



Muscle contributions to propelling the body upward differ between skipping and running

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ABSTRACT

Skipping represents a training alternative to running due to its lower knee contact forces and higher whole-body metabolic cost. The increased metabolic cost of skipping is associated with a higher vertical center-of-mass (COM) displacement during the support and flight phases of the skipping hop compared to running. However, skipping has lower muscle force impulses than running. Therefore, the study purpose was to compare the flow of mechanical power between body segments during skipping and running to determine the mechanisms enabling higher vertical displacement in skipping despite the lower vertical impulse. Running and skipping cycles were simulated in OpenSim for 5 adults (22.4 ± 2.2 y) using motion capture data collected at 2.5 m/s on an instrumented dual-belt treadmill. A segmental power analysis quantified muscle contributions to vertical body segment mechanical power, which were integrated over the stance phase of running (Run) and the hop (Skip 1) and step (Skip 2) of skipping to calculate mechanical work. Higher vertical work was done by the gluteus maximus, vasti, and soleus in Skip 1, primarily through power generation to the trunk, compared to power absorption in Run and Skip 2. Thus, despite lower muscle force impulses in Skip 1, muscles generate power through concentric contractions, leading to greater metabolic cost than in running. These muscle force impulses contribute to propelling the COM upward in Skip 1 (rather than decelerating downward COM motion in Run and Skip 2), which raises the COM and contributes to the greater COM displacement in skipping compared to running.

1. Introduction

Skipping, a gait that combines a step and a hop executed on one limb followed by a step and a hop on the contralateral limb, is a common warm-up and training activity in athletics to increase speed (Cissik, 2004) and has been used as a transitional rehabilitation activity between walking and running (Davies et al., 2015; Johnson et al., 2005; Sáez de Villarreal et al., 2015). A highly aerobic activity, skipping has a greater metabolic cost than running (McDonnell et al., 2019; Minetti, 1998), yet has the benefit of lower peak vertical ground reaction forces (GRFs) (Johnson et al., 2005; McDonnell et al., 2017) and knee contact forces (McDonnell et al., 2019; Roelker et al., 2022) compared to running. The increased metabolic cost of skipping was associated with a higher vertical displacement of the body's center-of-mass (COM) while the lower vertical GRFs were associated with the shorter step lengths of the

individual skipping steps (McDonnell et al., 2019). Higher vertical displacement of the COM is strongly correlated with higher vertical GRF impulse (Kirby et al., 2011), which can be achieved by increasing the GRF magnitude, duration, or both (Sánchez-Sixto et al., 2018). While skipping has lower peak vertical GRFs and a shorter or similar support phase duration than running (McDonnell et al., 2017), average vertical GRFs are greater during skipping than running (Minetti, 1998).

The greater displacement of the COM during skipping compared to running is attributable to 1) a greater change in the vertical COM position during the support phase of the hop step of skipping compared to the support phase of running, and 2) a greater change in COM position during the flight phase (McDonnell et al., 2017). While the change in COM position during flight is directly related to the take-off velocity, mechanical work (provided primarily by muscle forces) is required to produce the vertical GRF that raises the COM during the support phase.

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A muscle's contribution to mechanical work can be determined using a segmental power analysis, which quantifies how a muscle's force contributes to the mechanical power of each body segment. Previous studies used a segmental power analysis to identify the contributions of individual muscle forces to the biomechanical subtasks of body support and forward propulsion in running (Sasaki and Neptune, 2006a, 2006b). Given the higher vertical mechanical work required to generate the higher vertical displacement of the COM during skipping compared to running, one might assume this greater mechanical work is achieved by the production of greater muscle forces in skipping. However, our recent work revealed lower muscle force impulses in skipping compared to running (Roelker et al., 2022), and thus uncovered an intriguing biomechanical anomaly of a gait that combines lower muscle force impulses with higher vertical displacement. Investigating the differences in muscle contributions to mechanical power during skipping compared to running will allow us to identify the mechanisms underlying the generation of higher vertical mechanical work despite the lower muscle forces produced during skipping. Therefore, the purpose of this mechanistic study was to compare the flow of mechanical power between body segments during skipping and running to determine the mechanisms enabling higher vertical displacement in skipping despite lower muscle force impulses.

