


ORIGINAL ARTICLE

Muscle forces and fascicle behavior during three hamstring exercises

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Knowledge about muscular forces and fascicle behavior during hamstring exercises can optimize exercise prescription, but information on these outcomes across different exercises is lacking. We aimed to characterize and compare lower-limb muscle forces and biceps femoris long head muscle fascicle behavior between three hamstring exercises: the Nordic hamstring curl (NHC), single-leg Roman chair (RCH), and single-leg deadlift (DL). Ten male participants performed the exercises while full-body kinematics, ground reaction forces, surface muscle activation, and biceps femoris long head fascicle behavior were measured. Mean fascicle length was highest in the DL, followed by the RCH and NHC. Fascicle lengthening was higher in the NHC compared with the RCH and DL, with no difference between the RCH and DL. Biceps femoris short and long head, semitendinosus, and semimembranosus peak forces were generally higher in the NHC compared with the RCH and DL, while mean forces during the eccentric phase were generally not different between the NHC and RCH. Peak forces in the NHC coincided with low biceps femoris long head and semimembranosus muscle activation. The NHC generally has the highest peak hamstring muscle forces and results in more fascicle lengthening when compared to the DL and RCH. The NHC may therefore be most effective to promote increases in fascicle length. While the NHC may be effective to promote biceps femoris short head and semitendinosus strength adaptations, the RCH and DL may be more effective to promote strength increases in the biceps femoris long head and semimembranosus.

KEYWORDS

deadlift, musculoskeletal modeling, Nordic hamstring curl, single-leg roman chair, ultrasound

1 | INTRODUCTION

Hamstring injuries are one of the most common injuries in sports that involve high-speed running such as football and have a high risk of recurrence. Hamstring injuries frequently involve the biceps femoris long head and are

believed to occur during the late swing phase of high-speed running when the muscle-tendon unit reaches its peak length and develops a high force.¹ Modifiable risk factors for hamstring injuries include low levels of hamstring strength² (although the association is weak when considered in isolation^{3,4}), poor hamstring strength

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endurance,^{5,6} shorter biceps femoris long head fascicles,^{2,7} and altered intermuscular coordination (i.e. load sharing) between the medial and lateral hamstrings, and other muscles.^{5,8,9} A variety of exercises is being used to modify these risk factors in an attempt to prevent hamstring injuries.¹⁰⁻¹²

Since loading intensity has been found to be the primary stimulus for molecular responses and adaptations in both muscle and tendinous tissue,¹³⁻¹⁵ exercises that require high muscle forces are likely most effective at improving muscular strength and hereby reducing the risk for hamstring injuries. Further, increases in fascicle length are typically more pronounced following eccentric compared with concentric or isometric training,^{15,16} although they may also increase when training at longer muscle lengths or with a large range of motion.^{17,18} Exercises that require eccentric fascicle behavior or require force production at longer muscle lengths may therefore be beneficial to modify this risk factor. These findings collectively indicate that knowledge about the muscular forces and the fascicle behavior during exercises is essential as this allows practitioners and researchers to optimize exercise prescription and target-specific adaptations to maximize the effectiveness of the exercises. Further, such information can also inform the design of training studies that aim to investigate the chronic adaptations induced by different exercises.

Popular hamstring strengthening exercises include the Nordic hamstring curl (NHC), single-leg Roman chair hold (RCH), and single-leg deadlift (DL). Despite the increased focus on hamstring strengthening exercises, there is currently only a little evidence available on the muscular forces and the contraction mode of the hamstrings during these exercises. Indeed, although the NHC has been shown to be effective at reducing hamstring injuries (when compliance is adequate) and at improving sprint performance and hamstring strength¹⁹ and fascicle length,^{10,20} the hamstring muscle forces and fascicle behavior during this exercise that may explain these adaptations remain largely unknown, with only one study so far investigating fascicle behavior during a portion of the exercise.²¹ Similarly, the single-leg RCH has also been suggested to be an effective hamstring strengthening exercise because it is believed to also result in high hamstring muscle forces and to mimic the quasi-isometric hamstring action observed during (a part of) the late swing phase of running.^{1,22} Finally, hip dominant exercises such as the single-leg DL are also often used for hamstring injury prevention, in the rehabilitation process, and to enhance performance.²³⁻²⁶ Reasons for the popularity of the DL include the larger moment arms of the hamstrings around the hip compared with the knee,^{27,28} which theoretically results in larger muscle-tendon unit -and hence potentially fascicle

length changes during this exercise as compared to more knee-dominant exercises. Since the muscle forces and fascicle behavior during these exercises that may explain specific adaptations remain unknown, the aim of this study was to characterize and compare hamstring muscle forces and biceps femoris long head muscle fascicle behavior between three popular hamstring strengthening exercises (the Nordic hamstring curl, the single-leg Roman chair, and the single-leg deadlift) in an attempt to understand their potential role for modifying hamstring injury risk factors. We hypothesize that the NHC shows the highest peak hamstring muscle forces due to the potential eccentric muscle fiber action²⁹ and hypothesize that the DL shows the largest excursion in biceps femoris fascicle length throughout the exercise due to the large hip flexion and large moment arm of the hamstrings around the hip.

2 | METHODS

2.1 | General procedures

This cross-sectional study was registered after data collection but before data analysis in the Dutch trial register (nr. NL8438). The study consisted of two experimental sessions. The first session was used to familiarize the participants with the exercises and to determine the one-repetition maximum (1RM) for the RCH and DL. During the second session, the participants performed the RCH, DL, and NHC in a random order. Hamstring surface electromyographic activation, biceps femoris long head fascicle length, and lower-limb muscle forces were measured/estimated during the exercises. Participants were instructed to wear non-reflective shorts and refrain from strenuous exercise 24 hours before the sessions.

2.2 | Participants

Ten male participants (mean \pm SD age 23.2 ± 2.9 years, body height 1.80 ± 0.1 m; body mass 74.4 ± 9.9 kg) volunteered to participate. Inclusion criteria were: aged 18–30 years, participating in a sport that involves high-speed running for at least three times a week (e.g., soccer and athletics), prior experience with lower-body resistance training (though not necessary experience with the exercises employed within this study), and height of 1.70–1.99 m. Participants were excluded whether they had severe visual or hearing impairment, or a history of a previous injury to the leg or back within the previous 24 months. The study was approved by the local ethics committee (NL63290.068), and all participants signed informed consent prior to the measurements. The sample size calculation is specified in

Supplementary Material S1. The final sample included individuals who participated at a recreational or subnational level in soccer, American football, and athletics and also regularly performed strength training exercises. None of the participants underwent an operation for a lower leg or back injury in the past.

2.3 | Exercises

The participants performed the DL by standing upright on a force platform (AMTI OR6 series) while holding the barbell. They were then instructed to slightly flex the knee of the preferred leg, point the toes straight ahead, and transfer their weight on this leg. The participant then flexed the hip allowing the torso and barbell to lower to a point where the upper body was almost horizontal (Figure 1A), before extending their hip and returning to an upright position. More details regarding the instructions provided can be found in Supplementary Material S1.

