



Generalized modules reflect similar biomechanical subtasks across skipping and running

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ABSTRACT

Biomechanical and metabolic differences between skipping and running suggest the nervous system may require an alternative motor control strategy to execute skipping. Motor control strategies can be compared across gaits by muscle modules based on which muscles are coactivated (module composition) and whether the same module compositions are used across gaits (module generalization). The purposes of this study were to identify and compare the module composition of skipping and running and determine the module generalization present across these two gaits. Six healthy young adults performed 10 s skipping and running trials on a treadmill at 2.5 m/s while electromyography (EMG) was collected from 8 muscles. A non-negative matrix factorization extracted motor modules from the EMG data. Generalization of modules, both at the group and individual level, was determined with correlations of module weights. Participants required 3.7 ± 0.5 (range: 3–4) modules to control skipping and 3.8 ± 0.4 (range: 3–4) modules to control running. Three generalized modules were found across gaits at the group level, and at the individual level each participant had at least one generalized module. The generalized modules contributed to similar biomechanical subtasks across gaits, highlighting similar gross motor task demands. The unique biomechanical demands of the skipping hop resulted in gait-specific control of the tibialis anterior and gluteus medius. Future work is needed to identify the factors that influence the amount of generalization an individual uses across locomotor tasks and whether the degree of generalization impacts the performance of each gait.

1. Introduction

Skipping is a challenging fundamental motor skill which combines two unique motions (a step and a hop) into one gait (McDonnell et al., 2017; Robertson and Halverson, 1984), with elements of both walking (a brief double support phase) and running (a flight phase) (McDonnell et al., 2017). Skipping is often used as a warm-up activity for athletics (Cissik, 2004) and has been used as a transitional rehabilitation activity between walking and running (Davies et al., 2015; Johnson et al., 2005). Yet, there are biomechanical and metabolic differences between skipping and running. Skipping has greater whole-body energy expenditure (McDonnell et al., 2019; Minetti, 1998) and vertical displacement (McDonnell et al., 2017), but lower muscle force impulses (Roelker et al., 2022) and peak ground reaction forces (McDonnell et al., 2017)

compared to running. Peak joint torques also differ across running and skipping; the skipping hop has the highest hip torque, running has the highest knee torque, and the skipping step has the highest ankle torque (McDonnell et al., 2017). Additionally, joint contact forces differ between gaits, with running experiencing greater knee joint contact forces but lower hip and ankle contact forces (Roelker et al., 2022). These differences between running and skipping at the muscle, joint, and whole-body levels are indicative of different biomechanical demands between the two gaits. Furthermore, as the last fundamental locomotion pattern to develop in children, skipping emerges later than running and only after at least basic hopping proficiency has been achieved (Robertson and Halverson, 1984). Thus, while all gaits require foundational biomechanical subtasks such as body support and forward propulsion, the differences in biomechanical demands between these two

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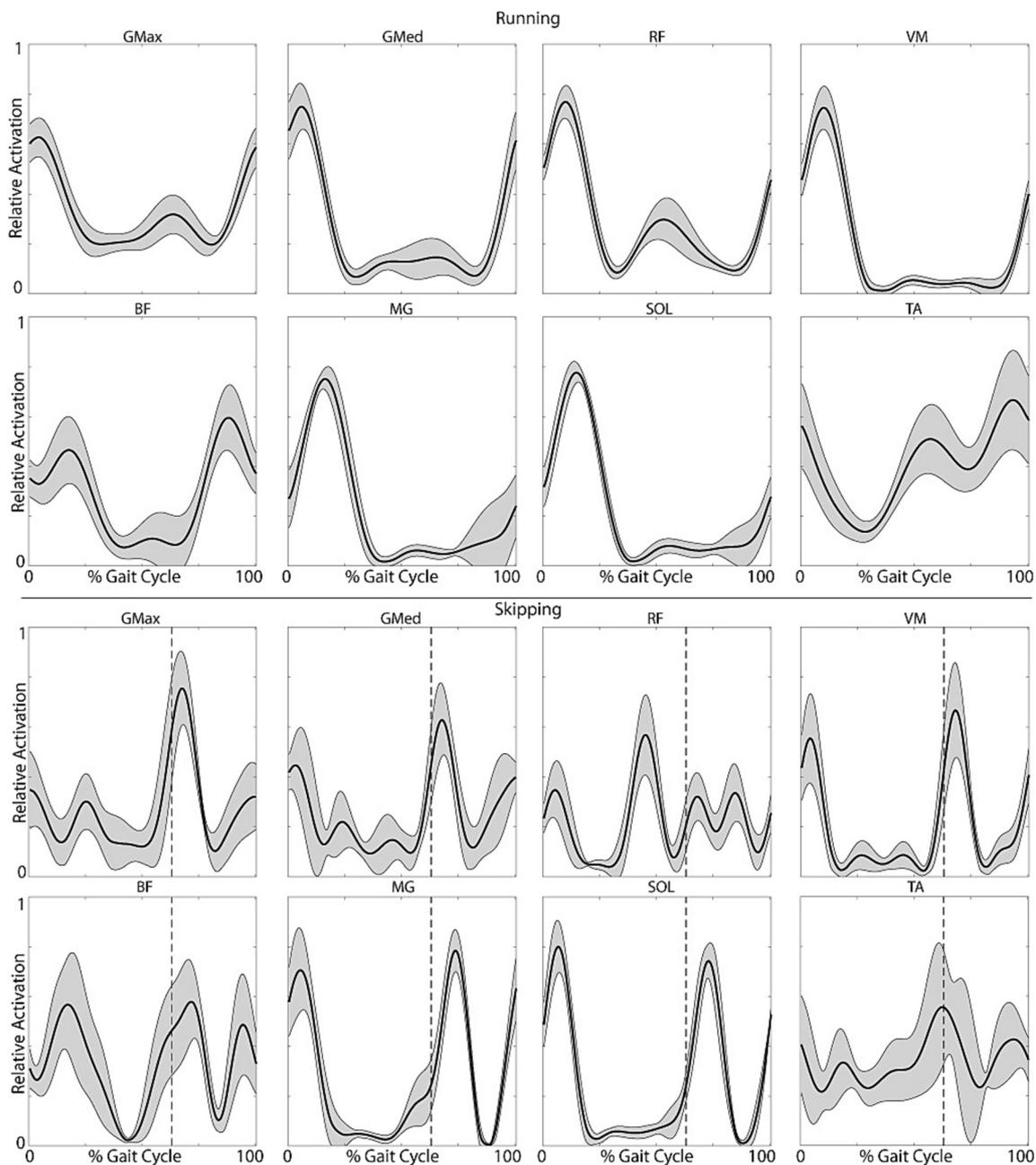


