



The effects of stride frequency manipulation on physiological and perceptual responses during backward and forward running with body weight support

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Received: 21 October 2019 / Accepted: 19 April 2020 / Published online: 29 April 2020
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Abstract

Purpose We investigated the influence of a change in stride frequency on physiological and perceptual responses during forward and backward running at different body weight support (BWS) levels.

Methods Participants ran forward and backward at 0% BWS, 20% BWS, and 50% BWS conditions on a lower body positive pressure treadmill. The stride frequency conditions consisted of forward and backward running at preferred stride frequency (PSF), PSF + 10%, and PSF - 10%. We measured oxygen uptake ($\dot{V}O_2$), carbon dioxide production, heart rate (HR), muscle activity from the lower extremity, and rating of perceived exertion (RPE). Furthermore, we calculated the metabolic cost of transport (CoT).

Results $\dot{V}O_2$, HR, CoT, and muscle activity from the rectus femoris were significantly different between stride frequency conditions ($P < 0.05$). $\dot{V}O_2$, HR, and CoT during running at PSF + 10% were significantly higher than when running at PSF, regardless of running direction and BWS ($P < 0.05$). However, RPE was not different between stride frequency conditions ($P > 0.05$: e.g., 12.8–13.8 rankings in RPE for backward running at 0% BWS).

Conclusions Manipulation of stride frequency during running may have a greater impact on physiological responses than on perceptual responses at a given speed, regardless of running direction and BWS. Individuals who need to increase their physiological demands during running may benefit from a 10% increase in stride frequency from the PSF, regardless of BWS and running direction.

Keywords Locomotion · Lower body positive pressure treadmill · Running direction · Stride frequency

Abbreviations

BWS	Body weight support
CoT	Cost of transport
EMG	Electromyography
HR	Heart rate
LBPP	Lower body positive pressure
partial η^2	Partial eta-squared
PSF	Preferred stride frequency

RPE	Rating of perceived exertion
$\dot{V}O_2$	Oxygen uptake

Introduction

Running is a popular exercise, however, 66% of runners sustained at least one injury within 2 years (Messier et al. 2018). Although the etiology of running-related injury is multifactorial in nature, the magnitude of impact loading during running may be associated with a lower extremity stress fracture (Milner et al. 2006). Gait retraining with real-time visual feedback of impact peak during running on a treadmill may be useful in reducing the impact loading and occurrence of running-related injury (Chan et al. 2018). Nevertheless, exploration of the other strategies to reduce the impact loading magnitude on the lower extremity, without decreasing physiological demands during running may be useful for minimizing the risk of running-related injury.

Communicated by Jean-René Lacour.

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For example, increasing body weight support (BWS) directly reduces the impact loading magnitude on lower extremity during running (Grabowski and Kram 2008). Metabolic costs during running decrease with increasing BWS at a constant running speed (Kline et al. 2015; Raffalt et al. 2013). However, the metabolic costs during running with increasing BWS can be maintained by increasing running speed (Kline et al. 2015), while still reducing the impact loading magnitude (Raffalt et al. 2013). Furthermore, BWS may not influence lower extremity muscle activity patterns during running at a constant speed (Liebenberg et al. 2011; Mercer et al. 2013), although an extreme change in BWS (i.e., a 80% increase in BWS) influenced gastrocnemius muscle activity patterns during running at individual's preferred speed (Masumoto et al. 2017).

Additionally, backward running reduces the impact loading magnitude on the lower extremities (Threlkeld et al. 1989), while producing greater metabolic costs (Flynn et al. 1994; Williford et al. 1998) than when running forward at the same speed. Previous investigations have mainly focused on physiological (Flynn et al. 1994; Williford et al. 1998) and biomechanical (Threlkeld et al. 1989) responses during backward and forward running at the same speed. However, when running with BWS, individuals may consistently select a unique combination of preferred speed and preferred stride frequency (PSF) for backward running and forward running in a way that resulted in similar metabolic costs (Masumoto et al. 2019).

Furthermore, manipulating stride frequency reduces the impact loading magnitude on lower extremity during forward running (Heiderscheidt et al. 2011). For example, a 10% increase in stride frequency from the PSF during forward running produced similar metabolic costs to that of forward running at the PSF (Hamill et al. 1995), while reducing the impact loading magnitude during running (Heiderscheidt et al. 2011). Additionally, increasing stride frequency by 10% from the PSF during forward running produced greater muscle activity than when running at the PSF, regardless of BWS (Masumoto et al. 2018). However, other studies (Cavanagh and Williams 1982; Snyder and Farley 2011) reported that for a given speed, individuals tend to select PSF that is close to the optimal metabolic cost during forward running, and a deviation from the PSF increases metabolic cost, although biomechanical responses during forward running may or may not explain the selection of PSF (Hobara et al. 2012; Masumoto et al. 2015, 2018). Nevertheless, none of the previous studies have investigated the influence of a change in stride frequency on physiological and perceptual responses during backward running with BWS.

Systematic manipulations of BWS, stride frequency, and running direction are necessary to determine the independent influence of these manipulation strategies on physiological and perceptual responses during running. The purpose

of this study was to investigate the influence of a change in stride frequency on physiological and perceptual responses during backward and forward running at different levels of BWS. We hypothesized that an increase in stride frequency may increase physiological and perceptual responses during running, regardless of BWS and running direction. Additionally, we hypothesized that the physiological responses during backward running may be similar and/or higher than that of running forward when running at individual's preferred speed, regardless of stride frequency and BWS. Furthermore, we hypothesized that an increase in BWS may decrease the physiological and perceptual responses during running, regardless of running direction and stride frequency.