2. Methods

The experimental and musculoskeletal modeling and simulation procedures used to collect and generate the data analyzed in this study have been previously described in detail (Roelker et al., 2022). Briefly, five healthy young adults (2 females; 22.4 ± 2.2 y; 1.70 ± 0.06 m; 74.5 ± 12.7 kg) provided written informed consent to participate in the study protocol approved by the East Carolina University Institutional Review Board. All participants reported they had no musculoskeletal, cardiovascular, or neurological diseases, illnesses, or injuries. None of the participants were using medications of any kind. For each gait, three 10 s trials were performed on an instrumented dual-belt treadmill (Bertec, USA) at 2.5 m/s. The speed of 2.5 m/s, which is slightly slower than the 2.68 m/s overground speed tested previously (McDonnell et al., 2019, 2017) was chosen for this study because it is a speed at which running and skipping can both be performed comfortably on the treadmill (Minetti, 1998). All participants had previously used a treadmill. When asked to report their comfort running and skipping on a treadmill on a scale from 0 (completely comfortable) to 5 (completely uncomfortable), the participants reported they were very comfortable running (0.4 ± 0.5) and generally comfortable skipping (1.6 ± 1.3) on the treadmill. Three-dimensional positions of reflective markers were recorded by a 10-camera motion capture system (Qualisys Medical AB) and electromyography (EMG; DELSYS, Boston, MA, USA) was recorded bilaterally at 1000 Hz from 8 muscles: gluteus maximus, gluteus medius, rectus femoris, vastus medialis, long head of the biceps femoris, medial gastrocnemius, soleus and tibialis anterior. The raw EMG was demeaned, filtered with a 4th order bandpass (30–300 Hz) zero-lag Butterworth filter, rectified, and filtered with a 4th order low-pass (4 Hz) zero-lag Butterworth filter. The EMG was then normalized to the maximum value from the respective 10 s trial. For each participant, the most representative running cycle (defined as right heel strike to subsequent right heel strike) and skipping cycle (defined as a leading limb hop (Skip 1) and trailing limb step (Skip 2) executed by the right limb) (Fig. 1) were identified from the 10 s trial using a functional measure of depth method (Sangeux and Polak, 2015) which determined the cycle closest to the median of all cycles in the trial based on the GRF data. In OpenSim 3.3 (Delp et al., 2007), a full-body 12 segment model with 92 musculotendon actuators (Hamner et al., 2010) was scaled for each participant. Each representative running and skipping cycle was simulated using a traditional OpenSim pipeline using Inverse Kinematics (Lu and O'Connor, 1999), Residual Reduction Algorithm (Delp et al., 2007) and Computed Muscle Control (CMC) (Thelen et al., 2003; Thelen and

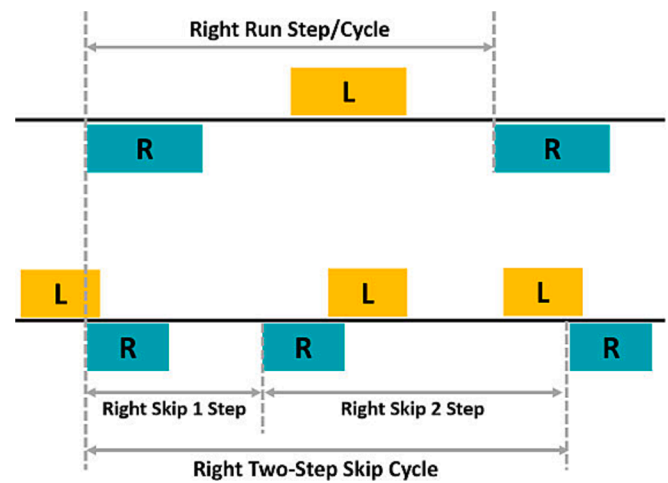


Fig. 1. Schematic descriptions of running and skipping steps and cycles on the right limb. For skipping, a step was defined as the period from one right heel strike to the subsequent right heel strike (including the stance phase and subsequent flight phase). The Skip cycle was defined as the sum of the Skip 1 and Skip 2 steps. For running, the Run cycle was the same as the Run step, which was defined as the period from one right heel strike to the subsequent right heel strike. (Figure adapted from Roelker et al., 2022, with permission).

Anderson, 2006). To validate the simulation results, error thresholds were applied according to OpenSim Best Practices (Hicks et al., 2015, 2012). For Scaling, maximum and root mean square (RMS) marker errors were required to be less than 2 cm and 1 cm, respectively. For Inverse Kinematics, maximum and RMS marker errors were required to be less than 4 cm and 2 cm, respectively. For Residual Reduction Algorithm and CMC: peak residual forces were required to be less than 5% of peak GRFs and peak translational and rotational coordinated errors were required to be less than 2 cm and 2°, respectively. In addition, CMC was performed with constraints such that the muscle excitation timing and patterns were consistent with those of the experimentally measured EMG data as described previously for this data set (Fig. 2; Roelker et al., 2022). Furthermore, to ensure that the CMC solution was primarily muscle-driven, for each participant peak isometric forces of all modeled muscles were uniformly increased until the peak reserve torque actuator magnitudes did not exceed 5% (range: 1.7–4.9%) of the peak joint moment for all coordinates (Hicks et al., 2015) for the participant's running and skipping simulations. Given this rigorous approach to ensure the simulations were muscle driven and consistent with the experimental EMG, and so that the model strength was the same for running and skipping simulations for a given participant, the required increase in peak isometric muscle forces ranged from 200% (model peak isometric forces multiplied by 2) to 350% (model peak isometric forces multiplied by 3.5) across participants.

