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RESEARCH ARTICLE

Robustness of hamstring muscle activation strategies following selective hypertrophy induced by Nordic hamstring curl and stiff-leg deadlift exercises

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Abstract

This study aimed to determine whether muscle activation distribution between hamstrings is modified after 9 wk of two resistance training programs that induce selective muscle hypertrophy. Using a blinded, randomized, controlled design, 36 resistance-untrained individuals were assigned to one of the three groups: control (CON), Nordic hamstring exercise (NHE), or stiff-leg deadlift (SDL). Strength gain was measured as changes in one-repetition maximum (1RM). Changes in semimembranosus (SM), semitendinosus (ST), and biceps femoris (BF) muscle volume were measured using three-dimensional (3-D) freehand ultrasound. Activation of each hamstring muscle head was assessed using surface electromyography during the trained exercise (or both for CON) performed at 80% of 1RM. We found a significant increase in 1RM after 9 wk for the NHE (37.4 ± 13.8%) and SDL (34.0 ± 21.2%) groups compared with CON. This strength gain was accompanied by selective hypertrophy of ST (24.3 ± 10.8%) and SM (11.2 ± 12.7%), for the NHE and SDL groups, respectively. However, statistical parametric mapping analyses revealed that muscle activation was not altered over time, between the groups, or by their interactions (all $P \geq 0.05$). Our findings demonstrate the robustness of muscle activation strategies over time despite training-induced selective hypertrophy. These results provide a deeper understanding of the complex interplay between neural drive and muscle mechanical characteristics. This provides additional impetus to study long-term effects of activation strategies (e.g., on the development of musculoskeletal disorders), as they seem to represent a trait-like characteristic rather than a transient state.

NEW & NOTEWORTHY We demonstrate that stiff-leg deadlift and Nordic hamstring exercises are effective in inducing selective hypertrophy of the semimembranosus (11.2%) and semitendinosus (24.4%), respectively. Hamstring muscle activation did not adapt to the change in the distribution of muscle volume. These resistance training exercises, commonly used in hamstring prevention and rehabilitation strategies, appear effective at increasing the force-generating potential of the targeted muscles in noninjured individuals, as their muscle volume increases without altering their activation strategies.

EMG; muscle coordination; muscle volume; resistance training

INTRODUCTION

It is widely accepted that the nervous system adapts muscle activation to minimize movement costs, aligning with the principles of optimal control theory (1). In this framework, the selection and weighting of muscle recruitment are shaped by biomechanical and physiological constraints. These include factors such as muscle architecture, mechanical advantage, fiber-type composition, and energetic efficiency. Consequently, muscle activation is thought to be preferentially biased toward muscles with a high proportion of slow-twitch fibers (2), larger moment arms (3), and greater force-generating capacities (4). This latter is usually characterized either by muscle volume (5) or by physiological cross-sectional area (i.e., PCSA = muscle volume × cos pennation angle/fascicle length) (6). For example, Hug et al. (7) used electromyography (EMG) to investigate the relationship between muscle activation distribution (i.e., the ratio of individual muscle activation relative to the total activation of the muscles of interest) and the distribution of PCSA across the vastii. They reported a strong positive correlation between the distribution of muscle activation and the distribution of PCSA in the vastus lateralis (VL) and vastus medialis (VM). Individuals with a higher PCSA in the VL compared with the VM showed a stronger activation bias toward the VL. Importantly, VL and VM exhibit a strong common neural input (8, 9), which limits the potential for exploring motor control flexibility. A recent study suggests that hamstring heads may not share significant common input (10). This aligns with the selective increase in semimembranosus (SM) activation during a submaximal [20% of maximal voluntary contraction (MVC)] isometric knee flexion task, in the presence of the selective atrophy of the previously injured biceps femoris (BF) (−4.1% of the overall hamstring volume) (11).

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Also, we can use this study to examine muscle activation and muscle volume in highly specialized populations, such as elite sprinters. When examining the noninjured limb, elite sprinters demonstrated a greater semitendinosus-to-hamstrings (ST/Hams) muscle volume ratio (37%) compared with a nonspecialized population (31%) (12). This selective hypertrophy of the semitendinosus (ST) is consistent with previous observations (13). Furthermore, the ST/Hams muscle activation ratio during submaximal isometric knee flexion was also higher in elite sprinters compared with nonspecialized individuals (31.3% vs. 29.3%), supporting the neuromechanical coupling hypothesis (4). However, the cross-sectional nature of these studies limits causal inference and warrants caution in interpretation.

Resistance training is a well-established strategy for enhancing strength and promoting muscle volume (i.e., hypertrophy). For the hamstrings, resistance training programs commonly incorporate both knee flexion- and hip extension-focused movements (14). It has been demonstrated that 10 wk of knee flexion-oriented movement, such as Nordic hamstring exercise, favored selective hypertrophy of the ST muscle, whereas a hip extension-oriented movement favored a more homogeneous (15) or SM-biased (16) hypertrophy. The hamstring muscle group is therefore an ideal model to understand the relationship between hypertrophy and muscle activation, as SM and ST exhibit large architectural differences (17). Specifically, SM exhibited a larger muscle volume (207 cm^3) compared with ST (173 cm^3), along with shorter fascicles (8.9 cm vs. 17.3 cm). Although SM exhibited a pennation angle of ~10.7°, whereas ST is typically classified as a fusiform muscle, these architectural differences resulted in a greater estimated force-generating capacity during knee flexion for SM [23.6 arbitrary unit (au)] compared with ST (10.6 au) (12). However, it remains unclear whether these muscle-specific differences influence changes in activation distribution. In other words, activation is likely to increase when a "strong" muscle with short muscle fibers, such as SM, exhibits hypertrophy (4), whereas such a change may be less expected in a less mechanically efficient muscle, such as ST. Also, it is possible that individuals develop different "good-enough" muscle activation strategies through motor exploration, experience, and training, leading to habitual rather than optimal strategies (18).

The distribution of muscle activation, often referred to as activation strategies, is a highly individualized characteristic, experimentally identified as an "individual muscle activation signature" (19). The uniqueness of these muscle activation strategies and their defining features has been observed during walking and pedaling (20). Moreover, the robustness of these strategies over time and across tasks has been investigated. For instance, Crouzier et al. (21) found that muscle activation strategies within the quadriceps and triceps surae remained consistent across various tasks (i.e., simple single-joint tasks, walking, and pedaling) in a large cohort of participants. In addition, these strategies exhibited high reliability between days. In other words, individuals who favored the activation of a specific muscle within a muscle group tended to maintain this preference over time. This robustness has also been demonstrated across different hamstring-strengthening exercises, such as the Nordic hamstring exercise and the stiff-leg deadlift (22). Despite this apparent robustness, the mechanical constraints of these tasks influence the distribution of activation between SM and ST across individuals (22). This provides initial evidence for some degree of flexibility in hamstring activation strategies. However, the numerous mechanical differences between the Nordic hamstring exercise and the stiff-leg deadlift (e.g., relative muscle length, moment arm, and involvement of synergistic muscles) make it difficult to isolate the specific contribution of each underlying mechanism to the observed changes in muscle activation strategies.