Methods

Participants

Nine individuals (5 males and 4 females: means \pm standard deviation: age = 33.2 ± 12.1 years, height = 176.1 ± 11.8 cm, body weight = 70.9 ± 14.7 kg) completed the study. Their running training distance, duration, and frequency were 26.1 ± 20.9 km/week, 36.1 ± 16.2 min/session and 4.3 ± 1.2 sessions/week, respectively. The participants were free from any diseases and injuries at the time of the study. All participants gave their written informed consent that was approved by the University Institutional Review Board.

Instrumentations

Oxygen uptake ($\dot{V}O_2$) and carbon dioxide production were measured using an automatic breath-by-breath gas exchange system (MOXUS Modular Metabolic System, AEI Technologies Co. Ltd., United States). Heart rate (HR) was measured continuously by a telemetry method (Polar Electro, Finland) and was recorded via the metabolic system. The $\dot{V}O_2$ and HR data from the final 30 s of each test were analyzed. Furthermore, we calculated the metabolic cost of transport (CoT). The calculation procedures for the CoT followed the previously described methods of Beck et al. (2017). Rating of perceived exertion (RPE) was measured using Borg's 6–20 scale (Borg 1982) during the final 30 s of each test.

Muscle activity from the right rectus femoris, the long head of the biceps femoris, tibialis anterior, and the lateral head of the gastrocnemius was measured at the sampling rate of 1500 Hz using a telemetry electromyography (EMG) system (TeleMyo 2400 T, G2, Noraxon, United States). Surface electrodes (Ambu[®] BlueSensor N, Ambu Inc., United States) were placed on each tested muscle (Hermens et al. 2000). A reference electrode was placed in combination with the rectus femoris lead. Prior to electrode placement, the skin

surface was shaved and abraded using a skin preparation gel (Skinpure, YZ-0019, Nihon Kohden Co. Ltd., Japan). The right knee angle was measured using an electrogoniometer (Model SG 150, Biometrics Ltd., United States) during the running tests.

Experimental procedures

Submaximal running test sessions (Days 1 and 2)

Participants performed submaximal forward and backward running test sessions on Days 1 and 2, respectively. Each of the test sessions were separated by at least one day and no more than 7 days. Participants were asked not to eat approximately 2 h prior to testing, although they were allowed to drink water during the tests.

Firstly, the preferred speed and PSF for each participant was determined during running for BWS condition, essentially following the previously described methods (Masumoto et al. 2017, 2018, 2019). During the preferred speed and PSF measurement session, we asked each participant to increase or decrease the running speed during forward (Day 1) and backward (Day 2) running at each BWS condition on a lower body positive pressure treadmill (G-Trainer Pro Version 1.20, Alter-G Inc., United States) until the participant indicated that a certain speed was most comfortable. The participants were not allowed to see the actual speed and BWS setting when measuring their preferred speed and PSF. We determined stride frequency by measuring the time to complete 20 strides during each test using a stopwatch. Each participant completed this procedure three times for each BWS condition with an approximately 1-min rest between the trials. Each participant was assigned a random test order for BWS conditions. We averaged the three obtained running speed and stride frequency values for each condition to represent the preferred speed and PSF for each condition. The preferred speed and PSF at each condition for each participant were used for each of the actual submaximal running tests (Days 1 and 2) as well as for the muscle activity and knee angular kinematics measurements (Day 3).

After determining the preferred speed and PSF, resting metabolic data were measured for 5 min. The resting $\dot{V}O_2$ values between Day 1 (4.0 ± 0.5 ml/kg/min) and Day 2 (4.3 ± 0.8 ml/kg/min) were similar (a paired *t* test: $P > 0.05$). Following the resting metabolic costs measurements, each participant ran forward (Day 1) and backward (Day 2) at specific BWS conditions: 0% BWS, 20% BWS, and 50% BWS. The stride frequency conditions were set at PSF-10%, PSF, and PSF + 10%. We used a digital audio metronome to help participants achieve the targeted stride frequency.

The running speed used for each condition was the preferred speed determined previously. For each condition, running speed was constant at the specific preferred speed for that condition. Participants were assigned a random testing order (BWS and stride frequency conditions). Each condition lasted about 6-min. The next condition started after the participants had rested and HR was within 10 beats/min of the resting HR.

Muscle activity and knee angular kinematics measurements session (Day 3)

At least a day after the completion of the two submaximal running test sessions on Days 1 and 2, participants returned to the laboratory for Day 3 which consisted of measuring EMG and knee angular kinematics during running.

To normalize EMG, each participant performed a maximal voluntary isometric contraction for each tested muscle (Hishlop and Montgomery 2007) before commencing the actual running tests. During the running tests, participants ran forward and backward at three different BWS (0% BWS, 20% BWS, and 50% BWS) and at three different stride frequency (PSF-10%, PSF, and PSF + 10%) conditions on the lower body positive pressure treadmill. Each participant was assigned a random test order (running direction, BWS, and stride frequency conditions). Participants were allowed time to practice each of the conditions before commencing the actual data collection. Participants performed approximately 30–60-s exercise bout for each condition.