For the NHC, the participants were positioned with each knee on a separate force platform and the ankles secured under a pad at a $\sim 90^\circ$ angle (Figure 1B). The participants were then instructed to lower their bodies towards the floor within ~ 7 – 8 s (as controlled by a metronome and by counting out loud) to ensure a controlled execution.³⁰ They were also instructed to continue resisting falling down after the break-point and to ‘catch’ their upper body as late as possible after the break-point to maximize the knee range of motion.

The RCH was performed on a custom-made roman chair whereby the pelvic support was secured to a force platform and performed as per the previously described protocol.¹² Briefly, the participants were lying prone, with

the pelvis supported by a pad, the hips and knees in slight flexion ($\sim 40^\circ$ and 40° , respectively), and the feet secured under the foot pad (Figure 1C). They were then asked to lift the barbell and to raise their trunk upwards until the trunk was approximately parallel to the ground, before taking their weight onto their preferred leg. This position was held for approximately 3 s to achieve an isometric condition of the hamstrings before lowering the weight in a controlled way.¹² Only the single-leg hold and barbell lowering phase were included in the analysis.

2.4 | Familiarization and determination of 1RM

During the first experimental session, each participant was shown a demonstration of the correct technique for all exercises by one of the investigators and then performed several practice repetitions of the NHC and a 1RM protocol for the RCH and DL (which also served as familiarization with the exercise) in the same order as the exercises were performed in the second session. For both the RCH and DL, the 1RM protocol was performed according to the guidelines of the National Strength and Conditioning Association (Supplementary Material S1). The 1RM was recorded to the nearest 1 kg, and all participants reached their 1RM within 2.6 ± 1.1 attempts. Mean \pm SD 1RM for the RCH and DL were 68.2 ± 8.8 and 63.5 ± 19.5 kg, respectively. For all individuals in the current study, the NHC was already supramaximal (i.e., they could not complete the exercise throughout the complete range of motion without falling), and no 1RM assessment was therefore required. The second experimental session was performed at least three days after the first experimental

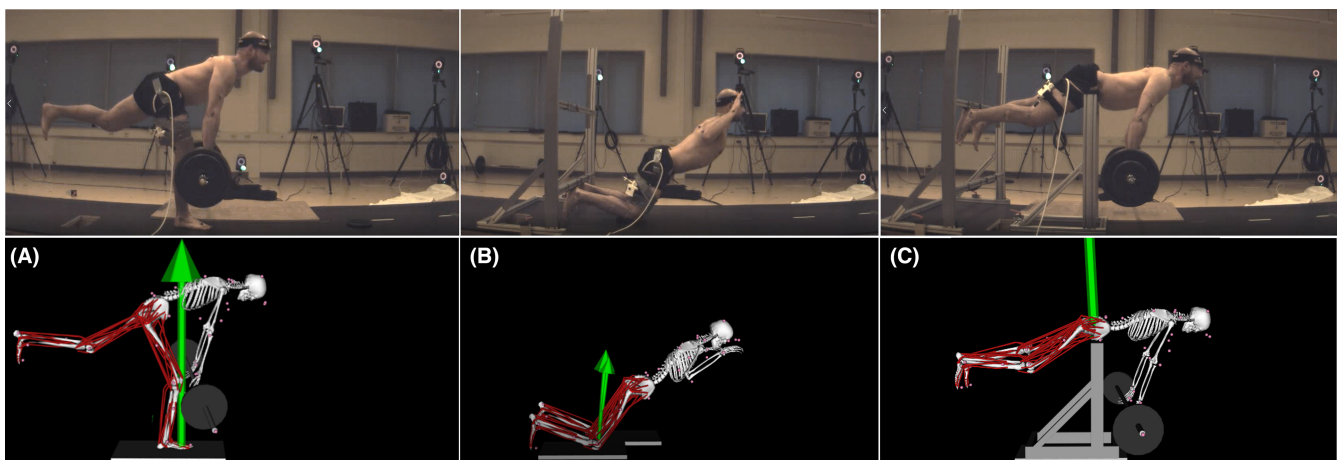


FIGURE 1 Experimental set-up for the single-leg deadlift (A), Nordic hamstring curl (B), and the single-leg Roman chair hold (C), and the corresponding OpenSim model for each exercise. Note that the top and bottom images are from a slightly different point of view. The green arrow depicts the ground reaction force vector. A video with synchronized video and musculoskeletal model movement can be viewed at the OpenScience framework: <https://osf.io/zfbwa/>

session to minimize the influence of delayed-onset muscle soreness. Indeed, eight participants reported no delayed-onset muscle soreness, and two participants reported only minor soreness.

2.5 | Data collection

When the participants entered the laboratory, 43 retroreflective skin markers were attached to the skin using a modified version of the full-body plug-in gait marker set. Modifications included (1) removal of the heel markers after subject calibration as these could not be used with the heel support in the RCH and NHC; (2) displacement of the anterior superior iliac spine markers in a vertical line with the greater trochanter and on the same horizontal height as the anterior superior iliac spine; and (3) addition of the medial knee and ankle markers (during both the calibration and dynamic trials). A 3D optoelectronic motion analysis system (VICON NEXUS v2.8.1, Oxford Metrics Group, Oxford, UK) with 15 cameras (11MX3+ and 4T20) was used to capture the kinematics at a sampling frequency of 200 Hz. All forces were sampled at 1000 Hz.

Surface electromyographic (sEMG) activation was collected using wireless surface electrodes (Cometa Pico, Cometa, Milan, Italy, $41 \times 16 \times 8.5$ mm, 7.6 g, interelectrode distance 25 mm). Skin preparation was done according to the SENIAM guidelines. Proximal and distal electrode pairs were placed at $\sim 35\%$ and $\sim 75\%$ from the ischial tuberosity to the fibula head over the bellies of the semitendinosus and biceps femoris long head, respectively. These locations were chosen as the SENIAM recommended mid-belly electrode position was not possible due to the ultrasound probe placement. Additionally, two pairs of electrodes per hamstring were used as this provides a better 'average' muscle activation since muscle activation is heterogeneous through the hamstrings.³¹ Care was taken to prevent the placement of the electrodes at the muscle-tendon junctions. Electrode pairs were also placed at the gastrocnemius medialis, gluteus maximus, vastus medialis, and rectus femoris in line with the SENIAM guidelines. Correct placement was identified by palpation and confirmed by visual observation of the sEMG signal during voluntary contractions.

Biceps femoris long head fascicle length changes were determined using a 128-element linear, flat-shaped ultrasound transducer in B-mode (Teleded ArtUs, Vilnius, Lithuania), sampling images at 26.6 ± 0.7 frames per second with a scanning depth of 50 mm, width of 60 mm, and beam angle of -5 to -10° .³² After application of water-soluble gel for acoustic coupling, the transducer was placed in a custom-made probe holder (Probefix Dynamic, USONO, Eindhoven, The Netherlands) at $\sim 60\%$ between the ischial tuberosity and the fibula head and

manually aligned with the presumed fascicle plane (see Supplementary Material S3 for example images of the probe placement and probe holder). The probe holder was then attached to the skin with bandages and tape to reduce errors associated with changes in transducer orientation, while care was taken to minimize the pressure that could interfere with fascicle behavior.³² The same researcher experienced with ultrasound data acquisition placed the ultrasound probe for each subject/trial during low-load practice reps of each exercise (i.e., assisted NHCs and low-load DLs and RCHs). Ultrasound videos were inspected directly after each trial, and the trial was repeated if the video was deemed unclear for further analysis.