We conducted a randomized controlled trial to investigate changes in the distribution of muscle activation among the hamstring heads following 9-wk resistance training program comprising either stiff-leg deadlift or Nordic hamstring exercise, promoting selective hypertrophy (i.e., increase in the volume of one muscle). According to biomechanical models suggesting minimization of the mechanical stress within muscles to avoid fatigue (23), we hypothesized that the distribution of muscle activation would shift toward selectively hypertrophied muscles, especially the SM, for the stiff-leg deadlift group. To control confounding factors, changes in lower limb kinematics between testing sessions were measured (24) using inertial measurement units (IMUs).

METHODS

Experimental Design

The experimental protocol included three experimental sessions: a familiarization session and two testing sessions, which were conducted before and after 9 wk of the resistance training program. The training program comprised a total of 27 training sessions. Muscle volume, one-repetition maximum (1RM), muscle activation, and lower limb kinematics were estimated during the testing sessions pre, and after 9 wk of resistance training program. Note that data from three-dimensional (3-D) ultrasound, 1RM, and its associated muscle activation were reported in a previous publication dealing with strength transfer between exercises (25).

Participants

The sample size calculation was based on the difference in hamstring hypertrophy distribution (+16% between ST and SM) reported by Bourne et al. (15). Each group required a minimum of 12 participants to detect a significant between-group difference, with a statistical power of 0.8 and a type I error rate set at 1%, due to the multiple planned comparisons. Thirty-six physically active (~9 h/wk) sports students participated in this study. Participants were familiar with resistance training, whereas none was following a specific hamstring-strengthening program before the start of the study. Inclusion criteria required participants to not be currently engaged in any specific lower limb training program and to have no history of lower limb injuries impacting the hamstrings (i.e., neither hamstring strain injury nor anterior cruciate ligament reconstruction, which may impact hamstring muscle integrity). Before the first experimental session, participants were randomly assigned to one of the three groups: control (CON, n = 12 with 10 males and 2 females, age: 19.6 ± 1.1 yr, height: 177.3 ± 7.7 cm, weight: 71.6 ± 10.6 kg), Nordic hamstring exercise (NHE, n = 12 with 10 males and 2 females, age: 20.3 ± 1.5 yr, height: 180.1 ± 9.1 cm, weight: 76.0 ± 11.1 kg), or stiff-leg deadlift

(SDL, $n = 12$ with 10 males and 2 females, age: 20.4 ± 1.4 yr, height: 178.5 ± 7.1 cm, weight: 69.5 ± 9.3 kg). Group allocation was performed using a 1:3 ratio before the first laboratory visits for familiarization. Group differences, Consolidated Standards of Reporting Trials (CONSORT) checklist (26), and flowchart graph are available in Supplemental Material. Participants were instructed to maintain their usual physical activities. During an initial meeting, participants were informed about the nature, aims, and risks associated with the experimental and training procedures, and written consent was obtained. This trial (NCT06164249) was conducted in accordance with the Declaration of Helsinki and was approved by the Ethics Committee (No. 2021-A02993-38).

Procedures

Familiarization session.

During the familiarization session, each participant was familiarized with both stiff-leg deadlift and Nordic hamstring exercises. Since the Nordic hamstring curl performed at body weight often constitutes supramaximal exercise (15), participants used a specific machine (Westside inverse curl pro; Watson, UK) equipped with a counterweight system that allowed off-loading participants' body weight and precisely quantify the load. After key execution criteria (detailed later) were presented and demonstrated by an experienced examiner, participants practiced 10 min per exercise to *1*) experience the full range of motion with a low resistance and *2*) perform 8–10 contractions at a moderate resistance while adhering to the execution criteria. If execution was validated by the examiner (otherwise, an additional set was performed), a progressive increase in load was performed over three to four sets to determine the maximal load for one repetition at a rating of perceived effort (RPE) of about eight (RPE 8) on a scale between 1 and 10 (27). This maximal load performance was recorded and later used during the first one-repetition maximum (1RM) assessment session (pre).

Nordic hamstring curl was performed from 90° knee flexion to full knee extension (thigh parallel to the floor) with a neutral spinal posture and complete hip extension (0°). Stiff-leg deadlift was performed with a shoulder-width stance, no lower limb rotation, and movement from 0° to 90° of hip flexion. Only slight knee unlocking was permitted, and a neutral spinal posture was maintained. For both exercises, participants were asked to perform the eccentric phase over 3 s before executing the concentric phase with the intention of achieving maximal speed.

Training program description.

The training protocol took place at the "Movement - Interactions - Performance" laboratory of Nantes University (France) between February and April 2024. It comprised 9 wk of training for the NHE and SDL groups, with three sessions per week. The CON group continued their usual activities without any changes.

The NHE and SDL groups performed a progressive 27-session training protocol using a load set at 80% of their 1RM (see details in Table 1). Participants were allowed to miss up to two training sessions during the entire protocol. If a third session was missed, it was made up the following week, which then included four sessions. A minimum rest period of 24 h was required between all sessions.

Table 1. *Training program for both the Nordic hamstring exercise and stiff-leg deadlift*

Week	Sessions	Sets	Repetitions	Load (%1RM)
1	3	2	5	80
2	3	3	6	80
3	3	4	7	80
		1RM reassessment		
4	3	4	7	80
5	3	5	7	80
6	3	6	8	80
		1RM reassessment		
7	3	5	7	80
8	3	5	6	80
9	3	3	5	80

1RM, one-repetition maximum.

Progressive changes in training volume (i.e., number of sets and repetitions) followed a pyramid structure (15) and are reported in Table 1. Execution criteria and participants safety were monitored by a certified trainer during the entire protocol, and simultaneous training sessions were limited to two participants (one per exercise). Importantly, the training protocol was conducted using the exact same execution criteria as during the 1RM assessment.

Resistance training monitoring.

Participants monitoring during the 9-wk training program was conducted using the HexFit application (Hexfit Inc., QC, Canada). This tool allowed participants to schedule laboratory appointments for experimental sessions and to book training slots for both NHE and SDL groups. The application also enabled precise tracking of external training loads throughout the 9 wk. In addition, it allowed the collection of data such as RPE, training-related comments, and fatigue levels.

Dietary supplementation.

In line with recommendations for protein intake during resistance training focused on hypertrophy (28), participants consumed a supplement on training days containing 22.0 g of protein and 2.0 g of carbohydrates (Whey Protein Bio, Alter Nutrition) under the examiner's supervision.

One-repetition maximum.