Data reduction

The procedures used to process data from raw form to dependent variables essentially followed the previously described methods (Masumoto et al. 2017, 2018). The greatest 1-s average EMG during maximal voluntary isometric contraction was calculated and used as a normalizing value. For each condition, EMG data were first processed by removing any zero offset and performing a full-wave rectifying procedure (i.e., absolute value). We then calculated the average EMG across 15 s within the data set for each muscle (Fig. 1).

We further processed EMG data by smoothing using a fourth-order, Butterworth, zero-phase lag low pass filter (cutoff frequency = 4 Hz) to analyze the muscle activity patterns. We extracted EMG data for 15 consecutive gait cycles, with each gait cycle defined by identifying maximum knee extension peaks. We then normalized stride time to 100% to calculate an average muscle activity pattern for each condition for each participant (Fig. 2).

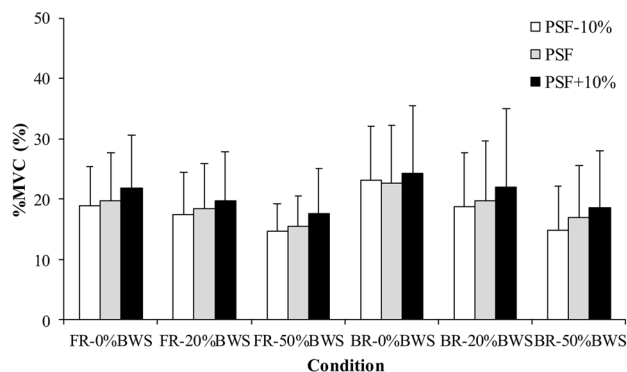
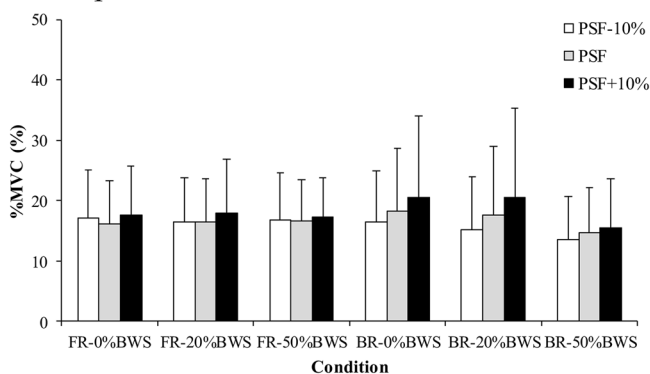
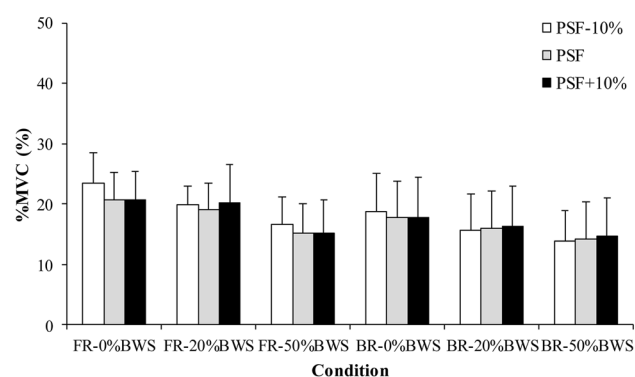
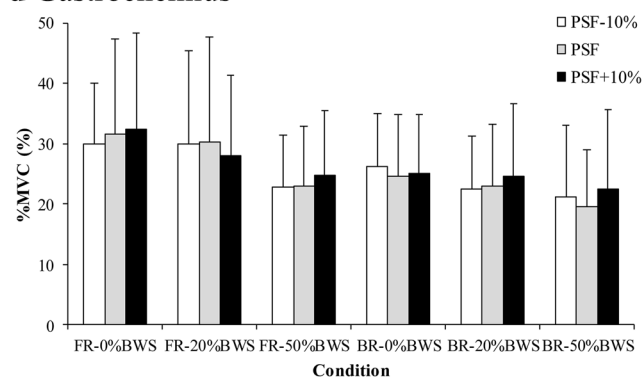
a Rectus Femoris^{b, c}**b Biceps Femoris**^{d, e}**c Tibialis Anterior**^b**d Gastrocnemius**^{a, b}

Fig. 1 Average muscle activity as a percentage of that observed during maximal voluntary contraction from the rectus femoris (**a**), biceps femoris (**b**), tibialis anterior (**c**), and gastrocnemius (**d**) during forward and backward running at different body weight support conditions at various stride frequencies. Data are presented as means \pm standard deviation. %MVC average muscle activity as a percentage of that observed during maximal voluntary contraction, *FR*

forward running, *BR* backward running, *BWS* body weight support, *PSF* preferred stride frequency. ^aSignificant running direction effect, $P < 0.05$. ^bSignificant body weight support effect, $P < 0.001$. ^cSignificant stride frequency effect, $P < 0.05$. ^dSignificant running direction and stride frequency interaction effect, $P < 0.05$. ^eSignificant running direction and body weight support interaction effect, $P < 0.05$

Statistical analyses

$\dot{V}O_2$, HR, CoT, RPE, muscle activity, and stride frequency were analyzed using a 2 (running directions) \times 3 (BWS) \times 3 (stride frequency) repeated measures analysis of variance. Preferred speed was analyzed using a 2 (running directions) \times 3 (BWS) repeated measures analysis of variance. When a significant main effect was observed, the difference function of the IBM SPSS Statistics version 19.0 was used as a subsequent post hoc test. When an interaction effect was observed, paired post hoc tests were used to detect differences between conditions. The level of statistical significance was set at $P < 0.05$.

