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Motor control strategies differ between monoarticular and biarticular quadriceps muscles during bipedal squats

Tom Maudrich[1,2] | **Pascal Tapper**[1] | **Martina Clauß**[1] | **Roberto Falz**[3] | **Johannes Lässing**[3] | **Rouven Kenville**[1,2]

[1]Department of Movement Neuroscience, Faculty of Sports Science, Leipzig University, Leipzig, Germany

[2]Department of Neurology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

[3]Department of Sport Medicine and Prevention, Faculty of Sports Science, Leipzig University, Leipzig, Germany

Correspondence
Rouven Kenville, Department of Movement Neuroscience, Faculty of Sports Science, Leipzig University, Leipzig 04109, Germany.
Email: rouven.kenville@uni-leipzig.de

The interplay between biarticular and monoarticular muscles of the knee and hip joints during bipedal squats (SQ_{BP}) requires adequate central-nervous control mechanisms to enable smooth and dynamic movements. Here, we investigated motor control between M. vastus medialis (VM), M. vastus lateralis (VL), and M. rectus femoris (RF) in 12 healthy male recreational athletes during SQ_{BP} with three load levels (50%, 62.5%, and 75% of 3-repetition maximum) following a standardized strength training protocol (3 sets of 10 repetitions). To quantify differences in motor control mechanisms in both time and frequency domains, we analyzed (1) muscle covariation via correlation analyses, as well as (2) common neural input via intermuscular coherence (IMC) between RF, VM, and VL. Our results revealed significantly higher gamma IMC between VM-VL compared with RF-VL and RF-VM for both legs. Correlation analyses demonstrated significantly higher correlation coefficients during ascent periods compared with descent periods across all analyzed muscle pairs. However, no load-dependent modulation of motor control could be observed. Our study provides novel evidence that motor control during SQ_{BP} is characterized by differences in common input between biarticular and monoarticular muscles. Additionally, muscle activation patterns show higher similarity during ascent compared with descent periods. Future research should aim to validate and extend our observations as insights into the underlying control mechanisms offer the possibility for practical implications to optimize training concepts in elite sports and rehabilitation.

KEYWORDS
intermuscular coherence, motor control, muscle covariation, squats, surface EMG

1 | INTRODUCTION

The bipedal squat (SQ_{BP}) is among the most commonly employed fundamental whole-body movements for building strength and improving posture as well as lower-body stability. Although several hundred muscles are involved in the execution of SQ_{BP},[1] extensors of the knee and hip joints are considered prime movers.[2] Particular

Tom Maudrich and Pascal Tapper contributed equally to the work.

importance is placed on the knee extensors, that is, the quadriceps femoris muscles comprising M. rectus femoris (RF), M. vastus lateralis (VL), M. vastus medialis (VM), and M. vastus intermedius (VI). During SQ_{BP}, these muscles perform a concentric knee extension and eccentrically resist knee flexion. Due to their high stress resistance, the muscles of the quadriceps femoris compensate for and transmit large forces in the hip and knee joint, and thus, assume a central biomechanical role during SQ_{BP}.[3] Despite this unity, both anatomical and functional distinctions can be made between individual quadriceps femoris muscles.

While the main function of the biarticular RF is to initiate hip flexion and support knee range of motion in both extension and flexion,[4] both monoarticular VM and VL work synergistically to provide adequate stability of the patella, by balancing the lateral and medial forces acting on the patella, during dynamic SQ_{BP}.[5] Electromyography (EMG) studies support this divergence, as RF shows different activation patterns during SQ_{BP} compared with VM and VL.[6] For example, studies observed lower activation of RF compared with VM and VL,[4] while VM showed increased activity compared with VL, regardless of external load.[6] On the contrary,[7] reported a non-significant trend of higher activity of the VL compared with VM during the concentric contraction of a parallel squat. Ideally, the close functional relationship between VM and VL leads to an activity ratio of 1:1, although this often differs under natural conditions.[8]

The interplay between biarticular and monoarticular muscles of the knee and hip joints during SQ_{BP} necessitates appropriate central-nervous control mechanisms to enable smooth, dynamic movements. It is assumed that muscles acting together within a movement, such as the muscles of the M. quadriceps femoris during SQ_{BP}, are functionally connected by the nervous system and share a common neural drive.[9] In simple terms, the activities of their motor units are affected by this common drive and consequently synchronized.[10] One method that allows the analysis of functional binding between muscles is intermuscular coherence (IMC).[11] IMC has been studied in a variety of movements and enables inferences about frequency-specific, shared neural drive among different muscles.[12] In this context, frequency bands reflect distinct aspects of movement-specific control mechanisms.[11] While multiple frequency bands carry information relevant to movement, synchronized activation between muscles in the range of gamma frequencies (~ >30 Hz) is at the center of compound motor control research.[13–15] Gamma IMC between lower extremity muscle pairs has been previously reported in several studies and is ascribed to the onset of movements as well as sensory integration processing.[15,16] Of particular interest are findings by Mohr and colleagues (2015, 2018) who demonstrated gamma IMC between VM and VL during isometric and dynamic SQ_{BP}. Previous research from our group also observed gamma IMC between homologous muscle pairs during SQ_{BP} underlining the importance of gamma IMC in compound movements and specifically SQ_{BP}. Still, it remains unresolved to what extent gamma IMC differs between RF, VM, and VL during SQ_{BP} performance. Further, it is unclear what effect different load levels have on IMC between these muscle pairs. Although there is some evidence of possible force-related modulation in IMC magnitude and frequency,[17] a systematic investigation of such changes in SQ_{BP} has not been conducted. Another approach to investigating motor control of multiple muscles during compound movements is the analysis of muscle covariation through correlation analysis.[18] In this context, covariation describes the similarity of activation time-courses between several functionally related muscle groups. For example, previous animal research revealed higher correlation coefficients between VM-VL compared with RF-VM and RF-VL during different phases of locomotion.[18] Similar to IMC analysis, a systematic investigation of the modulation of these parameters between bi- and monoarticular muscles during SQ_{BP}, as well as potential modulations depending on different load levels remain elusive. Importantly, coherence and correlation are not necessarily related and may, therefore, reflect individual aspects of motor control mechanisms.[18]

With the present study, we aimed to analyze alterations in motor control of bi- and monoarticular muscles of the knee and hip joint in dependence of different load levels during SQ_{BP}. To quantify such differences in both time and frequency domains, we analyzed (1) covariation via correlation analyses, as well as (2) common neural input via IMC between RF, VM, and VL. Based on contemporary literature, we hypothesized a higher correlation between VM-VL compared with RF-VM and RF-VL, as well as a modulation of gamma IMC as a function of load levels.