The 1RM was assessed for both exercises 4–10 days before and 4–7 days after the 9-wk training program. To support the training session, the 1RM was also reassessed at the start of the 10th (after 3 wk) and 19th training sessions (after 6 wk) (15). The 1RM evaluation session followed a standardized protocol to allow comparison across participants: participants completed a standardized warm-up comprising two rounds of 10 body weight single-leg bridge reps and 8 kg-loaded good morning exercise, with progressively increasing effort levels. This was followed by a specific warm-up (either Nordic hamstring curl or stiff-leg deadlift) comprising three sets of ten, six, and one repetitions performed at, respectively, 30%, 60%, and 90% of the maximal load that was determined during the familiarization session. After the warm-up, a progressive load increase (minimum = 2.5 kg) was used to estimate 1RM. If participants failed, a second trial was attempted after 3 min of rest. A valid 1RM required

1) a controlled three-second eccentric phase and *2*) compliance with the joint angles specified by the experimenter. Participants received verbal feedback on their technique and were encouraged throughout the 1RM attempts.

For the Nordic hamstring, the lower the additional weight, the better the performance. Given the influence of individual biomechanics on force production, the 1RM torque (Nm) was calculated as follows:

$$1RM = (BM \times g \times COMposition) - (CW \times LA) \quad (1)$$

where BM is the participant's body mass from Winter et al. (29), excluding (tibia and feet); g = 9.81 (gravitational acceleration); COMposition is the estimated center of mass position of the system (upper body); CW is the additional counterweight; and LA is the lever arm of the machine counterweight.

For SDL, the 1RM was the maximal load (kg) that could be lifted once over the range of motion (ROM). The 1RM for both the Nordic hamstring curl and stiff-leg deadlift was tested in randomized order.

Muscle volume assessment using 3-D ultrasound.

The freehand 3-D ultrasound method used in the present study has been validated for the hamstrings (30). The reproducibility tests show between-session coefficient of variation (CV) from 1.13 to 1.88% and intraclass correlation coefficients (ICCs) of 0.99 for the hamstring muscles. Participants lay prone on a massage table while ultrasound images of each hamstrings head were captured using an ultrasound scanner (Aixplorer version 12.3, SuperSonic Imagine, Aix-en-Provence, France) with a 10-2 MHz transducer (40 mm field of view: Vermon, Tours, France). Image depth and brightness were individually adjusted for each participant.

The transducer was fitted with a 3-D-printed rigid body containing four reflective markers. An optoelectric motion capture system with 10 cameras (Optitrack Flex 13, NaturalPoint), recording at 120 Hz, tracked the transducer's position. Ultrasound images and transducer position data were recorded using the open-source software 3-D Slicer (slicer.org; v.5.6.2; Perth, Australia). To ensure measurement reproducibility, the same examiner (T.M.) conducted all pre- and posttraining volume recordings. Furthermore, for each measurement, the examiner was blinded to the participant group assignments. A gel pad was used to minimize compression effects, and no pressure was applied to the transducer during imaging (30, 31).

Surface EMG.

Myoelectrical activity was recorded using surface EMG at pre and after 9 wk of training during the 80% of 1RM of the trained exercise for SDL and NHE groups and for both exercises for the CON group. Given the regional variation in EMG amplitude (32, 33), two pairs of bipolar EMG electrodes were placed on each biarticular hamstring head (SM, ST, and BF): at the proximal-middle and one at the distal-middle location. Before electrodes placement, the skin was shaved and cleaned with alcohol. Wireless surface electrodes (Cometa Pico, Cometa, Milan, Italy, interelectrode distance = 25 mm) were attached to the skin with double-sided tape (intersensor distance = 1 cm). Electrodes placement was verified with B-mode ultrasound to ensure alignment with the muscle fascicle plane and avoidance of neighboring muscle borders. To minimize crosstalk, EMG electrodes were placed on the midline of the most prominent superficial muscle belly of each hamstring head. Based on hamstring morphology (34), the electrode positions for BF and SM were slightly more distal than for ST. For EMG normalization, two maximal voluntary contractions (MVCs) (35) were performed at three different knee flexion angles (20°, 45°, and 80°; 0° = knee fully extended) with a fixed 90° of hip flexion (0° = full hip extension) to ensure about the maximal activation of each hamstring head and each electrode location (36). Given the importance of EMG signal normalization, electrodes were placed with participants in the same position as during MVC testing. Electrode placement was verified using manual passive knee joint mobilizations through the full ROM to ensure sufficient distance between each muscle's distal electrode and its corresponding tendon. All recordings were performed on the participants' dominant leg (i.e., the leg used to kick a ball).

Kinematic data.

Participants wear a set of seven IMUs (internal sampling rate = 1,000 Hz, accelerometer range = 16 *g*, gyroscope range = ±2,000°·s^{-1}, dynamic systematic uncertainty = 0.75°, MTw Awinda, Xsens Technologies, Enschede, The Netherlands), placed according to the Xsens protocol, by a single operator (T.M.). Xsens software was used to conduct sensor calibration routine and to record raw kinematics data at a 100-Hz sampling rate. The reproducibility of the method has already been investigated over time, showing high levels of agreement, particularly in the sagittal plane (ICC > 0.80 for hip, knee, and ankle) (37). Xsens equipment was also used to synchronize kinematic and EMG signal acquisitions via an external trigger.

Data Analysis

Hypertrophy.

Once data collection was complete, all muscle volumes were reconstructed and manually segmented using 3-D Slicer by the same blinded examiner for consistency. Manual segmentations were conducted every 6.0 mm at the hamstring insertions and every 10.0 mm in the muscle belly regions, representing ~30–50 slices per muscle. Hypertrophy of each individual muscle was considered as the relative changes in muscle volume between pre and after 9 wk.

Joint angles.

A generic lower-limb OpenSim musculoskeletal model was individually scaled to each participant anthropometry, and used to realize inverse kinematics analyze (Opensense, OpenSim 4.5) (38). Modelized knee and hip angles were used during the trained exercise to identify the onset and offset of each repetition and were further compared to ensure the consistency of kinematic patterns between pre, and after 9 wk of training.

We used the standard error of measurement (SE) of inertial sensors measuring sagittal knee and hip joint angles during squatting from a previous study (37), to calculate the smallest detectable change (SDC) (39). The SDC served as a threshold to identify participants who exhibited substantial changes in kinematics between the pretest and after 9 wk, as

such changes could influence muscle activation (24). Based on this approach, we determined that the SDC (mean of the ROM) for both knee and hip kinematics was ~11.6°. Participants whose kinematic changes for either knee or hip angle exceeded this threshold were excluded from further muscle activation analysis.

Muscle activation.