A segmental power analysis was used to determine the mechanical power each muscle generates, absorbs, or transfers to or from each segment in each gait (Fregly and Zajac, 1996). A muscle's contribution to segmental power was calculated as the product of the segment's mass, the instantaneous velocity of the segment and the muscle-induced acceleration of the segment, which was determined using an Induced Acceleration Analysis (IAA) performed in OpenSim. When the total vertical acceleration calculated by IAA was compared to vertical COM acceleration, average RMS errors across all subjects and gaits was 3.7 ± 3.6 m/s². Power is a scalar quantity; therefore, the individual segment powers can be summed to quantify a muscle's contribution to the power of any group of segments (Fregly and Zajac, 1989). Thus, muscle contributions to segmental power were determined for four body segment groups of interest: the trunk (sum of pelvis, torso and arms segment power), ipsilateral leg (sum of right femur, tibia and foot segment power), contralateral leg (sum of left femur, tibia and foot segment power), and whole body (sum of power to all segments). Individual muscle

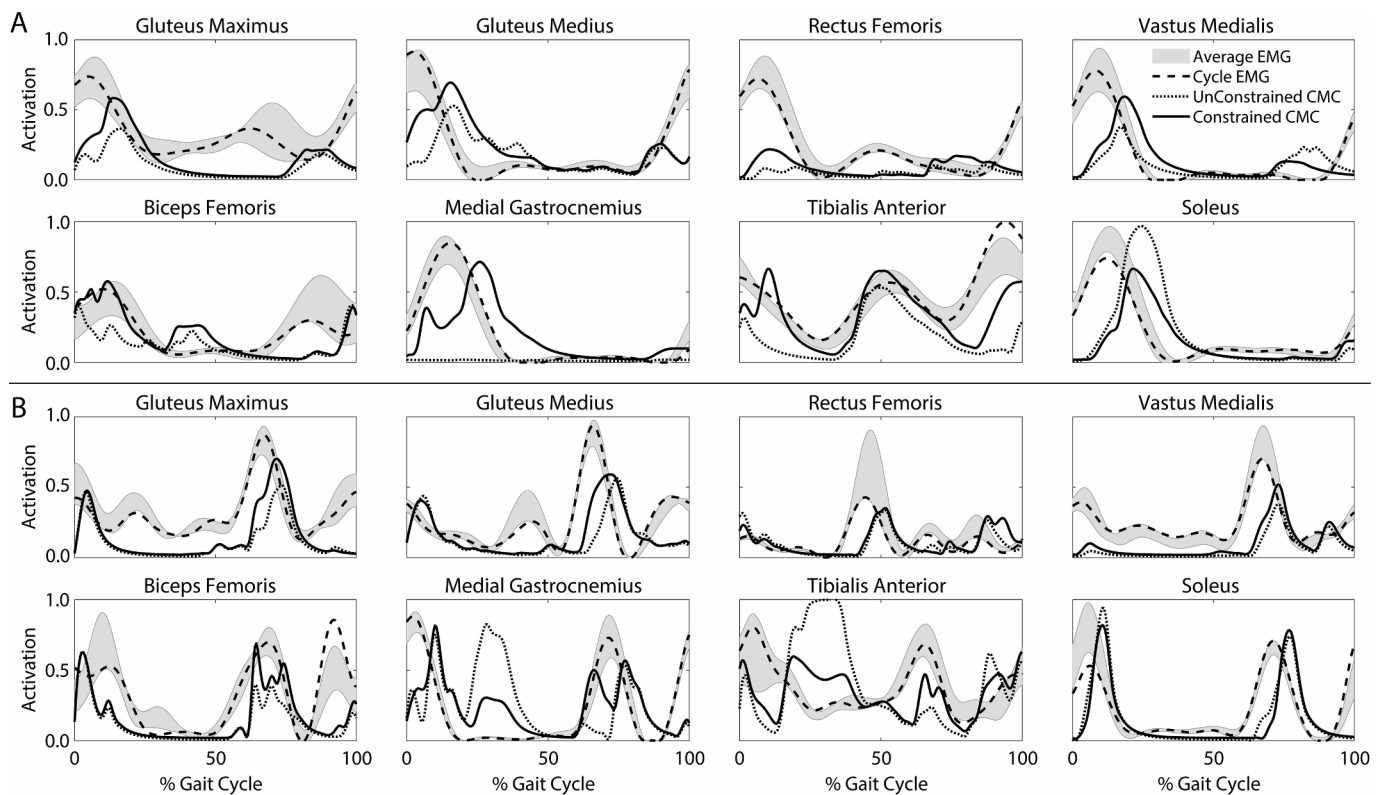


Fig. 2. Experimental and simulated muscle activation patterns from a representative subject for A) running and B) skipping. Experimental EMG is shown for each muscle over the simulated gait cycle (dashed line) and the average EMG (shaded area) across all collected gait cycles from the 10 s trials. The unconstrained (dotted line) and constrained (solid line) CMC activation patterns demonstrate the improved muscle activation timing with the CMC excitations constrained to EMG.

contributions to segmental power were then integrated over the stance phase of each step to determine each muscle's segmental work.

Separate one-way repeated measures ANOVA analyses compared muscle contributions to vertical segmental work on the whole body, trunk, ipsilateral leg, and contralateral leg between the stance phases of the Run, Skip 1, and Skip 2 steps. In addition, vertical COM kinematics including maximum and net vertical displacement, initial stance (i.e., landing) velocity, take-off velocity, and change in velocity during stance, as well as vertical ground reaction force (GRF) impulse and net vertical impulse (GRF impulse minus impulse due to body weight), were compared between steps using separate one-way repeated measures ANOVAs. Maximum vertical COM displacement was calculated as the distance between the maximum and minimum vertical COM position during stance and net vertical COM displacement was calculated as the vertical COM position at take-off minus the vertical COM position at initial contact. The change in vertical