After placement of the surface electromyographic (sEMG) electrode pairs, the participants performed a maximum voluntary contraction assessment for all measured muscles in a randomized order (Supplementary Material S1). Each maximum voluntary contraction was preceded by three practice reps of increasing intensity. The maximum voluntary contraction assessment was followed by a warm-up consisting of multiple repetitions of the RCH with increasing load (i.e., eight repetitions with body mass only, five repetitions with 30% of 1RM, and three repetitions of 70% of 1RM) followed by three repetitions of the NHC. After a static calibration trial in a T-pose, the participants completed 3–6 sets of each exercise using a 1RM load with the order of the exercises being randomized. Kinematic, kinetic, sEMG and ultrasound data were collected during all trials and synchronized using an electronic pulse. The rest period between the sets and different exercises was ~ 3 min, and the average of three trials from all exercises was used for further analysis. Identification of the start and end of each trial and time normalization was done using marker velocity and/or position data and was also visually checked (Supplementary Material S2).

2.6 | Data processing and analysis

Raw marker data were labeled in Vicon Nexus, gaps were filled with a combination of spline and rigid body fills and smoothed with a Woltring quintic spline filter. The labeled and filtered data were then further processed using custom-made scripts (Matlab2018b, The MathWorks Inc., Natick, MA, USA) to create a virtual marker on the anterior superior iliac spine using the Newington-Gage method. The measured marker trajectories and ground reaction forces were then processed using OpenSim 3.3 to determine joint angles, joint moments, and muscle forces with a modified full-body musculoskeletal model (Catelli model, 22 rigid body segments, 37 degrees of freedom, and 80 muscles) that was designed for tasks involving large hip and knee flexions.²⁷ For both the RCH and NHC, a modified version

of the Catelli OpenSim model was used whereby the order of connection of the different segments was changed such that the feet were the floating body and that inverse dynamics was calculated starting from the hands. The mass of the barbell was halved and summed with the mass of each hand to represent the barbell during the RCH and DL. This approach has recently been validated against more complex modeling approaches.³³ Additionally, the non-dominant leg was removed for analyses in the RCH and NHC, with its mass being added to the dominant leg (see Supplementary Material S2). The model's geometry and mass were scaled to the participant's individual segments length and total body mass using the scale tool. Inverse kinematics was used to determine joint angles from the measured marker trajectories, while internal joint moments were determined through inverse dynamics. Muscle-tendon unit lengths were determined using the muscle analysis tool, and these were used to compute the change in muscle-tendon unit length from minimum to maximum length. Muscle-tendon unit lengthening velocity was also determined by computing the change in length per second (see later for more details). The low pass (4th order) filter was set to 6 Hz to filter the ground reaction forces and marker trajectories. Muscle forces required to balance the joint moments were calculated through dynamic optimization³⁴ while minimizing the sum of muscle activations squared (see Supplementary Material S2). Muscle forces were subsequently extracted for the semitendinosus, semimembranosus, biceps femoris short and long head, gastrocnemius medialis and gluteus maximus, and their peak and mean values were used for further analysis. Joint moments and muscle forces were normalized for body mass using ratio scaling (i.e. Nm/kg and N/kg).

EMG signals were sampled at 1000 Hz, the offset was removed, full-wave rectified, and the signal was band-pass filtered at 20–450 Hz using a zero-lag 4th order Butterworth to remove motion artifacts and high-frequency noise using custom-made scripts in Matlab. Muscle activation was determined using a recursive root mean square (RMS) over a 100-ms window for both the MVC and experimental trials. The RMS was time-normalized, normalized to the maximum value that occurred in either the MVC or trial, averaged over the recorded trials within each participant and then averaged over all participants. The muscle activation recorded from the 2 pairs of electrodes on the hamstrings was averaged for each muscle prior to further analyses.

Ultrasound videos from each trial were exported to custom-made, semiautomated feature-identification software to determine fascicle length changes.³⁵ One researcher blinded to the exercise being analysed performed all analyses. All ultrasound data were filtered using a zero-lag 4th order Butterworth with a 6-Hz low-pass cut-off. Mean fascicle length, the excursion from minimum

to maximum length and the lengthening velocity were determined for each exercise. Further details regarding the ultrasound analysis are provided in Supplementary Material S3.

While most outcome parameters were determined over the whole duration of each exercise, some variables were determined during a specific phase only. To provide relevant information regarding the potential long-term strength adaptations¹³⁻¹⁵ and potential long-term adaptations in fascicle length,^{17,18} peak muscle forces and mean fascicle length were determined over the duration of the whole exercise (0–100%, Figure 2). Fascicle and muscle-tendon unit excursion magnitude may also provide important information regarding the potential long-term adaptations in fascicle length^{36,37} and were determined by computing the change from minimum to maximum length over the whole duration of each exercise. Fascicle and muscle-tendon unit lengthening velocities, and mean muscle forces were determined over specific phases that were expected to be associated with the eccentric contraction phase of the hamstring muscles. This was from the start of the movement to the lowest barbell position for the DL, from the start of barbell lowering to just prior to barbell ground contact for the RCH and from the start to end of the NHC (see also the grey areas in Figure 2). For the NHC, fascicle and muscle-tendon unit excursion magnitude and lengthening velocity were also determined from the break-point (i.e. initiation of the 'free fall') to the end of the NHC to differentiate the 'free fall' from the whole exercise (darker grey area in Figure 2). Such a distinction between phases within a single exercise was not made for the other exercises because the defined phases in the DL and RCH were not characterized by drastic changes in, for example, joint angular velocity.

2.7 | Statistical analysis

All statistical analyses were performed using SPSS Version 19.0.0.1 (IBM Corporation, Chicago, IL). A repeated-measures linear-mixed model fitted with a restricted maximum likelihood method and unstructured covariates was used to compare outcomes between exercises. Exercise was specified as a fixed factor, and Bonferroni corrections were used for post-hoc comparisons. The main outcomes used in statistical analyses were mean biceps femoris long head fascicle length, biceps femoris fascicle and muscle-tendon unit excursion, biceps femoris fascicle and muscle-tendon unit lengthening velocity, and mean and peak normalized muscle forces for the semitendinosus, semimembranosus, biceps femoris short and long head, gastrocnemius medialis and gluteus maximus. The level of significance for all tests was set to $\alpha = 0.05$. Mean \pm

