be very similar under dynamic conditions). In addition, segments are considered to be of zero mass and joints to be frictionless. The effective moment arm of tension in either vastus or rectus femoris is defined to be the external moment that would need to be applied to either the femur or tibia in order to maintain its moment equilibrium.

The geometry of the model is defined by reference to previous work (Figure 3). Firstly, the line of action of the patellar tendon (π) and the anterior and posterior cruciate ligaments relative to the longitudinal axis of the tibia are calculated as a function of tibiofemoral flexion angle (κ) using the data of Herzog and Read (Herzog and Read, 1993). The patella tilt relative to the femur (ρ) is defined relative to tibiofemoral flexion angle based on the work of Nha and colleagues (Nha et al., 2008). Finally, the angle of the line of action of vastus relative to the femur (μ) is a constant that is taken from the data set of Klein Horsman and colleagues (Klein Horsman et al., 2007). Now, given the four angles identified above, the angles of incidence of vastus (α) and the patellar tendon (β) on the patella can be determined based upon the geometry (Figure 3) for each tibiofemoral flexion angle. This in turn then allows the ratio of patellar tendon (P) to vastus (Q) force to be calculated from Equation 1 (based on the assumption that the patella is in static force and moment equilibrium):

$$\frac{P}{Q} = \frac{\cos \alpha}{\cos \beta}$$

... Equation 1

For rectus femoris, the analysis is markedly similar. The origin and insertion of rectus femoris is also taken from the Klein Horsman data (Klein Horsman et al., 2007). The main difference is that the angle of rectus femoris relative to the femur varies with hip flexion angle, resulting in a different P/Q ratio for rectus femoris.

Next, the origins and insertions of muscles and ligaments and the contact points between segments are defined, again using the data of Klein Horsman and colleagues (Klein Horsman et al., 2007). The following assumptions are made:

1. The contact position of the femur on the tibia remains fixed (within the tibial frame) throughout tibiofemoral flexion;

2. The contact position of the tibia on the femur is a function of tibiofemoral flexion angle. The articular surface of the femur is modelled as a circle and the femur is assumed to rotate and translate relative to the tibia in order that this circle remains in contact with the tibia;

3. The contact position of the patella on the femur is also a function of tibiofemoral flexion. This articular surface (representing the trochlea of the femur) is also modelled as a circle;

4. The vastus tendon is assumed to wrap around the circle representing the trochlea from 85° of tibiofemoral joint flexion. The rectus femoris tendon wraps around the trochlea from 95° of tibiofemoral joint flexion – this angle is based on the assumption that after wrapping around the trochlea the geometry of vastus and rectus femoris tendons are the same.

5. The contact position of the pelvis with the femur is fixed on the femur.

Finally, the forces and moments that arise due to tension in vastus and rectus femoris can be determined, again based on the following assumptions:

6. Force in either vastus or rectus femoris is 1N. The consequent tension in the patellar tendon is determined from Equation 1;

7. The cruciate ligaments are the sole restraint to anterior/posterior shear of the tibia relative to the femur and thus their loading is a direct result of tension in the patellar tendon. Of course, such an assumption neglects the fact that some of these shear forces would be borne by other ligaments, the joint capsule or the articular surfaces of the tibiofemoral joint. However, as all of these structures are a similar distance from the centre of mass of femur or tibia, the difference in the moment exerted is small.

8. The tibiofemoral contact force is equal and opposite to the sum of the patellar tendon and cruciate ligament forces and is directed through the centre of mass of the tibia;

9. The patellofemoral joint contact force is calculated from the vastus/rectus femoris force and the patellar tendon force based on the assumption that the patella is in force equilibrium, following the example of previous authors (van Eijden et al., 1986);

10. The hip joint contact force is equal and opposite to the tension in rectus femoris;

11. Forces create rotation of a segment about its centre of mass (the position of the centre of mass is taken from the Klein Horsman (Klein Horsman et al., 2007) data);

12. In this work, moments that act to extend the lower limb are positively valued, and moments that tend to flex the lower limb are negative.

Vertical Jump Data

The vertical jumping data used in this study are taken from Bobbert and van Ingen Schenau (1988). Firstly, the time series data for the ground reaction force, joint angles, joint moments and electromyography during vertical jumping were obtained by digitizing Figures 4, 5 and 7

of the article using Digitizeit (version 2.1.3; I. Bormann, Am Rohrbruch 41, 38108 Braunschweig, Germany; www.digitizeit.de; Figure 4). The raw moment data were then interpolated to produce time series data at regular intervals of 5 ms using the spline function of MATLAB® (R2015b; The MathWorks Inc, 1 Apple Hill Drive, Natick, MA 01760, United States). Finally, the mean joint moments were used to calculate the net moments acting upon the femoral and tibial segments, and these data were plotted relative to both time and knee flexion angle.

Statistical Analysis

The knee and hip joint angles taken from the Bobbert and van Ingen Schenau data (Bobbert and van Ingen Schenau, 1988) were used to find the effective moment arms of vastus and rectus femoris on femur and tibia (based on the geometry of the model) for the period of the jump where the knee was extending. The weighted average of the two effective moment arms was calculated based on their relative strength (Narici et al., 1992). Simple linear regression was used to find the relationship between the effective moment arms predicted by the model and the actual moment arms observed by Bobbert and van Ingen Schenau.