Fig. 1. Normalized EMG across participants for running (top) and skipping (bottom). Solid black lines represent the average across participants and the shaded grey areas represent \pm one standard deviation. Vertical dashed lines indicate the transition between the step and hop in skipping.

gaits suggest the neural control strategies used to execute running and skipping may feature aspects unique to each gait. For example, running and skipping share locomotor subtasks, including hip and knee extension, ankle plantarflexion, and achieving leg swing and toe clearance. On the other hand, while skipping involves rapid knee flexion and ankle dorsiflexion on the contralateral limb during the hop, running may have increased mediolateral stability requirements due to the absence of double limb support phases. These task-specific biomechanics may require unique control strategies.

An individual's motor control strategy can be quantified by muscle modules (e.g. Allen et al., 2017; Clark et al., 2010; Sawers et al., 2015), also referred to as muscle synergies. The theory of modular control posits, rather than the nervous system controlling each muscle individually, groups of muscles (i.e., modules), are activated together (Allen et al., 2017; Clark et al., 2010). The modular control strategy of a gait can be described by the complexity (the number of modules used to

execute the task), composition (which muscles are grouped together in each module), and activation timing (when each module is active during the motion) (Ting and Macpherson, 2005). A greater number of modules (i.e., greater complexity) is thought to indicate a greater ability to adapt to changing locomotor task demands (Routson et al., 2014), while reduced complexity is thought to indicate a reduced ability to fine-tune control and has been associated with poorer task performance (Clark et al., 2010) and reduced capacity to perform complex tasks well (Allen and Franz, 2018).

The use of identical modules across multiple locomotor tasks, known as module generalization, is indicative of an individual's coordination and locomotor function, with greater generalization associated with better functional performance (Allen et al., 2017, 2019; Sawers et al., 2015). Module generalization has been explored across various modes of bipedal locomotion including walking, running, unilateral skipping (henceforth referred to as galloping), and bilateral skipping (henceforth

referred to as skipping). Previous work determined that galloping, walking, and running can all be controlled by 4 modules, where three modules were shared across gaits and the fourth was specific to the given locomotor pattern (Pequera et al., 2021). In another study, 5 central activation patterns, which can be thought of as the module activation patterns, controlled 32 muscles during skipping, walking, and running (Ivanenko et al., 2008). Although the activation patterns differed between gaits, the skipping activation patterns were a near super-position of the walking and running activation patterns (Ivanenko et al., 2008), reflective of the combination of movements from both gaits. However, muscle composition of these central activation patterns was not compared across gaits; therefore, it is unclear if different muscles are coactivated by the nervous system during skipping compared to running. Whether it is the module activation timing or the module compositions which change in response to changes in task demands is a matter of debate, though it has been proposed that it is likely a combination of these two factors (module activation timing and composition) that respond to changing task demands (Lacquaniti et al., 2012). Thus, investigation of both activation patterns and module compositions is important to fully understand how motor control changes across gaits.

While the modular control of walking, galloping, skipping, and running have been explored, the specific composition of each module associated with individual module activation patterns have yet to be identified for skipping. Identifying the composition of the modules used to control skipping will build on these previous investigations of modular control complexity and activation patterns to further determine how the nervous system coordinates skipping compared to running and what generalization may exist in the control of these two gaits. Therefore, the purposes of this study were to identify and compare the module composition of skipping and running and determine the module generalization and gait specific modules present across these two gaits. Based on previous literature, we hypothesized similarities in the composition of modules for skipping and running would result in generalized modules, but the differences in task demands would require gait-specific modules. Specifically, running and skipping share locomotor subtasks, thus we expected generalized modules to reflect this overlap in gross biomechanics. In addition, given the unique aspects of each gait, such as the hop in skipping and lack of a double limb support phase in running, we hypothesized at least one gait-specific module in each gait.