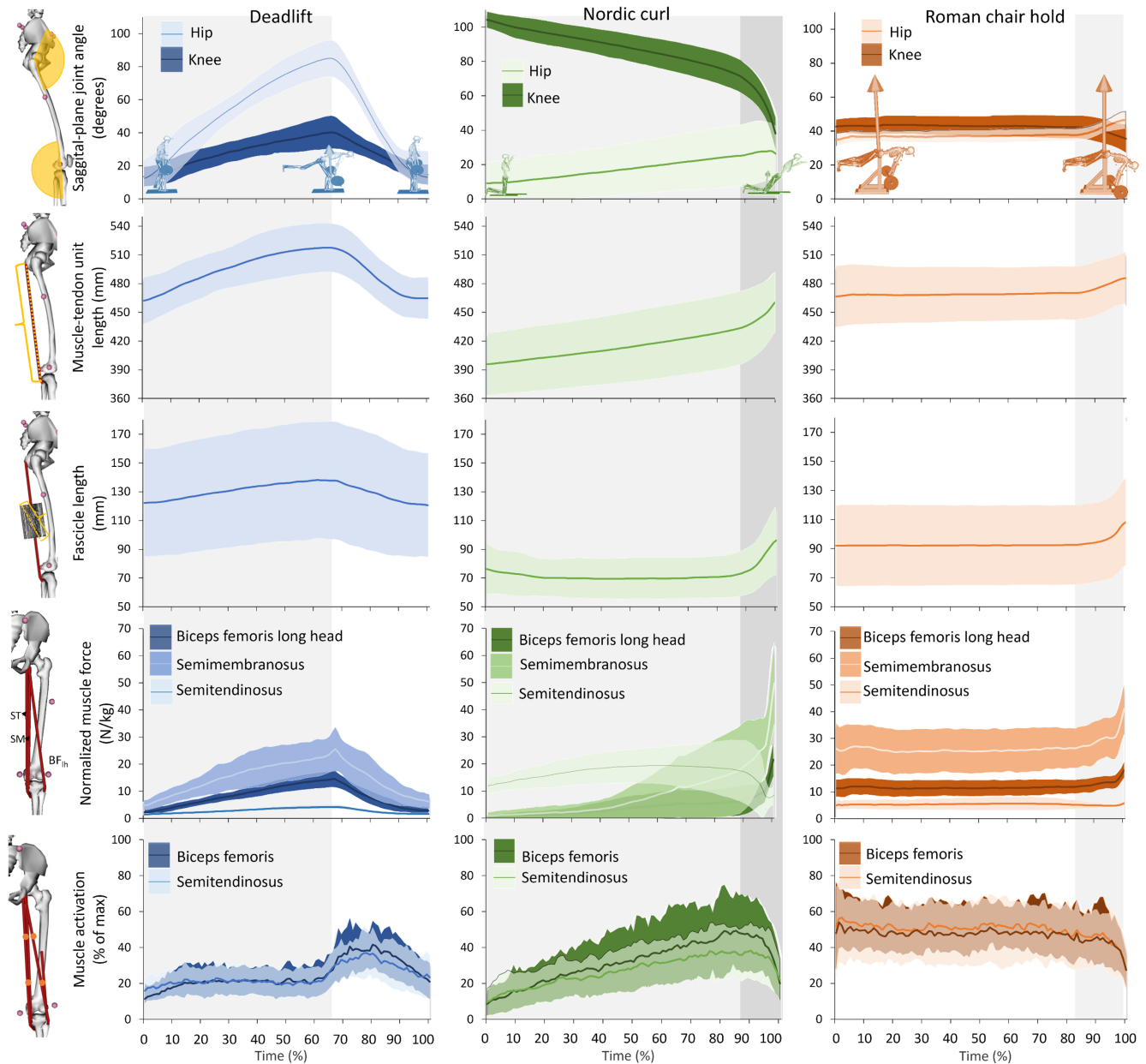


FIGURE 2 Top: Sagittal-plane joint angles during the single-leg deadlift (left), Nordic hamstring curl (middle) and single-leg Roman chair hold (right). Second row: Biceps femoris muscle-tendon unit length. Third row: Biceps femoris long head fascicle length. Fourth row: Biceps femoris long head, semimembranosus, and semitendinosus muscle forces. Fifth row: Experimentally measured muscle activation for the semitendinosus and biceps femoris, averaged over the proximal and distal measurement location. Each panel displays the group mean (solid line) \pm 1 SD (shaded band). The light grey area reflects the barbell lowering phase for the DL (0–66%) and RCH (83–100%), and start to break-point of the NHC (0–88%). The dark grey area reflects the period after the break-point until the end of the NHC (88–100%)

SD and 95% CIs were reported for all statistical analyses. Normality was assessed using Q-Q plots and histograms. Trial-to-trial reliability of biceps femoris long head fascicle length excursion magnitude and lengthening velocity was assessed using a two-way mixed-model intraclass correlation coefficient (ICC) for absolute agreement. We considered a score of <0.50 poor, 0.50–0.75 moderate, 0.75–0.90 good and >0.90 excellent.³²

3 | RESULTS

3.1 | Fascicle lengths

As depicted in Figure 2, biceps femoris long head fascicle length did not change substantially until the end of the exercise during the NHC and RCH. In contrast, fascicle length initially increased and thereafter decreased

in the DL. Mean fascicle length was highest during the DL, followed by the RCH and NHC, with all pairwise comparisons being significant (Table 1). Fascicle excursion was highest during the NHC when measured over the whole exercise, and this excursion was significantly higher compared with the DL. Fascicle excursion after the break-point in the NHC was still higher in magnitude, but not significantly different compared with the DL and RCH (Table 2). Mean fascicle lengthening velocity was highest in the RCH when compared to the DL and NHC. However, when computed only from the break-point to the end of the exercise, mean fascicle lengthening velocity was highest in the NHC followed by the RCH and finally the DL, with all pairwise comparisons being significant (Tables 1 and 2).

Biceps femoris long head fascicle excursion magnitude and velocity generally showed good reliability across trials with mean ICCs of 0.77 and 0.88 during the DL, 0.95 and 0.42 during the NHC and 0.81 and 0.80 during the RCH, respectively. Figure 3 shows ultrasound images from a random participant at different time points during each exercise and videos with synchronized ultrasound and Vicon videos can be viewed here: <https://osf.io/y82uw/>.

3.2 | Muscle forces

The NHC required significantly higher peak force production from the biceps femoris short head (71% and 89%), semitendinosus (74% and 82%) and semimembranosus (22% and 48%) compared with the RCH and DL, respectively (Table 3, Figure 4). The NHC also required significantly higher peak force production from the biceps femoris long head compared with the DL (35%), but there was no significant difference with the RCH. The RCH also showed significantly higher peak muscle forces for the biceps femoris short head (62%), semitendinosus (30%) and semimembranosus (33%) compared with the DL. Conversely, the DL required significantly higher peak gluteus muscle forces than the NHC and RCH (43% and 58%).

Since the peak forces in particular for the NHC lasted only very briefly, we also compared the mean muscle forces during the previously defined phases (Table 3). Briefly, the mean hamstring muscle forces were generally significantly higher in the NHC and RCH compared with the DL, but mostly not significantly different between the NHC and RCH. Peak hip and knee joint moments are reported in Table S1 and Figure S1. The agreement between experimentally measured and modelled muscle activation is shown in Figure S3 of Supplementary Material S4.