Results

The segmental moments derived from the Bobbert and van Ingen Schenau paper (Bobbert and van Ingen Schenau, 1988) for the period when the knee was extending (i.e. from -0.225s to take off at 0s) are plotted as a function of knee joint angle in Figure 5 (given that the focus of this study is on evaluating how the changing geometry of the patellofemoral joint that is commensurate with changes in tibiofemoral joint angle affects moment production). The difference between femoral and tibial extension moments decreased steadily as the knee

extended from approximately 104° to 52° (this change means that the tibial extension moment relative to the femoral extension moment was increasing – i.e. the proximal to distal pattern that was expected) and this trend only reversed in the last 0.05s of the jump, when the ground reaction force had already begun to rapidly decrease.

The effective moment arms of vastus on the tibial and femoral segments as a function of knee joint angle are illustrated in Figure 6A. As the knee extends during the propulsive phase of the jump, the effective moment arm on the tibial segment increases while the effective moment arm on the femoral segment decreases. The difference between these effective moment arms is also illustrated in Figure 6A, and it is clear that the greatest increase in the effective moment arm on the tibial segment relative to the femoral segment (as represented by a decreasing difference) occurs between a knee flexion angle of 40° and 80°. This difference is contrasted with the change in femoral/tibial extension moments experienced during vertical jumping taken from the Bobbert and van Ingen Schenau data (Bobbert and van Ingen Schenau, 1988) (in the right hand side panel of Figure 6A). The differences between tibial and femoral moments and effective moment arms are qualitatively similar from 104° to 56° of knee flexion, and are most notably similar between -0.10s and -0.05s.

A similar pattern is seen when considering rectus femoris (Figure 6B) – as the knee extends during the propulsive phase of the jump the effective moment arm on the tibial segment increases whereas the effective moment arm on the femoral segment decreases. However, there are two major differences. Firstly, the decrease in the effective moment arm on the femoral segment is much more pronounced when the knee is most flexed. Secondly, once the knee straightens past 80°, the effect of tension is to create flexion (not extension) of the femoral segment. Again, the difference in effective moment arms is illustrated in Figure 6B. It is clear that for rectus femoris there is a quite different pattern – the greatest change in the

effective moment arm on the tibial segment relative to the femoral segment occurs between approximately 80° and 104° degrees of knee flexion with a smaller change between 40° and 80°. Again there are qualitative similarities with the Bobbert and van Ingen Schenau data (Bobbert and van Ingen Schenau, 1988), but in this case there are greater similarities between -0.225s and -0.10s. The data in Figure 6 is also included in the supplemental information.

In Figure 7, the difference in the combined (weighted based upon the relative strengths of vastus and rectus femoris) effective moment arms of the complete quadriceps muscle group on the femoral and tibial segments at a given knee joint angle are plotted against the actual differences in moments reported by Bobbert and van Ingen Schenau (Bobbert and van Ingen Schenau, 1988) at the same joint angle (for the period from -0.225s to -0.05s). The two measures are highly correlated with the difference in the effective moment arm of the complete quadriceps muscle group accounting for 93% of the variation in the difference between the actual segmental moments ($R^2 = 0.926$; $p < 0.01$).

Discussion

The purpose of this study was to test the hypothesis that the patella plays a role in influencing the motor control of movement. The results of this study tend to support this hypothesis. In particular, these results demonstrate that the characteristic pattern of proximal to distal moment production observed in vertical jumping (at least from femur to tibia) could to a large part be explained simply by the presence of the patella and the changing geometry of the patellofemoral joint with changes in tibiofemoral joint angle. Such a result is of importance to the understanding of the control of human movement.

The mechanisms and motor control of movement are conundrums that have also fascinated researchers. The musculoskeletal system is a complex mechanical system with a great many degrees of mechanical freedom (Bernstein, 1967; Latash, 2012). Our principal mechanism for control of this system is through the coordinated activation of hundreds of muscles − that is, we have a control mechanism that also has a large number of degrees of freedom. The calculation of the particular sequence of activation of motor units that produces smooth coordinated motion and performing such calculations in fractions of a second is a problem that remains challenging even for current computing technologies, and so the way in which the brain is able to achieve this feat is largely a mystery - although a variety of potential theories have been advanced (Feldman, 1986, 2016; Latash et al., 2010; Latash, 2012; Scholz and Schöner, 1999, 2014). The results of this study, are consistent with hypotheses of motor control that relate to "mechanical intelligence" (Blickhan et al., 2007; Full et al., 2002; Full and Koditschek, 1999). In particular, that the mechanical arrangement of the musculoskeletal system itself can effectively reduce the number of degrees of freedom available in movement, by providing a strong mechanical imperative for a particular movement strategy. The results of this study lend weight to dynamic systems theories of motor control and movement − that is the idea that movement is the result of self organisation based upon the nature of the system and its environment (Schaal et al., 2007; Taga, 1995). Clearly, the geometry of the patellofemoral joint provides a fundamental mechanical constraint that means that, provided there is a strong contraction of the quadriceps muscle group, it is very likely that there will be a proximal to distal transfer of moments between femur and tibia as the knee extends. Furthermore, these results also provide insight into the variations in motor control that are often exhibited in skilled movement (that is certain key aspects of the movement are preserved, while other aspects vary (Bernstein, 1967; Rosenblatt et al., 2014; Yang and Scholz, 2005)). Clearly the presence of the patella exerts a very strong influence on the