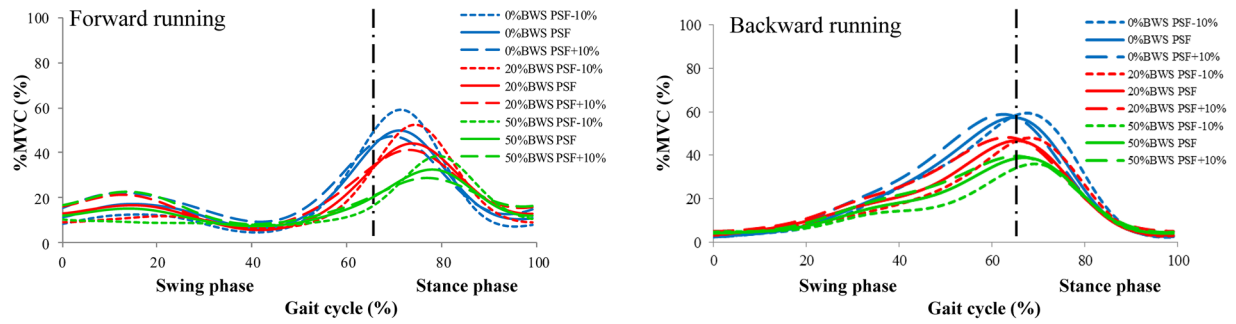
When an interaction effect was identified, Bonferroni corrected paired post hoc tests were used to detect differences between conditions ($\alpha = 0.0003$). Partial eta-squared (η^2) was reported. Muscle activity patterns (Fig. 2) and knee angle data (Fig. 3) were described qualitatively.

Results

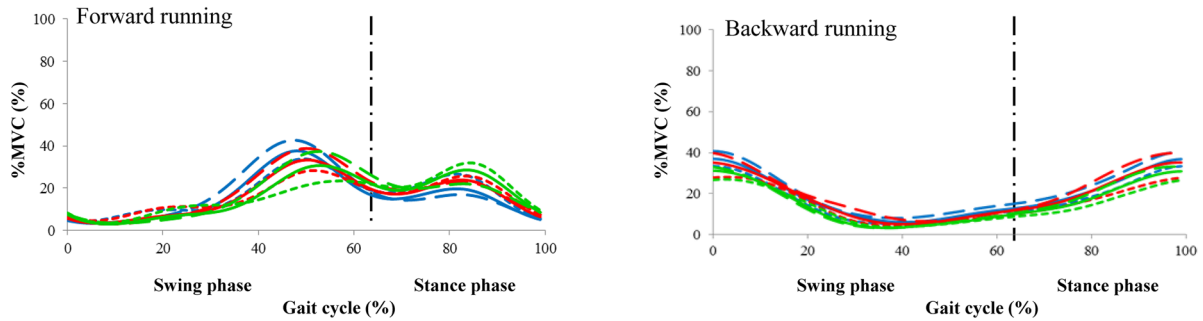
Metabolic costs and rating of perceived exertion

$\dot{V}O_2$ (Fig. 4a), HR (Fig. 4b), CoT (Fig. 4c), and RPE (Fig. 4d) were not influenced by the interaction of running direction, BWS, and stride frequency ($P > 0.05$). However,