TABLE 1 Mean \pm SD fascicle and muscle-tendon unit outcomes

	Mean difference (95% CI) ^a				
	DL	NHC	RCH	NHC vs DL	RCH vs DL
Fascicle outcomes					
Mean fascicle length whole exercise (mm)	138 \pm 44.3	72.3 \pm 13.9	92.8 \pm 24.8	-20.5 (-35.9 to -5.2)*	-45.5 (-67.7 to -23.3)*
Fascicle excursion whole exercise (mm)	15.4 \pm 5.2	28.6 \pm 10.9	16.0 \pm 10.9	12.6 (-1.6 to 26.7)	0.62 (-9.3 to 10.5)
Mean fascicle lengthening velocity (mm/s) ^b	2.0 \pm 1.8	3.6 \pm 2.4	11.4 \pm 9.0	-7.8 (-16.6 to 0.89)	9.4 (1.9 to 17.0)*
MTU outcomes					
MTU excursion whole exercise (mm)	55.6 \pm 16.0	63.5 \pm 6.3	15.4 \pm 5.4	48.1 (41.6 to 54.6)*	-40.2 (-57.1 to -23.2)*
Mean MTU lengthening velocity (mm/s) ^b	11.8 \pm 4.8	13.4 \pm 3.6	11.1 \pm 4.7	2.3 (-2.2 to 6.7)	-0.72 (-5.8 to 4.3)

Note: Values are means \pm SD.

Abbreviations: DL, single-leg deadlift; NHC, Nordic hamstring curl; RCH, single-leg Roman chair hold; MTU, muscle-tendon unit.

^aAdjusted for multiple comparisons using the Benferroni procedure.

^bDetermined from start to lowest barbell position in the DL, start of barbell lowering to just prior to barbell ground contact for the RCH and start to just prior to ground contact for the NHC.

*Mean differences accompanied by asterisks indicate significant ($p < 0.05$) differences after Bonferroni adjustment.

TABLE 2 Mean \pm SD fascicle and muscle-tendon unit outcomes after the break-point in the NHC

	Exercise			Mean difference (95% CI) ^a		
	DL	NHC	RCH	NHC vs RCH	NHC vs DL	RCH vs DL
Fascicle outcomes						
Fascicle excursion (mm) ^b	15.4 \pm 5.2	23.4 \pm 10.3	16.0 \pm 10.9	7.4 (−5.6 to 20.4)	7.9 (−2.7 to 18.5)	n.a.
Mean fascicle lengthening velocity (mm/s) ^b	2.4 \pm 1.7	31.7 \pm 17.2	11.4 \pm 9.0	20.2 (0.19 to 40.2)*	29.2 (12.0 to 46.4)*	n.a.
MTU outcomes						
MTU excursion (mm) ^b	56.9 \pm 15.5	27.7 \pm 9.7	15.4 \pm 5.4	12.3 (2.3 to 22.2)*	−29.2 (−47.7 to −10.8)*	n.a.
Mean MTU lengthening velocity (mm/s) ^b	11.8 \pm 4.8	37.1 \pm 14.3	11.1 \pm 4.7	26.0 (13.6 to 38.4)*	25.4 (9.4 to 41.4)*	n.a.

Note: Values are means \pm SD.

Abbreviations: DL, single-leg deadlift; NHC, Nordic hamstring curl; RCH, single-leg Roman chair hold; MTU, muscle-tendon unit.

^aAdjusted for multiple comparisons using the Benferoni procedure.

^bFrom start to lowest barbell position in the DL, start of barbell lowering to just prior to barbell ground contact for the RCH and break-point to just prior to ground contact in the NHC.

*Mean differences accompanied by asterisks indicate significant ($p < 0.05$) differences after Bonferoni adjustment.

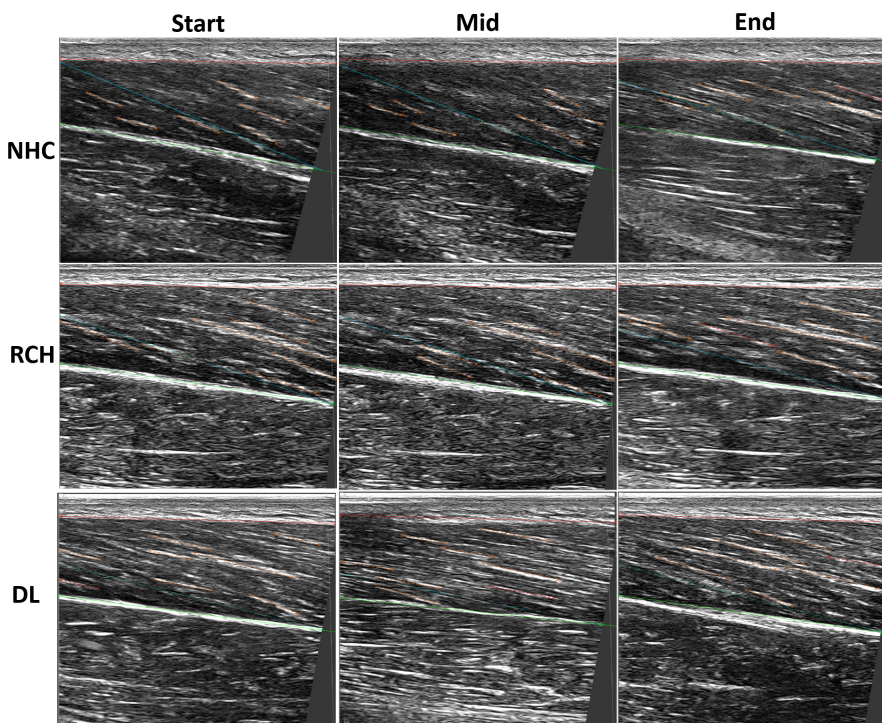


FIGURE 3 Ultrasound imaging screenshots during the start, midpoint and end of each exercise. NHC, Nordic hamstring curl; RCH, Roman chair hold; DL, deadlift. Red and green dashed lines depict the upper and lower aponeurosis, respectively. Dashed orange lines depict the fascicle snippets and the blue line depicts the reference fascicle computed based on the weighted contributed from each snippet. A video with synchronized ultrasound and Vicon video data is available from <https://osf.io/y82uw/>

4 | DISCUSSION

The aim of this study was to characterize and compare hamstring muscle forces and biceps femoris long head muscle fascicle behavior between the NHC, the single-leg RCH, and the single-leg DL. The most important findings are that the fascicle excursion magnitude was highest in the NHC, whereas the mean fascicle length was highest in

the DL. During the whole eccentric phase, fascicle lengthening velocity was highest in the RCH, while it was highest in the NHC when measured only after the break-point. Peak hamstring muscle forces were generally highest in the NHC, while mean hamstring muscle forces during the eccentric phase were generally higher for the NHC and RCH as compared to the DL, with mostly no significant differences between the NHC and RCH.

