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The Effect of Age and Joint Angle on the Proportionality of Extensor and Flexor Strength at the Knee Joint

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Functional movements require concerted actions of monoarticular and biarticular agonists and antagonists. Understanding age-related changes of muscle function on performance requires insight in the contributions of different muscles to joint moments. Young and elderly participants performed isometric knee extensions and flexions at combinations of knee and hip joint angles. This approach allowed assessing changes in contribution of monoarticular and biarticular knee joint flexors and extensors. Reduced moments were found for elderly persons (flexors: -43% ; extensors: -33%). In the flexor group, this reduction was mainly caused by retardation of the biarticular muscles; in the extensors, by reduced strength of the monoarticular muscles. This age-related reduction of joint moments occurred to be joint angle dependent for the extensors. In the flexor group, the reduction was almost invariant. Due to this difference in joint angle dependence, the proportionality between extensors and flexors varied over joint angles and differed with age. It has been discussed how this is related to changes in performances occurring with age.

ELDERLY people experience difficulty in their gait; they walk slower, with a smaller range of motion in their joints, and are more unstable, resulting in a higher incidence of falling (1–6). Changes in gait dynamics, possibly initiated by reduced muscle capacity, underlie these differences in gait parameters (7–13). An important aging effect is a redistribution of joint moments or powers. For example, DeVita and Hortobagyi (11) showed that the gait of elderly persons differs from that of younger persons with respect to the distribution of joint moments. They reported that elderly people generate larger hip joint extension moments during the stance phase of walking and reduced knee joint extension moments.

The distribution of moments over adjacent joints is governed by the tuning of monoarticular and biarticular agonistic and antagonistic muscles (14). In a multibody system, like the human leg, the distribution of joint moments determines the external force, i.e., the force applied to the ground. During walking, in the initial part of the stance phase, the force applied to the ground is directed forward and downward. When the stance phase proceeds, the forward component of this force decreases. Finally, in the second half of the stance phase, the horizontal component of this force is increasingly backwardly directed. Van Ingen Schenau and colleagues (14) have shown that, in a multibody system, specific patterns of coactivation of monoarticular and biarticular agonists and antagonists are required to efficiently produce a required movement pattern in combination with an appropriate direction and magnitude of an external force. For example, during walking, coactivation of the monoarticular hip joint extensor muscle (*m. gluteus maximus*) and the biarticular hip joint flexor and knee extensor muscle (*m. rectus femoris*) is the most efficient way to direct the external

force forward and simultaneously extend the knee and hip joints.

From the above it can be concluded that muscles do not simply function as joint moment generators, but also play an important role in the control of external forces. This implies that a biarticular muscle such as *rectus femoris* cannot be seen as just a part of the knee extensors. Instead biarticular muscle should be treated as a separate functional unit. Since the direction of the external force is determined by coactivation of antagonists, functional performance is not so much limited by maximal force capacity of a specific muscle. Instead, in a multibody system, it is the weakest link that sets the limit for a proper performance. Therefore, function of individual muscles should be evaluated at the joint angles (i.e., specific muscle lengths) that are relevant for the task. Furthermore, muscle function should be evaluated in the context of the muscles it cooperates with. For example, if the *m. rectus femoris* is relatively weak compared with the *m. gluteus maximus*, the ability to direct the force applied to the ground forwardly at the beginning of the stance phase will be hampered.

Commonly, muscle weakness has been assessed as a reduction in maximal joint moments (15–22). This approach ignores the individual contributions of monoarticular and biarticular muscles to, for example, extending knee joint moments. Recently, it has been shown that sports-specific specialization (e.g., running and cycling) has important consequences for the distribution between monoarticular and biarticular agonists. It was found that sports activity influenced the maximal joint moments and the optimal joint angles of individual muscles in the *m. quadriceps* group, but it did not influence the maximal knee extending joint moments of the *m. quadriceps* as

a whole (23,24). This indicates that subtle changes in individual muscle performance have profound effects on whole-body performance. It can be concluded that an understanding of human movement performance requires knowledge of adaptations in monoarticular and biarticular muscle separately.

Approaches that assess both maximal extending and flexing knee joint moments (25–27) acknowledge the need to have insight in the contributions of antagonistic muscle groups, but still lack the ability to understand contributions of monoarticular and biarticular muscles. Furthermore, these studies provide just a single value for a flexor:extensor ratio, being defined as the quotient of maximal flexor moment and maximal extensor moment (28–31). Implicitly it has been assumed in these studies that the proportion of flexor and extensor strength does not change with joint angles, and that maximal values for extensor and flexor muscles occur at similar joint angle combinations. The length dependency of muscle force makes both assumptions questionable. Recently, Aagaard and colleagues (32) showed that the flexor:extensor ratio depends on joint angle. From this it can be deduced that, to relate the flexor:extensor ratio to activities of daily living (walking stability, stair negotiation, sit-to-stand activity), it would be more appropriate to evaluate them at joint angle combinations (knee and hip joint angles) that are relevant for such a functional activity.