pattern of moment production during lower limb extension, such that there are a great many potential patterns of recruitment which will still yield the characteristic gross movement pattern that is seen during vertical jumping. As one reviewer of this paper described it, the great many potential variations in muscular activity "are funnelled by the mechanics into some manifold of the observed variability."

The coefficients of the line of best fit found in this study also have a physiological interpretation which does lend some support to the findings of this study. Firstly, the gradient is analogous to the force in the quadriceps implied by the regression analysis. A force of around 14,000N is certainly towards the upper end of the possible quadriceps forces, but is within a physiological range. Similarly, the value of the intercept (-660N) is equivalent to the inverse of the segmental moment applied to the tibia excluding the effect of the quadriceps. Again, this is towards the upper end of the possible physiological range, but is possible (for instance, the peak segmental tibial moment in the Bobbert and van Ingen Schenau study (Bobbert and van Ingen Schenau, 1988) is 590 N). Given the fact that the geometrical data sets for the model and the actual vertical jumping moments are from entirely distinct sources, the physiological coherence of the regression relationship found here is encouraging. It should also be noted that the relationship found here is based simply on there being a strong and constant contraction of the quadriceps. The period where this regression relationship was found also coincides with the period of greatest vastus and rectus femoris electromyographic activity found in the Bobbert and van Ingen Schenau paper (see Figure 4). Clearly, the strength of the relationship could easily be improved based upon variations in activation of the quadriceps muscle groups.

A patella structure is found in a very large number of mammalian, reptilian and avian species (Samuels et al., 2017), yet in this paper I focussed only on the human knee. The reason for

this is that to date despite a large number of studies describing the form of the patella in different species, the lever behaviour of the patella has largely not been quantified outside of the human model. The exception to this is the very recent work from John Hutchinson's group (Allen et al., 2017; Regnault et al., 2017). Future work should seek to test the hypotheses posed in this study in other animal models.

The patella is not the only structure of the lower limb that might provide a mechanical imperative for motor control – another candidate is the biarticular musculature of the lower limb. It is sometimes argued that the biarticular muscles contribute to the proximal to distal movement pattern of lower limb extension by transferring energy between segments. However the moment arms of gastrocnemius and the biarticular hamstrings also show a joint angle dependence. Although some of the evidence is equivocal, it may well be the case that this function is enhanced as the limb extends. For instance, the moment arm of gastrocnemius about the ankle certainly increases with increased plantar flexion and this is consistent with an increased moment being applied to tibia and foot as the limb extends. Similarly, in another previous study (Cleather et al., 2015), we showed that recruitment of either gastrocnemius or the biarticular hamstrings during closed kinetic chain activity (like vertical jumping), then requires a greater recruitment of the quadriceps (when contrasted with the same movement pattern in a lower limb only actuated by monoarticular muscles). As we have seen, greater relative force production by the quadriceps will tend to favour a proximal to distal pattern of moment production enhancing the influence of the patella.

In summary, the results of this study demonstrate the powerful influence that the geometry of the patellar mechanism exerts upon the coordination of jumping. This lends support to dynamic systems theories of motor control, at least for lower limb extension, as the characteristic patterns seen during movement may be a consequence of the structure of the

musculoskeletal system itself. Future research should seek to ascertain how other aspects of the musculoskeletal geometry vary with joint angle, and evaluate the effects of these relationships on moment production during movement.

References

Allen, V.R., Kambic, R.E., Gatesy, S.M., Hutchinson, J.R., 2017. Gearing effects of the patella (knee extensor muscle sesamoid) of the helmeted guineafowl during terrestrial locomotion. J. Zool. 303, 178–187. https://doi.org/10.1111/jzo.12485

Amis, A.A., Farahmand, F., 1996. Extensor mechanism of the knee. Curr. Orthop. 10, 102–109.

Arnold, E.M., Ward, S.R., Lieber, R.L., Delp, S.L., 2010. A Model of the Lower Limb for Analysis of Human Movement. Ann. Biomed. Eng. 38, 269–279. https://doi.org/10.1007/s10439-009-9852-5

Bernstein, N.A., 1967. The co-ordination and regulation of movements. Pergamon Press, Oxford.

Bishop, R.E.D., Denham, R.A., 1977. A note on the ratio between tensions in the quadriceps tendon and infra-patellar ligament. Eng. Med. 6, 53–54.