2. Methods

Six healthy young adults (3 female, 21.7 ± 1.3 y, 1.7 ± 0.1 m, 69.9 ± 12.4 kg) participated in the study. Informed consent was obtained from each participant prior to participation. All procedures were approved by the East Carolina University Institutional Review Board.

Participants performed 10 s skipping and running trials at 2.5 m/s on a dual-belt treadmill (Berotec USA, Worthington, OH). Participants were provided time to familiarize themselves with both skipping and running at the test speed on the treadmill prior to the data collection. Trials were collected in a randomized order with one minute rest between trials. Electromyography (EMG) data were collected at 1000 Hz from 8 muscles on the right leg: gluteus maximus (GMax), gluteus medius (GMed), rectus femoris (RF), vastus medialis (VM), biceps femoris (BF), medial gastrocnemius (MG), tibialis anterior (TA), and soleus (SOL). Participants were also asked to report their comfort level (0: completely comfortable, to 5: completely uncomfortable) performing each gait on the treadmill.

The raw EMG was demeaned, filtered with a bandpass (30–300 Hz) 4th order zero-lag Butterworth filter, rectified, and filtered with a low-pass (4 Hz) 4th order zero-lag Butterworth filter to create linear envelopes. The EMG was then normalized to the maximum value of the linear envelope for each trial type (Fig. 1). A run cycle was defined as right heel strike to right heel strike, and a skipping cycle was defined as beginning with the right heel strike at the start of the right step to heel strike at the end of the subsequent right hop. Cycles from each running and skipping

trial were time-normalized to 201 points, representing 0–100% of the gait cycle. For each participant and gait, the normalized EMG from all cycles (running: mean 12.7 ± 0.7 cycles, minimum 12 cycles; skipping: mean 7.2 ± 0.7 cycles, minimum 6 cycles) were concatenated into an $m \times t$ matrix (EMG_0), where m is the number of muscles ($m = 8$) and t is the number of time points ($201 \times \#$ of cycles). The concatenated matrices were normalized to unit variance (Torres-Oviedo and Ting, 2010) to ensure the variability of a single muscle does not unduly influence the factorization algorithm.

Non-negative matrix factorization (NNMF) (Lee and Seung, 1999) was used to identify modules from EMG_0 for each participant and gait. The NNMF algorithm extracts k modules ($k = 1-8$) defined by 2 matrices, an $m \times k$ matrix (W) representing the weights of each muscle within each module and a $k \times t$ matrix (C) representing the activation coefficient of each module at each time point. The product of W and C produces a reconstructed $m \times t$ matrix (EMG_r) such that the error between EMG_r and EMG_0 is minimized. First, a 500-sample bootstrap method (Roelker et al., 2021) was used to determine 95% confidence intervals (CIs) for the variability accounted for (VAF), calculated as: $VAF = 1 - ((EMG_0 - EMG_r)^2) / (EMG_0^2)$ (Clark et al., 2010). The VAF was calculated for each of the 500 samples for each individual muscle (mVAF) and for the total VAF across all muscles (tVAF). The number of modules required to sufficiently reconstruct EMG_0 was determined when the lower bound of the 95% CI for tVAF was greater than 90% and either the minimum lower bound of the 95% CI for mVAF was greater than 90% or the addition of one module increased minimum mVAF by less than 5% (Clark et al., 2010). After the number of required modules was determined for a given participant and gait, NNMF was repeated for the required number of modules with EMG_0 as the input into the NNMF procedure to extract the activation patterns for each module. In addition, since the NNMF algorithm does not return W and C in the same order for every sample, module compositions from the NNMF performed on EMG_0 were used as seeds for a k-means clustering approach to sort the module compositions from the bootstrapped samples. Once the bootstrapped modules were sorted, for each sample, each module's muscle weights were normalized to the maximum weight within a module, resulting in a range of 0–1 for the muscle weights. Similarly, the module activation patterns were normalized to the maximum activation within a module, resulting in a range of 0–1 for the module activations. From the bootstrapped samples, a 95% CI was created for the muscle weights within each module.

Within a gait, similar modules across subjects were identified using hierarchical cluster analysis (Allen and Franz, 2018) of the module weights (Ward linkage; Minkowski difference, $p = 2$). The number of clusters for each gait was determined as the minimum number resulting in no cluster containing more than one module from the same participant. Modules generalized across gaits were identified by Pearson's correlation coefficients of the module weights (composition) with $r \geq 0.707$ (Hayes et al., 2014). With $m = 8$ muscles and 6 degrees of freedom ($df = m-2 = 6$), a two-tailed test with $\alpha = 0.05$ has a critical r value of 0.707. The correlation of module weights was assessed both with the average module weights across all participants with that module (group-level generalization) and between all modules within each individual participant (within-subject generalization). A Chi-squared test was used to compare the number of modules between gaits and a paired t -test was used to compare the tVAF between gaits at each value of k . For all statistical tests, α was set *a priori* at 0.05.