TABLE 3 Peak and mean \pm SD Muscle forces

	Exercise				Mean difference; (95% CI) ^a		
	DL	NHC	RCH		NHC vs RCH	NHC vs DL	RCH vs DL
Normalized peak muscle force (N/kg)							
Muscle force BF _{sh}	1.6 \pm 0.3	14.7 \pm 9.1	4.2 \pm 1.2		10.5 (1.3 to 19.7)*	13.1 (4.3 to 21.9)*	2.6 (-1.3 to 3.9)*
Muscle force BF _{lh}	14.9 \pm 3.1	23.0 \pm 4.9	17.8 \pm 2.7		5.2 (-0.1 to 10.5)	8.1 (4.2 to 11.9)*	2.9 (-1.3 to 7.1)
Muscle force ST	4.3 \pm 0.7	23.7 \pm 7.9	6.1 \pm 1.5		17.5 (9.5 to 25.7)*	19.4 (12.2 to 26.5)*	1.8 (0.01 to 3.5)*
Muscle force SM	27.3 \pm 8.9	52.5 \pm 11.8	41.0 \pm 8.7		11.6 (1.7 to 21.4)*	25.2 (10.4 to 40.0)*	13.6 (1.4 to 25.8)*
Muscle force GastroMed	20.9 \pm 4.0	110.2 \pm 57.9	43.5 \pm 29.1		66.7 (8.1 to 125.4)*	89.4 (34.4 to 144.4)*	22.7 (-5.8 to 51.1)
Muscle force GlutMax	48.7 \pm 11.8	27.9 \pm 10.3	20.5 \pm 5.0		6.4 (-3.5 to 16.3)	-21.8 (-40.9 to -2.7)*	-28.2 (-40.4 to -16.0)*
Normalized mean muscle force (N/kg) ^b							
Muscle force BF _{sh}	1.3 \pm 0.3	11.7 \pm 6.3	2.8 \pm 0.5		8.9 (2.7 to 15.1)*	10.4 (4.4 to 16.4)*	1.5 (0.98 to 2.1)*
Muscle force BF _{lh}	8.7 \pm 1.8	10.7 \pm 3.8	12.6 \pm 2.4		-1.9 (-6.4 to 2.5)	2.0 (-1.8 to 5.7)	3.9 (0.66 to 7.2)*
Muscle force ST	2.9 \pm 0.5	13.9 \pm 8.1	5.4 \pm 1.7		8.5 (-0.12 to 17.1)	11.0 (3.4 to 18.6)*	2.5 (0.80 to 4.2)*
Muscle force SM	16.2 \pm 4.9	28.8 \pm 12.1	28.2 \pm 7.4		0.59 (-10.5 to 11.6)	12.6 (-0.23 to 25.4)	12.0 (2.4 to 21.6)*
Muscle force GastroMed	14.4 \pm 2.7	20.8 \pm 8.5	13.6 \pm 8.0		6.4 (-0.77 to 13.5)	6.4 (-3.1 to 17.5)	-0.79 (-8.3 to 6.7)
Muscle force GlutMax	29.4 \pm 6.2	6.3 \pm 3.8	17.7 \pm 4.0		-11.3 (-16.1 to -6.58)*	-23.1 (-32.1 to -14.0)*	-11.7 (-19.1 to -4.3)*

Note: Values are means \pm SD.

Abbreviations: DL, single-leg deadlift; NHC, Nordic hamstring curl; RCH, single-leg Roman chair hold; BF_{sh}, biceps femoris short head; BF_{lh}, biceps femoris long head; ST, semitendinosus; SM, semimembranosus; GastroMed, gastrocnemius medialis; GlutMax, gluteus maximus.

^aAdjusted for multiple comparisons using the Bonferroni procedure.

^bMean muscle forces were determined from the start to the lowest barbell position in the DL, start of barbell lowering to just prior to barbell ground contact for the RCH and break-point to just prior to ground contact for the NHC. These phases included active fascicle lengthening.

*Mean differences accompanied by asterisks indicate significant ($p < 0.05$) differences after Bonferroni adjustment.

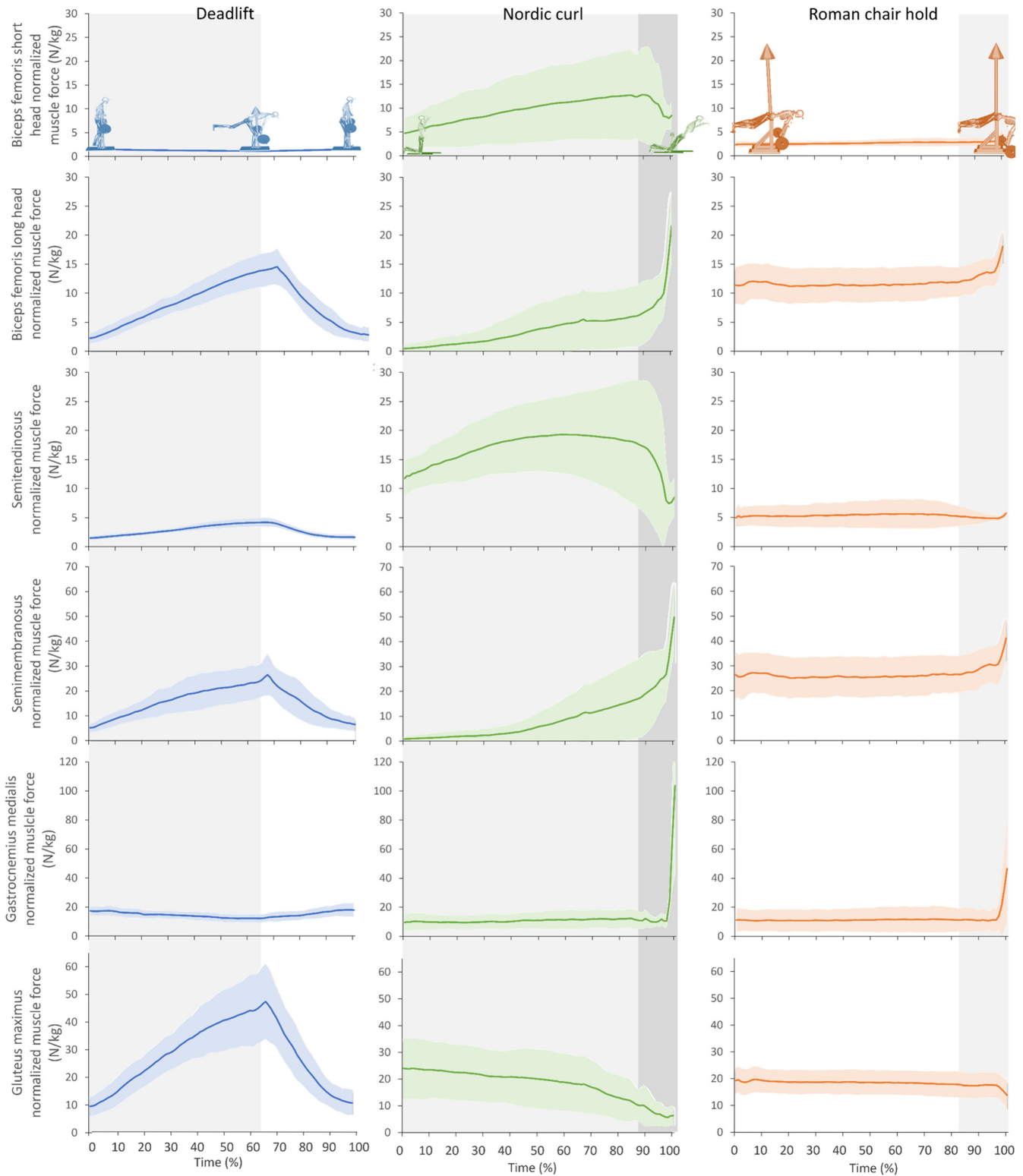


FIGURE 4 Normalized muscle forces during the single-leg deadlift (left), Nordic hamstring curl (middle) and single-leg Roman chair hold (right). Each panel displays the group mean (solid line) ± 1 SD (shaded band). The light grey area reflects the barbell lowering phase for the DL (0–66%) and RCH (83–100%), and start to break-point of the NHC (0–88%). The dark grey area reflects the period after the break-point until the end of the NHC (88–100%)