2 | MATERIALS AND METHODS

2.1 | Participants

Twelve healthy male recreational athletes (aged 24.5 ± 3.1 years [mean ± SD], body mass 81.4 ± 7.3 kg, height 183.2 ± 4.9 cm, weight training experience 2.8 ± 2.7 years) participated in this study. All participants were aged between 18 and 35 years, had at least 1 year of weight training experience, and had no current or previous history of lower limb injury. Leg dominance of all participants was assessed by inquiring the preferred leg for kicking a ball. Based on this assessment, the majority of participants were classified as right-leg dominant ($n = 9$),

with only three participants being classified as left-leg dominant. Intentions, procedures, as well as potential risks and benefits, were communicated to the participants and were confirmed by signing an informed consent form according to the Declaration of Helsinki. The study was approved by the ethics committee of Leipzig University (ref.-nr. 271/21-ek).

2.2 | Procedures

All participants completed a series of standardized SQ_{BP} on a smith machine (Technogym Germany GmbH, Germany) at three load conditions: 50%, 62.5%, and 75% of the individual three-repetition-maximum (3-RM) (see Figure 1A). Individual 3-RM corresponds to the maximum amount of weight a person can lift for three repetitions.[19] To ensure adequate recovery and minimize fatigue, all three load conditions were performed on separate days, 1 week apart. In addition, participants were instructed to avoid any resistance training for the lower extremities during the 72 h before testing days. On each of the three testing days, 3 sets of 10 repetitions were completed for each load with a 4-min rest period between each set.[19] SQ_{BP} was standardized according to the following criteria. Firstly, individual knee flexion angles (mean: 69.8 ± 7.2°) corresponding to a parallel squat, that is, a position where the femur is parallel to the ground, were determined. For this purpose, all participants slowly descended in the smith machine until they reached the desired squat position. A digital protractor was used to obtain individual knee angles at this position. A custom-built laser Sharp® IR-Sensor (Sharp Business Systems Deutschland GmbH, Germany) attached to the smith machine recorded the time course of the vertical position of the barbell and angular trajectories were derived from the resulting data. Angular trajectories were then synchronized with an auditory feedback device, where a sound was triggered once the established knee angle was reached during each contraction. This ensured a standardized range of motion within and across participants. To maintain a constant pace, one repetition cycle consisted of three consecutive movement periods, descent, ascent, and hold, each with a duration of 2 s (see Figure 1B). The start of each movement period was visually cued via a monitor located in front of the participants. Lastly, the stance was set to shoulder width with both feet externally rotated at 10°, and participants were instructed to keep their feet planted throughout the SQ_{BP}.

In the first testing session, individual 3-RM values were determined. For this purpose, all participants first

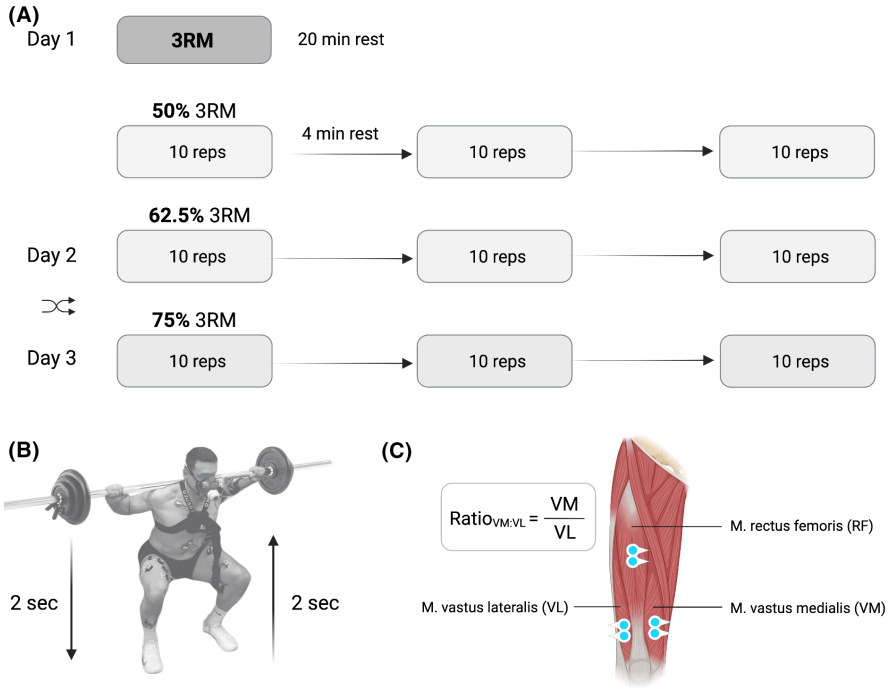

FIGURE 1 Experimental Setup. (A) Participants completed three experimental sessions separated by a week. On the first day, the individual 3-repetition maximum (3RM) in the smith-machine back squat was determined. Thereafter, 3 sets of 10 repetitions each with 50% of 3RM were performed interspaced by a resting period of 4 min. This procedure was repeated with 62.5% 3RM and 75% 3RM loads on separate days. The order of squatting loads for day 2 and day 3 was randomized. (B) Participants performed SQ_{BP} on a smith-machine with 2 s descend, 2 s ascend and 2 s hold at the top. (C) Surface EMG was recorded from bilateral M. rectus femoris (RF), M. vastus medialis (VM), and M. vastus lateralis (VL). Created with BioRender.com