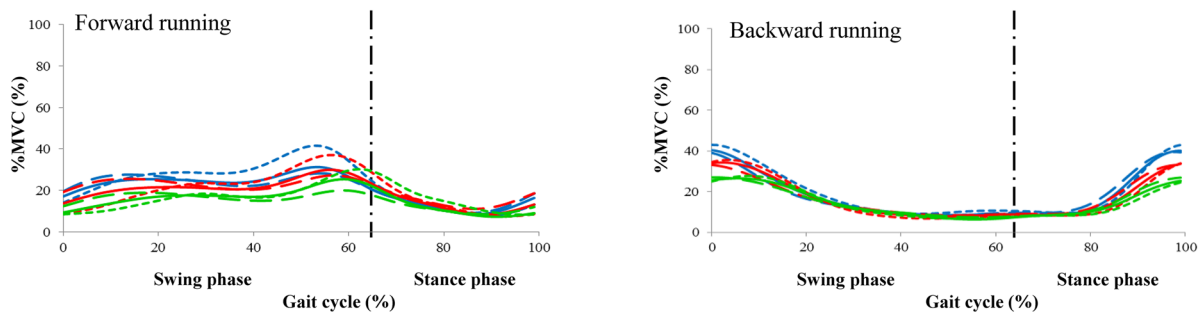
a Rectus Femoris



b Biceps Femoris



c Tibialis Anterior



d Gastrocnemius

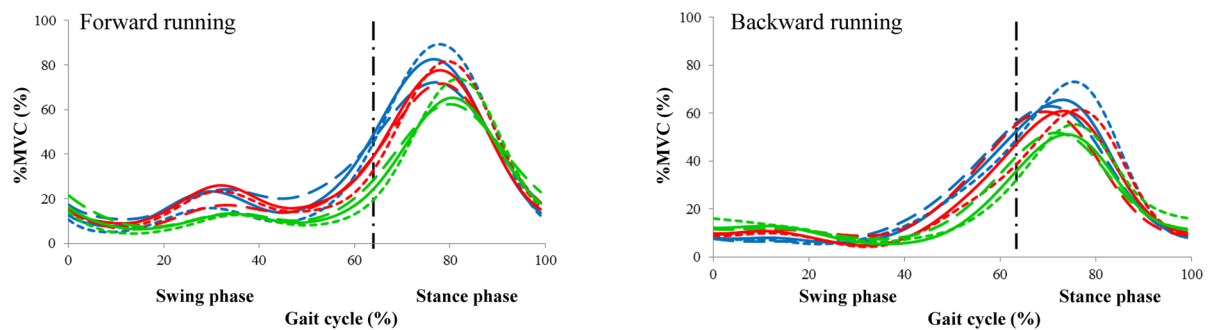
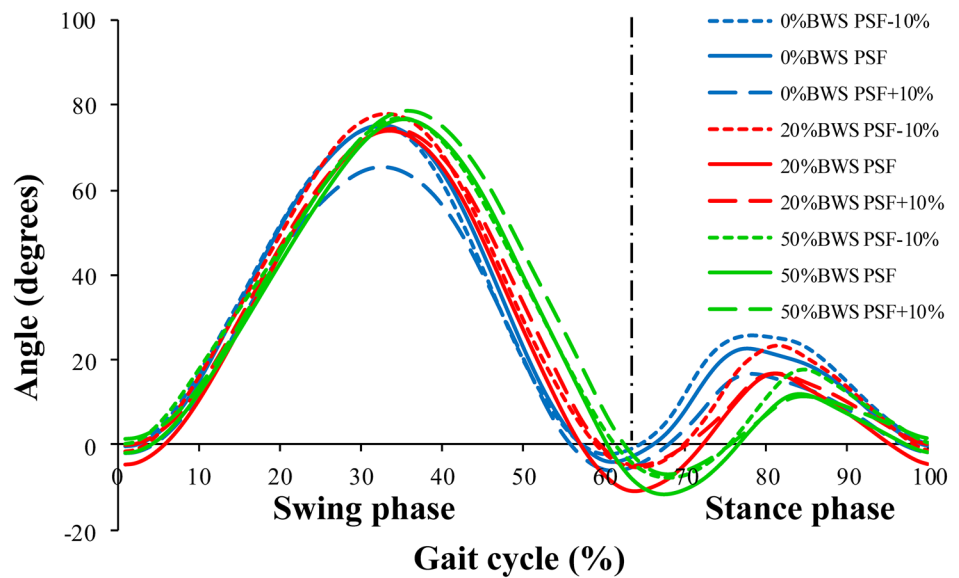


Fig. 2 Average muscle activity patterns from the rectus femoris (a), biceps femoris (b), tibialis anterior (c), and gastrocnemius (d) during forward and backward running at different body weight support con-

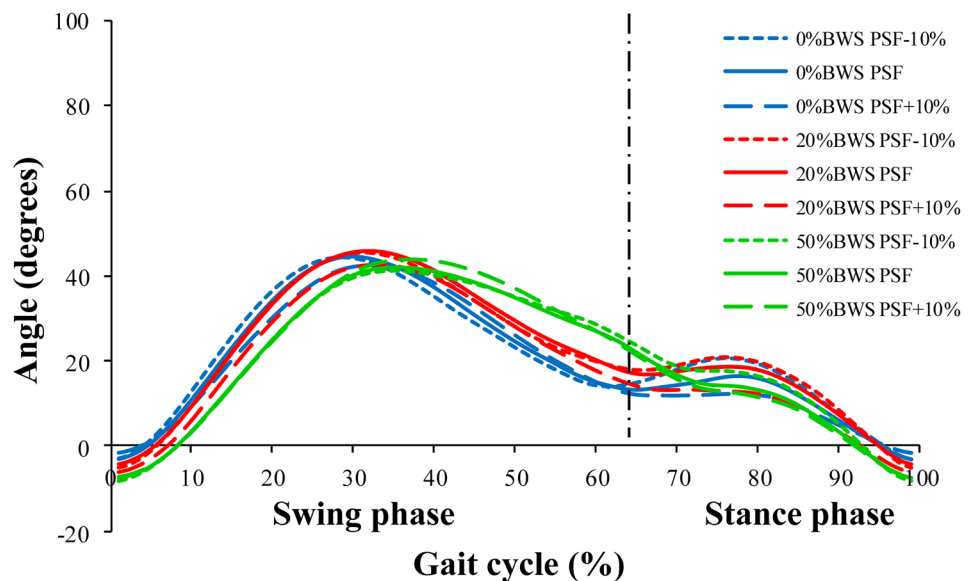
ditions at various stride frequencies. %MVC average muscle activity as a percentage of that observed during maximal voluntary contraction, PSF preferred stride frequency, BWS body weight support

Fig. 3 Knee angle data during forward (a) and backward (b) running at different body weight support conditions at various stride frequencies. It should be noted that the knee angle is below 0° in some parts—it may possibly be resulted from an artifact of the electrogoniometer position. *PSF* preferred stride frequency, *BWS* body weight support

a Forward Running



b Backward Running

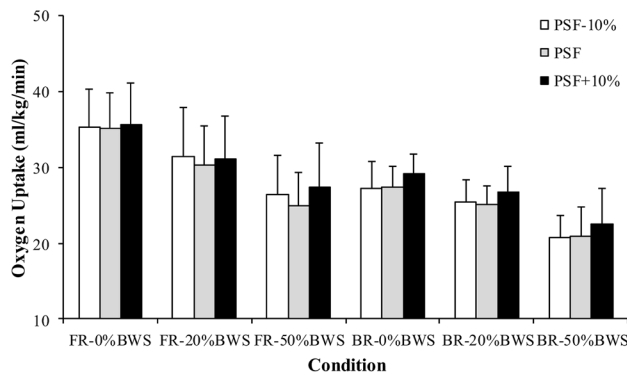


CoT was influenced by the interaction of running direction and BWS ($P < 0.01$, partial $\eta^2 = 0.625$).