COM velocity was calculated by subtracting the take-off velocity from the velocity at initial contact. Post-hoc t-tests with Bonferroni corrections for multiple comparisons identified pairwise differences between steps. All statistical analyses were performed in MATLAB 2023a (Mathworks Inc., Natick, MA) with an α value of 0.05 set *a priori*. All p-values reported in the text are from the post-hoc tests. The p-values reported in the Tables are identified as from the ANOVA or pairwise comparisons. In addition to our primary analysis of muscle contributions to vertical segmental power, comparisons of overall muscle contributions to segmental power and muscle contributions to anteroposterior segmental power between Run, Skip 1 and Skip 2 are presented in the Appendix for completeness.

3. Results

3.1. Vertical COM kinematics and kinetics

Differences in the vertical COM trajectory (Fig. 3A) between the Run

and Skip 1 steps resulted in greater maximum ($p < 0.001$; Fig. 3C) and net vertical ($p < 0.001$; Fig. 3D) COM displacements in Skip 1 than Run (Table 1). Skip 2 also had a greater maximum COM displacement than Run ($p < 0.001$) and a greater negative net vertical COM displacement than Run and Skip 1 ($p \leq 0.008$). Skip 1 had greater landing and take-off vertical COM velocities compared to Run and Skip 2 ($p \leq 0.04$), while Run had a greater take-off ($p = 0.04$), but not landing ($p = 0.12$), velocity than Skip 2 (Fig. 3B). Run had a higher vertical GRF impulse than Skip 2 ($p < 0.001$; Fig. 3E,F), but there was no difference in net vertical impulse ($p \geq 0.26$; Fig. 3G) between any of the three steps. There were also no differences in the change in vertical COM velocity between the three steps ($p \geq 0.43$).

3.2. Muscle contributions to vertical segmental power

Significantly higher vertical work was performed on the whole body in Skip 1 (Fig. 3H) compared to Run ($p = 0.009$) and Skip 2 ($p < 0.001$). Individual muscle contributions to vertical segmental power differed between all three steps in both magnitude and direction of power flow (Fig. 4A), which resulted in significant differences in segmental power work on individual body segments between the three steps (Fig. 4B; Table 2). The plantar flexors (soleus and gastrocnemius) were the primary contributors to the higher vertical work performed on the whole body in Skip 1, with smaller positive contributions from the quadriceps (vasti and rectus femoris) and gluteal muscles (gluteus maximus and medius) and negative contributions from the tibialis anterior, hamstrings, and iliopsoas. In contrast, the plantarflexors, quadriceps and gluteal muscles performed net negative or net zero work on the whole-body during Run and Skip 2.