EMG signals were digitized at 2,000 Hz and band-pass filtered (30–300 Hz) using a 2nd-order Butterworth filter. The signals were then rectified and low-pass filtered at 6 Hz to generate individual EMG envelopes (40). The peak value of each EMG envelope over the six MVCs was used as the maximal reference value for normalizing EMG signals to obtain an estimate of muscle activation. Activation was expressed as a percentage of the range of motion (ROM) of the eccentric phase for each exercise. For each muscle, the normalized activation of the two electrodes was averaged to obtain a representative value of the whole muscle activation. Data from five repetitions performed at 80% of 1RM were averaged, representing ~60% of the total repetition range (41). This procedure allowed us to compare the following ratios of normalized activation over the range of motion at pre and after 9 wk of training:

$$\frac{\text{Activation}_{\text{muscle1}}(\%\text{max})}{\text{Activation}_{\text{muscle1}}(\%\text{max}) + \text{Activation}_{\text{muscle2}}(\%\text{max}) + \text{Activation}_{\text{muscle3}}(\%\text{max})} \times 100 \quad (2)$$

The SM/Hams, ST/Hams, and BF/Hams activation ratios were considered as an index of the contribution of each muscle to the whole activation of the hamstrings (12, 22, 42). As mentioned earlier, this calculation was also performed with muscle volume to estimate the distribution of force generating capacities before and after 9 wk.

Statistical Analysis

The data normal distribution was verified using the Shapiro–Wilk test. Outliers were detected using Grubbs' test (43), resulting in the exclusion of one participant of the CON group from the analysis.

The effect of the 9-wk training program on 1RM in the trained exercise (NHE or SDL) was evaluated using a two-way repeated-measures analysis of variance (ANOVA) to compare the effect of time (pre and after 9 wk) on relative strength gains between control and trained groups (CON vs. NHE; CON vs. SDL).

A linear mixed-effects model was used to evaluate differences in changes in muscle volume (%) (i.e., hypertrophy) between groups (CON, NHE, and SDL) and muscles (SM, ST, and BF). Group and muscle were modeled as fixed effects, along with their interaction (group × muscle) to examine whether hypertrophy responses differed across muscles depending on the group. To account for interparticipant variability, participant was included as a random effect.

Statistical parametric mapping (SPM 30, v0.4, www.spm1d.org) was used to compare muscle activation patterns with high temporal resolution. Two three-way repeated-measures ANOVAs were used to determine whether time (pre and after 9 wk), muscle (SM, ST, and BF), group [NHE vs. CON (during Nordic hamstring curl); SDL vs. CON (during stiff-leg deadlift)], and their interactions altered normalized activation over the range of motion. For each ratio (SM/Hams; ST/Hams; and BF/Hams), two two-way repeated-measures ANOVA were used to determine whether time (pre and after 9 wk), group [NHE vs. CON (during Nordic hamstring curl); SDL vs. CON (during stiff-leg deadlift)], and their interactions altered the distribution of muscle activation. In case of an interaction at any timepoint across the range of motion, locations of the differences were tested using paired-sample t tests with Bonferroni correction. The significance level was set at $P < 0.05$. Effect sizes were also calculated using Cohen's d (44) and interpreted as trivial, small, moderate, and large at <0.35, 0.35–0.80, 0.80–1.50, and >1.50, respectively (45). All statistical analyses and data visualizations in this study were performed using MATLAB (MATLAB; The MathWorks, Natick, MA) and Prism (v.10.1.1, GraphPad Prism, Boston, MA) software.

RESULTS

Training session attendance was 96.6 ± 3.7% for the NHE group and 94.8 ± 4.0% for the SDL group.

Joint Angles

A total of eight participants exhibited a larger variation in knee and/or hip joint angles between pre and after 9 wk compared with the MDC previously calculated (cf. METHODS). Thus, three and one participants were excluded from the NHE and SDL groups, respectively. Three and one participants were excluded from the CON group during Nordic hamstring exercise and stiff-leg deadlift, respectively. The kinematics of the remaining participants is depicted in Fig. 1.

One-Repetition Maximum

In the Nordic hamstring exercise, the NHE group showed a significantly larger increase in 1RM compared with the CON group [mean difference = 18.8%, 95% confidence interval (CI): 3.0%–34.5%, $P = 0.02$, $d = 0.8$]. On average, participants in the NHE group exhibited a 37.4 ± 13.8% increase in 1RM after 9 wk of training (201.1 ± 60.2 Nm and 274.6 ± 81.6 Nm at pre and post, respectively). In the stiff-leg deadlift exercise, the SDL group showed a significantly larger increase in 1RM compared with the CON group (mean difference = 21.6%, 95% CI: 7.2%–36.1%, $P = 0.01$, $d = 1.0$). On average, participants in the SDL group exhibited a 34.0 ± 21.2% increase in 1RM (103.5 ± 22.9 kg and 136.0 ± 23.0 kg at pre and post, respectively).

