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REVIEW ARTICLE

Intra- and Inter-Muscular Variations in Hamstring Architecture and Mechanics and Their Implications for Injury: A Narrative Review

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Abstract
Understanding the architecture, anatomy, and biomechanics of the hamstrings may assist in explaining the mechanisms that affect and improve their function. The aim of this review is to specifically examine intra- and inter-muscular variations in architecture and mechanical properties of the hamstrings. Of the hamstrings, the long head of the biceps femoris shows the shortest and more pennated fibers. The semimembranosus has a similar muscle architecture with a long head of the biceps femoris but it has a different proximal attachment as well as a different moment arm compared with the long head of the biceps femoris. For the same joint motion, the semitendinosus displays less relative strain than the other hamstrings probably owing to a greater length, longer fascicles and, possibly, a longer tendon. Intra-muscular variations in architecture are documented but their implications are currently unclear. Proximally, the long head of the biceps femoris has shorter and more pennated fibers coupled with a narrower aponeurosis than distally, while the semitendinosus is the only muscle that entails a tendinous inscription. In conclusion, some of the identified intra- and inter-muscular variations in architecture may help explain why some muscles sustain injuries more than others. In the same line, exercises designed for the hamstrings may not provide the same stimulus for all components of this muscle group. Future research could examine whether intervention strategies that target specific muscles or specific areas of the hamstrings may offer additional benefits for injury prevention or rehabilitation of their function.

Key Points

- Inter-muscular differences in hamstring architecture may explain the greater injury potential of the long head of the biceps femoris relative to other hamstrings
- The existence of distinct areas within each hamstring muscle is documented but the functional implications are unclear. Proximo-distal differences in architecture have been linked with higher strains in the proximal area of the long head of the biceps femoris
- Future studies could examine the effectiveness of interventions that target specific muscles or specific areas within a component of the hamstrings

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1 Introduction

The hamstring is a group of muscles that acts simultaneously at two joints by flexing the knee and extending the hip. Hamstring muscle function is important for the performance of dynamic activities such as sprinting [1]. Hamstring injuries and recovery represent an important sport injury and a high rate of recurrence that exceeds 30% [2]. Hamstring muscle function is also considered important for maintaining knee joint stability [3].

The hamstring muscle group consists of the semimembranosus (SM), the semitendinosus (ST), and the long head of the biceps femoris (BFlh). The short head of the biceps femoris (BFsh) is a mono-articular muscle that shares a common tendon with the BFlh and it is frequently considered as a hamstring muscle. Other muscles, such as the gracilis, also share common functions with the hamstrings, but these muscles will not be considered in this review. Injury mechanisms and rates vary not only between the hamstrings but also within each hamstring component. Specifically, of the four hamstrings, the BFlh is injured most, followed by the SM and then the ST [2]. In addition, most injuries occur in the proximal area of the muscle, mainly in the muscle–tendon junction [2]. The BFlh is most frequently injured during sprinting, while the SM is injured during excessive stretching [4].

Despite the extensive research on hamstring injury mechanics and epidemiology, the precise mechanical behavior of the hamstring muscle group and their components has not been clarified yet [2, 4]. This is partly owing to significant variations in architecture and anatomy within each hamstring muscle as well as between the hamstring components [2]. Muscle architecture is defined as the organization of the muscle and tendinous tissue relative to the line of action of the muscle–tendon unit (MTU) [5]. Modeling studies have identified the role of architecture in hamstring injury and rehabilitation [6]. However, new data have emerged and there is an increased demand for more effective therapeutic interventions. The aim of this review is to specifically examine the latest research on the inter- and intra-muscular differences in hamstring architecture.

2 Literature Search

The articles selected for review were obtained via searches of SPORTDiscus and MEDLINE between 1966 and October 2017. The keywords used in this search were: 'architecture', 'anatomy', 'mechanics', 'hamstring', 'knee flexor', 'hip extensor', 'muscle strain', 'injury', and 'mechanism'. From the abstracts returned, articles were included for review if they related to hamstring architecture, anatomy, or mechanical properties.

3 Inter-Muscular Variability

The mechanical characteristics of each hamstring muscle are largely determined by the morphology and mechanical properties of the MTU. In turn, the MTU behavior overall is determined by the properties of its individual components, i.e., the fascicles, tendons, and aponeuroses as well as their interactions [7]. If the mechanical properties of each of these components differ between the individual hamstrings, then fundamental force-generation properties such as the force–length curve might also differ. Quantification of such differences will assist in better understanding injury mechanics and how the hamstrings respond to exercise.

3.1 Muscle

The main architecture variables include muscle–tendon unit length (*L*MTU), muscle length (ML), fascicle length (FL), pennation angle (PA), physiological cross-sectional area (PCSA), and anatomical cross-sectional area and muscle volume (Fig. 1). Because the sarcomere represents the basic functional unit of the muscle, a comparison of fiber lengths between muscles is more appropriate when the effects of sarcomere length are taken into consideration [8].

Architecture variables reported in the literature are presented in Tables 1 and 2. Traditionally, compared with the large quadriceps musculature, the hamstrings are considered as muscles designed for low force production and a high contractile and stretching velocity [9, 10]. For example, by taking the sum of all individual muscle components, the hamstring group displays lower muscle mass and PCSA and, hence, a lower force generation potential than the quadriceps [8]. In contrast, the normalized (to sarcomere length) FL:ML ratio is greater for the hamstring muscle group than the quadriceps, indicating a greater excursion potential of the hamstrings than the quadriceps [8]. Another traditional view has been that the hamstrings, mainly the BFlh, consist of type II (fast-twitch) muscle fibers and therefore they are more susceptible to injury [11]. However, recent evidence has shown that this is not the case [12].