3. Results

All subjects reported being comfortable running on the treadmill (mean: 0.17 ± 0.37 ; range: 0–1) and were equally or less comfortable (but not uncomfortable) skipping on the treadmill (mean: 0.83 ± 0.69 ; range: 0–2). Participants used either 3 or 4 (mean: 3.7 ± 0.5) modules to control skipping and either 3 or 4 (mean: 3.8 ± 0.4) modules to control running. Although the number of modules required did not differ

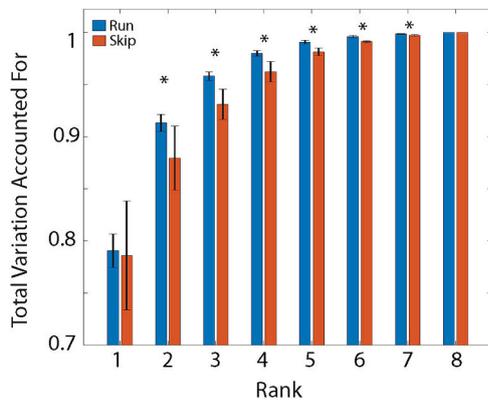


Fig. 2. The total variability accounted for at each rank (i.e., number of modules extracted by NNMF) for running (blue) and skipping (red). * indicates a significant difference between gaits. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Module compositions.

Module Abbreviation	Primary Muscles	Gait(s) present
GluteQuad	GMax, Gmed, VM, RF*	Skipping, Running
PF	MG, SOL	Skipping, Running
BFTA	BF, TA	Skipping, Running
RFTA	RF, TA	Skipping
TA	TA	Running
GMedQuad	GMed, RF, VM	Running

* The RF was highly weighted in the GluteQuad module in running, but less so in skipping

between gaits ($p = 0.97$), the tVAF for running was greater than the tVAF for skipping when 2 through 7 modules were extracted (Fig. 2; all $p < 0.05$).

3.1. Module compositions for skipping and running

In skipping, all modules could be sorted into one of four separate clusters (Table 1, Fig. 3). Each unique module was observed in 4–6 participants. For this study, modules have been named based on the primary muscles activated in the module. The GluteQuad module was observed in 4 participants and characterized by GMax, GMed, and VM activity during the stance phase of the hop. The PF module was observed in all 6 participants and characterized by MG and SOL activity during the stance phase of the step and hop. The BFTA module was observed in all 6 participants and characterized by BF and TA activity during the stance-swing transition of the step and the hop, as well as the swing phase of the hop. The RFTA module was observed in all 6 participants and was characterized by RF and TA activity during the swing phase of the step and the stance-swing transition of the hop.

In running, modules were sorted into five clusters (Table 1, Fig. 4). The GluteQuad module was observed in all 6 participants and characterized by GMax, GMed, VM, and some RF activity primarily during early stance and late swing, with moderate activation during early swing. The PF module was observed in 5 participants and characterized by MG and SOL activity during stance. The BFTA module was observed in all 6 participants and characterized by BF and TA activity during late swing. The TA module was observed in 3 participants and characterized by TA activity in early stance and throughout swing. The GMedQuad module was observed in 3 participants and characterized by GMed, RF, and VM activity during stance and late swing.

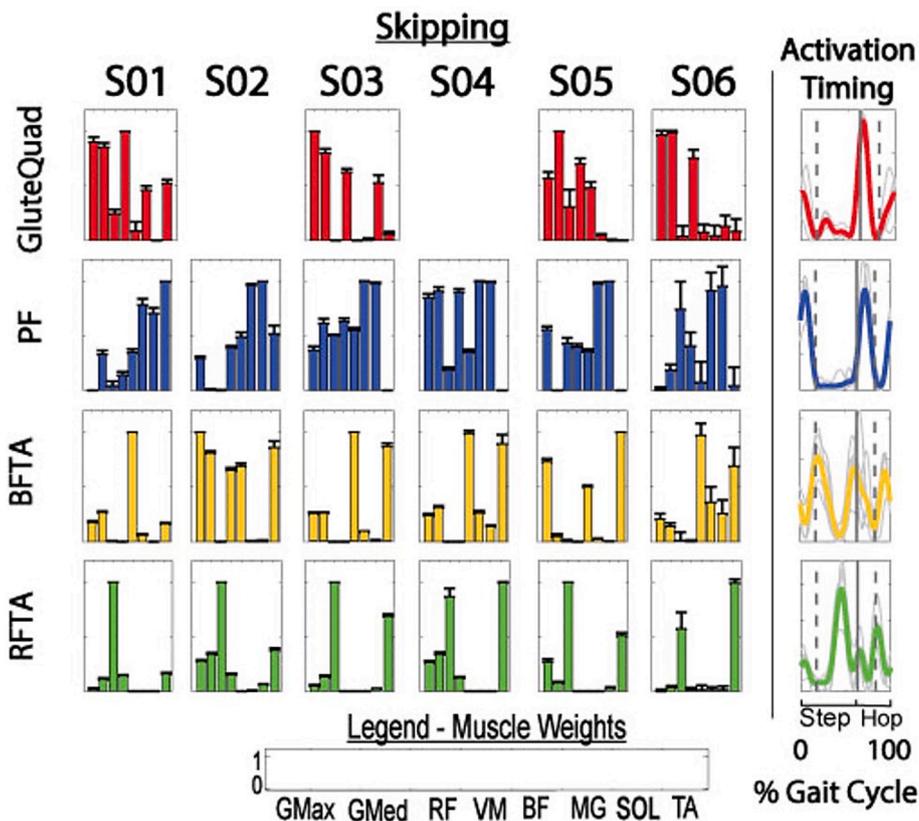


Fig. 3. Skipping module weights and activation patterns. Muscle weights (left) for each participant (column), organized by cluster (row). Bar heights indicate mean muscle weight and error bars represent the standard deviation across bootstrap samples. For each module, the mean (bold, colored line) and individual (grey lines) module activation patterns are shown (right). Vertical dashed and solid black lines indicate the stance/swing transition and step/hop transition, respectively.