performed 10 repetitions with an empty barbell to warm up and become familiar with the task. Thereafter, one set of five repetitions with added submaximal load and another set of three repetitions with added submaximal load were performed. From there, the actual 3-RM was determined by single trials of incrementally increasing load. Once 3 clean repetitions of a load level were completed, the load was increased in the next attempt. Between each attempt, there was a rest period of at least 4 min. In case participants were not able to complete 3 clean repetitions of a load level, the previous load level was assumed to be 3-RM. After 3-RM determination (mean: 97.3 ± 23.9 kg), participants were allowed to rest for 20 min to reduce potential fatigue effects.

Next, the actual SQ_{BP} task with 50% of 3-RM load was performed. All participants completed another warm-up procedure consisting of 5 min on a cycle ergometer (120 watts; 75 rpm) followed by one set of 10 repetitions without external load, 5 repetitions with 50% of the subsequent testing load, and finally 3 repetitions with 75% of the subsequent load. Finally, three sets of 10 repetitions with 50% of 3-RM load were performed in the previously described standardized manner. This procedure was repeated for the remaining two load conditions on separate days. To minimize any sequence effects, the order of the following testing loads (62.5% 3-RM, 75% 3-RM) was randomized. All testing sessions were performed in the University Human Performance Laboratory.

2.3 | Data recording

Muscle activity of M. rectus femoris (RF), M. vastus medialis (VM), and M. vastus lateralis (VL) was recorded bilaterally (see Figure 1C) using a wireless Desktop Transmission System (NORAXON Inc.). To ensure optimal signal quality during recording, the skin of each participant was shaved, abraded, and cleaned with alcohol. Subsequently, gel-coated self-adhesive electrodes (interelectrode distance of 20 mm) were mounted on standardized electrode positions according to SENIAM recommendations.[20] Electrode positions were kept constant between sessions according to anatomical landmarks. Pairwise EMG electrodes were placed in parallel to muscle fiber orientations. Data were recorded at a sampling frequency of 1500 Hz. During recording, the input impedance of the amplifier was set at >100 MΩ, bandpass filtering was applied in the frequency range of 10–500 Hz, and common-mode rejection (CMRR) was set at >100 dB. To enable normalization of EMG activity, maximum voluntary contraction (MVC) values were determined for each muscle at the beginning of every single testing session. To determine the MVC of RF, VM, and VL, two maximal isometric contractions (5 s) of the quadriceps femoris muscle were performed according to.[21] Amplitude normalization of all trials in a testing session was carried out using the maximum RMS value of both maximal contractions of each participant for each muscle separately. To reduce any fatigue effects, a thirty-second rest period was granted between each MVC trial.

2.4 | Preprocessing

Initially, all data were normalized to individual MVC values and separated into 30 trials of descent and ascent periods. Onsets and offsets of movement periods were determined based on the angular trajectories derived from the path progression of the barbell. All data were filtered using a high-pass filter at 20 Hz (4th order Butterworth filter). As the power density function of surface, EMG signals has insignificant contributions at frequencies <10 Hz, this is a common processing step to improve signal quality.[22]

2.5 | Time-domain analyses

First, root-mean square values were calculated for all trials individually to obtain amplitudes of MVC-normalized EMG activity. RMS values were then averaged per set, yielding three RMS values per condition (50%, 62.5%, and 75%), movement period (descent and ascent), and muscle (RF, VM, and VL) for each participant. MVC-normalized amplitudes of RF, VM, and VL were analyzed for each leg separately by a four-way repeated-measures analysis of variance (ANOVA) with the factors MUSCLE (RF, VM, VL), LOAD (50%, 62.5%, 75%), PERIOD (descent, ascent), and SET (Set 1, Set 2, Set 3).

Next, $Ratio_{VM:VL}$ was calculated by dividing MVC-normalized amplitudes of VM by those of VL.[23] To analyze differences in $Ratio_{VM:VL}$, a four-way repeated-measures ANOVA was carried out using the factors SIDE (Right, Left), PERIOD (descent, ascent), LOAD (50%, 62.5%, 75%), and SET (Set 1, Set 2, Set 3).

Finally, to investigate coordination between quadriceps muscles during SQ_{BP}, we evaluated the similarity between muscle activations by computing the Pearson correlation between the activation time-courses of all three possible muscle pairs (VM-VL, RF-VM, RF-VL) for each leg separately. Therefore, EMG data was low-pass filtered at 20 Hz (4th order Butterworth filter) and time-normalized. Pearson correlation was carried out on time-normalized EMG data. To enable statistical comparison between conditions, Pearson correlation coefficients were normalized using Fisher transform. To analyze differences in these correlations between conditions, two four-way repeated-measures ANOVAs with the factors MUSCLE (VM-VL,

RF-VM, RF-VL), PERIOD (descent, ascent), LOAD (50%, 62.5%, 75%), and SET (Set 1, Set 2, Set 3) were performed, for each leg separately.

Post hoc Bonferroni tests were used to identify differences in potential main effects, whereas simple main effect tests were used to assess interactions, if applicable. If sphericity assumptions were violated, Greenhouse–Geisser adjustments of the *p*-values were used. Effect size was evaluated by way of ηp^2 (Eta partial squared) where 0.01–0.06 constitutes a small effect, 0.06–0.14 a medium effect, and >0.14 a large effect or Cohens d for pairwise post hoc comparisons. All statistical analyses were conducted with JASP version 0.16.1 (University of Amsterdam, Amsterdam, Netherlands) with the level for significance set at $p < 0.05$.