Latest research findings have made clear that not all hamstrings have a parallel muscle fiber configuration but there are differences in fiber arrangement between them [8, 13–17] (Tables 1, 2). In particular, the BFlh and SM display greater PCSA and pennation and, therefore, a greater force generation capacity than the ST and BFsh. In fact, the SM PCSA is similar to that reported for rectus femoris, vastus intermedius, and vastus medialis [8, 17]. In contrast, the ST and BFsh displayed almost a double normalized (to sarcomere length) FL/ML ratio and, hence, a greater excursion capacity compared with SM and BFlh (Tables 1, 2) [8, 17].

Examination of current evidence indicates that there is a considerable variability in the range of values for each architectural characteristic of the hamstrings reported in the literature (Tables 1, 2). These variations are particularly important as they may lead to different conclusions regarding hamstring muscle function. For example, the BFlh has been reported to have a PA range of 0°–28° (Table 1). Similarly, some studies have reported that the ST has a parallel fiber configuration, [9, 18] while others have found a greater PA reaching 12.0° [8, 15] (Table 2). Further, a wide range of FL values of the ST has been reported with values starting from 9.0 cm [10] up to 23.8 cm [18]. This variability in reported data may be mainly attributed to a different area of the muscle and a different joint position at which architectural parameters are being measured [14, 16]. This indicates that conclusions regarding the role of architecture in hamstring muscle function are highly specific to the area of the muscle being examined.

These inter-muscular differences in muscle architecture have an impact both on hamstring force-generation capacity as well as injury potential [2]. In terms of performance, simple model predictions have shown that for the same change

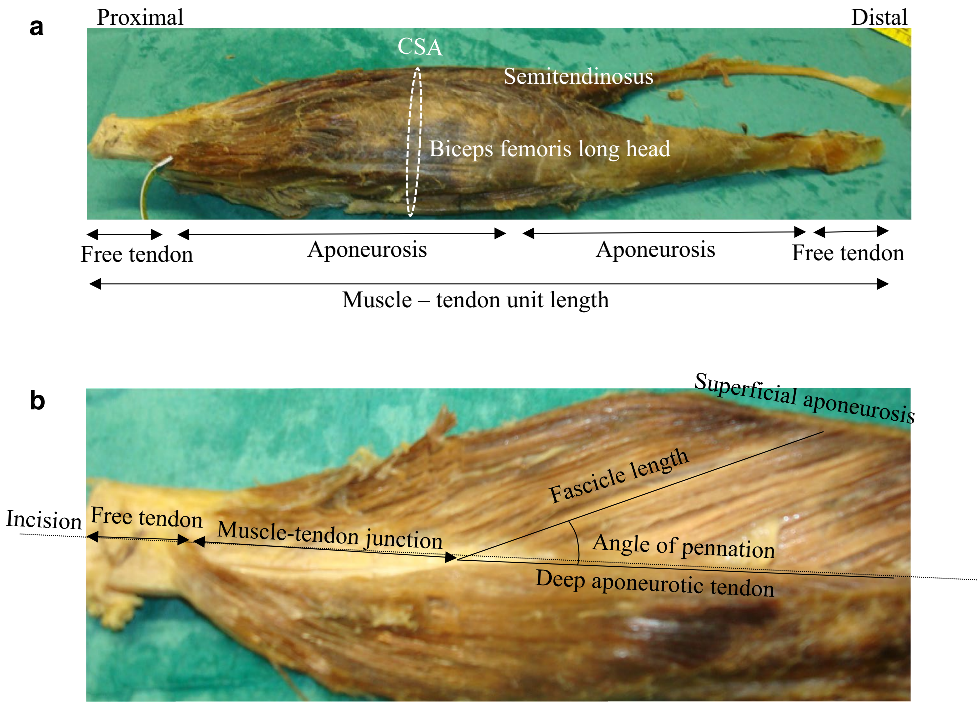

Fig. 1 **a** Example image of the biceps femoris long head and semitendinosus after being removed from the skeleton [17]. Illustration of muscle–tendon unit length, distal and proximal free tendon, and aponeuroses length of the biceps femoris long head. The cross-sectional area (CSA) is measured after cutting the muscle cross-sectionally (not shown). **b** Proximal area of the biceps femoris long head after the muscle has been incised to allow measurement of architecture. Architecture variables are illustrated

Table 1 Muscle architecture parameters of the long and short heads of the biceps femoris as they appear in the literature

Study	Biceps femoris long head			Biceps femoris short head		
	PA (°)	FL (mm)	*L*MTU (cm)	PA (°)	FL (mm)	*L*MTU (cm)
Wickiewicz et al. [9]	0	8.5	34.2	23.3	14	27.0
Ward et al. [8]	11.6	9.8	34.7	12.3	11	22.4
Makihara et al. [18]	28	7.3	31.2	–	–	–
Woodley and Mercer [14]	–	7.0	43.8	–	12.4	29.1
Chleboun et al. [13] (cadavers)	17.0	8.0	–	–	–	–
Chleboun et al. [13] (in vivo)	14.0	8.8	–	–	–	–
Friedrich and Brand [10]	7	7.3	27.4	15	11.7	22.3
Alexander and Vernon [95]	17.0	–	–	0	–	–
Kellis et al. [15] (cadavers)	13.5	7.6	39.2	–	–	–
Kellis et al. [15] (in vivo)	13.9	8.0	38.7	–	–	–
Kellis et al. [17]	13.5	7.0	38.9	13.2	10.4	28.5
Van der Made et al. [23]	–	–	42	–	–	29.8
Kumazaki et al. [31]	–	7.4	39.1	–	13.0	15.1
Klein Horstman et al. [96]	30	8.5	–		0	9.1
Spoor et al. [97]	15	–	–	–	–	–
Delp et al. [98]	0	10.9	–	23.0	–	–
Pierrynowski and Morrison [99]	15		–	0	–	–
Blackburn et al. [84]	14	14.1	–	–	–	–
Timmins et al. [100]	12.8	11.1	–	–	–	–
Potier et al. [101]	13.9	5.7	–	–	–	–
Timmins et al. [102]	13.3	11.1	–	–	–	–