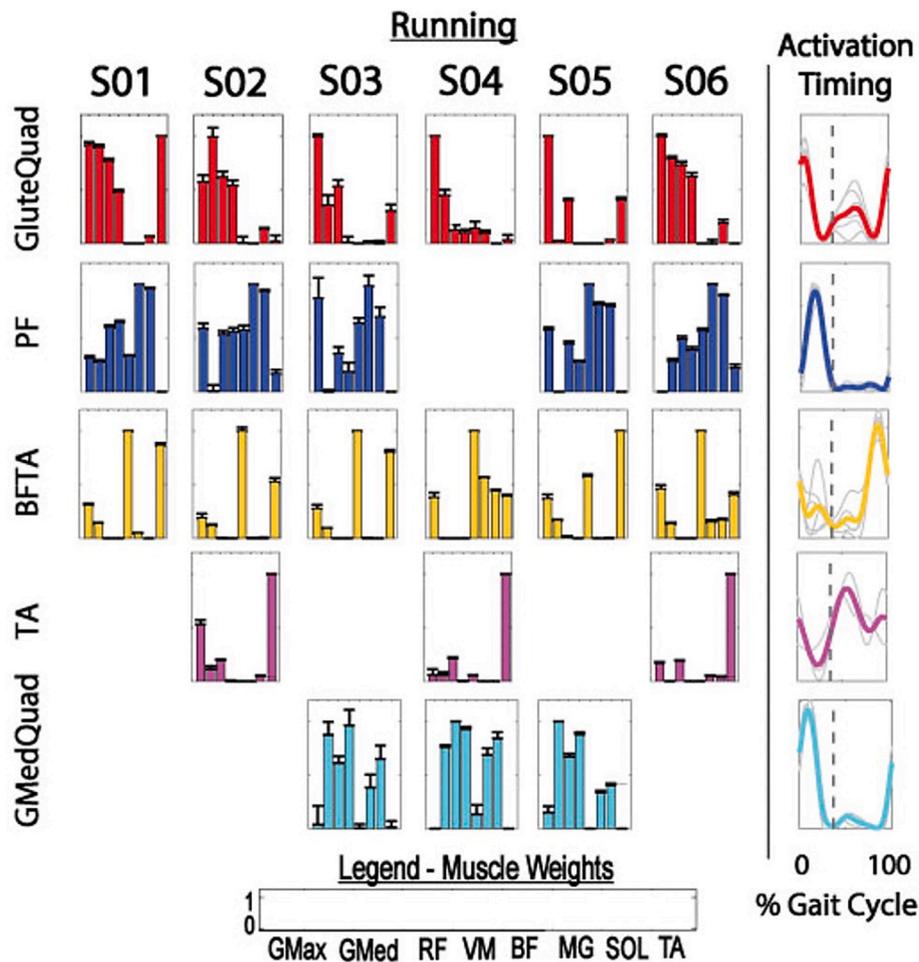


Fig. 4. Running module weights and activation patterns. Muscle weights (left) for each participant (column), organized by cluster (row). Bar heights indicate mean muscle weight and error bars represent the standard deviation across bootstrap samples. For each module, the mean (bold, colored line) and individual (grey lines) module activation patterns are shown (right). Vertical dashed black lines indicate the stance/swing transition.

3.2. Module generalization across skipping and running

Three generalized modules were found across gaits at the group level: GluteQuad ($r = 0.714$), PF ($r = 0.830$), and BFTA ($r = 0.967$; Fig. 5). When generalization was assessed at the individual level (within a participant), each participant had at least one generalized module (mean: 1.8 ± 1.1 ; range: 1–4) across gaits. The generalized modules observed within participants included the GluteQuad in one participant (S06, $r = 0.755$), PF in three participants (S02, S05, S06; r range: 0.750–0.802), BFTA in five participants (S01, S03, S04, S05, S06; r range: 0.713–0.987), and the running TA module was correlated with the skipping RFTA module in two participants (S04, S06; r range: 0.806–0.917).

4. Discussion

The purposes of this study were to 1) identify and compare the module composition of skipping and running and 2) determine the generalization of modular control between these two gaits. We hypothesized running and skipping would share generalized modules reflecting the control of biomechanical subtasks shared between gaits. Supporting this hypothesis, all participants exhibited some degree of generalization. We further hypothesized participants would use gait-specific modules, reflecting gait-specific tasks. Supporting this hypothesis, all but one participant had at least one gait-specific module. The shared control strategies between these two gaits supports the idea of a common motor control foundation for cyclic locomotor tasks.

4.1. Module compositions in skipping and running

The control of skipping and running required 3 or 4 modules for the participants in this study, which is consistent with what has been reported for walking (Allen and Franz, 2018) and running (Oliveira et al., 2016; Pequera et al., 2021; Santuz et al., 2022) and suggests skipping can be similarly executed with a relatively small set of modules. Previous work comparing skipping and running control found all participants to require the same number of central activation patterns (Ivanenko et al., 2008). The present study expanded on this earlier work by comparing modules across participants based on module composition to determine which muscles are coactivated and found that each participant's running and skipping modules could be grouped into one of four components based on the module composition: 1) hip and knee extensors (GluteQuad, GMedQuad), 2) plantarflexors (PF), 3) knee and ankle flexors (BFTA), and 4) hip and/or ankle flexors (RFTA, TA).