4.1 | Muscle-tendon unit and fascicle behavior

Since the biceps femoris long head has a larger moment arm at the hip compared to the knee,^{27,28} we expected larger changes in muscle-tendon unit length during movements involving primarily hip flexion such as the DL compared to movements involving primarily knee extension such as the NHC. In contrast to this hypothesis, the increase in muscle-tendon unit length was largest in the NHC, followed by the DL and finally the RCH (Table 1). This likely reflects the relatively large increase in knee angle during the NHC, combined with a slight increase in hip flexion, while hip flexion in the DL was also combined with knee flexion, hereby reducing total muscle-tendon unit excursion (Figure 2). In line with these findings, the increase in biceps femoris fascicle length over the total duration of the exercise was largest in the NHC, followed by the RCH and DL, with no significant difference between the DL and RCH. Almost all fascicle length changes during the NHC occurred after the break-point (~82%, Table 2), where biceps femoris long head fascicle velocity and force rapidly increased, while experimentally measured muscle activation rapidly decreased (Figure 2). Similarly, during the RCH, fascicle lengthening was also associated with a reduced muscle activation. In contrast, fascicle lengthening during the DL occurred with higher constant muscle activation and at a higher absolute fascicle length, but also a slower velocity compared to the NHC. The implications of these findings are discussed in Section 4.4.

Only one other study has attempted to quantify hamstring fascicle behavior during strength training exercises and also found that biceps femoris long head fascicles actively lengthen during the NHC.²¹ However, this study investigated fascicle behavior only from 85% of the peak force until peak force (i.e. break-point). The magnitude of fascicle lengthening found in that study was highly consistent (~4.9 mm) to the magnitude of fascicle lengthening found in our study from the start of the exercise up to the break-point (~5.6 mm). The slight differences may primarily reflect differences in the exact phase measured, and differences in technical performance (e.g. alterations in pelvis orientation).

4.2 | Muscle force

Peak hamstring muscle forces were generally higher in the NHC as compared to the RCH and DL. Mean muscle forces during the eccentric phase were generally also higher during the NHC and RCH as compared to the DL, but typically not significantly different between the NHC

and RCH. Since all exercises are performed with a (near) maximum (DL and RCH) or supra-maximum (NHC) load, the differences in the (peak) muscle forces between exercises may partially be explained by the force-length-velocity properties of muscle fibers. Specifically, individuals typically start the NHC with a neutral hip and 90° knee flexion and drop down after approximately 155° of knee flexion,³⁸ which corresponds to the findings in our study, where the knee angle at break-point was ~72° (Figure 2). Cadaver data suggests that the hamstring sarcomeres function on the ascending limb of the force-length curve in this joint configuration, whereas they may function closer to optimum length with the joint configuration in the RCH.³⁹ Conversely, during the DL, the hamstring sarcomeres may function more on the descending limb of the force-length curve.³⁹ The higher peak muscle force for most hamstrings in the NHC compared to the RCH is therefore likely due to the rapid increase in fascicle length, that yields high forces based on the force-velocity relation of muscle fibers, despite a potentially suboptimal operating length.²⁹ Similarly, the lower peak forces and mean forces during the eccentric phase of the DL when compared to the NHC and RCH may reflect the lower force potential at the descending limb of the force-length curve, which is also not substantially increased according to the force-velocity properties due to a slow fascicle lengthening velocity.

While the knee-dominant NHC primarily involved relatively high loading of the semitendinosus, the hip-dominant DL had relatively low semitendinosus force production and relatively larger biceps femoris long head force production (Figure 4). This differential contribution is (largely) consistent with evidence from (high-density) electromyographic experiments and transverse relaxation times (T_2) of magnetic resonance imaging^{31,40-42} and likely reflects the different moment arms -and hence mechanical advantage- of the muscles around the hip and knee joint. Specifically, the biceps femoris long head and semitendinosus have a relatively similar moment arm at the hip, while the semitendinosus has a larger moment arm at the knee.⁴³ Exercises that primarily involve knee movement and hereby create a larger knee moment may therefore result in higher loading of the semitendinosus, while exercises that primarily involve hip movement and hereby create a larger hip moment result in higher loading of the biceps femoris long head.¹⁰ Conversely, exercises that do not involve substantial joint movement and are performed with only slight knee and hip joint flexion such as the supine hamstring bridge -which bears most similarity to the single-leg RCH- typically results in approximately equal activation of the lateral and medial hamstrings,⁴⁴ which is also largely in line with the observed muscle forces during the RCH.

Interestingly, after the break-point of the NHC, biceps femoris short head and semitendinosus muscle forces decreased, while biceps femoris long head and semimembranosus muscle forces rapidly increased (Figure 4). This differential contribution of these muscles is also consistent with findings from surface electromyographic experiments,⁴⁵ and partly consistent with suggestions of higher force production by the semimembranosus and biceps femoris long head at intermediate hamstring lengths based on their architecture.⁴⁶ Specifically, although the long fibers in the semitendinosus suggest that this muscle is better suited to produce force at longer muscle-tendon unit lengths as compared to the shorter fibered biceps femoris long head and semimembranosus, the higher lengthening velocity of shorter fibers may result in higher force production in shorter fibered muscles according to the force-velocity relationship,²⁹ which could therefore mean it is beneficial to preferentially recruit these muscles.

4.3 | Limitations

There are several limitations to this study that should be considered when interpreting the findings. First, the dynamic optimization was solved for one to two degrees of freedom per joint, which likely resulted in a slight underestimation of the actual muscle forces. Nevertheless, the fiber length and muscle activation estimated by dynamic optimization generally agreed well with the experimentally measured fascicle length and muscle activation (Figures S3 and S7, respectively), which increases our confidence in the muscle forces. Additionally, we compared the joint moments from the set-up of two force platforms below each knee as used for the NHC, with a second set-up where we measured ground reaction forces at one knee and one heel and showed that the results were very similar (Figure S5 and S6). Moreover, the rapid increase in the knee joint moment during the fall in the NHC is also in line with previous findings among relatively strong individuals (personal communication with T. Alt based on findings reported in³⁰).