FL fascicle length, *MTU* muscle–tendon unit length, *PA* pennation angle

Table 2 Muscle architecture parameters of the semitendinosus and semimembranosus as they appear in the literature

Study	Semitendinosus			Semimembranosus		
	PA (°)	FL (mm)	*L*MTU (cm)	PA (°)	FL (mm)	*L*MTU (cm)
Wickiewicz et al. [9]	5.0	15.8	31.7	15	6.3	26.2
Ward et al. [8]	12.9	19.3	29.7	15.1	6.9	29.3
Makihara et al. [18]	0	23.8	26.8	31	6.0	28.5
Woodley and Mercer [14]	–	9.0	43.8	–	5.0	43.8
Friedrich and Brand [10]	6.0	9.0	28.3	16	6.4	20.8
Alexander and Vernon [95]	0	–	–	16	–	–
Kellis et al. [15] (cadavers)	13.4	18.9	39.0	–	–	–
Kellis et al. [15] (in vivo)	13.3	20.4	38.1	–	–	–
Kellis et al. [17]	9.1	14.9	47.0	15.5	5.4	40.4
Van der Made et al. [23]	–		44.3	–	–	38.7
Kumazaki et al. [31]	–	17.8	38.2	–	6.3	38.2
Klein Horstman et al. [96]	0	14.2	–	25	8.1	–
Spoor et al. [97]	10	–	–	15	–	–
Delp et al. [98]	5.0	20.1	–	15	8.0	–
Pierrynowski and Morrison [99]	0	–	–	15	–	–
Haberfehlner et al. [69]	15.0 (dl) 19.7 (pl)	9.7 (dl) 8.0 (pl)	37.7	–	–	–

dl distal, *FL* fascicle length, *MTU* muscle–tendon unit length, *PA* pennation angle, *pl* proximal

in length, the BFsh produces greater force at shorter lengths, the SM and BFlh produce almost 80% of total hamstring force at intermediate lengths, and the ST produces a low force at longer muscle lengths [17]. For example, the shorter SM fascicles attaching at larger angles (12.5°, 112.3 mm length) would be expected to generate high relative peak forces over shorter length ranges [17]. This can be compared with the immediately adjacent, architecturally dissimilar ST (6.5°, 162.1 mm), which is designed to generate lower peak forces over greater length ranges [17]. This may verify the suggestion that muscles within synergistic groups tend to vary their architecture so that they can produce forces with broad magnitude, range, and velocity characteristics [5]. In terms of injury, muscles with greater fiber lengths have a greater lengthening capacity than muscles consisting of shorter fibers [5]. Hence, when all hamstrings contract when they lengthen (eccentrically), muscles with shorter fibers may display a greater injury risk [19]. This may predispose the BFlh and SM to high rates of strain injury.

3.2 Tendon

Tendon mechanical behavior is generally assessed via the stress–strain relationship; that is, the relative change in length (strain) as a result of a change in load applied to the tendon. The slope of the stress–strain curve represents its stiffness. A stiffer tendon can transfer muscle forces to the bone more rapidly than a less stiff tendon. More compliant tendons may cause the muscle fascicles to shorten more to take up the excess compliance in the tendons [20]. This may lead to the damping of excessive forces but it may bring muscle fibers to a less optimal region of the force–length curve [6, 21].

Muscle–tendon unit, proximal, and distal tendon lengths of the four hamstrings reported in the literature are presented in Fig. 2. The longest free tendon (the portion of the tendon that has no muscle fibers inserting into it) is displayed by the ST distally while proximally the SM and BFlh tendons have similar lengths. The SM shows the highest distal tendon cross-sectional area (CSA) followed by the BFlh and finally the ST [22]. Proximally, qualitative observations from cadaveric studies [14, 15, 17, 23] indicate that the BFlh and SM have somewhat thicker (hence, having greater CSA) free tendons than the ST, but this has yet to be confirmed experimentally. Keeping everything else constant, a longer free tendon is linked with a greater excursion capacity (and compliance) than a shorter tendon. Similarly, a tendon with a greater CSA would be stiffer than a tendon with a smaller CSA [20]. However, these data are not sufficient to compare the three muscles, as tendon stiffness is largely determined by its length, CSA, and the density of the tendinous tissue [20]. Young's modulus (the stiffness normalized to tendon CSA and length) provides a measure of tendon material properties irrespective of its geometric characteristics. To our knowledge, Young's modulus differences between the four hamstring muscles have not been investigated. As a result, it is difficult to make general conclusions regarding differences in tendon properties between the hamstrings.