Blickhan, R., Seyfarth, A., Geyer, H., Grimmer, S., Wagner, H., Günther, M., 2007. Intelligence by mechanics. Philos. Trans. R. Soc. Lond. Math. Phys. Eng. Sci. 365, 199–220. https://doi.org/10.1098/rsta.2006.1911

Bobbert, M.F., van Ingen Schenau, G.J., 1988. Coordination in vertical jumping. J. Biomech. 21, 249–262. https://doi.org/10.1016/0021-9290(88)90175-3

Buff, H.-U., Jones, L.C., Hungerford, D.S., 1988. Experimental determination of forces transmitted through the patello-femoral joint. J. Biomech. 21, 17–23. https://doi.org/10.1016/0021-9290(88)90187-X

Cleather, D.J., Bull, A.M.J., 2012. The development of lower limb musculoskeletal models with clinical relevance is dependent upon the fidelity of the mathematical description of the lower limb. Part 1: equations of motion. Proc. Inst. Mech. Eng. [H] 226, 120–132.

Cleather, D.J., Southgate, D.F.L., Bull, A.M.J., 2015. The role of the biarticular hamstrings and gastrocnemius muscles in closed chain lower limb extension. J. Theor. Biol. 365, 217–225. https://doi.org/10.1016/j.jtbi.2014.10.020

Cleather, D.J., Southgate, D.F.L., Bull, A.M.J., 2014. On the role of the patella, ACL and joint contact forces in the extension of the knee. PloS One 9, e115670. https://doi.org/10.1371/journal.pone.0115670

Correa, T.A., Baker, R., Kerr Graham, H., Pandy, M.G., 2011. Accuracy of generic musculoskeletal models in predicting the functional roles of muscles in human gait. J. Biomech. 44, 2096–2105. https://doi.org/16/j.jbiomech.2011.05.023

DeFrate, L.E., Nha, K.W., Papannagari, R., Moses, J.M., Gill, T.J., Li, G., 2007. The biomechanical function of the patellar tendon during in-vivo weight-bearing flexion. J. Biomech. 40, 1716–1722. https://doi.org/10.1016/j.jbiomech.2006.08.009

Feldman, A.G., 2016. The Relationship Between Postural and Movement Stability. Adv. Exp. Med. Biol. 957, 105–120. https://doi.org/10.1007/978-3-319-47313-0_6

Feldman, A.G., 1986. Once more on the equilibrium-point hypothesis (lambda model) for motor control. J. Mot. Behav. 18, 17–54.

Full, R.J., Koditschek, D.E., 1999. Templates and anchors: neuromechanical hypotheses of legged locomotion on land. J. Exp. Biol. 202, 3325–3332.

Full, R.J., Kubow, T., Schmitt, J., Holmes, P., Koditschek, D., 2002. Quantifying Dynamic Stability and Maneuverability in Legged Locomotion. Integr. Comp. Biol. 42, 149–157. https://doi.org/10.1093/icb/42.1.149

Gill, H., O'Connor, J., 1996. Biarticulating two-dimensional computer model of the human patellofemoral joint. Clin. Biomech. 11, 81–89. https://doi.org/10.1016/0268-0033(95)00021-6

Gwinner, C., Märdian, S., Schwabe, P., Schaser, K.-D., Krapohl, B.D., Jung, T.M., 2016. Current concepts review: Fractures of the patella. GMS Interdiscip. Plast. Reconstr. Surg. DGPW 5. https://doi.org/10.3205/iprs000080

Herzog, W., Read, L.J., 1993. Lines of action and moment arms of the major force-carrying structures crossing the human knee joint. J. Anat. 182, 213–230.

Huberti, H.H., Hayes, W.C., Stone, J.L., Shybut, G.T., 1984. Force ratios in the quadriceps tendon and ligamentum patellae. J. Orthop. Res. 2, 49–54.

Kaufer, H., 1971. Mechanical function of the patella. J. Bone Jt. Surg.-Am. Vol. 53, 1551–1560.

Klein Horsman, M.D., Koopman, H.F.J.M., van der Helm, F.C.T., Poliacu Prose, L., Veeger, H.E.J., 2007. Morphological muscle and joint parameters for musculoskeletal modelling of the lower extremity. Clin. Biomech. 22, 239–247. https://doi.org/10.1016/j.clinbiomech.2006.10.003

Latash, M.L., 2012. The Bliss of Motor Abundance. Exp. Brain Res. Exp. Hirnforsch. Exp. Cerebrale 217, 1–5. https://doi.org/10.1007/s00221-012-3000-4

Latash, M.L., Levin, M.F., Scholz, J.P., Schöner, G., 2010. Motor Control Theories and Their Applications. Med. Kaunas Lith. 46, 382–392.

Mason, J.J., Leszko, F., Johnson, T., Komistek, R.D., 2008. Patellofemoral joint forces. J. Biomech. 41, 2337–2348. https://doi.org/10.1016/j.jbiomech.2008.04.039

Narici, M.V., Landoni, L., Minetti, A.E., 1992. Assessment of human knee extensor muscles stress from in vivo physiological cross-sectional area and strength measurements. Eur. J. Appl. Physiol. 65, 438–444.