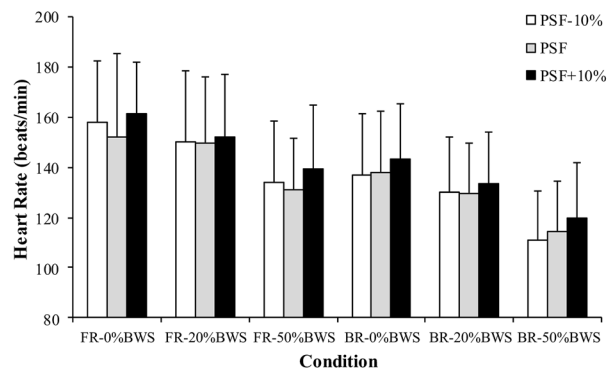
$\dot{V}O_2$ ($P < 0.01$, partial $\eta^2 = 0.768$) and HR ($P < 0.001$, partial $\eta^2 = 0.879$) were significantly different between running directions. Specifically, $\dot{V}O_2$ and HR during backward running were averages of 19% and 13% lower than that of forward running, respectively, regardless of BWS and stride frequency. The pairwise comparisons indicated that CoT during backward running was an average of 65% greater than that of forward running only when running at 0% BWS conditions ($P < 0.0003$). However, RPE was not different between running directions ($P > 0.05$).

Additionally, $\dot{V}O_2$ ($P < 0.001$, partial $\eta^2 = 0.925$), HR ($P < 0.001$, partial $\eta^2 = 0.891$), and RPE ($P < 0.001$, partial $\eta^2 = 0.729$) were significantly different between BWS conditions. For example, $\dot{V}O_2$ ($P < 0.001$, partial $\eta^2 = 0.800$), HR ($P < 0.05$, partial $\eta^2 = 0.526$), and RPE ($P < 0.05$, partial $\eta^2 = 0.527$) during running at 20% BWS were 7–14%, 2–7%, and 0.6–1.4 rankings lower than when running at 0% BWS, respectively, regardless of running direction and stride frequency. The pairwise comparisons indicated that CoT during forward running at 20% BWS was 20–24% lower than that of running at 0% BWS ($P < 0.0003$). $\dot{V}O_2$ ($P < 0.001$, partial $\eta^2 = 0.957$), HR ($P < 0.001$, partial