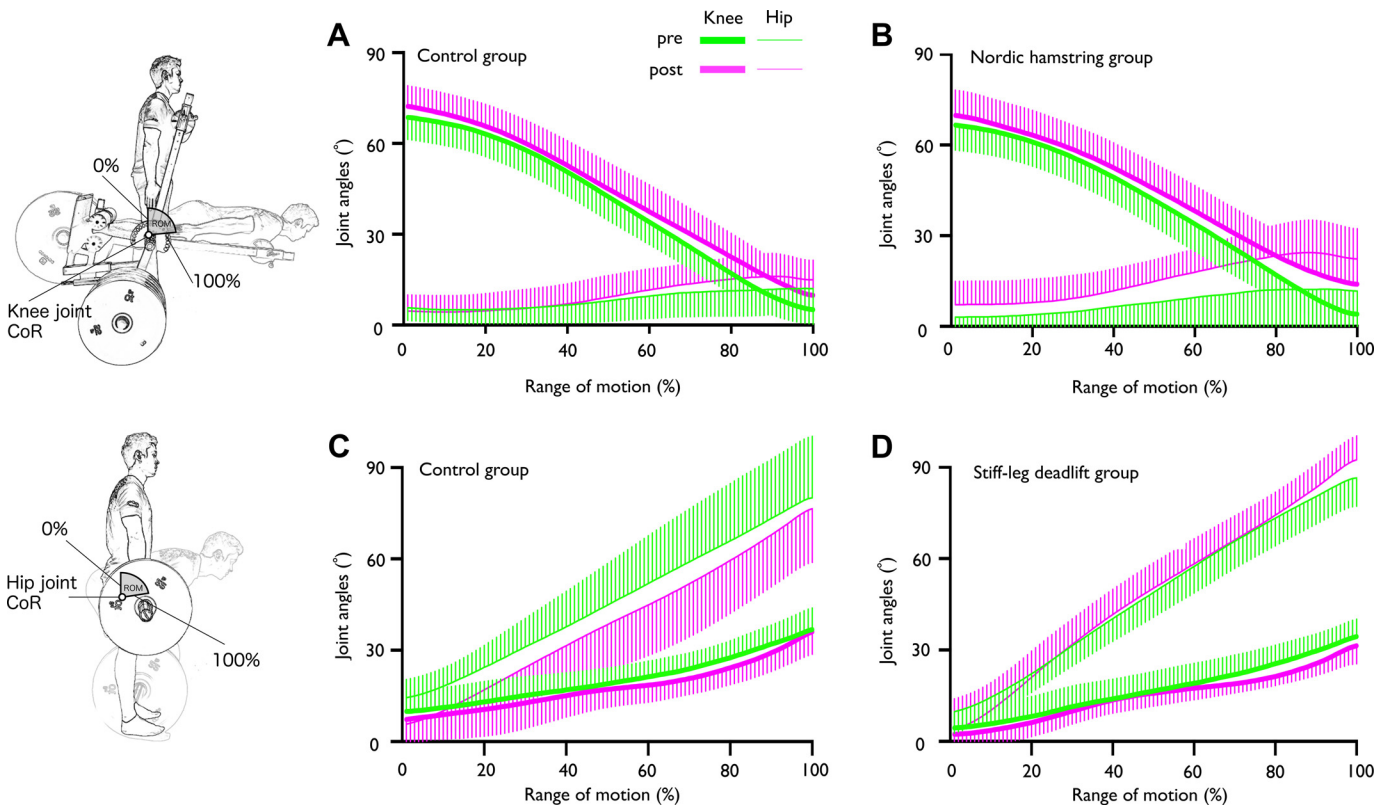

Figure 1. Knee and hip joint angles for the Nordic hamstring (NHE) and stiff-leg deadlift (SDL) exercises. The knee and hip joint angles are represented by thick and thin curves, respectively, with green curves indicating pre (before) and pink curves indicating post data (after 9 wk). The joint angles are shown as a function of the range of motion (from 0 to 100%) during the eccentric phase of the movement. *A* and *C* show data for the control group (CON) during Nordic hamstring exercise and stiff-leg deadlift. *B* and *D* show data for the trained groups during their respective exercise (i.e., Nordic hamstring for the NHE group, and stiff-leg deadlift for the SDL group). For clarity, the standard deviation was not represented. CoR, center of rotation; ROM, range of motion.

Muscle Hypertrophy

The linear mixed-effects model revealed a significant group effect ($P = 0.004$) and a group × muscle interaction effect on changes in muscle hypertrophy ($P < 0.001$). Post hoc tests showed that both the NHE and SDL groups experienced significant overall hamstrings hypertrophy compared with the control group ($P < 0.001$ and $P = 0.044$, respectively). No significant difference in overall hypertrophy was observed between the NHE and SDL groups ($P > 0.05$).

Regarding muscle-specific hypertrophy, the NHE group exhibited significant hypertrophy of the ST (24.4 ± 10.8%) compared with both the CON group (0.2 ± 5.9%; $P < 0.001$, $d = 2.83$) and the SDL group (5.5 ± 9.3%; $P < 0.001$, $d = 1.96$). The SDL group, in contrast, showed significant hypertrophy of SM (11.2 ± 12.7%) compared with the CON group (2.3 ± 4.2%; $P = 0.02$, $d = 0.92$), but not compared with the NHE group (4.6 ± 5.8%; $P = 0.24$, $d = 0.69$). For the BF, no significant differences in hypertrophy were observed between any of the groups ($P \geq 0.39$, $d \leq 0.58$).

Muscle Activation

Muscle activation patterns during both Nordic hamstring curl and stiff-leg deadlift are depicted in Fig. 2. SPM analyses revealed no significant effect of time, group or time × muscle × group (all $P \geq 0.05$) on muscle activation during the trained exercise. The main effect of muscle was observed for both Nordic hamstring ($P < 0.001$) and stiff-leg deadlift exercises ($P < 0.001$). Post hoc analysis revealed that ST activation was lower than that of BF and SM across the entire ROM of the stiff-leg deadlift exercise, whereas no differences were observed between BF and SM. During Nordic hamstring curl, BF exhibited greater muscle activation than SM (29%–69% of the ROM) and ST (38%–100% of the ROM). We also found that SM showed higher activation than ST (54%–100% of the ROM).

The distribution of activation averaged over the ROM at pre and after 9 wk, as a function of muscle hypertrophy, is depicted in Fig. 3. We did not find any significant time, group, and time × group effect (all $P \geq 0.05$) on the distribution of muscle activation during the trained exercise. Table 2 depicts the distribution of activation averaged over the range of motion of both exercises.

DISCUSSION

Our findings demonstrate a robustness of muscle activation distribution despite significant selective hypertrophies of the semimembranosus (11.2%) and semitendinosus (24.4%), induced by the stiff-leg deadlift and Nordic hamstring exercise, respectively (Fig. 3). This absence of changes in muscle activation could lead to an increase in force imbalance