The plantar flexors performed net positive vertical work during Skip 1 due to power generation to all segment groups. In contrast, during Skip 2 the plantar flexors absorbed power from the trunk and ipsilateral leg which produced net negative work. In Run, the plantar flexors absorbed

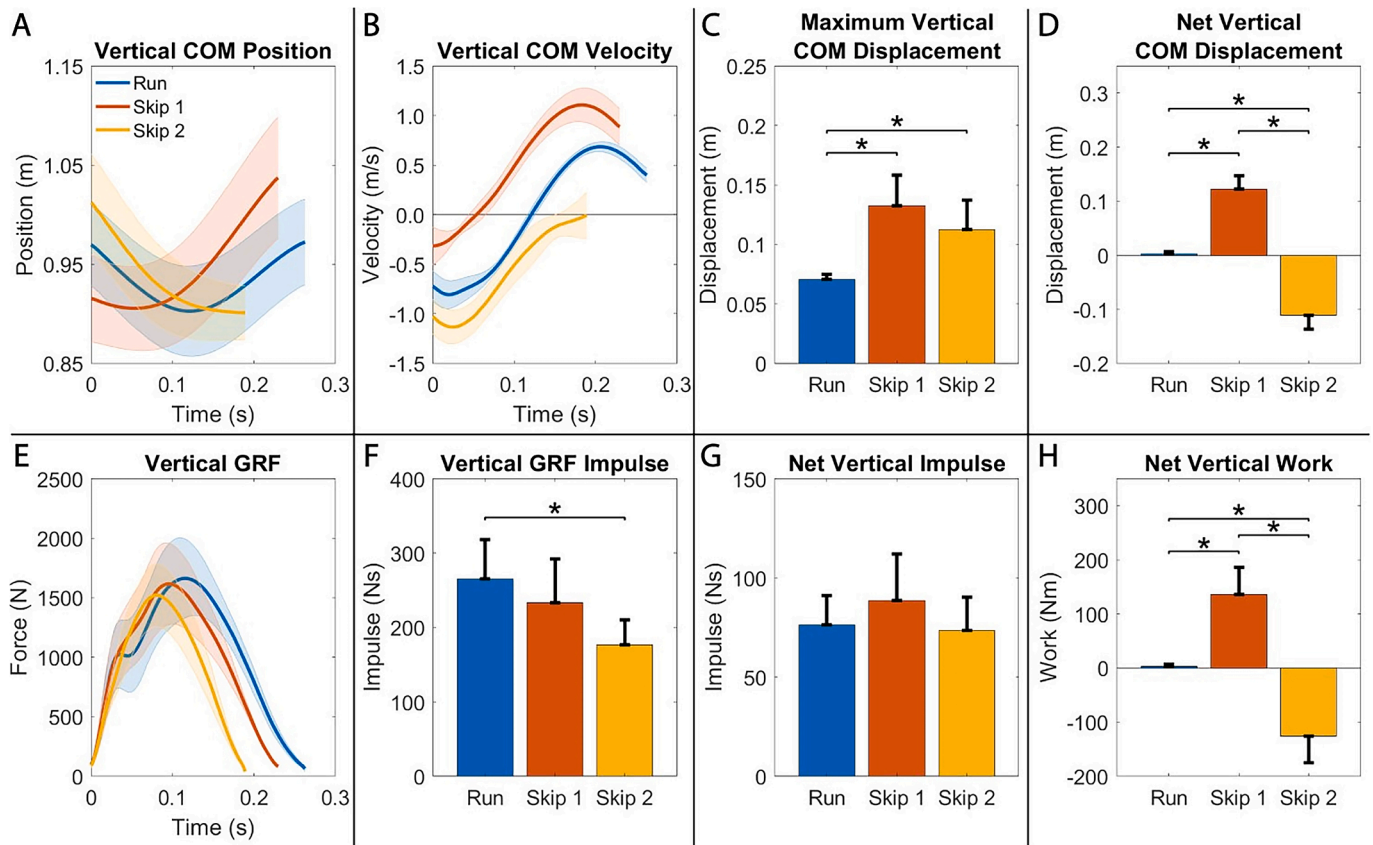


Fig. 3. Vertical center of mass (COM) kinematics and kinetics during the stance phase of running and skipping steps. * indicate pairwise difference between steps.

Table 1
Vertical COM Kinematics during Stance.

Measure	Run	Skip 1	Skip 2	ANOVA p-value
Maximum Vertical COM Displacement (m)	0.071 ± 0.004	0.133 ± 0.026	0.113 ± 0.025	< 0.001 ^{a,b}
Net Vertical COM Displacement (m)	0.003 ± 0.004	0.122 ± 0.025	-0.113 ± 0.026	< 0.001 ^{a,b,c}
Vertical COM Landing Velocity (m/s)	-0.71 ± 0.15	0.32 ± 0.19	-1.03 ± 0.17	0.002 ^{a,c}
Vertical COM Take-Off Velocity (m/s)	0.39 ± 0.07	0.88 ± 0.18	-0.01 ± 0.24	< 0.001 ^{a,b,c}
Change in Vertical COM Velocity (m/s)	1.10 ± 0.20	1.19 ± 0.09	1.02 ± 0.17	0.317

Symbols indicate significant pairwise differences between steps:

- a: Run vs Skip 1.
- b: Run vs Skip 2.
- c: Skip 1 vs Skip 2.

power from the trunk and ipsilateral leg in the first half of stance and generated power to these segments during the second half of stance, which resulted in near net zero work.