Muscle weakness and reduced lower extremity strength have been associated with mobility and stability problems in elderly persons (15–18,33,34). It is known that the negative influence of aging on muscle function can be different for different muscle groups (26,27). Potentially, this can result in age-related changes in the proportionality of the force that can be generated by these muscles. Consequently, reduced stability in elderly people can be the result of a redistribution of joint moments to compensate for differences in muscle weakness between different groups. To substantiate this idea, it will be necessary to evaluate the age-related changes in the force–length relation of monoarticular and biarticular agonists and antagonists. It is the aim of this study to investigate how the knee joint moment generated by monoarticular and biarticular flexor and extensor differs between younger and older participants.

METHODS

Participants

Ten young male adults (23.1 ± 2.4 years) and 10 male elderly adults (64.6 ± 3.4 years) participated in this study. All participants, both elderly and young, were active runners. To be included in the study, participants had to run at least 20 km/week. In this way, differences due to nonstandardized adaptation conditions (e.g., differences in sport activities) were largely excluded. After participants had been familiarized with the procedure of the study; all participants gave written informed consent to participate. The human ethical review committee of Maastricht University approved the study.

Experimental Setup

After warming up on a cycle-ergometer, the participants were positioned on a dynamometer (Cybex II; CSMI, Stoughton, MA). Before testing, the participants were acquainted with the protocol and the test setup. Participants were instructed to execute maximal, voluntary, isometric contractions with the right leg. They were instructed to develop subsequently a maximal extending and a maximal flexing knee joint moment. During the contractions, the participants were fixed to the chair of the dynamometer by Velcro strips over the pelvis and thigh. The lateral epicondyle of the right femur was aligned with the axis of rotation of the dynamometer.

Protocol

During a test, the participants performed 20 maximal, voluntary, isometric contractions. The contractions were carried out at combinations of four different hip joint angles and five different knee joint angles. The hip joint angle was set at 5°, 35°, 65°, or 100°. A completely extended trunk, with the legs and the trunk aligned, was defined as zero degrees. The knee joint angle was varied between 0°, 20°, 50°, 80°, and 110°. The extended leg was defined as zero degrees; increasing angle values corresponded to increasing flexion at the knee joint. In random order, the different joint configurations were applied. Between subsequent maximal, voluntary, isometric contractions, the participants were allowed 3 minutes of rest. Each of the respective extension and flexion contractions at one hip and knee joint configuration lasted approximately 2 seconds. Immediately after the contractions at one joint configuration, the participant was positioned in the joint configuration for the next contractions. In this way, standardization of preconditioning of the elastic components of the muscle–tendon complex was provided. The passive knee joint moment was recorded for 1 second before the respective extension and flexion contractions. This passive moment resulted from the weight of the limb and of the arm of dynamometer, and from the tension of passive structures in the limb. The passive moment could have a positive (knee extending) or negative (knee flexing) value. Subsequently, the gross active knee joint extension and flexion moments were assessed.

Data Analysis

For both extension and flexion, the net active knee joint moment was calculated by subtracting the passive knee joint moment from the maximal gross active knee joint moment. The maximal gross active knee joint moment was defined as the average value of the highest joint moment that was sustained for at least 0.5 seconds.

To separate the contribution of the monoarticular muscles (*mm. vasti* and *m. biceps femoris caput breve*) from their biarticular counterparts (*m. rectus femoris* and biarticular part of the hamstrings), a procedure described by Savelberg and Meijer (24) was applied. In this approach, use is made of the fact that changing the knee joint angle will affect the lengths of both monoarticular and biarticular muscles, whereas manipulating the hip joint angle changes only the length of the biarticular muscle and thus only affects the

contribution of the biarticular muscle to the joint moment. By comparing joint moments generated at similar knee joint angles but different hip joint angles, changes in the contribution of the biarticular muscles with changing length of the biarticular muscles can be distilled. By subtracting the biarticular contribution from the total joint moment, the contribution of the monoarticulars was obtained. A model by Hawkins and Hull (35) was used to relate knee and hip joint angles to lengths of the biarticular muscles. Subsequently, these raw data for biarticular muscles were fitted to a first or second degree polynomial in order to obtain a moment–angle relation for this muscle. The degree of the polynomial was determined by polynomial regression; it was allowed to vary between individuals. The contributions of the monoarticular muscles as a function of knee joint angle were obtained by subtracting the fitted contribution of the biarticular muscles from the respective total joint moments. Finally, a polynomial was fitted through these data, resulting in moment–angle relationships for the monoarticular muscles. This approach allowed for analysis of the amplitude and shape of the moment–angle curves of monoarticular and biarticular muscles. Also, from this analysis, it could be concluded whether the isometric force of a muscle group increases or decreases with joint angle variation. This change in contribution of a muscle group was expressed relative to the contribution at a combination of reference knee and hip joint angles. The reference joint angle combination was 0° at the knee joint and 80° at the hip joint. It is important to notice that this approach did not enable assessing absolute values for knee joint moments generated by the monoarticular muscle groups or the biarticular muscle groups. These changed contributions will be referred to as ΔM_{vasti} (*m. vasti*), ΔM_{RF} (*m. rectus femoris*), $\Delta M_{\text{monoHam}}$ (*m. biceps femoris caput breve*), and ΔM_{biHam} (biarticular component of the hamstrings moment). The minimal extending or flexing knee joint moment that was generated will be referred to as the nonattributable extending or flexing joint moment. So for extension and flexion, the joint moment generated at a specific combination of knee and hip joint angles consists of the moment attributable to the biarticular muscle group, the moment attributable to the monoarticular muscle group, and a moment that cannot be exclusively attributed to either the monoarticular or the biarticular muscle group:

$$M_{\text{tot}}(i, j) = M_{\text{bi}}(i, j) + M_{\text{mono}}(i, j) + M_{\text{non-attr}}$$

where i and j represent specific knee and hip joint angles.

To evaluate the quality of this procedure for attributing total joint moments to either monoarticular or biarticular muscle groups, a correlation coefficient for each of the 20 combinations of joint angles was calculated for measured joint moments and the sum of moments attributed to monoarticular or biarticular muscle and the nonattributable moment. This correlation coefficient was calculated for each participant for both the extension moments and the flexor moments. Data sets with a correlation coefficient of less than 0.65 were not considered in the analysis.

The maximal changes in the contribution of individual monoarticular and biarticular extensor muscles were ex-

Table 1. Participant Characteristics

Characteristic	Young	Elderly	<i>p</i>
Age (y)	23.1 (2.4)	64.6 (3.4)	<.001*
Body length (m)	1.86 (0.08)	1.75 (0.03)	<.001*
Body mass (kg)	76.7 (6.2)	75.6 (5.2)	.337
% Fat	8.4 (1.1)	19.6 (3.9)	<.001*

Notes: Average values (standard deviation).

**p* denotes level of statistical significance between young and elderly participants.

pressed as a percentage of the maximal extension joint moment, for example:

$$\begin{aligned} \% \Delta M_{\text{vasti}} \\ = \text{maximal } \Delta M_{\text{vasti}} / \text{maximal extension joint moment} \end{aligned}$$

Similarly, the monoarticular and biarticular flexor muscles were related to the maximal flexion joint moment. These values express to what extent changing the joint angles affects the ability of a muscle to contribute to a joint moment. Similarly, both nonattributable joint moments were expressed as a percentage of the respective maximal extension and maximal flexion moments. To monitor changes in the optimal length of muscles, the joint angle at which a muscle contributed maximally was assessed. To evaluate the balance between flexor and extensor muscle capacity, an HQ ratio was determined for each combination of knee and hip joint angles:

$$\begin{aligned} \text{HQ ratio} \\ = 10 \log(\text{flexion joint moment} / \text{extension joint moment}) \end{aligned}$$

Statistical Analysis

Student's *t* test was applied to analyze the differences between young and elderly persons in the characteristics of moment–angle curves of total joint moments and of individual muscles.

RESULTS

Apart from their age, participants also differed with respect to body length and body composition. Younger participants were significantly larger and had less body fat (Table 1).

Distribution Between Flexor and Extensor Moments

In elderly participants, both the maximal and minimal extension and flexion joint moments were significantly reduced compared with the young participants (Table 2). The difference between the extensor joint moments of young and elderly participants depended on the knee joint angle. At large flexed knee joint angles, the difference was found to be, on the average, 33%. At small extended knee joint angles, the difference between young and elderly participants was, on the average, 18%. In the flexors, the effect of aging was larger, on the average, the maximal difference amounted to 43%, the minimal difference was 35%. For the flexor moment, the joint angle dependence of this age-related change was less prominent than for the extensor moment (Figure 1).