Some anatomical variations in tendon attachments are worth noting as they may also have an influence on the

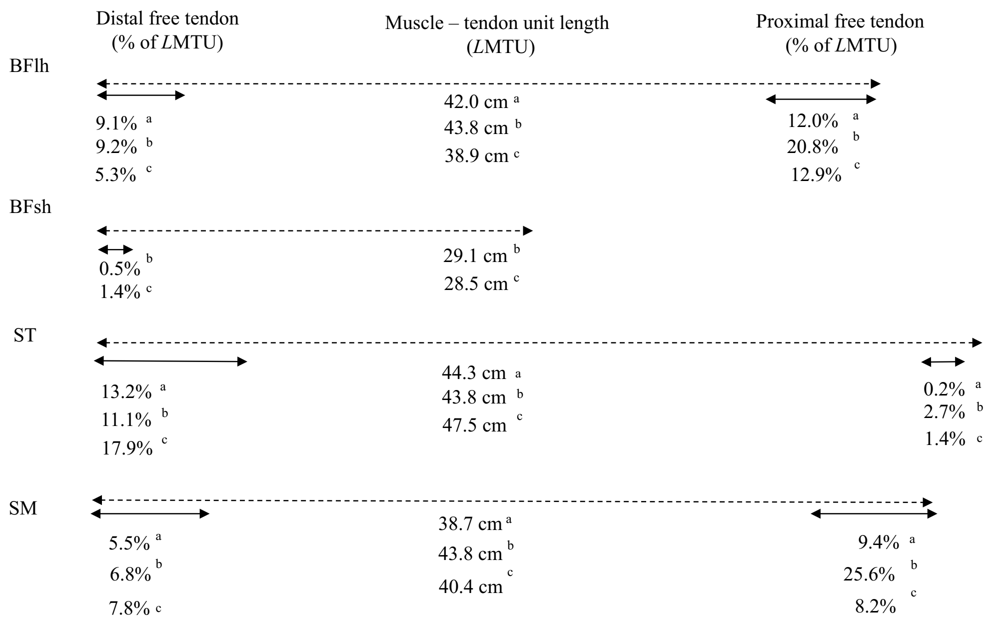

Fig. 2 Indicative values of whole muscle–tendon unit length (*L*MTU), distal and proximal free tendon length of the biceps femoris long head (BFlh), biceps femoris short head (BFsh), semitendinosus (ST), and semimembranosus (SM). [a]Data from van der Made et al. [23] [b]Data from Woodley and Mercer [14]. [c]Data from Kellis et al. [17]

mechanical properties of each hamstring. Proximally, the most proximal region of the BFlh is composed of tendon, the ST is composed of muscle, while the SM originates vertically from two directions [24]. For this reason, it has been proposed that BFlh is more vulnerable to excessive forces between tissues than the ST and SM [24]. This is confirmed by simulation studies showing greater muscle tissue strains in the proximal BFlh muscle–tendon junction (relative to the other areas of the muscle), which were attributed to a smaller CSA of the muscle proximally than neighboring regions [25]. Finally, a challenge for future research is whether the continuity of the BFlh origin with the sacrotuberous ligament indicates that there is a link between the function of the sacroiliac joint, the gluteus maximus, and the BFlh [24].

Distally, tendon attachments vary between the hamstrings. In particular, the long distal ST free tendon wraps around the tibia and it is divided into several bands before it inserts into the pes anserinus [26]. Some bands or “arms” were also observed along the SM distal tendon, some of which intertwine with the branches of the posterior oblique ligament [27, 28]. It has been proposed that this arrangement allows the contribution of the SM to rotatory stability and control of hyperextension of the knee [27, 28]. Finally, large inter-individual differences in muscle anatomy and tendon attachments to the bones may contribute to corresponding differences in the mechanical responses of tendons [27]. For example, it has been proposed that the existence of hypertrophic slips between the hamstrings can alter muscle extensibility [29]. In theory, a reduced tendon CSA and a line of action closer to the joint center of rotation can also reduce the muscle moment arm, [22] but this has to be verified experimentally.

3.3 Muscle–Tendon Unit Mechanics

Reduced resistance to stretch and muscle strength are frequently considered as injury risk factors [2]. However, if the hamstrings have different *L*MTUs, then one may suggest that it is not the extensibility or force-generation capacity of the hamstrings as a group, but rather the properties of each individual MTU that are important for muscle injury. For this reason, measurement of *L*MTU represents the first step in comparing individual hamstring properties.

Hamstring *L*MTU values vary significantly between studies (Tables 1, 2) [30]. Of the four hamstrings, the ST displays the greatest length and the BFsh the shortest [8, 14, 17]. Knee extension is associated with an increase in whole hamstring *L*MTU [31–33]. However, the amount of length change differs between individual hamstring components. In absolute terms, the highest *L*MTU change is displayed by the ST, followed by the SM, the BFlh, and finally the BFsh [31–33]. When the values are expressed relative to the resting values, the BFsh and ST display the greater change in length (~ 17–20%), followed by the BFlh (~ 11–14.7%), and finally the SM (~ 12.5%) [31, 32]. The greater ST whole MTU strain and length change can be attributed to its greater knee moment arm change and FL as the hamstrings are stretched [32]. Isolating the effects of hip angle from those of knee angle on *L*MTU has been only documented for the BFlh muscle, but findings are conflicting [33, 34]. More specifically, direct measurements in cadavers have shown that BFlh length increased by almost ~ 30% during hip flexion and only 5% during knee extension [33]. However, estimates using ultrasound have shown much less lengthening of the MTU (~ 13%), which did not differ between hip and knee joint movement [34]. Therefore, more research is required to examine this issue.

Hamstring muscle properties may also be affected by the movement of the pelvis owing to their proximal attachment to the ischial tuberosity [35]. There are suggestions that a greater anterior pelvic tilt increases hamstring length thus increasing injury risk [36, 37]. Alternatively, simulation has shown that overactive hamstrings can induce posterior pelvic tilt [38]. An altered pelvic position has also be linked with significant leg asymmetries in horizontal forces during running in athletes with a previous hamstring injury [39]. Further, anterior pelvic tilt increases the muscle stiffness of all hamstrings compared with non-tilt and this increase appears to be lower for the ST than the BFlh and SM [40]. It is therefore clear that changes in pelvis position may alter hamstring muscle length and this effect may vary amongst the hamstrings.