The net work performed by the quadriceps in each step was largely due to their contributions to the trunk. In Skip 1, the quadriceps generated power to the trunk, resulting in net positive work. In Run, the quadriceps absorbed more power from the trunk in the first half of stance than they generated power to the trunk during the second half of stance, which resulted in net negative work by the vasti and rectus femoris. In Skip 2, the quadriceps performed net negative work due to power absorption from the trunk.

The gluteal muscles generated positive vertical work in Skip 1 by transferring power from the trunk and contralateral leg to the ipsilateral leg during early stance and generating power to the trunk and

contralateral leg in mid-to-late stance. In contrast, during Run the gluteus maximus primarily absorbed power from all segments during the first half of stance and the gluteus medius transferred power between the trunk and contralateral leg, which resulted in net negative work. In Skip 2 the gluteal muscles performed net negative work due to power absorption from the ipsilateral leg by gluteus maximus and from the trunk and contralateral leg by gluteus medius.

4. Discussion

The purpose of this study was to compare the flow of mechanical power between body segments during skipping and running to determine the mechanisms enabling higher vertical displacement in skipping, despite lower muscle force impulses (Roelker et al., 2022). The simulation analysis revealed that muscle contributions to vertical segmental power differed between the three steps in both magnitude and direction of the power flow, which revealed differences in the mechanisms by which muscles contribute to propelling the COM upward between gaits. During Skip 1, the gluteus maximus and medius, quadriceps and plantar flexor muscles perform large positive vertical work, primarily through power generation to the trunk, which leads to the large vertical displacement of the COM. In contrast, these muscles perform negative work during Run and Skip 2, absorbing power from the trunk.

A greater net vertical impulse during the stance phase will produce a greater change in vertical COM velocity. During the flight phase, the body's COM follows projectile motion such that the vertical displacement is directly proportional to the square of the vertical take-off velocity. Thus, a greater take-off velocity will produce a higher vertical displacement during flight. However, in this cohort there were no significant differences in the net vertical impulse nor in the change in vertical COM velocity between the three steps. Still, the lower negative landing velocity (and thus less negative kinetic energy) of Skip 1