Table 2. Joint Moment Characteristics

Characteristic	Young	Elderly	<i>p</i>
HQ			
Minimal HQ ratio	-0.38 (0.06)	-0.40 (0.05)	.214
Maximal HQ ratio	0.26 (0.14)	0.08 (0.10)	.002*
Quadriceps			
Maximal extension moment	231.4 (70.1)	155.1 (40.3)	.004*
Minimal extension moment	53.7 (12.5)	43.7 (8.9)	.027*
% Range extension moment	74.8 (8.3)	70.6 (8.4)	.134
% Nonattributable extension moment	14.5 (11.5)	21.0 (15.5)	.152
Maximal ΔM_{vasti}	170.1 (74.7)	99.9 (45.4)	.010*
% ΔM_{vasti}	71.6 (10.0)	61.8 (13.9)	.044*
Optimal joint angle vasti	79.7 (16.0)	80.8 (13.4)	.435
Maximal ΔM_{RF}	41.1 (23.0)	31.3 (20.5)	.165
% ΔM_{RF}	18.1 (9.4)	21.4 (14.0)	.277
Optimal length RF	1.06 (0.14)	1.15 (0.16)	.084
Hamstrings			
Maximal flexion moment	126.2 (35.5)	73.4 (22.6)	.0004*
Minimal flexion moment	68.8 (30.1)	45.7 (15.5)	.022*
% Range flexion moment	46.0 (19.9)	36.9 (14.7)	.126
% Nonattributable flexion moment	37.5 (16.0)	48.9 (12.6)	.061
Maximal $\Delta M_{\text{monoHam}}$	46.7 (29.7)	27.9 (7.2)	.049*
% $\Delta M_{\text{monoHam}}$	36.4 (13.5)	36.0 (7.0)	.471
Optimal angle monoHam	84.1 (41.5)	87.9 (24.4)	.410
Maximal ΔM_{biHam}	53.8 (26.5)	19.9 (10.8)	.002*
% ΔM_{biHam}	42.4 (15.7)	25.8 (13.9)	.018*
Optimal length biHam	1.2 (0.0)	1.18 (0.07)	.173

Notes: Group means (standard deviations).

**p* denotes level of statistical significance between young and elderly participants.

Variables are explained in the text.

RF = rectus femoris.

The HQ ratio was not a constant. It was found to vary with the knee and hip joint angle in both young and elderly participants (Figure 2). It varied from -0.4 to 0.26. Negative values indicated extensor dominance, and positive values indicated flexor dominance. Maximal values of HQ ratio occurred at an extended knee joint angle, and minimal values at approximately 80° of flexion of the knee joint. The effect of hip joint angle on HQ ratio was small compared with the knee joint angle effect. Between both groups of participants, significant differences in the HQ ratio were found. The maximal HQ value was significantly smaller for the elderly participants (0.08 ± 0.10) than it was for the younger participants (0.26 ± 0.14). Minimal HQ ratio did not differ between groups.

Contribution of Monoarticular and Biarticular Extensors

The ΔM_{vasti} curves of all participants displayed a parabolic pattern (Figure 3) with a peak at approximately 80° of flexion. The optimal knee joint angle for this muscle group did not differ between both groups of participants. Both the maximal value of ΔM_{vasti} and the relative contribution of the *mm. vasti* (% ΔM_{vasti}) were significantly less in the elderly participants than in the young participants (Table 2). In the elderly participants, the relative amplitude of *mm. vasti* was 10% less than in the young participants (Table 2).

For the *m. rectus femoris*, maximal ΔM_{RF} and % ΔM_{RF} were not different between both groups (Figure 4). The

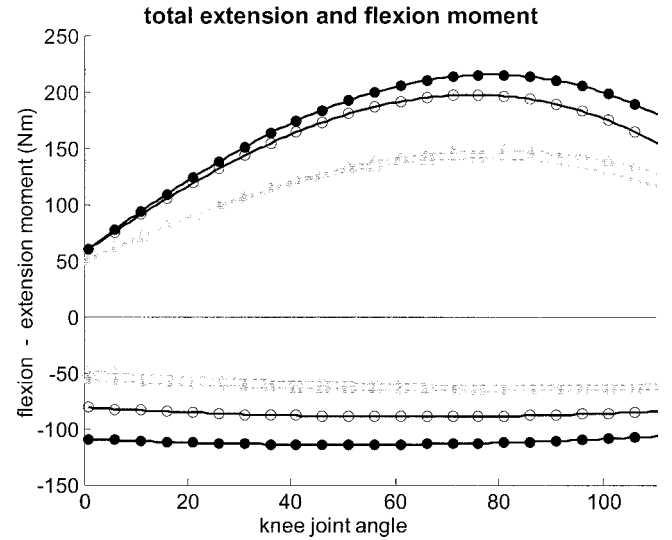


Figure 1. Averaged total extension and flexion knee joint moments as a function of knee joint angle. At 0°, the knee joint is fully extended; increasing values represent increasing flexion of the knee joint. Extension joint moments have been presented as positive values; the negative curves present the flexion joint moments. The grey curves with triangles give the average curves for the elderly participants ($n = 10$); the black lines with the circles represent data for young participants ($n = 10$). Moreover, the affect of hip joint angle has been presented. Curves with filled circles or triangles give data for complete forward flexion at the hip joint; open circles represent data for hip joint extension.

course of the curves for participants was found to vary considerably. In 7 of 10 young participants, *rectus femoris* operated on the descending part of the joint moment-length curve. In the elderly participants, 5 of 10 operated on the descending part. All other participants had their *rectus femoris* operating on the ascending side.

The amount of the extensor moment that could not be attributed to either the monoarticular or the biarticular muscle group did not differ between young and elderly participants. It amounted to 15%–20% of the maximal extending joint moment (Table 2).