Important information regarding hamstring mechanical responses to stretch can be provided through quantification of hamstring stiffness. Again, very few studies have provided quantitative values of whole hamstring stiffness. Prediction models based on kinematic and anthropometry data have shown that during a slow stretching exercise (from 70° to ~ 20° of knee flexion and the hip flexed 120°–135°) the highest stiffness is displayed by the BFlh (~ 2500 N/cm^2), followed by the SM (~ 2000 N/cm^2) and finally the ST (1500 N/cm^2) [32]. Consequently, although the ST displays the highest length change, the BFlh provides the greater resistance to stretch during a typical hamstring stretching exercise.

Recent studies have quantified stiffness using ultrasound-based shear-wave elastography [40–43]. This technique provides an index of material stiffness underneath the probe and its findings differ from whole muscle stiffness findings estimated based on length and force values [32]. One of the calculated parameters is the elastic shear modulus, which is the ratio of shear stress to shear strain; the higher the ratio the stiffer the underneath area [40–43]. It has been shown that the ST displays the lowest shear elastic modulus amongst the hamstrings during passive lengthening [40–42]. However, it is worth noting that the muscle that displays the highest shear elastic modulus differs between static and dynamic stretches, between joint positions and movements. First, static stretching of the hamstrings from a 45° knee flexion angle increases the shear elastic modulus of the SM more than the BFlh and ST; when the stretch is performed from 90° of knee flexion, the shear elastic modulus is similar between the SM and BFlh while the ST shear modulus is the lowest [40, 41]. Second, the changes in the elastic modulus during slow dynamic passive stretching are conflicting as some investigators have reported that passive stretching of the knee led to a greater peak elastic modulus of the BFlh than the other hamstrings, [42] while others have reported that it is the SM that displays the greater elastic modulus [43]. Third, hip flexion stretching exercises increased the shear elastic modulus of the ST and SM more than knee extension stretches; the opposite was observed for the BFlh [43]. These results may reflect differences in FL between the three hamstring muscles, as the ST has the longest fascicles and the SM has the shortest fascicles (Table 2).

3.4 Fascicle and Tendon/Aponeurosis Interactions

If the tendon and muscle contributions to MTU behavior differ between the individual hamstrings, this means that for the same force or change in LMTU each hamstring displays a different tendon and fiber response. Assuming that tendons are arranged in series with the muscle fascicles, a change in total *L*MTU is the result of the compliances of the tendon and fascicles [44]. The slope of the FL–*L*MTU curve is often referred to as the “compliance ratio”. When this ratio is less than one, then the change in FL that occurs as the relaxed muscle is lengthened through its physiological range is much less than the total change in *L*MTU [45]. Hence, the tendon contributes substantially to the total length changes in the relaxed MTU, even though it is intrinsically less compliant tissue than muscle [46]. Such evidence for all hamstring muscles is currently missing. It has been shown that the slope of the FL–*L*MTU curve was 0.42 [45] and 0.49, [34] for the SM and BF, respectively. Consequently, changes in FL account for 42% (SM) and 49% (BFlh) of change in *L*MTU. This indicates that the tendon (including the aponeuroses) contributes about half of the total compliance of the relaxed MTU, mainly because the tendon tissue is much longer than the muscle fascicles. These investigators, therefore, concluded that tendons and aponeuroses contribute significantly to passive lengthening of the SM and BFlh [34, 45]. However, no comparisons between the two muscles can be made as the findings were obtained during different exercises.

Comparisons of in-series elasticity of the MTU between muscles have also been made by calculating the tendon slack length-to-muscle fiber length ratio [44]. Slack tendon (including aponeuroses) length is the threshold length at which a stretched tendon begins to develop force. Optimal fiber length is the length at which the fiber produces maximum isometric force. Assuming a constant elastic modulus and CSA, the larger the ratio, the longer the tendon relative to its fibers, and the more compliant the MTU. Based on published evidence, the SM shows almost a 1.5 and 3 times greater tendon:fiber length ratio than the BFlh and ST, respectively [7, 44]. Consequently, the contribution of tendon change in length to *L*MTU change would be greater for the SM, followed by the BFlh and finally the ST. Such information fits well with predictions that BFlh fibers are excessively stretched when tendon compliance decreases [1, 6].

Relaxed muscles do not immediately develop tension when they are lengthened. Tension begins when the muscle is lengthened beyond a certain length, frequently called slack length [47]. Slack length is usually assumed to be the length measured with the joint in its mid-position [48] or when the net joint torque is zero, [49, 50] but there is no reason to believe that either joint position should correspond to the true slack length [51]. For the hamstrings, resting length is frequently taken as the position where the passive knee flexion moment is almost zero, which is in the range of 30°–40° of knee flexion [52]. Some evidence indicates that as the knee is passively extended from a 110° to 20° angle of knee flexion, the angle where the elastic modulus starts to increase (defined as slack angle) does not vary between the individual hamstring components and it occurs at approximately 80°–90° of knee flexion [42]. However, further evidence is necessary to determine the position where whole MTU, fascicles, or tendons are slack and whether this differs between individual hamstring components.