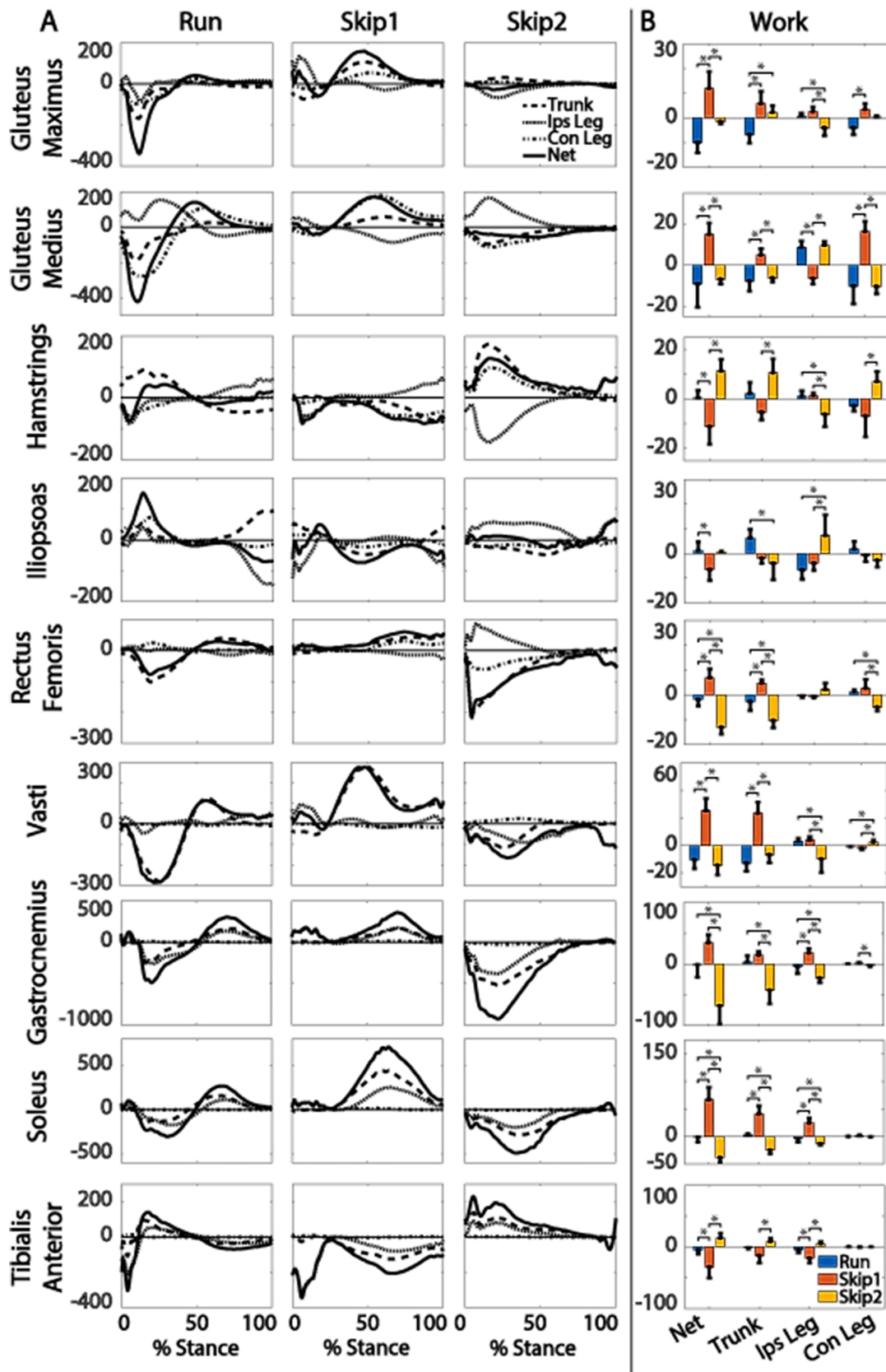


Fig. 4. Muscle contributions to vertical segmental A) power (W) and B) work (J) on the whole body (Net), trunk (Trunk), ipsilateral leg (Ips Leg), and contralateral leg (Con Leg). Due to the linear transformation between segment power and acceleration (Fregly and Zajac, 1996), the segment power analysis quantifies a muscle's contribution to a segment's motion such that positive (negative) segmental power indicates that a muscle accelerated (decelerated) a segment in the direction of movement. * indicates pairwise differences between steps.

Table 2

P-values for ANOVA and pairwise comparison of muscle contributions to vertical segmental work between steps.

Muscle	Body	ANOVA	Run vs Skip 1	Run vs Skip 2	Skip 1 vs Skip 2
Gluteus Maximus	Net	<	<	0.094	0.011
		0.001	0.001		
	Trunk	0.004	0.004	0.028	0.6191
	Ipsilateral Leg	0.005	0.601	0.035	0.005
Gluteus Medius	Contralateral Leg	0.004	0.004	0.069	0.237
	Net	0.003	0.006	1.0000	0.011
	Trunk	0.002	0.002	1.0000	0.005
	Ipsilateral Leg	<	<	1.0000	< 0.001
Hamstrings	Contralateral Leg	<	<	1.0000	< 0.001
	Net	<	0.042	0.055	< 0.001
		0.001			
	Trunk	0.002	0.081	0.050	0.001
Iliopsoas	Ipsilateral Leg	0.008	1.000	0.018	0.015
	Contralateral Leg	0.019	0.967	0.105	0.021
	Net	0.025	0.042	1.000	0.061
	Trunk	0.014	0.058	0.018	1.000
Rectus Femoris	Ipsilateral Leg	0.008	1.000	0.011	0.034
	Contralateral Leg	0.122			
	Net	<	0.001	< 0.001	< 0.001
		0.001			
Vasti	Trunk	<	0.002	0.001	< 0.001
		0.001			
	Ipsilateral Leg	0.041	1.000	0.103	0.065
	Contralateral Leg	0.002	1.000	0.012	0.003
Gastrocnemius	Net	<	<	1.000	< 0.001
		0.001	0.001		
	Trunk	0.001	<	0.643	< 0.001
		0.001	0.001		
Soleus	Ipsilateral Leg	0.013	1.000	0.031	0.022
	Contralateral Leg	0.004	0.487	0.030	0.004
	Net	<	0.188	0.011	< 0.001
		0.001			
Tibialis Anterior	Trunk	0.002	0.926	0.008	0.002
	Ipsilateral Leg	<	0.014	0.041	< 0.001
		0.001			
	Contralateral Leg	0.010	0.989	0.055	0.012
Tibialis Anterior	Net	<	<	0.005	< 0.001
		0.001	0.001		
	Trunk	<	<	0.005	< 0.001
		0.001	0.001		
Tibialis Anterior	Ipsilateral Leg	<	<	0.040	< 0.001
		0.001	0.001		
	Contralateral Leg	0.095			
	Net	<	0.023	0.102	< 0.001
Tibialis Anterior		0.001			
	Trunk	0.003	0.059	0.181	0.003
	Ipsilateral Leg	<	0.014	0.063	< 0.001
		0.001			
Tibialis Anterior	Contralateral Leg	0.295			
	Leg				

Bold values indicate statistically significant differences in vertical segmental work.

required less work to redirect the COM upward so that the COM moves upward earlier in stance. The earlier change in direction of the COM during Skip 1 allows the muscles to contribute to the upward acceleration of the COM through more of stance and provide the higher vertical COM displacement in Skip 1 compared to the other two steps.