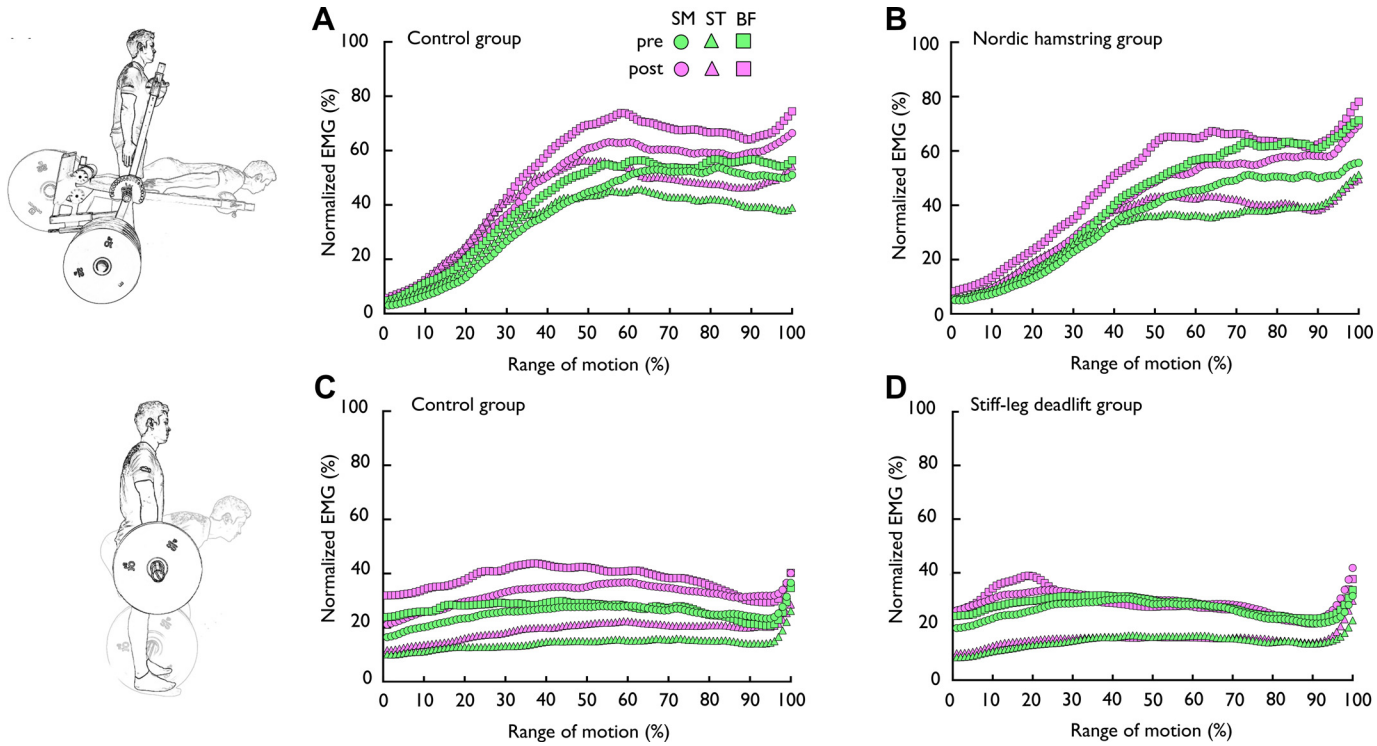

Figure 2. Normalized electromyographic activity (EMG) for each hamstring head for the Nordic hamstring exercise (NHE) and stiff-leg deadlift (SDL). Pre- (before) and post (after 9 wk) EMG data are represented with green and pink symbols, respectively [circle for semimembranosus (SM), triangle for semitendinosus (ST), and square for biceps femoris (BF)]. The data are presented as a function of the range of motion (from 0 to 100%) during the eccentric phase of the movement. *A* and *C* show data for the control group (CON) during Nordic hamstring exercise and stiff-leg deadlift. *B* and *D* show data for the trained groups during their respective exercise (i.e., Nordic hamstring for the NHE group, and stiff-leg deadlift for SDL group).

between semimembranosus and semitendinosus for SDL group whereas it could decrease for NHE group. These results provide a deeper understanding of the complex interplay between neural drive and muscle mechanical characteristics. This provides additional impetus to study long-term effects of activation strategies (e.g., on the development of musculoskeletal disorders), as they seem to represent a trait-like characteristic rather than a transient state.

Nordic Hamstring- and Stiff-Leg Deadlift-Induced Strength Gains (1RM)

It is well known that Nordic hamstring curl-based resistance training enhances maximal knee flexion strength. The strength gains occur early (6%–14% after 4 wk) (46) and continue to increase over time (47, 48). For instance, Andrews et al. (47) reported approximately a 40% increase in eccentric knee flexion torque following 9 wk of Nordic hamstrings training. This is close to the 37.4 ± 13.8% increase in 1RM presently observed in the NHE group after 27 training sessions. In contrast, stiff-leg deadlift training has been less investigated. Kawama et al. (16) reported 20%–26% increases in maximal isometric knee flexion torque after 10 wk with two and three weekly sessions of stiff-leg deadlift. Note that their protocol used lower loads (60% of body mass) and emphasized maximal range of motion to target flexibility and hamstrings structural adaptations. In our study, which used higher loads (180% of body mass on average), we also observed significant strength gains in the stiff-leg deadlift exercise ~34.0 ± 21.2% increase in 1RM for the SDL group, after 27 training sessions. Overall, this finding underscores the effectiveness of our protocol in promoting strength gains in the trained exercise.

Nordic Hamstring- and Stiff-Leg Deadlift-Induced Muscle-Specific Hypertrophies

According to our hypothesis, both NHE and SDL groups exhibited significant and similar whole hamstring hypertrophy (11.4 ± 6.5% and 7.0 ± 8.1%, respectively, vs. CON group = 0.6 ± 1.5%). Noticeably, hypertrophy was larger in the SM (11.2 ± 12.7%) and ST (24.4 ± 10.8%) for stiff-leg deadlift training and Nordic hamstring exercises, respectively. These results align with Bourne et al. (15), who reported 15%–16% hamstring hypertrophy for both Nordic hamstring and 45° hip extension exercises, with a selective hypertrophy of the ST (21%) compared with BF (6%) and SM (6%) for Nordic hamstring group. Using low loads during stiff-leg deadlift, Kawama et al. (16) reported a selective hypertrophy of the SM (6.5%). Taken together with the current study, it is now well established that Nordic hamstring promotes the distribution of hypertrophy to ST, whereas stiff-leg deadlift promotes the distribution of hypertrophy to SM.

Distribution of Muscle Activation before Training

Muscle activation during Nordic hamstring exercise has been extensively studied (22, 32, 49). This exercise is