4.2. Module generalization

By comparing module compositions across gaits, we identified three generalized modules with similar compositions which had similar relative activation timing (e.g., early stance) across the two gaits, building on previous work that found skipping control patterns to be a combination of walking and running activation patterns (Ivanenko et al., 2008). To gain further insight into the module generalization, we performed a segmental power analysis similar to our previous work (Roelker et al., 2025). Detailed results can be found in the Appendix.

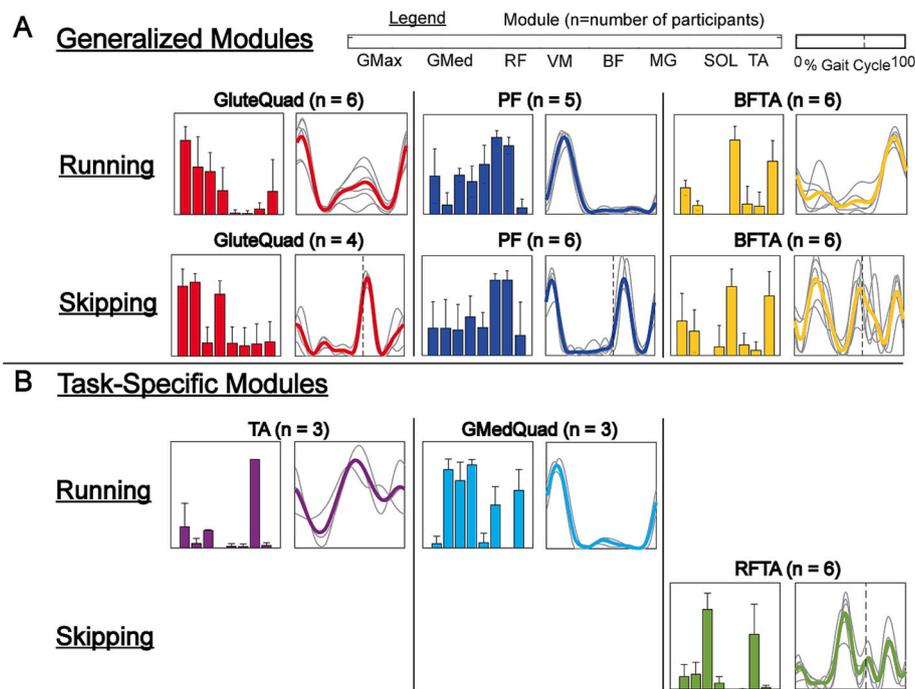


Fig. 5. Generalized modules (A) between skipping and running as determined with correlations between group averages of module weights. Task-specific modules (B) for running and skipping. For each module, muscle weights (left) and activation (right) are shown for running (top) and skipping (bottom). Bar heights indicate mean muscle weight and error bars represent the standard deviation across participants. For each module, the mean (bold colored line) and individual (grey lines) module activation patterns are shown. Vertical dashed line in skipping activation plots denotes the step/hop transition. The count of participants with each module is listed above the given module ($n = \text{count}$).

Together, these findings suggest that these generalized modules control similar biomechanical subtasks common to the execution of both running and skipping. For both gaits, GluteQuad contributed to braking and vertical support during stance, PF provided braking and vertical support during stance, and BFTA controlled leg swing during swing phase. Moreover, each participant exhibited at least one generalized module across gaits. However, the amount of generalization varied across participants, with some participants only exhibiting one generalized module, while one subject (S06) executed both gaits with all four modules generalized between running and skipping. The amount of generalization across these two movements in each participant may be reflective of the automaticity of running and skipping for each individual (Allen et al., 2019).

4.3. Differences in modular control between skipping and running

Similar to previous studies (Ivanenko et al., 2008; Pequera et al., 2021), there was no difference in the number of modules required to control skipping compared to running. However, running had higher tVAF than skipping when 2 or more modules were used, which may indicate the control of skipping requires some additional complexity than that of running (Roelker et al., 2021), but not so much that additional modules are required. Moreover, aligning with our hypothesis, gait-specific modules were observed. These task-specific modules centered around the control of the tibialis anterior which, in addition to being coactivated with the biceps femoris in all participants in both gaits, experienced gait-specific control. In skipping, all participants exhibited a module with coactivation of the hip and ankle flexors (RFTA). The presence of the RFTA module across all participants in skipping reflects the unique biomechanical action of the hip and ankle flexors to control the ipsilateral leg drive during the contralateral hop of the skipping gait (~30–50% of the skipping cycle, Fig. 3). Alternatively, in running where there is no hop, the TA was controlled independently or coactivated in the GluteQuad module. Running also had a separate GMedQuad module in 3 participants. This separate GluteMed control

may be related to the greater need during running than skipping to counteract the gravitational moment about the ipsilateral leg during stance (Neptune and McGowan, 2016).