The positive vertical work done on the trunk by the gluteus maximus, gluteus medius, rectus femoris, vasti, and soleus accelerates the COM upward during the support phase of Skip 1, which results in a large

vertical COM displacement. In contrast, the negative vertical work done on the trunk by these muscles during Run decelerates the downward motion of the COM. However, muscles perform positive work through concentric contractions, which are more metabolically costly than eccentric contractions which perform negative work (Bigland-Ritchie and Woods, 1976). Thus, despite lower muscle force impulses in Skip 1 compared to Run (Roelker et al., 2022), those muscle forces generate positive power through concentric contractions, leading to greater metabolic cost in skipping compared to running (McDonnell et al., 2019; Minetti, 1998; Roelker et al., 2022). The greater concentric work performed in Skip 1 compared to Run explains the relationship between higher vertical COM displacement and greater metabolic cost in skipping compared to running (McDonnell et al., 2019).

This study has some limitations that should be considered when evaluating the results. First, running and skipping gait cycles were simulated for 5 participants with muscle work compared for four body segment groups across several muscles. While a larger cohort would provide greater power to confirm the findings of this study are representative of the general population, whether a muscle performs positive or negative work in each step is related to differences in biomechanics of running and skipping, which would not be expected to change with additional subjects. Moreover, the running and skipping COM kinematics and GRFs observed in this study are consistent with the literature (Johnson et al., 2005; McDonnell et al., 2017; Minetti, 1998) and muscle contributions to segmental power during running are comparable to those previously reported (Sasaki and Neptune, 2006b), which provides confidence in the current findings. Specifically, our findings for muscle contributions to vertical power to the ipsilateral leg and trunk for the soleus, gastrocnemius, hamstrings, and vasti (Fig. 3) are quantitatively similar in magnitude and qualitatively similar in timing to those presented in Sasaki and Neptune (Fig. 6 in 2006b). Still, given the large number of statistical tests performed in this study, these results should be interpreted as provisional and should be confirmed in a larger study. Another important consideration is that running and skipping trials were performed on a treadmill in this study to ensure the gaits were performed at the same speed. While there may be some differences in how individuals perform the gaits on the treadmill compared to overground, previous research suggests treadmill running is biomechanically comparable to overground running (Van Hooren et al., 2020). In addition, participants were provided the opportunity to practice each gait condition at the test speed on the treadmill prior to data collection to promote comfort running and skipping on the treadmill. Secondly, while the average BMI of our participants (25.5, range 20.3–28.7) does fall into the overweight category, no participant fell into the obese category (BMI > 29.9). Furthermore, BMI is a poor indicator of percent body fat and of health, particularly at the individual level, as it does not take into account important factors of health, such as lean muscle mass (Brooks et al., 2007; Burkhauser and Cawley, 2008; Nuttall, 2015; Romero-Corral et al., 2008). In addition, participants were free from disease and injury and were not taking any medications. Thus, we feel confident in classifying the participants as healthy young adults.

In summary, our results suggest the higher vertical displacement and greater metabolic cost of skipping compared to running are attributable to the greater concentric work performed during Skip 1 by the gluteal muscles, quadriceps, and plantarflexors. The less negative landing velocity of Skip 1 enables these muscles to generate more positive vertical work during stance leading to greater COM displacement during stance and greater take-off velocity, which increases COM displacement during flight compared to running. Thus, by comparing muscle contributions to mechanical power in running and skipping, we identified the mechanisms underlying the biomechanical anomaly observed in skipping of lower muscle force impulses generating higher vertical displacement. The greater concentric work performed in the gluteal muscles, quadriceps, and plantarflexors in skipping compared to running may be important for clinicians to consider when prescribing skipping or running in training programs or rehabilitation protocols depending on

an individual's goals.

CRedit authorship contribution statement

Sarah A. Roelker: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **John D. Willson:** Writing – review & editing, Resources, Project administration, Data curation. **Paul DeVita:** Writing – review & editing, Resources, Project administration, Data curation. **Richard R. Neptune:** Writing – review & editing, Supervision, Resources, Project administration, 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 material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jbiomech.2025.112545>.

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