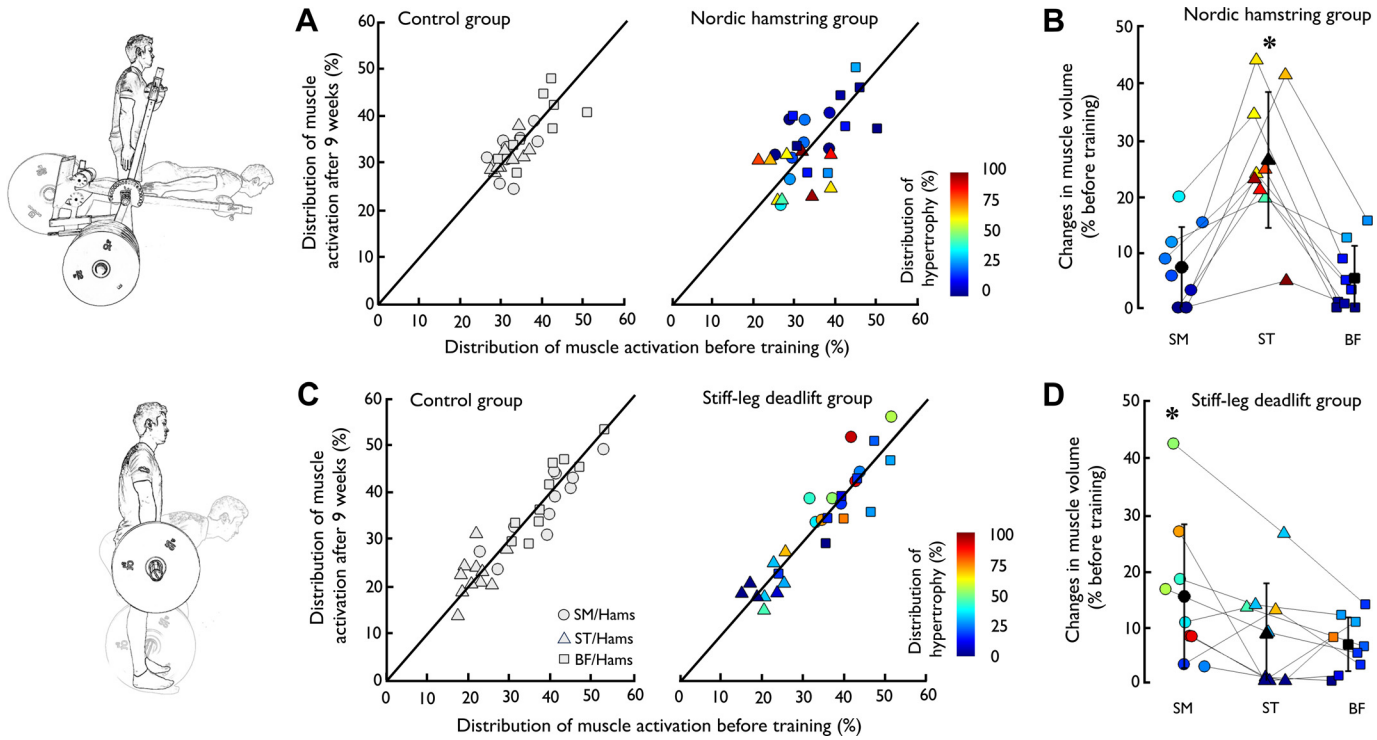

Figure 3. Scatter plots of the distribution of muscle activation and hamstring hypertrophy. Scatter plots of the distribution of activation before and after 9 wk in controls (*A*; *left*) and training groups (*C*; *right*). The *left* panels of *A* and *C* show data for the control group (CON) during Nordic hamstring exercise and stiff-leg deadlift, whereas the *right* panels of *A* and *C* show data for the trained groups during their respective exercise (i.e., Nordic hamstring for the NHE group, and stiff-leg deadlift for SDL group). The distribution of muscle hypertrophy is depicted through a color scale from 0% to 100% (i.e., 100% means that only one muscle exhibits hypertrophy). Magnitude of hypertrophy for each hamstring head for the Nordic hamstring group (*B*) and stiff-leg deadlift group (*D*) (symbols in bolt represent means ± SD). Each colored symbol represents a participant. *Significant difference in muscle volume between, before, and after training; $P < 0.05$. BF, biceps femoris; Hams, Hamstring; SM, semimembranosus; ST, semitendinosus.

commonly performed at body weight, which often represents a supramaximal condition for participants (i.e., they are not able to resist over the full ROM) (15, 48). Many lightening options can be used (e.g., dedicated machine, slope platform, and elastic bands) to enable participants to perform the Nordic hamstring curl at a maximal or submaximal intensity over the full ROM. Using elastic bands, Boyer et al. (22) reported that eccentric contraction of the Nordic hamstring curl performed at 1RM (over the full ROM) elicits averaged muscle activation ~48.6%, 55.9%, and 64.5%, for SM, ST, and BF, respectively. According to Henneman's size principle in motor unit recruitment (50), the use of 80% of 1RM in the current study largely reduces the magnitude of activation. When averaging both NHE and CON groups during Nordic hamstring curl at pre, we found, in mean, 35.4%, 32.0%, and 42.5% for SM, ST, and BF, respectively. During stiff-leg deadlift, Boyer et al. (22) found that the activation of SM, ST, and BF was ~42.8%, 30.9%, and 44.6%, respectively, whereas the current study reported values ~25.4%, 14.1%, and 27.1%, respectively, at pre for both SDL and CON groups. Regardless of the magnitude of muscle activation, its distribution among the hamstring heads varied between both exercises. Using functional magnetic resonance, it has been shown that the SM was the least involved muscle during the Nordic hamstring exercise, whereas the BF and ST showed similar levels of involvement (51), or higher involvement for the ST (15). The lower involvement of ST in the current study may be explained by the inclusion of extended knee extension in the ROM, which favors the contribution of the BF compared with ST (32). During the stiff-leg deadlift, the largest distribution of activation to the SM and BF compared with ST, was in accordance with previous studies (22, 52). Beyond this generality, a large interindividual variability in the distribution of muscle

Table 2. *Distribution of hamstrings activation during Nordic hamstring and stiff-leg deadlift before (pre) and after 9 wk (post)*

Exercise	Nordic Hamstring						Exercise	Stiff-Leg Deadlift					
Ratio	SM/Hams, %		ST/Hams, %		BF/Hams, %		Ratio	SM/Hams, %		ST/Hams, %		BF/Hams, %	
Time	Pre	Post	Pre	Post	Pre	Post	Time	Pre	Post	Pre	Post	Pre	Post
NHE group	30.9 ± 7.5	33.3 ± 6.8	29.7 ± 6.8	28.0 ± 6.0	39.3 ± 8.6	38.7 ± 8.7	SDL group	39.2 ± 7.6	40.3 ± 9.1	20.7 ± 4.0	21.3 ± 5.0	40.1 ± 9.4	38.4 ± 9.8
CON group	30.8 ± 6.1	31.8 ± 6.1	30.8 ± 4.9	30.7 ± 4.2	37.9 ± 7.9	37.5 ± 8.1	CON group	38.2 ± 7.9	36.9 ± 9.2	21.2 ± 4.2	22.2 ± 4.9	40.6 ± 4.8	41.3 ± 12.3

BF, biceps femoris; CON, control group; Hams, hamstring; NHE, Nordic hamstring group; SDL, stiff-leg deadlift group; SM, semimembranosus; ST, semitendinosus.

activation was observed, the magnitude of which varied between muscles (Fig. 3). The consequences of these activation strategies on muscle force and their relationship with the distribution of hypertrophy will be investigated in the future.

Invariance of Muscle Activation Distribution Post Training in the Presence of Selective Hypertrophy

To the best of our knowledge, this was the first study that experimentally investigated the possible changes in the distribution of muscle activation in the presence of selective hypertrophy due to training. Previous works were interested in the ability of the central nervous system to face a reduction of muscle volume after a muscle strain injury (11, 53, 54) or even in a paralyzed individual muscle (18). In the presence of a selective atrophy of the BF, Avrillon et al. (11) reported an alteration of the distribution of muscle activation during submaximal isometric knee flexion at 20% of MVC, but not at 50% of MVC. More specifically, they showed that a reduction in BF volume led to a decreased contribution of this muscle during the task, which was compensated by an increased activation of the SM. However, De Rugy et al. (18) demonstrated that muscle coordination is habitual rather than optimal, as the activation of all synergist muscles, including the paralyzed muscle, was increased to meet the mechanical demand of the task. Accordingly, we did not find any significant changes in the distribution of muscle activation over the ROM of both stiff-leg deadlift and Nordic hamstring exercises (Table 2), despite the presence of substantial muscle hypertrophy. This finding partially contradicts biomechanical models that propose a neuromechanical coupling between force-generating capacities and activation (23). However, the experimental evidence supporting this coupling remains limited. Observations of neuromechanical coupling have been confined to cross-sectional studies during isometric submaximal conditions, specifically involving the vastii (7) and gastrocnemii muscles (8), or inferred by integrating findings from several studies (9, 10). In contrast, the present results do not support the flexibility of the neuromechanical coupling. It is likely that, at least in the case of the hamstrings, other biomechanical features, such as moment arm, force-length relationship, and fascicle length, exert a greater influence on muscle activation than muscle volume, particularly during dynamic contractions (3). Moreover, given that muscle hypertrophy is reversible, individuals may adopt "motor habits," defined as a set of valid distributions of activations that accomplish the task without necessarily minimizing cost. A longitudinal investigation conducted over a longer time scale would be necessary to determine whether these strategies evolve toward more optimal patterns with increased experience.