2.6 | Frequency-domain analyses

Median frequencies (MDF) were analyzed to investigate potential fatigue effects. MDF was estimated using built-in MATLAB functions, where MDF is defined as the frequency at which the EMG power spectrum is divided into two regions of equal amplitudes. MDF was finally compared between all conditions for each leg via separate four-way repeated-measures ANOVAs with factors MUSCLE (RF, VM, and VL), PERIOD (descent, ascent), LOAD (50%, 62.5%, 75%), and SET (Set 1, Set 2, Set 3).

To analyze differences in IMC, high-pass filtered EMG data were first concatenated in a contraction-wise manner, that is, 10 contractions of individual trial lengths (grand average of 0.9 ± 0.1 s) corresponding to durations of muscle activity, per movement period, set, and leg for each muscle separately (RF, VM, VL). Signal envelopes were extracted from concatenated EMG data using Hilbert transform. Equal trial lengths for analyzed muscle pairs were ensured by way of zero-padding without compromising temporal relationships between pairwise signals.[24] IMC was estimated between pairs of concatenated EMG data (VM-VL, RF-VM, RF-VL) using Welch's method with a Hanning window of 125 samples, no overlap, and a frequency resolution of 1.46 Hz.[11] Significance of IMC results was established through individual confidence limits according to[25]:

$$CL_{\alpha} = 1 - \left(1 - \frac{\alpha}{100}\right)^{\frac{1}{N-1}} \quad (1)$$

where α is the significance set to 5%, N is the number of epochs (grand average of 105 ± 2.7 epochs), and CL is the confidence limit above which observed coherence values were deemed significant. IMC estimates were then integrated over the gamma band (30–60 Hz) to yield IMC areas and used for further statistical analysis. Examining areas of coherence is considered superior in comparison with the analysis of peaks and frequencies of coherence estimates.[26,27] To avoid skewness and normalize variance, IMC areas were log-transformed before statistical analyses.[27] A separate four-way ANOVA for each leg (right and left) was carried out using the factors MUSCLE (VM-VL, RF-VM, RF-VL), PERIOD (descent, ascent), LOAD (50%, 62.5%, 75%), and SET (Set 1, Set 2, Set 3) to analyze differences in gamma IMC area between conditions.

3 | RESULTS

3.1 | Time-domain

Initially, mean amplitudes between all conditions and investigated muscles were analyzed. For the right leg, repeated-measures ANOVA revealed a significant effect for LOAD ($F_{(2,22)} = 5.353$, $p = 0.013$, $\eta p^2 = 0.327$) and PERIOD ($F_{(1,11)} = 60.016$, $p < 0.001$, $\eta p^2 = 0.845$). Post hoc comparisons showed mean amplitudes were significantly higher during ascent vs. descent (mean difference [MD] = 0.246, SE = 0.032, $p < 0.001$, d = 0.920), as well as during 62.5% vs. 50% (MD = 0.177, SE = 0.062, $p = 0.029$, d = 0.660), and 75% vs. 50% (MD = 0.176, SE = 0.062, $p = 0.029$, d = 0.657). No other significant main effect was found (all $p > 0.05$). For the left leg, repeated-measures ANOVA revealed a significant effect for LOAD ($F_{(2,22)} = 5.015$, $p = 0.016$, $\eta p^2 = 0.313$) and PERIOD ($F_{(1,11)} = 55.308$, $p < 0.001$, $\eta p^2 = 0.834$). Post hoc comparisons showed mean amplitudes were significantly higher during ascent vs. descent (MD = 0.283, SE = 0.038, $p < 0.001$, d = 0.848), as well as during 75% vs. 50% (MD = 0.202, SE = 0.066, $p = 0.016$, d = 0.606). No other significant main effect was found (all $p > 0.05$).

Concerning $Ratio_{VM:VL}$, repeated-measures ANOVA revealed a significant effect for SET ($F_{(2,22)} = 7.727$, $p = 0.003$, $\eta p^2 = 0.413$, see Figure 2A). Post hoc comparisons showed $Ratio_{VM:VL}$ to be significantly reduced in Set 3 when compared to Set 1 (MD = 0.019, SE = 0.005, $p = 0.002$, d = 1.134). No other significant main effect or interaction was found (all $p > 0.05$).

With regards to the Pearson correlation between muscle activation time-courses of the right leg, a significant effect for the factor PERIOD ($F_{(1,11)} = 49.699$, $p < 0.001$, $\eta p^2 = 0.819$, see Figure 3) was revealed. Post hoc comparisons indicated that correlation coefficients were higher during ascent compared with descent (MD = 0.388, SE = 0.055, $p < 0.001$, d = 1.651). No other main effects or interactions were found (all $p > 0.05$). Similarly, for the left leg, a significant effect for the