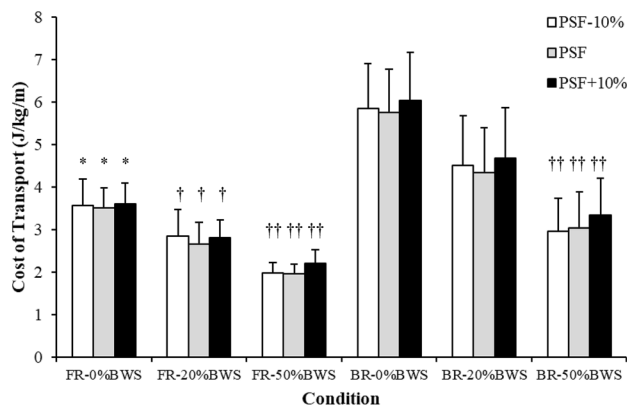
a Oxygen Uptake ^{a, b, c}



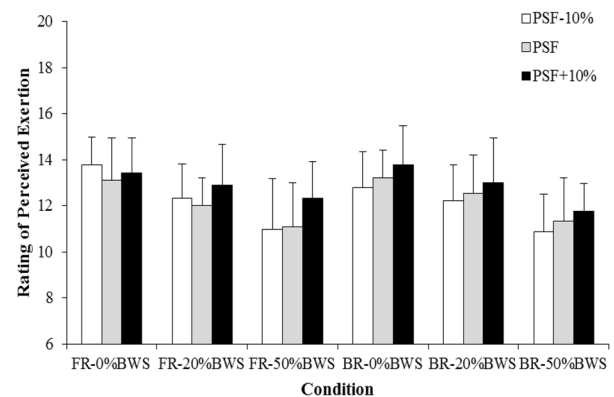
b Heart Rate ^{a, b, c}



c Cost of Transport ^{c, d}



d Rating of Perceived Exertion ^b



e Stride Frequency ^{c, e}

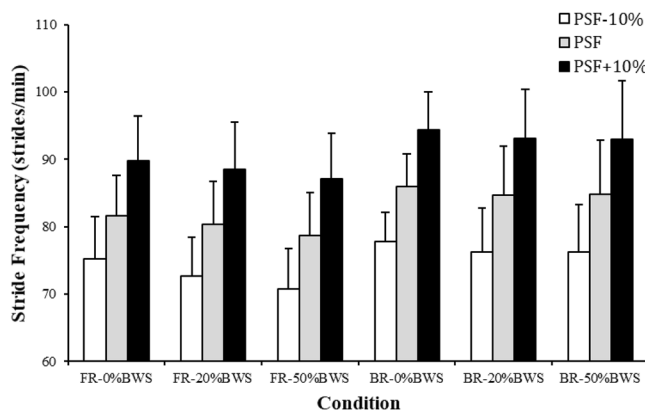


Fig. 4 Oxygen uptake (a), heart rate (b), cost of transport (c), rating of perceived exertion (d), and stride frequency (e) during forward and backward running at different body weight support conditions at various stride frequencies. Data are presented as means ± standard deviation. *FR* forward running, *BR* backward running, *BWS* body weight support, *PSF* preferred stride frequency. ^aSignificant running direction effect, $P < 0.01$. ^bSignificant body weight support effect, $P < 0.001$. ^cSignificant stride frequency effect, $P < 0.05$. ^dSignificant running direction and body weight support interaction effect, $P < 0.01$. ^eSignificant running direction and stride frequency interaction effect, $P < 0.05$. *Significant difference between forward running and backward running at the same body weight support condition, $P < 0.0003$. †Significant difference between 0 and 20% body weight support conditions, $P < 0.0003$. ††Significant difference between 0 and 50% body weight support conditions, $P < 0.0003$

nificant running direction and body weight support interaction effect, $P < 0.01$. ^eSignificant running direction and stride frequency interaction effect, $P < 0.05$. *Significant difference between forward running and backward running at the same body weight support condition, $P < 0.0003$. †Significant difference between 0 and 20% body weight support conditions, $P < 0.0003$. ††Significant difference between 0 and 50% body weight support conditions, $P < 0.0003$

$\eta^2=0.965$), and RPE ($P<0.001$, partial $\eta^2=0.802$) during running at 50% BWS were 22–29%, 14–19%, and 1.1–2.8 rankings lower than when running at 20% BWS, respectively, regardless of running direction and stride frequency. The pairwise comparisons indicated that CoT during forward and backward running at 50% BWS was 39–49% lower than that of running at 0% BWS ($P<0.0003$).

Furthermore, $\dot{V}O_2$ ($P<0.05$, partial $\eta^2=0.390$), HR ($P<0.01$, partial $\eta^2=0.552$), and CoT ($P<0.01$, partial $\eta^2=0.507$) were significantly different between stride frequency conditions. Specifically, $\dot{V}O_2$ ($P<0.05$, partial $\eta^2=0.530$), HR ($P<0.01$, partial $\eta^2=0.677$), and CoT ($P<0.05$, partial $\eta^2=0.608$) during running at PSF+10% were averages of 6%, 4%, and 7% higher than when running at PSF, respectively, regardless of running direction and BWS. However, RPE was not different between stride frequency conditions ($P>0.05$).

Stride frequency

Measured stride frequency (Fig. 4e) was not influenced by the interaction of running direction, BWS, and stride frequency condition (i.e., each stride frequency category) ($P>0.05$). The measured stride frequency was different as designed across stride frequency condition ($P<0.001$, partial $\eta^2=0.994$).

The measured stride frequency was influenced by the interaction of running direction and stride frequency (i.e., each stride frequency category) ($P<0.05$, partial $\eta^2=0.363$). However, the pairwise comparisons indicated that the measured stride frequency was not significantly different between running direction conditions ($P>0.0003$). For example, the measured stride frequency during forward running at 0% BWS was not significantly different from that of backward running at 0% BWS when running at PSF. Furthermore, the pairwise comparisons indicated that the measured stride frequency was not significantly different between BWS conditions ($P>0.0003$). For example, the measured stride frequency during forward running at 0% BWS was not significantly different from that of forward running at 20% BWS when running at PSF.

Muscle activity

Muscle activity from the rectus femoris (Fig. 1a), tibialis anterior (Fig. 1c), and gastrocnemius (Fig. 1d) were not influenced by the interaction of running direction, BWS, and stride frequency ($P>0.05$).

Muscle activity from the biceps femoris (Fig. 1b) was influenced by the interaction of running direction and BWS ($P<0.05$, partial $\eta^2=0.351$) and by the interaction of running direction and stride frequency ($P<0.05$, partial

$\eta^2=0.354$). However, the pairwise comparisons indicated that muscle activity from the biceps femoris was not significantly different between conditions ($P>0.0003$).

Muscle activity from the gastrocnemius was significantly different between running directions ($P<0.05$, partial $\eta^2=0.410$). Specifically, gastrocnemius during backward running was an average of 17% lower than that of forward running, regardless of BWS and stride frequency.

Additionally, muscle activity from the rectus femoris ($P<0.001$, partial $\eta^2=0.678$), tibialis anterior ($P<0.001$, partial $\eta^2=0.736$), and gastrocnemius ($P<0.001$, partial $\eta^2=0.680$) were significantly different between BWS conditions. For example, muscle activity from the rectus femoris ($P<0.01$, partial $\eta^2=0.603$) and tibialis anterior ($P<0.05$, partial $\eta^2=0.520$) during running at 20% BWS were averages of 11% and 10% lower than when running at 0% BWS, respectively, regardless of running direction and stride frequency. Muscle activity from the rectus femoris ($P<0.01$, partial $\eta^2=0.699$), tibialis anterior ($P<0.01$, partial $\eta^2=0.797$), and gastrocnemius ($P<0.001$, partial $\eta^2=0.811$) during running at 50% BWS were averages of 25%, 24%, and 21% lower than when running at 20% BWS, respectively, regardless of running direction and stride frequency.