Nha, K.W., Papannagari, R., Gill, T.J., Van de Velde, S.K., Freiberg, A.A., Rubash, H.E., Li, G., 2008. In vivo patellar tracking: Clinical motions and patellofemoral indices. J. Orthop. Res. 26, 1067–1074. https://doi.org/10.1002/jor.20554

Ogihara, N., Makishima, H., Aoi, S., Sugimoto, Y., Tsuchiya, K., Nakatsukasa, M., 2009. Development of an anatomically based whole- body musculoskeletal model of the Japanese macaque (Macaca fuscata). Am. J. Phys. Anthropol. 139, 323–338. https://doi.org/10.1002/ajpa.20986

Regnault, S., Allen, V.R., Chadwick, K.P., Hutchinson, J.R., 2017. Analysis of the moment arms and kinematics of ostrich (Struthio camelus) double patellar sesamoids. J. Exp. Zool. Part Ecol. Integr. Physiol. 327, 163–171. https://doi.org/10.1002/jez.2082

Rosenblatt, N.J., Hurt, C.P., Latash, M.L., Grabiner, M.D., 2014. An apparent contradiction: increasing variability to achieve greater precision? Exp. Brain Res. 232, 403–413. https://doi.org/10.1007/s00221-013-3748-1

Samuels, M.E., Regnault, S., Hutchinson, J.R., 2017. Evolution of the patellar sesamoid bone in mammals. PeerJ 5, e3103. https://doi.org/10.7717/peerj.3103

Schaal, S., Mohajerian, P., Ijspeert, A., 2007. Dynamics systems vs. optimal control - a unifying view, in: Cisek, P., Drew, T., Kalaska, J.F. (Eds.), Computational Neuroscience: Theoretical Insights into Brain Function. Elsevier Science Bv, Amsterdam, pp. 425–445.

Scholz, J.P., Schöner, G., 2014. Use of the uncontrolled manifold (UCM) approach to understand motor variability, motor equivalence, and self-motion. Adv. Exp. Med. Biol. 826, 91–100. https://doi.org/10.1007/978-1-4939-1338-1_7

Scholz, J.P., Schöner, G., 1999. The uncontrolled manifold concept: identifying control variables for a functional task. Exp. Brain Res. 126, 289–306.

Soo Im, H., Goltzer, O., Sheehan, F., 2015. The Effective Quadriceps and Patellar Tendon Moment Arms Relative to the Tibiofemoral Finite Helical Axis. J. Biomech. 48, 3737–3742. https://doi.org/10.1016/j.jbiomech.2015.04.003

Taga, G., 1995. A Model of the Neuro-Musculo-Skeletal System for Human Locomotion .1. Emergence of Basic Gait. Biol. Cybern. 73, 97–111. https://doi.org/10.1007/BF00204048

van Eijden, T.M.G.J., Kouwenhoven, E., Verburg, J., Weijs, W.A., 1986. A mathematical model of the patellofemoral joint. J. Biomech. 19, 219–223. https://doi.org/10.1016/0021-9290(86)90154-5

Vanlerberghe, C., Boutry, N., Petit, F., 2018. Genetics of patella hypoplasia/agenesis. Clin. Genet. https://doi.org/10.1111/cge.13209

Varadarajan, K.M., Gill, T.J., Freiberg, A.A., Rubash, H.E., Li, G., 2010. Patellar tendon orientation and patellar tracking in male and female knees. J. Orthop. Res. 28, 322–328. https://doi.org/10.1002/jor.20977

Yang, J.F., Scholz, J.P., 2005. Learning a throwing task is associated with differential changes in the use of motor abundance. Exp. Brain Res. 163, 137–158. https://doi.org/10.1007/s00221-004-2149-x

Zatsiorsky, V.M., Latash, M.L., 1993. What is a joint torque for joints spanned by multiarticular muscles? J. Appl. Biomech. 9, 333–336.
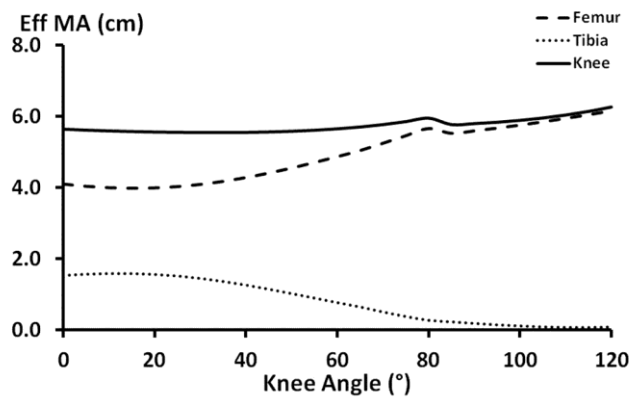
Figure Legends