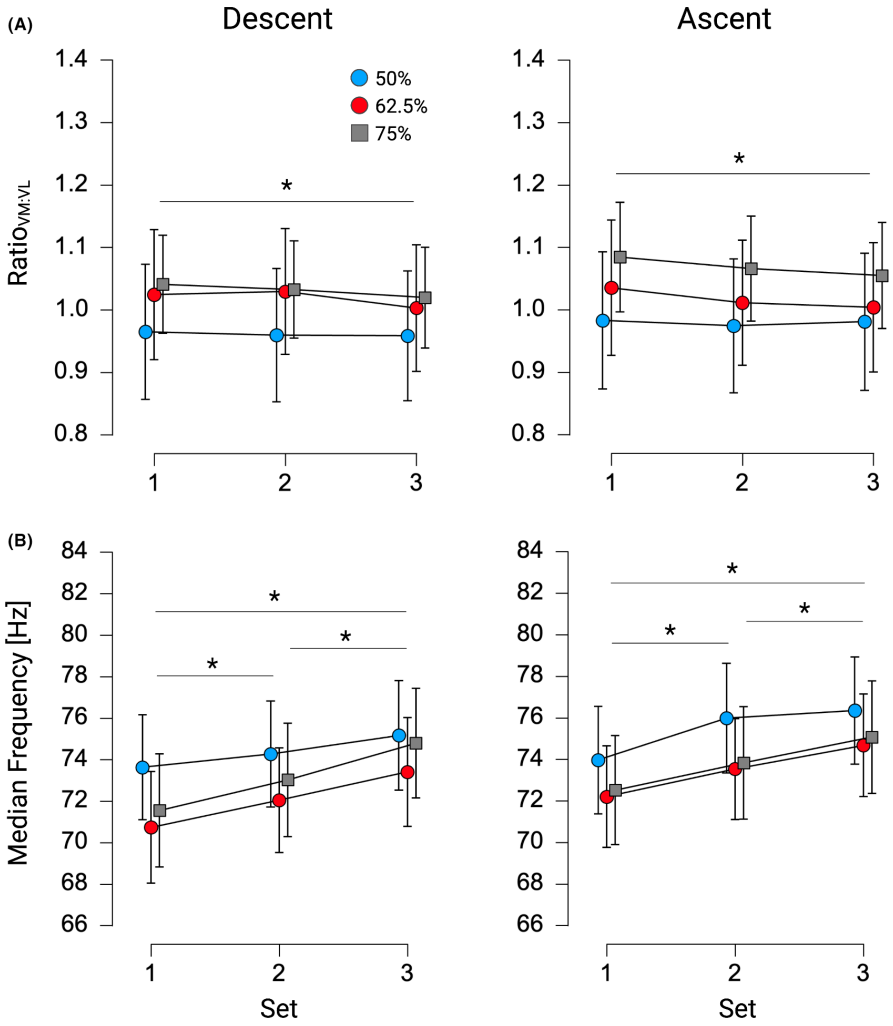

FIGURE 2 Results of time-domain and frequency-domain analyses. (A) Ratio$_{VM:VL}$ significantly decreased from set 1 to set 3. No significant effect of LOAD was observed. (B) MDF significantly increased gradually from set 1 to set 3. Again, no significant effect of LOAD was observed.

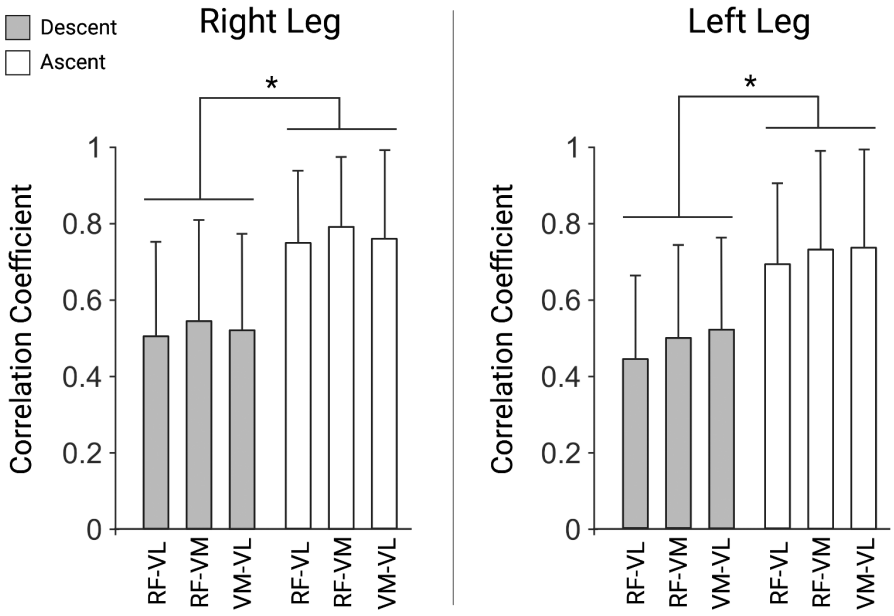

FIGURE 3 Pearson correlation coefficients between muscle activation time-courses. Correlation coefficients are higher during ascent compared with descent for all muscle pairs investigated.

factor PERIOD ($F_{(1,11)} = 46.933$, $p < 0.001$, $\eta p^2 = 0.810$, see Figure 3) was found. Post hoc comparisons again indicated that correlation coefficients were higher during ascent compared with descent (MD = 0.345, SE = 0.050, $p < 0.001$, d = 1.366). No other main effects or interactions were found (all $p > 0.05$).

3.2 | Frequency-domain

To monitor potential fatigue-related effects, MDF was compared between all conditions. For the right leg, repeated-measures ANOVA revealed a significant effect for MUSCLE ($F_{(2,22)} = 12.989$, $p < 0.001$, $\eta p^2 = 0.541$) and SET ($F_{(2,22)} = 52.321$, $p < 0.001$, $\eta p^2 = 0.826$, see Figure 2B). Post hoc comparisons showed MDF to be significantly higher in RF compared with both VM (MD = 16.627, SE = 3.450, $p < 0.001$, d = 1.391) and VL (MD = 13.264, SE = 3.450, $p = 0.003$, d = 1.110). Furthermore, MDF was elevated in Set 3 when compared to Set 2 (MD = 0.916, SE = 0.247, $p = 0.004$, d = 1.071) as well as compared to Set 1 (MD = −2.494, SE = 0.247, $p < 0.001$, d = 2.919) and in Set 2 compared to Set 1 (MD = 1.579, SE = 0.247, $p < 0.001$, d = 2.919). No other significant main effect was found (all $p > 0.05$). For the left leg, the same significant main effects MUSCLE ($F_{(2,22)} = 4.806$, $p = 0.001$, $\eta p^2 = 0.304$) and SET ($F_{(2,22)} = 53.061$, $p < 0.001$, $\eta p^2 = 0.828$, see Figure 2B) were found. Post hoc comparisons showed MDF to be significantly higher in RF compared with VM (MD = 11.698, SE = 3.813, $p = 0.017$, d = 0.886). Furthermore, MDF was elevated in Set 3 when compared to Set 2 (MD = 1.342, SE = 0.239, $p < 0.001$, d = 1.620) as well as compared to Set 1 (MD = −2.459, SE = 0.239, $p < 0.001$, d = 2.970) and in Set 2 compared to Set 1 (MD = 1.118, SE = 0.239, $p < 0.001$, d = 1.350). No other significant main effect was found (all $p > 0.05$).