High correlation coefficients between measured and calculated joint moments were found both for elderly 0.94 ± 0.04 and young participants 0.94 ± 0.03 .

Contribution of Monoarticular and Biarticular Flexors

Participants reported the flexion contractions to be harder to execute. This was reflected in lower correlation coefficients between measured and calculated joint moments, 0.77 ± 0.08 and 0.73 ± 0.07 , respectively, for young and elderly participants. For one of the young participants and for two of the elderly participants, the correlation coefficient was less than 0.65. These data were not considered in the analysis.

All biarticular hamstrings operated on the ascending side of the joint moment-length curve; flexion of the hip joint or extension of the knee joint, which both lengthen the muscle, resulted in increased forces. The absolute and relative ranges of this muscle group (ΔM_{biHam} and % ΔM_{biHam}) were significantly reduced in elderly participants (Table 2, Figure 5). The shape of the joint moment-joint angle relationship

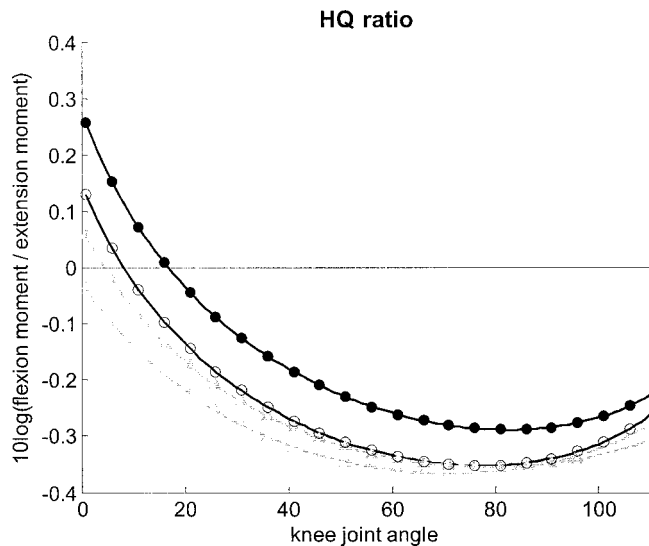


Figure 2. Average HQ ratios as a function of knee joint angle. At 0° , the knee joint is fully extended; increasing values represent increasing flexion of the knee joint. Positive values of HQ represent flexor dominance. The grey curves with triangles give the average curves for the elderly participants ($n = 10$); the black lines with the circles represent data of young participants ($n = 10$). Moreover, the affect of hip joint angle has been presented. Curves with filled circles or triangles give data for complete forward flexion at the hip joint; open circles represent data for hip joint extension.

for monoarticular hamstrings (Figure 6) varied widely between participants. Fifty percent of the participants operated on the descending side of the force-length curve, knee flexion being associated with increasing moments. The other 50% of the participants operated around the peak of the force-length curve, displaying an optimal knee joint angle at approximately 40° of knee joint flexion. The distribution of these patterns was found to be independent of age group.

The nonattributable flexion moment did not differ as a function of age. Compared to the nonattributable extension moment, it was found to be larger, on average, 37% for the young participants and 48% for the elderly participants.

DISCUSSION

Numerous studies have been carried out exploring the change in muscle force that occurs with aging. In many of these studies, muscle force has been operationalized as the maximal extending knee joint moment. The approach for this study was that muscle force is joint angle dependent, and that it is questionable whether maximal force has functional relevance. Moreover, it was acknowledged that the relation between the extensor and the flexor moment at any joint angle is of functional importance. It was hypothesized that aging affects the ratio between flexor and extensor knee muscle strength, and that changes in this ratio would vary with joint angle configuration. Furthermore, the study aimed at quantifying the contribution of monoarticular and biarticular muscles to changes in total joint moments. It was hypothesized that differentiation in the adaptations of contributing monoarticular and biarticular muscles underlies the variability in changes in this ratio. The

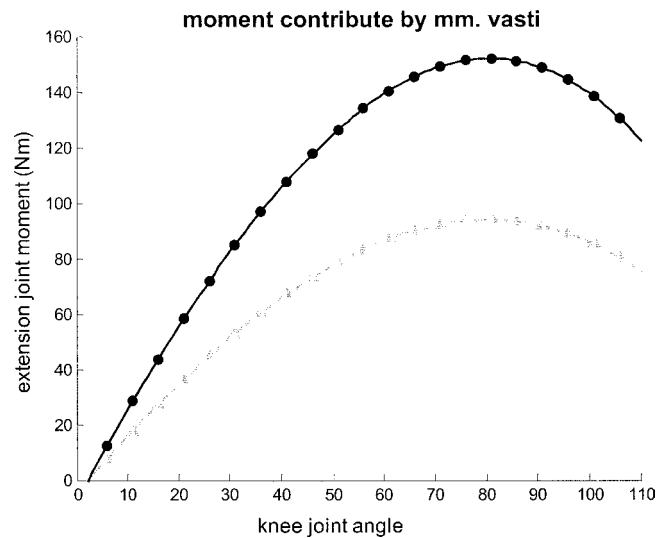


Figure 3. The change in the contribution of the monoarticular *mm. vasti* to the extending knee joint moment (ΔM_{vasti}) as a function of the knee joint angle. At 0° , the knee joint is fully extended; increasing values represent increasing flexion of the knee joint. The moment generated at the fully extended knee joint and flexed hip joint has been taken as the reference joint moment. The grey curves with triangles give the average curves for the elderly participants ($n = 10$); the black lines with the circles represent data for young participants ($n = 10$).