Published information does not allow a comparison of changes of tendon, fascicle, and aponeurosis length of each hamstring during passive lengthening or active shortening. Passive knee extension is accompanied by an almost two-fold greater distal aponeurosis strain for the BFlh (14.6%) compared with ST (7.4%) [50]. This indicates that the distal BFlh tendon/aponeurosis is stretched more than the corresponding ST aponeurosis during passive knee extension. The greater BFlh displacement may facilitate its lengthening, as this muscle has shorter and more pennated fascicles (Table 1) than the ST (Table 2) [5, 50]. However, further study is necessary to quantify FL, *L*MTU, and tendon length changes of all hamstrings during passive stretching to verify the above findings.

Less information is available about the mechanical properties of the hamstring MTUs during voluntary activation of the hamstrings [50, 53]. During isometric contractions, the BFlh fascicles shorten approximately by 20%, [54] while the distal tendon/aponeurosis lengthens by approximately 14% [50]. Because changes in total *L*MTU have not been quantified, the contribution of the muscles and tendons to whole MTU mechanical behavior remains unclear. It has been observed, however, that during ramping isometric contractions performed from the prone position, the tendon/aponeurosis strain of the ST is greater than the corresponding BFlh strain [50]. However, owing to a higher passive strain, when the hamstrings contract from full knee extension, the BFlh tendon/aponeurosis remains lengthened while the ST tendon/aponeurosis is displaced in the opposite direction as both tendons accommodate muscle shortening [50]. The reverse is observed when the contraction is performed from a higher knee flexion angle.

Inter-muscular differences in activation and torque-generation capacity are frequently attributed to differences in the moment arm [6, 14, 55]. Of the three bi-articular hamstrings, the ST displays the highest sagittal moment arm around the knee and the hip [55]. Further, the BFlh shows a greater hip sagittal moment arm than the SM whilst the opposite occurs for the knee moment arm. It is difficult to isolate the influence of the moment arm on the mechanical properties of the hamstrings from the effects of other factors. In theory, hip flexion requires a much greater change in length of the ST, followed by the BFlh and finally the SM. Knee extension requires a greater change in length of the ST, followed by the SM and finally the BFlh. Based on experimental and simulation data, it has been shown that when the hip flexes and the knee extends rapidly, as occurs in sprinting, the ST and BFlh lengthen slightly more than the SM [6]. However, as the knee flexes during the terminal swing phase, the BFlh experiences less shortening than the other hamstrings, as a result of a shorter knee joint moment arm [6].

4 Intra-Muscular Variability

Variability in architecture is a common feature of many human muscles. A challenging question is whether these variations can result in variable force-generation and local fiber length changes along each individual hamstring. This may facilitate our understanding of why injuries occur at specific locations [2] and may assist the design of individualized rehabilitation programs depending on the region of the muscle that sustains injury.

4.1 Compartmentalization

The existence of separate areas of neuromuscular compartments within a muscle is known as "compartmentalization" [56–58]. Each compartment is activated depending on the functional demands placed on that muscle [56, 59]. Such regions have been observed in each of the hamstring muscles, [14] thus raising the question whether compartmentalization influences their function (Fig. 3).

The division of the ST into two compartments each receiving a separate nerve supply has attracted most attention [14, 60–69] (Fig. 3). It has been suggested that because of their anatomical arrangement, compartment function reflects the regular stress–strain events that occur between fibers or motor units arranged in series [70]. Selective activation of compartments or motor unit areas may result in the performance of specific movements related to this particular muscle or enhance force transmission to the tendons when one part of the muscle is injured [56, 58, 70]. However, fascicle lengths in humans have been reported to be similar [14, 65, 69] or different [64, 67] between compartments.

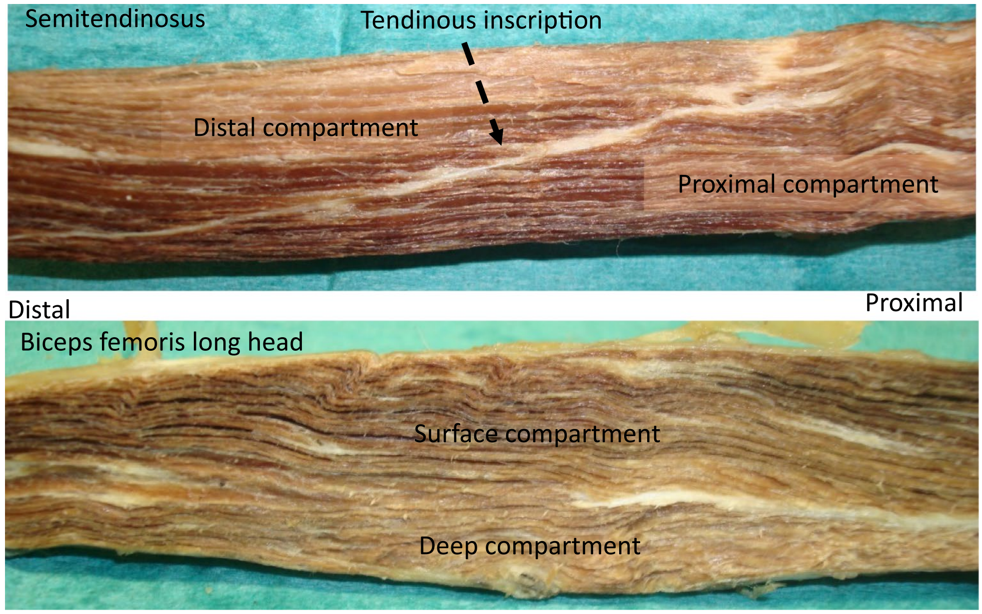

Fig. 3 Sagittal representative view from the mid-region of the semitendinosus and the long head of the biceps femoris. The muscles have been incised along the mid-line to illustrate fascicle direction [17]. The tendinous inscription divides the semitendinosus into a distal and a proximal region. In the biceps femoris, a more superficial region with fascicles attaching to the central tendon as opposed to a deeper region where fascicles have a different direction is identified

Activation differences between compartments have not been examined in humans; only one study has shown that acute metabolic responses to eccentric exercise differ between the two compartments [71]. This can be attributed to various factors such as a different activation of each compartment during exercise or the existence of intrinsic differences between the muscle compartments themselves or both.