The selective change in muscle volume of SM and ST provides an interesting model to study the flexibility of motor control for two main reasons. First, SM and ST exhibit significant differences in muscle characteristics. SM has a larger volume and shorter fascicle length compared with ST (12), making it a good candidate for reducing the metabolic cost of contraction (4). However, despite this metabolic advantage, the selective increase in SM muscle volume in the SDL group was not accompanied by a selective change in muscle activation (Fig. 3). Second, in the case of the selective hypertrophy of SM, the strongest hamstring head (17), combined with unchanged muscle activation, this could result in a greater force imbalance within the hamstrings whereas hypertrophy of the ST had the opposite effect, helping to limit this imbalance. This is an interesting model to better understand the complex interplay between neural drive and muscle mechanical characteristics. Although the increase in force-generating capacities has not been assessed in the current study, three main reasons led us to believe that this assumption is reasonable. First, a mean increase in volume of approximately 24.4% was observed in the ST fusiform muscle (for review, see Ref. 17), where changes in muscle volume can be considered as changes in PCSA (55). Second, the resistance training content (i.e., 80% 1RM with both eccentric and concentric contractions) used in the current study would favor an increase in muscle volume and pennation angle compared with fiber length, resulting in increasing PCSA as previously shown (56). Third, the complex interplay between changes in pennation angle, fiber length (and consequently fascicle length), and fiber cross-sectional area in response to overload acts together at increasing muscle strength. In their review, Jorgenson et al. (57) posits that muscle CSA increases in pennate muscles during overload are often primarily driven by longitudinal growth, reflected by increases in fascicle length, rather than radial growth (i.e., increases in mean fibers cross-sectional area). Alternatively, when overload predominantly induces radial growth, this may lead to concurrent increases in pennation angle and fiber cross-sectional area, without significant changes in fascicle length. It is unlikely that an increase in muscle volume in the current study led to a decrease or no changes in force-generating capacities. Taken together, it is likely that the central nervous system does not favor or counteract force imbalance among hamstrings after a 9-wk hypertrophy-based resistance training program. Future studies should investigate changes in muscle activation strategies in the presence of selective muscle atrophy, such as that induced by acute muscle strain or surgery. This would help determine whether targeting the atrophied muscle during rehabilitation is effective in restoring baseline activation strategies.

Limitations

Certainly, our study has limitations that must be addressed. First, Shapiro–Wilk test results demonstrate a non-normality in 11.4% of the muscle activation raw data. This is not inherently problematic in the context of SPM, as the model residuals were normally distributed. SPM, like other parametric methods based on the general linear model, relies on the assumption of normality in the residuals rather than in the raw observations themselves (58). Furthermore, with a sample size of 15 per group, the central limit theorem supports the robustness of the analysis against modest deviations from normality (59). Previous studies have shown that SPM remains valid and reliable under such conditions, provided that the residuals satisfy distributional assumptions (60, 61). Therefore, it is unlikely that the observed non-normality in the input data has adversely affected the integrity or interpretability of the results. Second, we measured the distribution of muscle activation during exercises performed at high intensity (80% 1RM). Avrillon et al. (11) reported that a history of muscle strain injury induced an alteration in muscle

activation during isometric submaximal contraction performed at 20% of MVC but not at 50% of MVC. This is likely because a higher activation of the hamstring muscles is required to perform the task. During such tasks, fewer degrees of freedom are available to modify the activation distribution while maintaining the goal of the task. However, muscle activation averaged over the ROM during stiff-leg deadlift was ~25.4%, 14.1%, and 27.1% for SM, ST, and BF, respectively. It is unlikely that the mechanical constraints of the tasks, at least for stiff-leg deadlift, have limited the flexibility of the neural drive. Third, neuromechanical coupling has been exclusively reported during isometric contractions. One might assume that the characterization of the distribution of the activation during the eccentric contraction could have influenced the results of the current study. However, previous works suggest that BF activation either decreases or remains unchanged following injury (62, 63). Such results were obtained during eccentric maximal contractions that involve a specific neural control, more prone to elicit neuromuscular inhibition at both the supraspinal and spinal levels compared with concentric or isometric tasks (64). We are confident that the absence of changes in the distribution of muscle activation is not fully explained by muscle contraction type. Fourth, the kinematics were not constrained during testing, which may have introduced variability in the distribution of muscle activation. We used the MDC as a threshold to exclude participants exhibiting a substantial variability in knee and hip joint angles. This approach allowed us to compare the distribution of activation in the trained exercise, which is relevant for training settings. Nonetheless, further studies should also incorporate standardized contractions on a dynamometer in the presence of selective hypertrophy. Finally, it is well known that bipolar surface EMG recordings of muscle electrical activity have limitations, particularly regarding crosstalk and normalization procedures (65). We paid particular attention to these issues by using ultrasound imaging to identify the different hamstring heads and to place the electrodes as far as possible from neighboring muscles (66). We also implemented multiple normalization conditions during various MVC tasks to maximize the likelihood that participants activated their muscles to their full capacity (36), enabling comparisons between muscles and participants (66). Taken together, these considerations make it unlikely that the methodological limitations primarily explain the conclusions drawn in the current study.

Conclusions

It is a long-held belief that muscle activation could change with muscle hypertrophy. The hamstring muscle group was a relevant model to experimentally address this belief due to *1*) the large differences in force-generating capacities reported between semimembranosus and semitendinosus, and *2*) the ability of stiff-leg deadlift and Nordic hamstring to target one of these muscles, respectively. In the presence of selective hypertrophy of the semimembranosus (11.2%) and semitendinosus (24.4%), we did not find any changes in the distribution of muscle activation during submaximal contractions performed during stiff-leg deadlift and Nordic hamstring curl. These resistance training exercises, which are commonly used in hamstring prevention and rehabilitation strategies, appear effective at increasing the force-generating potential of the targeted muscles in noninjured individuals as their muscle volume increases without altering their activation strategies.

DATA AVAILABILITY

Data will be made available upon reasonable request.

SUPPLEMENTAL MATERIAL

Supplemental Material: https://doi.org/10.6084/m9.figshare.29195720.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

T.M., A.H.C., A.N., V.D., and L.L. conceived and designed research; T.M., A.H.C., A.N., V.D., and L.L. performed experiments; T.M. analyzed data; T.M. and L.L. interpreted results of experiments; T.M., A.H.C., V.D., and L.L. prepared figures; T.M., A.H.C., A.N., V.D., and L.L. drafted manuscript; T.M., A.H.C., A.N., V.D., and L.L. edited and revised manuscript; T.M., A.H.C., A.N., V.D., and L.L. approved final version of manuscript.

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