results provide support for all three components of the hypothesis. Whereas at flexed knee joint angles extensor dominance has been found, flexor dominance occurred at more extended knee joint angles of young participants. This underlines that the proportion of flexor and extensor

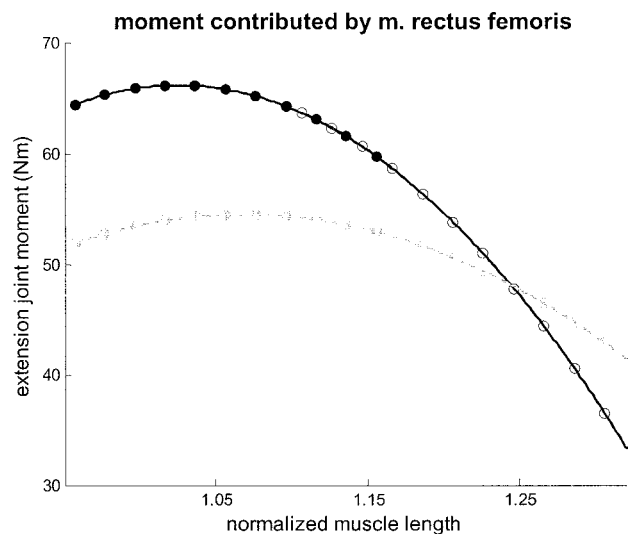


Figure 4. The change in the contribution of the biarticular *m. rectus femoris* to the extending knee joint moment (ΔM_{RF}) as a function of the normalized muscle length (35). The moment generated at the fully extended knee joint and flexed hip joint has been taken as the reference joint moment; in this configuration of knee and hip joint, the *m. rectus femoris* is at its shortest length. The grey curves with triangles give the average curves for the elderly participants ($n = 10$); the black lines with the circles represent data for young participants ($n = 10$). Moreover, the affect of hip joint angle has been presented. Curves with filled circles or triangles give data for complete flexion of the hip joint; open circles represent data for hip joint extension.

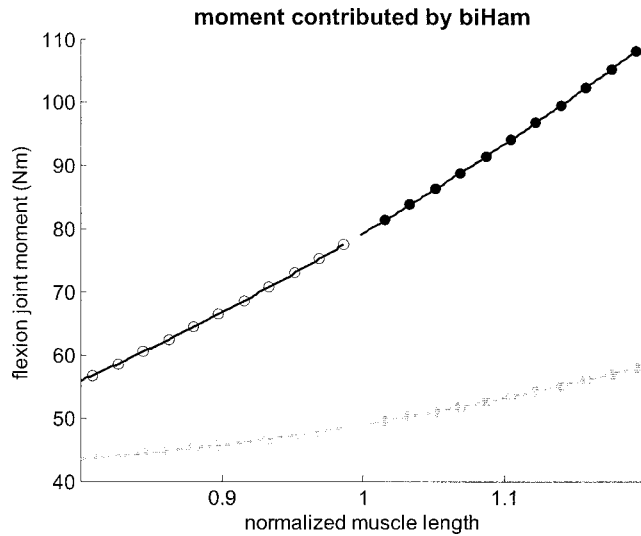


Figure 5. The change in the contribution of the biarticular part of the hamstring to the flexing knee joint moment (ΔM_{biHam}) as a function of the normalized muscle length (35). The moment generated at the fully extended knee joint and flexed hip joint has been taken as the reference joint moment; in this configuration of the knee and hip joint, the biarticular component of the hamstring is at its largest length. The grey curves with triangles give the average curves for the elderly participants ($n=8$); the black lines with the circles represent data for young participants ($n=9$). Moreover, the affect of hip joint angle has been presented. Curves with filled circles or triangles give data for complete flexion of the hip joint; open circles represent data for hip joint extension.

capacities is joint angle dependent. In elderly participants, a similar increase of extensor dominance with knee joint flexion has been found. However, the flexor dominance that was found in the young participants at extended knee joints did not occur in elderly participants. This indicates that HQ ratio is affected by aging. Moreover, it was found that monoarticular and biarticular muscles contributed unevenly to changes in the total extending or flexing joint moments.