A second limitation is that the RCH and the DL were performed with a 1RM load, while loads of 70–90% are typically used in training. The differences in the maximum joint moments and muscle forces are therefore likely larger when lower loads are used in these exercises compared to the NHC. However, since the NHC is considered a supramaximal exercise, we deliberately chose to use a 1RM load for a valid comparison of the maximum muscle force requirements. Additionally, although supramaximal, the NHC has effectively been used already ~3 days post injury,⁴⁷ suggesting the high loads used in the RCH and DL can also be used early in rehabilitation. Further, most

participants were limited by balance issues during the DL rather than strength perse and were able to hold multiple 1RM loads in the RCH with relatively short rest periods, suggesting that the differences in joint moments and muscle forces do reflect the differences in a typical high-load training session. Similarly, although all exercises do have a different time under tension, this comparison best reflects the typical implementation of these exercises in practice.

Third, changes in the probe and muscle orientation during the exercises may have affected the measurements of fascicle length.³² Although we attempted to quantify changes in probe orientation relative to the leg axis of rotation, small changes in knee marker positions as a result of soft tissue artifacts hampered this analysis, in particular during the NHC. Nevertheless, visual inspection showed only very small changes in probe orientation during all exercises, suggesting that changes in muscle orientation are more likely to have affected the measurements. Indeed, during the DL we were unable to analyse data from three subjects due to changes in muscle orientation. Related to this, the ultrasound probe field of view is only 60 mm, which required us to extrapolate fascicle length beyond the field of view, in particular during the DLs were fascicles achieved lengths more than twice the field of view. Yet we believe that the use of weighted fascicle parts to determine a reference fascicle reduced the extrapolation error as compared to other commonly used ultrasound analyses algorithms because more information within the field of view is used to determine fascicle length and orientation.³² Moreover, the sampling frequency of the ultrasound probe is ~27 Hz, which reduced the accuracy of the quantified fascicle lengthening velocity during the more rapid fall in the NHC. These limitations suggest that in particular the absolute fascicle lengths and differences between exercises should be interpreted with caution. Nevertheless, the generally good reliability for fascicle length outcomes and the relation with experimentally measured muscle activation increases our confidence in the observed contraction mode during all exercises. For example, biceps femoris muscle activation remained constant while muscle force increased during the eccentric phase of the DL, while muscle activation increased as muscle force increased during the quasi-isometric phase of the NHC. If muscle fascicle behaviour would have been eccentric during the majority of the NHC, muscle activation would likely also have remained constant with an increase in force, similar to the DL and in line with the Force-Velocity relationship.

A final limitation relates to the potential that our sEMG signals contain cross-talk from neighbouring muscles due to the relatively large interelectrode distance, and selective muscle activation should therefore be interpreted with caution.

4.4 | Perspective

The findings of this study have several applications for hamstring injury prevention, rehabilitation and performance enhancement. First, the larger fascicle excursion (and higher fascicle lengthening velocity when measured only after the break-point) in combination with high peak and mean hamstring muscle forces in the NHC may more effectively promote increases in sarcomere and fascicle length⁴⁸ than the DL and RCH.^{36,37,49} In particular, the fascicle excursion magnitude (i.e. relaxation strain) is an important predictor of the increase in fascicle length or increase in the number of sarcomeres in series due to training.^{36,37} In support of this, increases in biceps femoris fascicle length have been shown to be larger following NHC training as compared to stiff-legged DL training.⁵⁰ Moreover, since almost all fascicle lengthening and the high fascicle lengthening velocities occurred after the break-point, the NHC might need to be supramaximal to more effectively promote architectural adaptations. This is consistent with findings of larger increases in fascicle length following weighted NHC's compared to unloaded NHC's,⁵¹ but contrasts suggestions of others to primarily perform assisted NHC's.³⁰

Second, a combination of exercises may be required to optimally train hamstring strength because the investigated exercises target different muscles. Specifically, although the peak hamstring muscle forces were generally higher in the NHC as compared to the RCH and DL, the peak forces for the biceps femoris long head and semimembranosus in the NHC lasted only very short compared to the peak forces in the DL and were also associated with a strong reduction in muscle activation (Figure 2). This in turn may reflect less motor unit recruitment during the eccentric phase.¹⁵ As a result, these brief high peak forces may not provide an effective stimulus for long-term strength adaptations. In support of this, semitendinosus and biceps femoris short head anatomical cross-sectional area increased significantly following 5 weeks of NHC training, but there was a substantially smaller non-significant increase in biceps femoris long head and semimembranosus cross-sectional area.¹⁰ Nevertheless, the peak force for all hamstring muscles except for the biceps femoris long head was higher in the NHC compared with high-speed running in experienced runners up to approximately $9.5 \text{ m}\cdot\text{s}^{-1}$.^{52,53} During the RCH, only semimembranosus peak force was higher compared to sprinting, with the other hamstrings being only slightly lower. Collectively, the NHC and RCH may therefore present an effective supplemental exercise to strengthen the hamstrings for the high forces experienced during high-speed running. Additionally, the DL required significantly higher gluteus muscle forces, with

the peak muscle force being higher than reported during high-speed running.⁵³ While findings of higher muscle activation during sprinting compared to (heavy) resistance training exercises^{11,54} are often used to imply that resistance training exercises cannot achieve the same loading as sprinting, the findings of the current study therefore suggest that some heavy resistance training exercises *can* elicit higher or approximately comparable muscle forces as sprinting and hence be used as an effective training stimulus to increase maximal force production at slow velocities. For example, high loads and hence muscle forces are effective at improving voluntary activation⁵⁵ and may also improve the single-joint rate of force development,⁵⁶ both of which can be beneficial to improve sprint performance. Yet it is important to emphasize that the transfer of these mechanisms to improved sprint performance will depend on many other factors such as the similarity in fascicle operating lengths and velocities, and inter-muscular coordination.

5 | CONCLUSION

The findings of this study indicate that the NHC has generally the highest peak hamstring muscle forces and results in more eccentric fascicle lengthening along with a higher velocity during the specific braking phase compared to the DL and RCH. Collectively, these findings suggest the NHC may be most effective to promote increases in fascicle length, although both the DL and RCH may also be effective at promoting increases in fascicle length. Further, while the NHC may be an effective exercise to promote strength adaptations for the biceps femoris short head and semitendinosus, the RCH and DL may be more effective to promote strength increases in the biceps femoris long head and semimembranosus. Long-term studies are required to confirm these suggested implications.

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CONFLICTS OF INTEREST

All authors declare that they have no conflict of interest. All results are presented clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation.

AUTHOR CONTRIBUTIONS

The authors are involved in devising research (BVH, PW, BV, KM, and MD), data collection (BVH and PT), data analysis (BVH and SVR), and manuscript writing (BHV). All authors provided suggestions, revisions, and edits to the manuscript, approved the final version, and agreed with the author order.

DATA AVAILABILITY STATEMENT

C3D files and files used in OpenSim are available from the OpenScience framework at <https://osf.io/e8r2j/>. Further data is available from the corresponding author upon reasonable request.

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