Significant IMC was observable at gamma frequencies across all participants and conditions (see Figure 4 for an exemplary visualization of VM-VL IMC).

Log-transformed IMC areas were subsequently analyzed between all conditions. Regarding the right leg, repeated-measures ANOVA revealed a significant main effect for MUSCLE ($F_{(2,22)} = 29.019$, $p < 0.001$, $\eta p^2 = 0.725$, see Figure 5). Post hoc tests showed increased gamma IMC for the monoarticular muscle pair VM-VL compared with RF-VL (MD = 0.379, SE = 0.051, $p < 0.001$, d = 1.052) and RF-VM (MD = 0.254, SE = 0.051, $p = 0.001$, d = 0.707). No other significant main effect or interaction was found (all $p > 0.05$). Similarly, for the left leg, a significant effect for the factor MUSCLE was found ($F_{(2,22)} = 35.617$, $p < 0.001$, $\eta p^2 = 0.764$, see Figure 5). Pairwise post hoc tests again indicated increased gamma IMC for the monoarticular muscle pair VM-VL compared with RF-VL (MD = 0.394, SE = 0.047, $p < 0.001$, d = 1.085) and RF-VM (MD = 0.255, SE = 0.047, $p = 0.001$, d = 0.702). Furthermore, higher gamma IMC was observed for RF-VM compared with RF-VL (MD = 0.139, SE = 0.047, $p = 0.023$, d = 0.382). No other significant main effect or interaction was found (all $p > 0.05$).

4 | DISCUSSION

In this study, we aimed to investigate differences in motor control of biarticular and monoarticular muscles of the knee and hip joints as a function of different load levels during SQ_{BP}. Our results demonstrate significantly higher gamma IMC between VM-VL compared with RF-VL and RF-VM for both legs. Correlation analyses revealed significantly higher correlation coefficients during ascent compared with descent across all analyzed muscle pairs. Load levels only affected MVC-normalized amplitudes, which increased significantly with higher loads. In addition, amplitudes were significantly increased during ascent compared with descent. $Ratio_{VM:VL}$ was significantly higher for Set 1 compared with Set 3 with no influence of load or movement period. Median frequency increased significantly over all sets and was also elevated when comparing RF to VM and VL in the right leg as well as RF to VM in the left leg. All results and their implications are discussed below.

Coordination of multiple muscles requires neural strategies to enable dynamic adaptations of individual muscle functioning during task performance. IMC is assumed to reflect efficient neural control strategies due to the close relationship between IMC and functional binding across muscles.[28] Here, we observed gamma IMC between biarticular and monoarticular knee extensors during SQ_{BP}. This finding is in line with previous research observing gamma IMC between RF, VM, and VL during SQ_{BP},[13–15] as well as related movements such as bilateral[29] and unilateral leg extensions.[16] On a functional level, gamma IMC is associated with sensorimotor integration processes,[30] which in turn are related to task dimensionality and the consequent importance of afferent feedback for accurate task performance.[31] This link between gamma IMC and task dimensionality is supported by previous studies showing tasks that require effortful processing and integration, for example, due to force demands, task novelty, or task complexity to exhibit strong gamma IMC.[15,32]

A central finding in this study is increased gamma IMC between VM-VL compared with RF-VM and RF-VL, indicating stronger functional coupling between the monoarticular VM and VL compared with the biarticular RF. All three muscles work together throughout the full range of motion of SQ_{BP}, although specific functional roles differ. Monoarticular VM and VL contract eccentrically during descent and support the transition between descent and ascent by decelerating the descent period.[33] During most of the ascent period, VM and VL contract concentrically at high recruitment levels, while reducing their output during the last third of the ascent period.[33] Although VM and VL exhibit functional unity, their activity and thus their roles during SQ_{BP} are not identical. For instance, VM