In this study, we found for people in their seventh decade compared with young adults, the total knee extensor moment decreased by 33% on the average and the total knee flexor moment by 43%. These values are similar to the reduction in extensor moment reported in literature (36). The literature on age effects on knee joint flexors is limited. Macaluso and colleagues (27) reported a reduction of 47% for women in their seventh decade. Häkkinen and colleagues (25) reported reductions between 20% and 35% for women and men, respectively. Also the absolute values of joint moments resemble those reported for young and elderly persons in the literature (16,19,26,37,38).

In conventional approaches, only one HQ value (28–31,39) based on maximal knee joint extension moment and knee joint flexion moment has been determined. In such an approach, the present differences would not have been found. In that case, it would have been concluded that the relative contribution of flexors and extensors is neither affected by age nor by joint angle configuration (0.54 vs 0.47 NB, not reported in results). The present study showed that proportionality of flexors and extensors changed with age and that it was joint angle dependent. This is relevant for

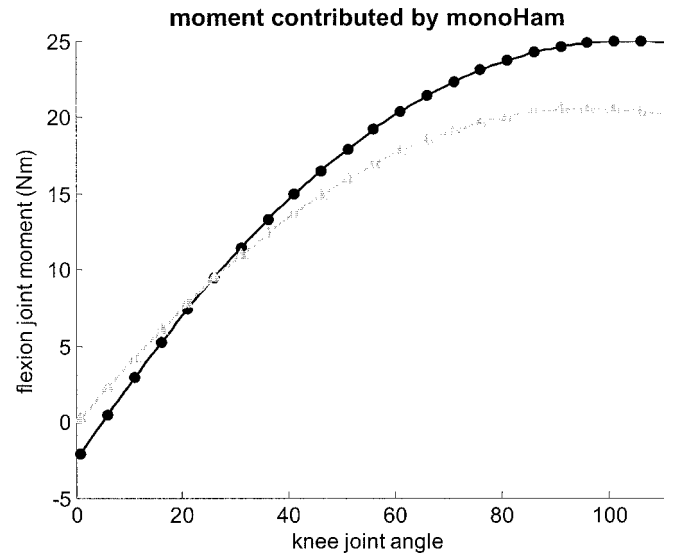


Figure 6. The change in the contribution of the monoarticular part of the hamstring to the flexing knee joint moment ($\Delta M_{\text{monoHam}}$) as a function of the knee joint angle. At 0° , the knee joint is fully extended; increasing values represent increasing flexion of the knee joint. The moment generated at the fully extended knee joint and the flexed hip joint has been taken as the reference joint moment. The grey curves with triangles give the average curves for the elderly participants ($n=8$); the black lines with the circles represent data for young participants ($n=9$).

relating changes in muscle capacity to functional performance, for example, rising from a chair or ambulation.

In gait, both the knee and hip operate during major parts of the stance phase at relatively extended joint angles [knee: 10° to 30° ; hip: -30° to 10°] (11). Particularly at these joint configurations, the largest differences in the HQ ratios of elderly and young participants have been found. In the young participants, at 10° of knee joint flexion, the flexors generated larger joint moments than the extensors, while in the elderly participants, the extensors generated clearly larger moments than the flexors. At 30° of knee joint flexion, extensor dominance has been found for both groups of participants. However, in the elderly participants, the extensors were more prominent (thus a smaller HQ ratio). The reduction of flexor muscle strength in the elderly participants was only slightly affected by the knee joint angle. In contrast, the reduced extensor strength in the elderly participants occurred most prominent at large, more flexed knee joint angles and was almost absent at extended knee joint angles (Figure 1). DeVita and Hortobagyi (11) reported that, for normal walking in elderly participants, there was a reduction in peak extending knee joint moment compared with young participants. Around the hip, they found enlarged extension moments and reduced flexion moments in elderly participants. The maximal net extending knee joint moment in walking, which occurs when the knee joint is approximately 20° flexed, was reduced from approximately 75 Nm in young participants to approximately 30 Nm in elderly participants. In the present study, we found that the average maximal extended knee joint moment at this particular knee joint angle was approximately 75 Nm for elderly participants.