4.4. Limitations

An individual's familiarity with the task or their comfort level may play a role in the variability found in both the unique module compositions and the amount of generalization across gaits. However, all subjects reported being comfortable running on the treadmill and were equally or less comfortable (but not uncomfortable) skipping on the treadmill. Additionally, the performance of these gaits on the treadmill may have inherently constrained movement in comparison to overground gait; however, previous work comparing the modular complexity of overground versus treadmill running found no differences (Mileti et al., 2020; Oliveira et al., 2016). The sample size is small and all participants were healthy young adults. While this may limit the applicability of these results to other populations, the module compositions identified for running in this study are consistent with prior work (Oliveira et al., 2016; Santuz et al., 2018, 2022), providing confidence in our results. Furthermore, the literature suggests that gaits that have large differences in kinematics, like running and skipping, can be compared with smaller samples such as in the comparison of walking and running in Biewener et al. (2004). In addition, this study evaluated modular control at a single fixed speed in both gaits, which does not account for the potential effect of speed on modular control. However, modules have been shown to be of similar composition across running speeds (Ivanenko et al., 2004). Overall, this study provides initial information to better understand module generalization across gaits and the relationship between neuromuscular coordination and biomechanical subtasks across gaits.

5. Conclusion

This study identified generalized control between running and

skipping, which supports the idea of a common foundation for cyclic locomotor tasks. While we found variation in module composition across participants, all modules could be grouped into four primary components for both gaits, including generalized modules executing independent plantarflexor control, coupled hip and knee extensor control, and coupled knee and ankle flexor control. These modules were associated with similar biomechanical subtasks between gaits, which suggests similar gross motor task demands in running and skipping, while modules unique to each gait provide control to gait-specific biomechanical subtasks. The current findings support the use of skipping as a training activity for running, as the generalization between the two gaits suggests skipping may reinforce neuromuscular control patterns for the shared biomechanical subtasks seen in running. However, the differences between the gaits suggest the need to also train running-specific tasks (e.g., gluteus medius control) separately. Furthermore, the difference in the amount of generalization between gaits observed across our participants suggests there is a need to identify the factors that influence the amount of generalization an individual uses across locomotor tasks and whether the degree of generalization impacts the performance of each gait.

CRedit authorship contribution statement

Abigail K. Salvatore: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis. **John D. Willson:** Writing – review & editing, Methodology, Data curation. **Paul DeVita:** Writing – review & editing, Methodology, Data curation. **Richard R. Neptune:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Sarah A. Roelker:** Writing – review & editing, Visualization, Validation, Supervision, Software, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jbiomech.2026.113197>.

References

- Allen, J.L., Franz, J.R., 2018. The motor repertoire of older adult fallers may constrain their response to balance perturbations. *J. Neurophysiol.* 120 (5), 2368–2378. <https://doi.org/10.1152/jn.00302.2018>.
- Allen, J.L., Kesar, T.M., Ting, L.H., 2019. Motor module generalization across balance and walking is impaired after stroke. *J. Neurophysiol.* 122 (1), 277–289. <https://doi.org/10.1152/jn.00561.2018>.
- Allen, J.L., McKay, J.L., Sawers, A., Hackney, M.E., Ting, L.H., 2017. Increased neuromuscular consistency in gait and balance after partnered, dance-based rehabilitation in Parkinson's disease. *J. Neurophysiol.* 118 (1), 363–373. <https://doi.org/10.1152/jn.00813.2016>.
- Biewener, A.A., Farley, C.T., Roberts, T.J., Temaner, M., 2004. Muscle mechanical advantage of human walking and running: Implications for energy cost. *J. Appl. Physiol.* 97 (6), 2266–2274. <https://doi.org/10.1152/jappphysiol.00003.2004>.
- Cissik, J.M., 2004. Means and methods of speed training, Part I. *Strength Condition.* J. 26 (4), 24–29. <https://doi.org/10.1519/00126548-200408000-00002>.
- Clark, D.J., Ting, L.H., Zajac, F.E., Neptune, R.R., Kautz, S.A., 2010. Merging of healthy motor modules predicts reduced locomotor performance and muscle coordination