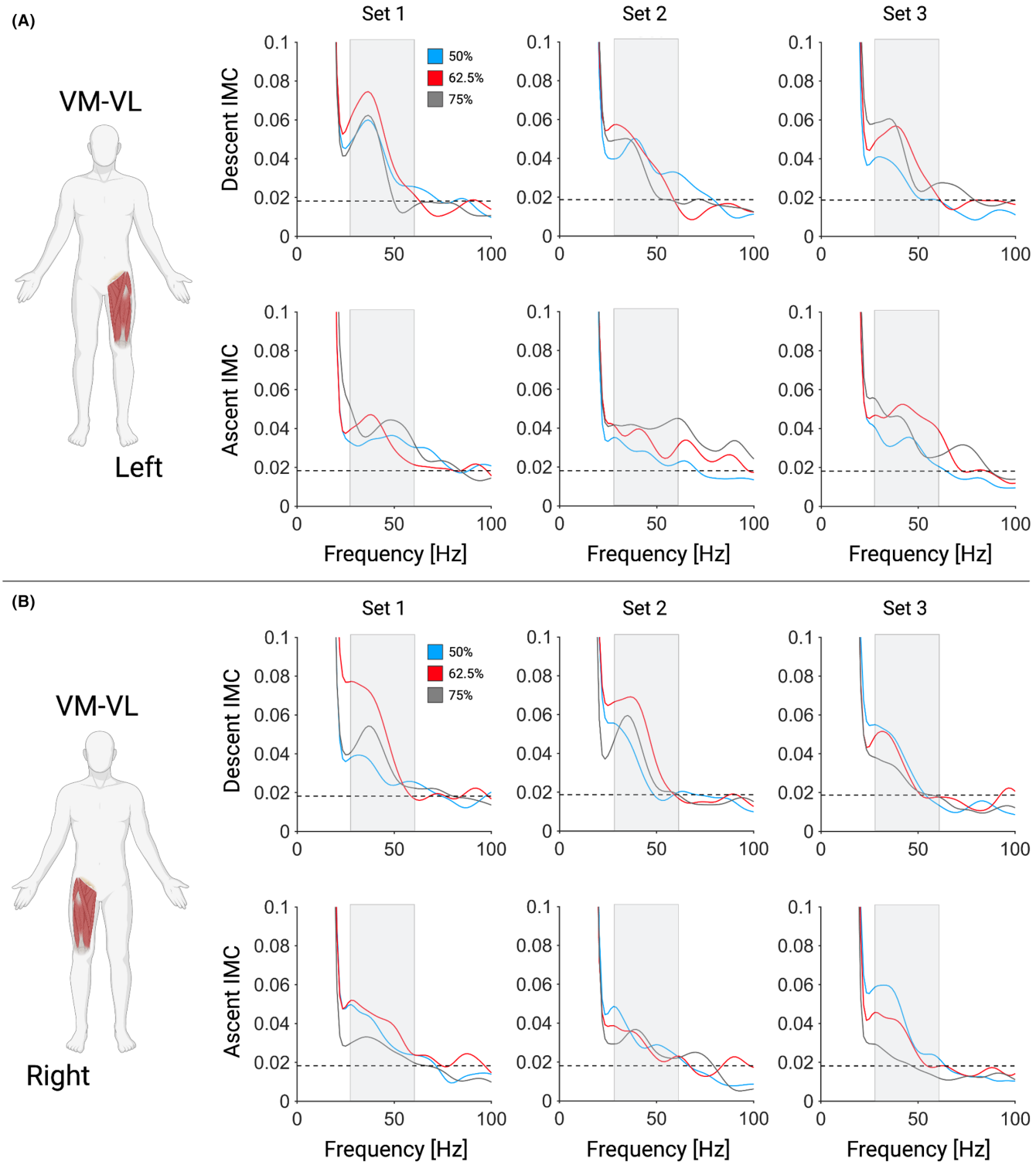

FIGURE 4 Intermuscular Coherence (IMC) between VM and VL. Significant IMC was observable at gamma frequencies (gray rectangle) across all participants and conditions for both the left and right leg. Dashed horizontal lines indicate confidence limits above which coherence was deemed significant. Created with BioRender.com

shows lower variability in activity than VL during SQ_{BP}.[33] Biarticular RF also increases its activity during descent. However, RF contracts concentrically during the final part of the descent, highlighting the additional role of RF as a hip flexor.[34] During the first half of the ascent, RF contracts eccentrically to counteract hip extension, while RF ceases its activity at the end of the ascent period.[33] Consequently, while all three muscles work together to facilitate SQ_{BP}, VM, and VL primarily mediate lateral and medial forces acting on the knee joint, while RF assumes

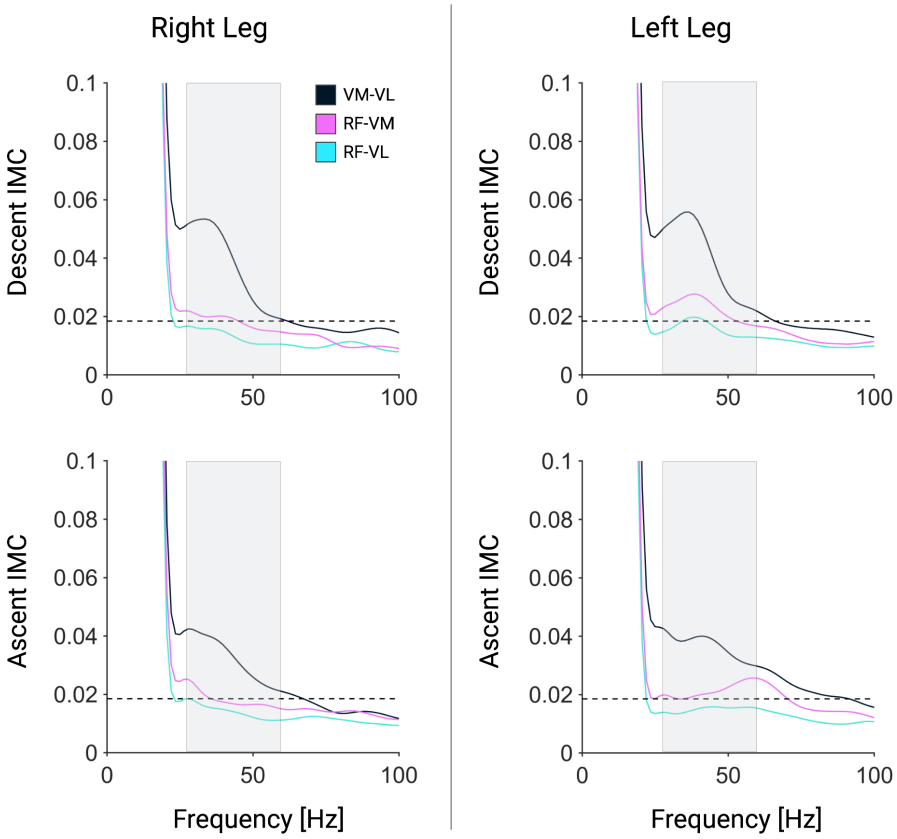

FIGURE 5 Grand averaged intermuscular coherence (IMC) for VM-VL, RF-VM, and RF-VL. Monoarticular muscle pairs (VM-VL) show significantly higher IMC values compared with mono-biarticular muscle pairs (RF-VM and RF-VL). Dashed horizontal lines indicate confidence limits above which coherence was considered significant.

additional functions related to maintaining stability in both the knee and hip joints.[33,34] The observed increase in VM-VL gamma IMC might therefore relate to a more balanced force development enabled by increased synchronous control of VM and VL during SQ_{BP}.[15] Indirect evidence for this is found in patients suffering from anterior knee pain (AKP). AKP, as well as patellofemoral pain, are thought to result from an inadequate balance between lateral and medial forces on the knee joint.[35] Accordingly, IMC is reduced between VM-VL in AKP patients compared with healthy individuals.[36] The close functional coupling between VM-VL is also illustrated by the stability of $Ratio_{VM:VL}$ observed in this study. Here, $Ratio_{VM:VL}$ did not vary significantly between load levels or movement periods and only decreased when comparing the first and third set. We, therefore, propose that higher gamma IMC between VM-VL reflects a more synchronous control mechanism of the central-nervous system that enables balanced force development and transmission in the knee joint during SQ_{BP}.