Figure 1. Effective moment arm of the vastus muscle group on femur and tibia and the combined relative effect. Positive moment arms act to extend the lower limb (figure reproduced from Cleather et al. (Cleather et al., 2014) under the terms of the Creative Commons Attribution License).
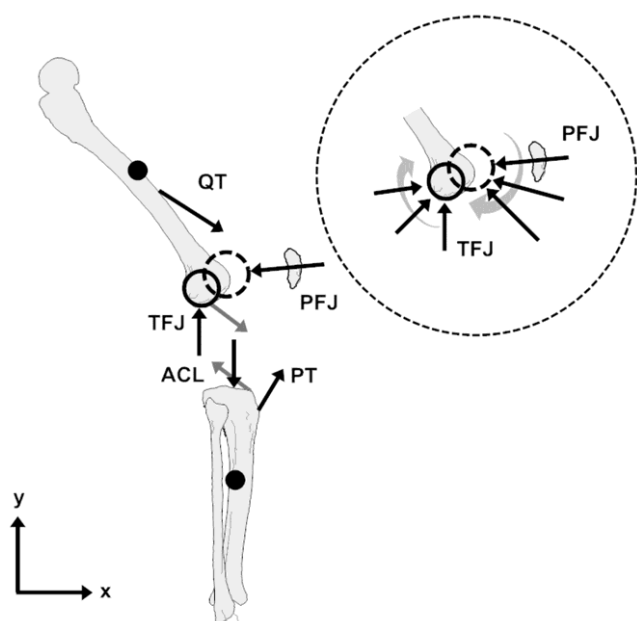
Figure 2. Rotation of femur and tibia about their centre of masses (QT = vastus or rectus femoris tendon force (vastus shown); PFJ = patellofemoral joint contact force; TFJ = tibiofemoral joint contact force; PT = patellar tendon force; and cruciate ligament forces – anterior cruciate ligament (ACL) force is shown here). The dotted circle illustrates the changing point of force application of PFJ and TFJ on the femur as the knee flexes (figure reproduced from Cleather et al. (Cleather et al., 2014) under the terms of the Creative Commons Attribution License).
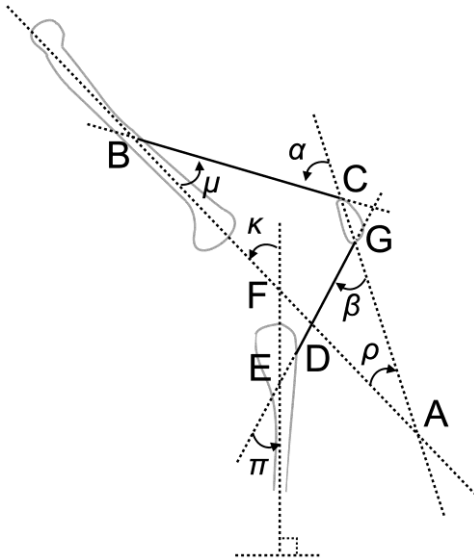