Monoarticular and biarticular extensors contribute equally to this moment. As the contraction during gait will not be isometrical, the actual joint moment generated by these muscles will be less than 75 Nm. Although some caution has to be considered when comparing the joint moments assessed in this study to net joint moments derived for gait, it can be suggested that the reduced capacity of knee joint extensors found in this study is a factor in the changes in gait dynamics reported for elderly participants (11). Comparing muscle capability and activities of daily living (ADL) requirements, Hortobagyi and colleagues (40) came to a similar conclusion. They found that elderly persons performed ADL tasks near their maximal joint moments. In rising from a chair, the range of joint movement is relatively large compared to walking. Both the knee and hip joints go from 90° of flexion to full extension. In such large range-of-motion tasks, the dependence of HQ ratio on joint angle would be a relevant factor. Hughes and colleagues (16) showed that, in elderly persons at 60° of flexion, the net joint moment required during rising from a chair was 97% of the available isometric strength. However, Corrigan and Bohannon (15) concluded that reduced extensor strength is not the complete explanation of stand-up performance. In rising from a chair, coactivation of the hamstrings is necessary to allow hip extension (41). In this study, we found that at more extended knee joint angles, the HQ ratio was lower in elderly participants. Consequently, at these joint angles, knee extensor capacity might be compromised by required hamstring activity. To investigate whether this is really a factor in rising problems in elderly persons, the actual requirements and capacities of these muscle groups have to be investigated. This study showed that for relating muscle capacities to different functional movements, for example, walking or rising from a chair, it is not satisfying to evaluate muscle capacity as the maximal force generated at one joint angle. Muscle capacity varies with joint angles.

The relative flat pattern of the flexor moment is striking. Naively, a parabolic curve, such as the extensor moment curve, resembling the force-length diagram of individual sarcomeres would have been expected. This flatness is a major factor in the joint angle dependence of the HQ ratio, and also accounts for the age-related changes in this ratio. The separation of the joint moments from moments contributed by monoarticular and biarticular muscles shows that both the biarticular extensor (*m. rectus femoris*) and the biarticular part of the hamstrings have a rather flat joint moment-length curve. In the extensor group, the contribution of the monoarticular group is dominant and overrules the flat appearance of the biarticular muscle. However, in the flexor group, the biarticular muscles contribute most to the flexor moment and thus dominate the flexor joint-moment curve. Heterogeneity in the mean sarcomere length of different fibers in the biarticular muscles may underlie the flat contour of the moment-angle curves of these muscles (42). This heterogeneity of mean sarcomere length allows these biarticular muscles to generate force at a wide range of muscle lengths.

Force-length or, as in this study, joint moment-joint angle diagrams provide insight in changes in both longitudinal and cross-sectional muscle structure. A shift in the

maximal force (joint moment) generated indicates that cross-sectional changes (number of muscle fibers, muscle fiber thickness, or muscle quality) have occurred. A change in the optimal length (working range) of a muscle indicates longitudinal adaptations (number of sarcomeres in a series). The optimal joint angle (optimal length) of all four muscle groups considered in this study was unaffected by age. From this it can be concluded that the number of sarcomeres in a series in these muscles was not affected by aging. Given that the involved participants participated in similar sport activities (e.g., running) and a previous conclusion that the number of sarcomeres in a series adapt to task requirements (23,24,43), this is not a surprising result.

Within the limits of the applied approach and presently available methods, the redundancy of the locomotor systems prohibits definite calculations of changes in the maximal joint moments generated by the specific muscle groups. Additional information about muscle morphology will be required to attribute the remaining joint moment to either the monoarticular or biarticular muscle group. A future combination of the present approach with a magnetic resonance imaging-based assessment of physiological cross-sectional areas of individual muscles (44) might provide a way to deal with this redundancy. To get some insight into the effect of age on maximal muscle force, the relative maximal contribution of each muscle group to a joint moment ($\% \Delta M_{\text{vasti}}$, etc.) has been calculated. Analysis of this reveals that, in the extensor group, the contribution of the monoarticular group ($\% \Delta M_{\text{vasti}}$) was significantly reduced in elderly participants, whereas, in the flexor group, a significant reduction occurred in the biarticular group ($\% \Delta M_{\text{biHam}}$; Table 2). As the nonattributable moments have not been affected by age, this can be interpreted as an indication that the reduced extension moment in elderly participants is for a considerable part caused by retardation in the monoarticular vasti, whereas the reduction in the flexion moment seems to be the consequence of less capacity of the biarticular muscle group.

Based on this study, two major conclusions with respect to the relation between muscle functioning and age can be drawn. The first is that the reduction in muscle function that is known to occur with age is not occurring in all muscles and muscle groups at a similar extent. A differentiation of effects between and within muscle groups has been found to exist. Second, this study showed that the decline in muscle function that has been found to be associated with aging is joint angle dependent. Therefore, when evaluating muscle properties, assessing one value, a maximal moment, or a ratio at maximal moment will not be sufficient. When relating muscle changes to functional movements, it is necessary to consider changes at relevant joint angles. Walking problems could be related to muscle changes at extended knee and hip joints. When trying to understand sit-to-stand difficulties, it might be more relevant to consider changes at flexed knee and hip joints. Different degrees of retardation in different muscles of a muscle group give indications for training and reconditioning protocols. For the elderly group tested in this study, it is advised to focus on strengthening monoarticular extensors and biarticular flexors.

Moreover, with respect to functionality, this study provides evidence that the changes in gait dynamics and chair-rising that have been reported to occur in elderly persons can be associated with adaptations in specific muscles. This kind of knowledge opens possibilities for designing intervention programs addressing specific muscles involved for specific tasks.

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