In contrast, minimal compartment differences in animal ST activation have been reported [61, 62, 72]. Based on the current experimental evidence, therefore, no safe conclusions can be made regarding the effects of compartmentalization on human ST muscle function. Two reports, however, are worth considering. First, in animal muscles, existing evidence indicates that the arrangement has very limited functional importance for the function of a parallel fibered muscle, such as the ST [61]. Second, modeling of fusiform muscles, such as the ST, showed minimal proximo-distal variations in fascicle strain [73]. These observations point to a rather low functional importance of compartmentalization for ST whole muscle function. However, more research is necessary in this direction.

The tendinous inscription that divides the ST muscle into two compartments has also received some attention [14, 65, 66, 68, 74]. The inscription consists of two “arms”, a long (lateral) arm of an average length of 6.5 cm and a shorter (medial) arm of approximately 2.4 cm [14, 65, 68]. As the hamstrings contract or lengthen, the shape of the tendinous inscription, measured using two-dimensional ultrasound, shows a non-uniform change [65, 74] owing to its ‘V’ shape along the muscle. The functional implications of the inscription for the ST and hamstrings are unclear. One may suggest that the whole complex behaves like a single unit because the inscription is entirely intra-muscular and it has a parallel alignment with fibers. Alternatively, it can by hypothesized that the inscription can assist in transferring forces from the fibers to the tendons, [75] it may increase resistance to stretch, [14, 65] it may protect the muscle against gross injury, [23] or it may alter local muscle-cell metabolism and fluid uptake between the two regions of the muscle [71]. The protective role of the inscription, if any, may be enforced by the observation that most injuries occur in the proximal region of the BFlh and SM, [2] which is located immediately adjacent to the ST inscription.

Apart from the ST muscle, there is no information on the role of compartments in the function of the other hamstrings. Distinct activation differences between different regions of the cat BFlh or the SM of the toad have been observed [62, 72, 76] but these findings have limited application to human muscles. Consequently, the role, if any, of compartments in hamstring muscle function and mechanical behavior remains unclear.

4.2 Proximo-Distal Variability

Variations in architecture has been reported along the length of each hamstring component [8, 16]. The BFlh has longer fibers and greater pennation angle proximally than distally while the opposite is observed for the ST [16]. Qualitative examination of cadaver data [14] indicates that the SM has slightly longer and less pennated fibers proximally than distally.

The implications of architecture variations for hamstring function are relatively unclear as they are based on several assumptions, i.e., a greater FL results in a greater excursion capacity whilst a greater PA indicates a relatively greater whole muscle force capacity and a lower strain [73]. One explanation is that variation in the architectural arrangement of muscle fibers allows regions with greater pennation to produce greater forces, while other regions are in line with the tendon to allow greater efficiency of the force transfer [77, 78]. Basic planimetric modeling showed that contraction of the proximal BFlh fibers would display greater excursion (because of longer fibers) and force potential (owing to greater pennation) compared with distal fibers [16]. This is in line with Bennett et al [54]. who found that the proximal BFlh fascicles shortened 40% more than the distal fascicles and had significantly greater cumulative shortening at high force levels. In the same line, research evidence based on finite element modeling showed larger amounts of tissue strain in the region near the proximal muscle–tendon junction compared with more distal regions of the muscle during active BFlh muscle lengthening [79, 80]. This contradicts recent reports indicating that in pennated muscles, regions with high pennation show less fiber strain than regions of low pennation [73].

Less information is available for the paralleled ST muscle; [16] the longer and more pennated proximal fibers may indicate a greater excursion capacity distally than proximally. However, simulations have shown that proximo-distal variability in parallel fibered muscles has minimal influence on their function; [73] instead, the outer/superficial fibers of the muscle experience lower strains than central fibers, [73] which has been partly observed in vivo [65]. The variability effect on ST function is further complicated by the existence of the tendinous inscription along its length.

Another potential explanation for heterogeneous fascicle strain within a muscle could be the regional variation of aponeuroses morphology and function [81]. Aponeuroses can act as stiff springs in both longitudinal and transverse directions depending on muscle loading [82]. Simulation based on magnetic resonance imaging has shown that muscles such as the BFlh with one narrow (proximally) and one wide (distally) aponeurosis display greater strains in the area adjacent to the musculotendinous junction [79]. Hence, they are more susceptible to injury as opposed to muscles with two wide aponeuroses such as the SM and ST, [79] particularly during active lengthening [53]. Aponeurosis size is expected to be most strongly related to the maximum force transmitted from fibers through these tissues to the tendons [83]. Before drawing general conclusions, however, one should take into consideration that the proximal BFlh aponeurosis size is highly variable and is not related to muscle or tendon CSA or muscle strength [83]. This variability may result in inter-individual variation in strains displayed by the fascicles of the proximal region of the muscle [82].