Notably, and contrary to our hypothesis, gamma IMC was not modulated as a function of external load. Different load levels, and thus, different force levels can influence IMC,[26] with studies demonstrating load-dependent reductions of beta IMC (15–25 Hz) in patients and healthy adults.[17] Although we could not replicate this finding for gamma IMC, our results do not rule out a load-dependent modulation of gamma IMC. This absence might relate to the underlying mechanism of gamma IMC, meaning that a load-dependent modulation of gamma IMC within compound movements may be less apparent in individual muscles and more pronounced when analyzing several muscles collectively. Support for this assumption is provided by Mohr et al. (2015), who demonstrated that more force-intensive, complex variants of the squat, associated with increased muscle activation, showed decreased gamma IMC compared with less intense and less complex variants. Additionally, the high load levels, that is, high intensity, used in this study could explain the lack of a load modulation of gamma IMC. Studies on load-dependent modulation of beta IMC observed that the strongest modulation occurred between low load levels (10% MVC, 20% MVC, and 40% MVC) compared with higher load levels (>50% MVC).[17] A further influencing factor could involve differences in peripheral fatigue between load levels. However, we did not observe any effect of load level on median frequency, making such an influence unlikely. Accordingly, the absence of a load-dependent modulation of gamma IMC may be explained by the fact that the analysis was limited to a few individual muscles of SQ_{BP}, as well as the high load levels. In any case, further research is needed to better understand this relationship.

Apart from the analysis of common input via IMC, examining the similarity between task-related activation patterns of multiple muscles can reveal additional insights into their functioning and underlying mechanisms.[18] Our

findings demonstrate significantly higher correlation coefficients across all muscles in ascent compared with descent. One reason for this may lie in the aforementioned differences in internal joint dynamics between ascent and descent while performing SQ_{BP}. During ascent, VM, VL, and RF contract mostly concentrically compared with descent where the contraction is predominantly eccentric.[33] It is known that motor output is more variable during eccentric contractions compared with concentric contractions.[37] First, EMG amplitudes are mostly lower during eccentric contractions,[38] which is also seen in this study. Furthermore, several studies have demonstrated differential recruitment patterns,[39] differences in excitatory drive and excitability of the motor neuron pool,[40] as well as greater force capacity[40] and more afferent input through muscle spindles[41] during eccentric contractions. Accordingly, higher correlation coefficients during ascent potentially reflect a more uniform concentric contraction pattern during ascent, which leads to greater similarity between muscle actions during this period. Still, more evidence is needed to support these findings. Future studies using, for example, high-density EMG (HD-EMG) should further investigate this interplay to better understand the underlying mechanisms.

4.1 | Limitations

We selected only male participants in this study to prevent variance issues due to possible sex differences in central-nervous structure and function,[42] and differences in activation patterns during squat performance.[43] Therefore, our results can only be applied to an all-male population and cannot be generalized to female populations. For example, as men and women have different quadriceps-angles (Q-angles), it will be interesting to dissect the potential influence of such biomechanical differences between women and men on lower extremity motor control. Future studies should aim to analyze an all-female group in a follow-up study to contextualize the present results and investigate potential differences in motor control mechanisms of mono- and biarticular muscles of the quadriceps femoris as a function of gender.

4.2 | Perspective

With this study, we provide novel evidence that motor control during SQ_{BP} is characterized by differences in common input between biarticular and monoarticular muscles. We additionally demonstrate a higher similarity of muscle activation patterns during ascent compared with descent. Interestingly, both modulations are unaffected by external load levels. In recent years, the focus of physical training, especially in the context of prevention and rehabilitation, has shifted to fundamental exercises such as SQ_{BP}. Here, we studied SQ_{BP} as it is commonly performed in practice, for example, in strength training or rehabilitation programs (3 sets of 10 repetitions with different load levels). The systematic study of fundamental exercises in natural settings holds great potential for promoting the ecological validity of applied research. Future research should aim to validate and extend our observations as insights into the underlying control mechanisms offer the possibility for practical implications to optimize training concepts in elite sports and rehabilitation. Lastly, an interesting question for future studies centers on the role of the hamstrings during SQ_{BP}. Due to the biomechanics of SQ_{BP}, the hamstrings perform opposing functions during a movement cycle, for example, both flexion and extension in the knee joints (*Lombard's paradox*). To provide a more complete description of lower extremity motor control, an extended analysis focusing on further biarticular muscles of the lower extremities such as the hamstrings or gastrocnemius seems to be useful.

AUTHOR CONTRIBUTIONS

TM, RF, JL & RK designed the study. PT acquired the data. TM, PT, MC & RK analyzed the data and wrote the manuscript. RF & JL provided critical revision. All authors interpreted the data, contributed to the manuscript, reviewed it, approved the content of the final version, and agree to be accountable for all aspects of the work. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

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CONFLICT OF INTEREST

The author(s) declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at https://figshare.com/articles/dataset/Data_-_QuadCoord/20222859.

ORCID

Tom Maudrich https://orcid.org/0000-0003-4367-4008
Rouven Kenville https://orcid.org/0000-0001-9093-8470

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