Figure 3. The geometry of the knee model used in this study (κ = tibiofemoral flexion angle; π = patellar tendon angle (relative to the tibia); ρ = patellar tilt angle (relative to the femur); μ = angle of vastus (or rectus femoris − not illustrated) relative to the femur; α = angle of incidence of vastus or rectus femoris on the patella; β = angle of incidence of patellar tendon on the patella; figure reproduced from Cleather et al. (Cleather et al., 2014) under the terms of the Creative Commons Attribution License).
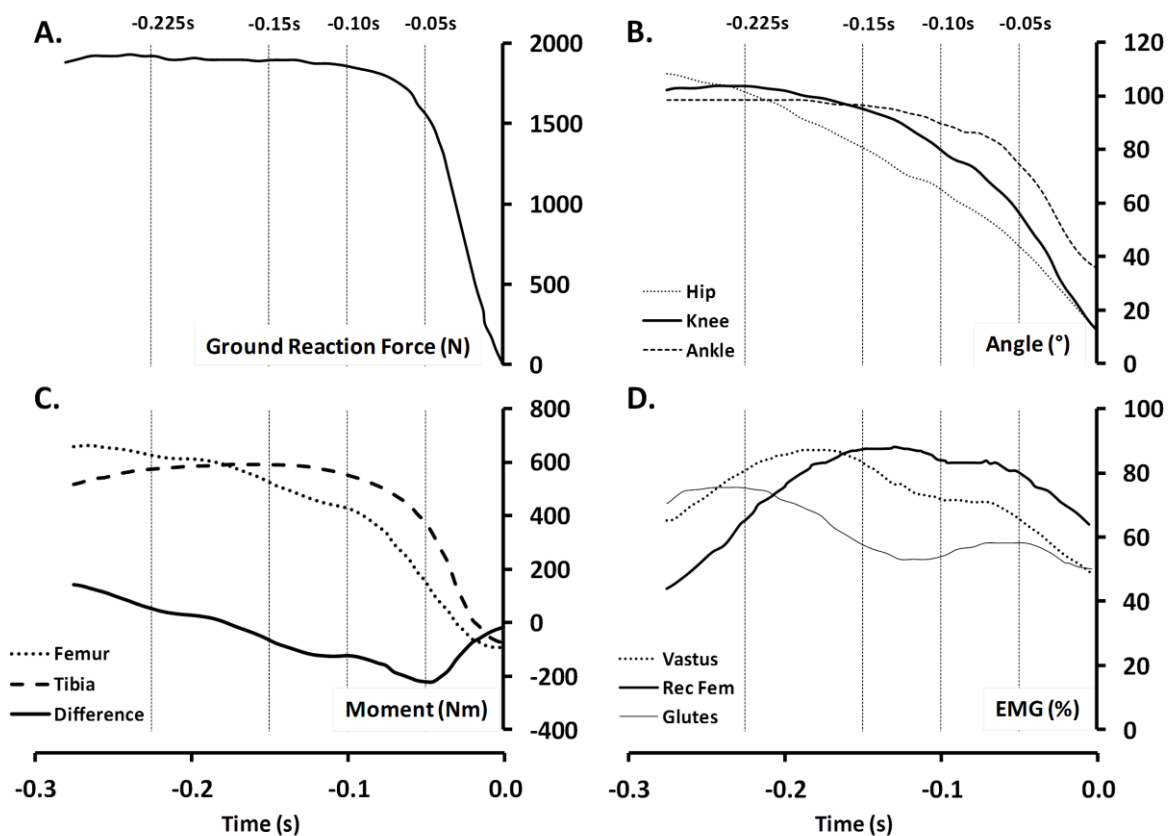
Figure 4. Kinematics and kinetics of vertical jumping extracted from the data of Bobbert and van Ingen Schenau (Bobbert and van Ingen Schenau, 1988) (A - ground reaction forces; B - joint angles; C - segmental moments; D - electromyography).
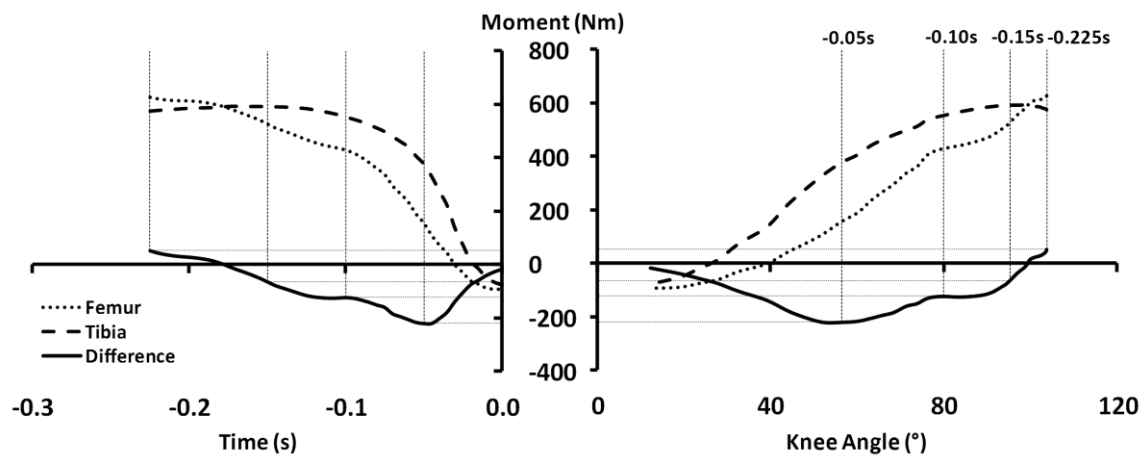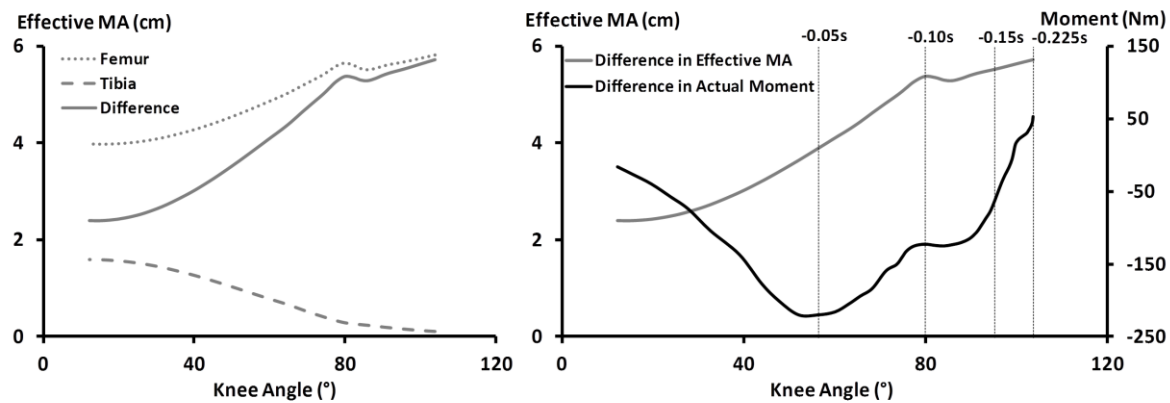
Figure 5. Moments acting on femur and tibia during vertical jumping as taken from Bobbert and van Ingen Schenau (Bobbert and van Ingen Schenau, 1988). Positive moment arms act to extend the lower limb.