- complexity post-stroke. *J. Neurophysiol.* 103 (2), 844–857. <https://doi.org/10.1152/jn.00825.2009>.
- Davies, G., Riemann, B.L., Manske, R., 2015. Current concepts of plyometric exercise. *Int. J. Sports Phys. Ther.* 10 (6).
- Hayes, H.B., Chvatal, S.A., French, M.A., Ting, L.H., Trumbower, R.D., 2014. Neuromuscular constraints on muscle coordination during overground walking in persons with chronic incomplete spinal cord injury. *Clin. Neurophysiol.* 125 (10), 2024–2035. <https://doi.org/10.1016/j.clinph.2014.02.001>.
- Ivanenko, Y.P., Cappellini, G., Poppele, R.E., Lacquaniti, F., 2008. Spatiotemporal organization of motoneuron activity in the human spinal cord during different gaits and gait transitions. *Eur. J. Neurosci.* 27 (12), 3351–3368. <https://doi.org/10.1111/j.1460-9568.2008.06289.x>.
- Ivanenko, Y.P., Poppele, R.E., Lacquaniti, F., 2004. Five basic muscle activation patterns account for muscle activity during human locomotion: basic muscle activation patterns. *J. Physiol.* 556 (1), 267–282. <https://doi.org/10.1113/jphysiol.2003.057174>.
- Johnson, S.T., Golden, G.M., Mercer, J.A., Mangus, B.C., Hoffman, M.A., 2005. Ground-reaction forces during form skipping and running. *J. Sport Rehabil.* 14 (4), 338–345. <https://doi.org/10.1123/jsr.14.4.338>.
- Lacquaniti, F., Ivanenko, Y.P., Zago, M., 2012. Patterned control of human locomotion: control of human locomotion. *J. Physiol.* 590 (10), 2189–2199. <https://doi.org/10.1113/jphysiol.2011.215137>.
- Lee, D.D., Seung, H.S., 1999. Learning the parts of objects by non-negative matrix factorization. *Nature* 401 (6755), 788–791. <https://doi.org/10.1038/44565>.
- McDonnell, J., Willson, J.D., Zwetsloot, K.A., Houmar, J., DeVita, P., 2017. Gait biomechanics of skipping are substantially different than those of running. *J. Biomech.* 64, 180–185. <https://doi.org/10.1016/j.jbiomech.2017.09.039>.
- McDonnell, J., Zwetsloot, K.A., Houmar, J., DeVita, P., 2019. Skipping has lower knee joint contact forces and higher metabolic cost compared to running. *Gait Posture* 70, 414–419. <https://doi.org/10.1016/j.gaitpost.2019.03.028>.
- Mileti, I., Serra, A., Wolf, N., Munoz-Martel, V., Ekizos, A., Palermo, E., Arampatzis, A., Santuz, A., 2020. Muscle activation patterns are more constrained and regular in treadmill than in overground human locomotion. *Front. Bioeng. Biotechnol.* 8, 581619. <https://doi.org/10.3389/fbioe.2020.581619>.
- Minetti, A.E., 1998. The biomechanics of skipping gaits: a third locomotion paradigm? *Proc. R. Soc. Lond. B* 265 (1402), 1227–1233. <https://doi.org/10.1098/rspb.1998.0424>.
- Neptune, R.R., McGowan, C.P., 2016. Muscle contributions to frontal plane angular momentum during walking. *J. Biomech.* 49 (13), 2975–2981. <https://doi.org/10.1016/j.jbiomech.2016.07.016>.
- Oliveira, A.S., Gizzi, L., Ketabi, S., Farina, D., Kersting, U.G., 2016. Modular control of treadmill vs overground running. *PLoS One* 11 (4), e0153307. <https://doi.org/10.1371/journal.pone.0153307>.
- Pequera, G., Ramírez Paulino, I., Biancardi, C.M., 2021. Common motor patterns of asymmetrical and symmetrical bipedal gaits. *PeerJ* 9, e11970. <https://doi.org/10.7717/peerj.11970>.
- Robertson, M.A., Halverson, L.E., 1984. *Developing children—their changing movement: a guide for teachers.* Lea & Febiger.
- Roelker, S.A., DeVita, P., Willson, J.D., Neptune, R.R., 2022. Differences in muscle demand and joint contact forces between running and skipping. *J. Appl. Biomech.* 38 (6), 382–390. <https://doi.org/10.1123/jab.2022-0011>.
- Roelker, S.A., Koehn, R.R., Caruthers, E.J., Schmitt, L.C., Chaudhari, A.M.W., Siston, R. A., 2021. Effects of age and knee osteoarthritis on the modular control of walking: a pilot study. *PLoS One.* <https://doi.org/10.1101/2020.05.22.20110536>.
- Roelker, S.A., Willson, J.D., DeVita, P., Neptune, R.R., 2025. Muscle contributions to propelling the body upward differ between skipping and running. *J. Biomech.* 181, 112545. <https://doi.org/10.1016/j.jbiomech.2025.112545>.
- Routson, R.L., Kautz, S.A., Neptune, R.R., 2014. Modular organization across changing task demands in healthy and poststroke gait. *Physiol. Rep.* 2 (6), e12055. <https://doi.org/10.14814/phy2.12055>.
- Santuz, A., Ekizos, A., Janshen, L., Mersmann, F., Bohm, S., Baltzopoulos, V., Arampatzis, A., 2018. Modular control of human movement during running: an open access data set. *Front. Physiol.* 9, 1509. <https://doi.org/10.3389/fphys.2018.01509>.
- Santuz, A., Janshen, L., Brüll, L., Munoz-Martel, V., Taborri, J., Rossi, S., Arampatzis, A., 2022. Sex-specific tuning of modular muscle activation patterns for locomotion in young and older adults. *PLoS One* 17 (6), e0269417. <https://doi.org/10.1371/journal.pone.0269417>.
- Sawers, A., Allen, J.L., Ting, L.H., 2015. Long-term training modifies the modular structure and organization of walking balance control. *J. Neurophysiol.* 114 (6), 3359–3373. <https://doi.org/10.1152/jn.00758.2015>.
- Ting, L.H., Macpherson, J.M., 2005. A limited set of muscle synergies for force control during a postural task. *J. Neurophysiol.* 93 (1), 609–613. <https://doi.org/10.1152/jn.00681.2004>.
- Torres-Oviedo, G., Ting, L.H., 2010. Subject-specific muscle synergies in human balance control are consistent across different biomechanical contexts. *J. Neurophysiol.* 103 (6), 3084–3098. <https://doi.org/10.1152/jn.00960.2009>.