5 Future Directions and Implications

Based on the reviewed literature, there are several aspects regarding the mechanical behavior of the hamstring MTUs that need further clarification. In particular, differences in tendon architecture between the hamstrings are unclear. Further, the presence of the long distal free tendon of the ST and the tendinous inscription is often ignored (Table 2). This affects comparisons of *L*MTU and FL between the hamstrings and may result in an erroneous interpretation of the ST mechanical properties. The absence of analysis of SM mechanical properties significantly limits conclusions regarding inter-muscular variations in injury and the responses of the hamstrings to exercise. Similarly, incomplete data regarding the mechanical role of tendon, aponeurosis, and fascicle interactions during passive conditions have been found while for dynamic (concentric and eccentric) tests information is very scarce. Although evidence indicates that MTU stiffness correlates with tendon stiffness, muscle CSA and strength, and fat thickness, [84] inter-muscular differences in each of these factors are currently unknown. It is unclear whether the in-series or in-parallel arrangement of different compartments and proximo-distal variations in architecture influences whole muscle mechanical properties.

This paucity of information is also related to methodological difficulties in quantifying such interactions in vivo. The interactions of tendons, aponeuroses, and fascicles are far more complex than those often presented in the literature [85]. The assumption of the in-series arrangement of the aponeuroses with the muscle fascicles is not always supported by experimental data [82, 86]. For example, there is evidence that the tibialis anterior aponeurosis behaves like an in-series element during isometric contractions, but not during concentric or eccentric conditions [85]. In most cases, muscle fascicle curvature and transverse tendon/aponeurosis strains have not been measured while in vivo data are based on two-dimensional imaging of the muscles. This can result in an erroneous interpretation of mechanical properties of the hamstrings. In addition, the calculation of force exerted by each individual muscle component is made under certain assumptions; this makes quantification of stress–strain curves of each muscle and tendon difficult.

Within the above limitations, implications of variations in architecture for hamstring injury could be identified. A comparison of MTU properties between the hamstrings indicates that ST injury incidents are low, probably owing to its lowest resistance to stretch and greater *L*MTU than the rest of the hamstrings. Further, architecture variations can assist in explaining the highest injury rate of the BFlh compared with the other hamstrings. In particular, it has been shown that during the late swing phase of sprinting, the BFlh displays the highest peak MTU strain amongst the hamstrings [87]. The greater BFlh MTU strain does not necessarily indicate a greater fascicle elongation [88] and this is supported by the higher tendon:FL ratio and PA displayed by the BFlh and SM compared with the ST [7, 44].

In addition, because of a shorter moment arm around the knee, the BFLh has a lower torque capacity at longer lengths compared with the ST and SM [6, 87]. Assuming an equal contribution of torque to whole hamstring torque around the knee, it could be suggested that as the hamstrings resist forced lengthening by exerting torque around the knee, the BFlh has to exert greater force compared with the ST and SM. Using a simple theoretical model, it has been estimated that when the hamstrings actively lengthen (eccentric contraction) within the same time frame, the BFlh fibers must produce a greater muscle force than the other hamstrings, as a result of their greater change in length [89]. This, assumes, however, that tendon properties and muscle activation are similar between the hamstrings, which is currently unknown.

However, of the three hamstrings, the BFlh displays greater stiffness during dynamic movements, [32] a greater passive lengthening but less active shortening of the aponeurosis from a lengthened position, [50] and a narrower aponeurosis proximally than distally [79]. In addition, absolute FL changes [54] and local muscle strains [25] during contractions of the BFlh are greater proximally than distally. All these factors might result in an increase in tissue strains near the proximal aponeurosis of the BFlh during active lengthening, thus increasing injury risk [25]. This risk may also increase following an injury, as a reduction in aponeurosis size and altered compliance near the injured area of the muscle has been reported [79, 90].

It appears that the SM displays greater local muscle stiffness (probably owing to greater lengthening of the fascicles) than the other hamstring muscles, while during dynamic stretches the BFlh may experience equal or even greater resistance to stretch. One may wonder whether this finding is linked with the observation that the SM is injured mostly during long stretching exercises, while the BFlh is injured during fast dynamic movements [4]. The factors that contribute to such differences are unclear. It has been proposed that as a result of different titin mechanics, the SM has lower passive extensibility than the BFlh while the opposite occurs in active contractions [91]. Future research could examine whether inter-muscular differences in the proximal attachment and fiber orientation along each muscle may affect local strains. It may also be necessary to re-model hamstring muscle kinematics by taking intra- and inter-muscular variability in architecture into consideration.

Based on the reviewed evidence, interesting questions regarding exercise responses of the hamstrings arise. For example, are dynamic stretches better for restoring BFlh compliance than static stretches? Are hip stretches better to increase SM compliance while knee stretches are better for a BFlh stretch? Which muscle is affected most by combined hip and knee stretching exercises? Recent studies [92–94] have identified regional-specific responses of the hamstrings to different exercises, thus strengthening the argument that specific exercises or exercise programs can selectively activate individual hamstring muscles. This can be elaborated further by examining whether specific combinations of joint motion, contraction type, and exercise instructions may 'target' a specific hamstring muscle. Similarly, it would be interesting to understand whether an injury to one area/compartment is compensated by altered mechanical behavior of the other compartment. In this occasion, therapeutic modalities such as electrical stimulation can be used to selectively activate a specific area of the muscle.

6 Conclusion

While the hamstrings may have a common function as a group, there are significant intra- and inter-muscular differences in their design that may influence their force-generation capacity as well as responses to external loading demands. These intra- and inter-muscular variations might suggest that hamstring exercises do not provide the same stimulus to all hamstring components. Future research could examine whether specific intervention strategies can be used to prevent specific hamstring muscles from sustaining injuries. Similarly, rehabilitation programs designed for each specific muscle–tendon region sustaining an injury may be more beneficial than programs designed for the hamstrings as a whole.

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