A. Vastus

Effective MA (cm)

- ······· Femur
- – – Tibia
- —— Difference

Knee Angle (°)

Effective MA (cm)   Moment (Nm)

-0.05s -0.10s -0.15s -0.225s

- —— Difference in Effective MA
- —— Difference in Actual Moment

Knee Angle (°)

B. Rectus Femoris

Effective MA (cm)

- ······· Femur
- – – Tibia
- —— Difference

Knee Angle (°)

Effective MA (cm)   Moment (Nm)

-0.05s -0.10s -0.15s -0.225s

- —— Difference in Effective MA
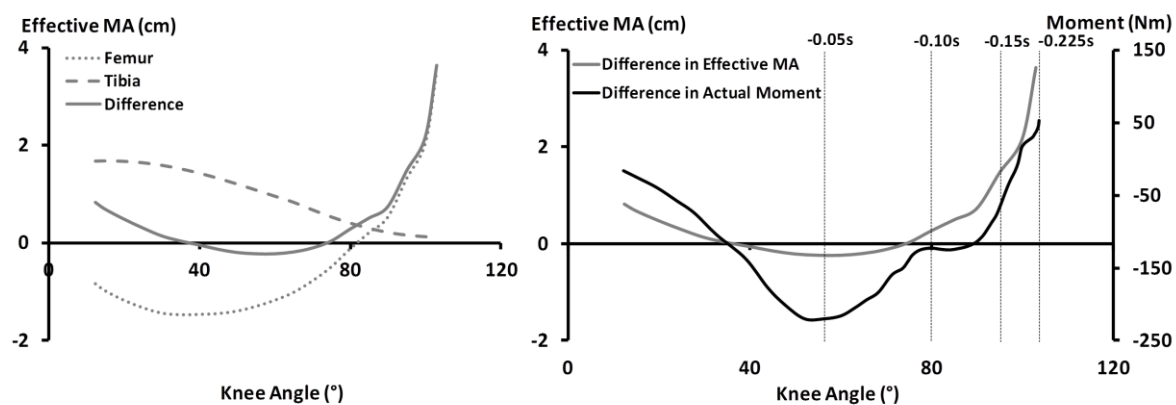- —— Difference in Actual Moment

Knee Angle (°)

Figure 6. Comparison of effective moment arms of vastus (A) and rectus femoris (B) on femur and tibia during vertical jumping derived from the model (left hand panel). The difference between the effective moment arms from the model is compared to the actual difference in moments found during vertical jumping by Bobbert and van Ingen Schenua (Bobbert and van Ingen Schenau, 1988) (right hand panel).
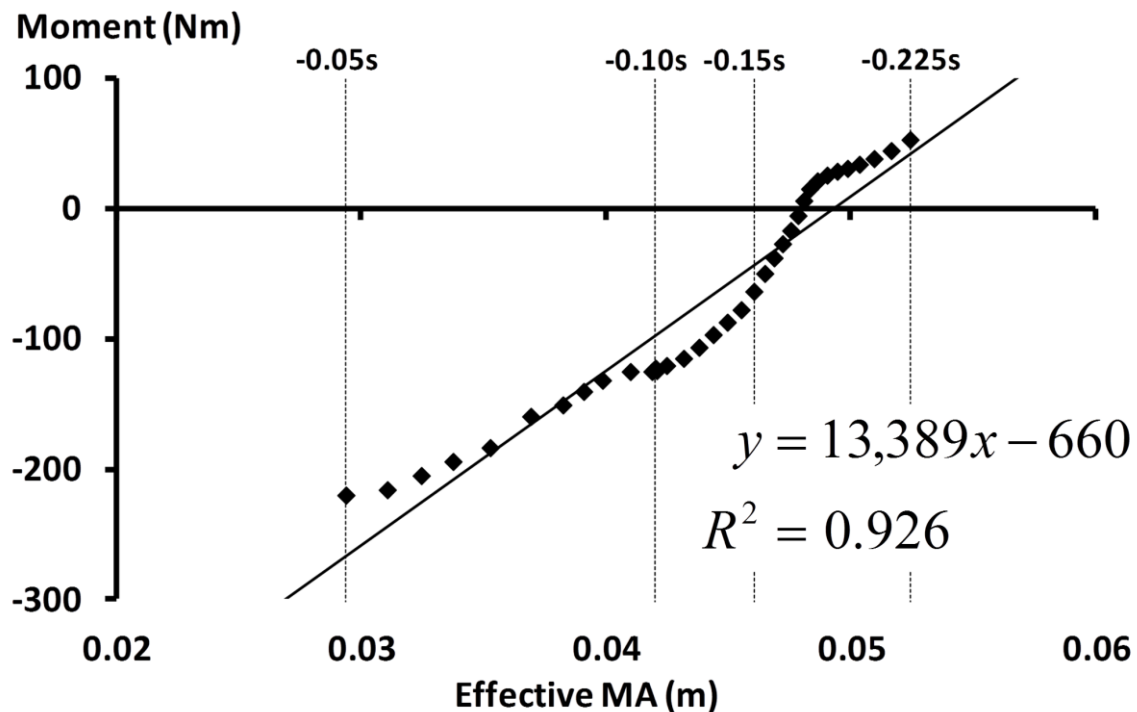

Figure 7. Relationship between the difference in actual femur and tibia moments from Bobbert and van Ingen Schenau (Bobbert and van Ingen Schenau, 1988) and the difference in effective moment arm of the quadriceps muscle group derived from the model (the combined effective moment arm of vastus and rectus femoris is weighted based on relative strength).