Furthermore, muscle activity from the rectus femoris was significantly different between stride frequency conditions ($P<0.05$, partial $\eta^2=0.343$), regardless of running direction and BWS. However, the subsequent post hoc test indicated that muscle activity from the rectus femoris was not significantly different between conditions ($P>0.05$).

Preferred Running Speed^{a, b}

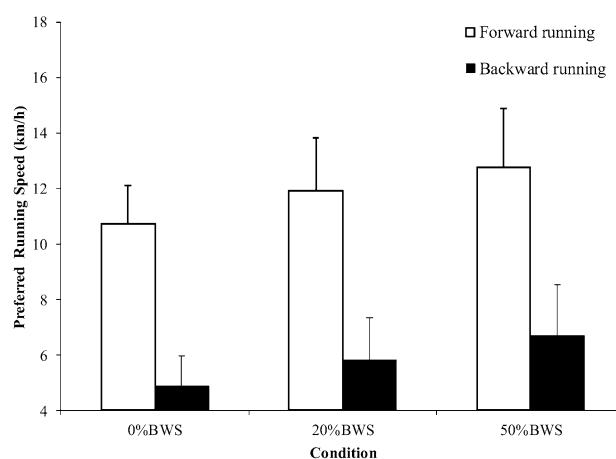


Fig. 5 Preferred running speed during forward and backward running at different body weight support conditions. Data are presented as means \pm standard deviation. BWS body weight support. ^aSignificant running direction effect, $P<0.001$. ^bSignificant body weight support effect, $P<0.001$

Preferred speed

Preferred speed (Fig. 5) was not influenced by the interaction of running direction and BWS ($P > 0.05$).

Preferred speed was significantly different between running directions ($P < 0.001$, partial $\eta^2 = 0.981$). Specifically, preferred speed during backward running was an average of 51% lower than that of forward running, regardless of BWS.

Furthermore, preferred speed was significantly different between BWS conditions ($P < 0.001$, partial $\eta^2 = 0.690$). For example, preferred speed at 20% BWS were an average of 15% higher than when running at 0% BWS ($P < 0.05$, partial $\eta^2 = 0.578$), regardless of running direction. Preferred speed at 50% BWS was an average of 28% higher than when running at 20% BWS ($P < 0.01$, partial $\eta^2 = 0.753$), regardless of running direction.

Discussion

This study was designed to determine the influence of changes in stride frequency, BWS, and running direction on physiological and perceptual responses during running. We observed that manipulations of stride frequency and running direction influenced metabolic costs during running, although RPE was similar between stride frequency conditions and between running direction conditions. Furthermore, a change in BWS influenced metabolic costs, RPE, and lower extremity muscle activity during running. Through systematic manipulations of stride frequency, BWS, and running direction, these observations suggest that lower extremity muscle activity may be an important determinant of RPE during running at a given speed, regardless of stride frequency, BWS, and running direction.

Influence of stride frequency on running mechanics

We observed that a 10% increase in stride frequency from the PSF during forward running produced 1%, 3%, and 10% increases in the $\dot{V}O_2$ for 0% BWS, 20% BWS, and 50% BWS conditions, respectively. Additionally, increasing stride frequency by 10% from the PSF during forward running produced 3%, 6%, and 12% increases in the CoT for 0% BWS, 20% BWS, and 50% BWS conditions, respectively. To our knowledge, no research has investigated the influence of a change in stride frequency on metabolic costs during running with BWS. However, Hamill et al. (1995) reported that metabolic costs during forward running on a treadmill (i.e., 0% BWS) were similar between the PSF and PSF + 10%

conditions, which is in general agreement with our observations of forward running at 0% BWS. Nevertheless, Mercer et al. (2008) reported that the influence of the change in stride frequency from the PSF (e.g., PSF-10%) on metabolic cost during forward running on a treadmill was greater for slower speed (e.g., 3.13 m/s versus 4.02 m/s). We observed that a 10% increase in stride frequency from the PSF during backward running produced 6%, 6%, and 8% increases in the $\dot{V}O_2$ for 0% BWS, 20% BWS, and 50% BWS conditions, respectively. Furthermore, a 10% increase in stride frequency from the PSF during backward running resulted in mean increases in the CoT of 5%, 8%, and 10% for 0% BWS, 20% BWS, and 50% BWS conditions, respectively. Our observations indicate that the impact of an increase in stride frequency on metabolic costs during running was the greatest at the greatest level of BWS, regardless of running direction.

Furthermore, we observed that a change in stride frequency did not influence RPE during running, indicating similar perceived effort during running at different stride frequency conditions. These observations suggest that individuals may not be able to perceive ~12% difference in metabolic costs that resulted from a 10% increase in stride frequency from the PSF during running at a given speed, regardless of BWS and running direction.

Influence of body weight support on running mechanics

We observed that $\dot{V}O_2$, HR, CoT, and muscle activity during running at 20% BWS were on average 10%, 5%, 22%, and 10% lower than when running at 0% BWS, respectively. Furthermore, a 50% increase in BWS from the 0% BWS condition during running produced averages of 25%, 16%, 45%, and 23% decreases in the $\dot{V}O_2$, HR, CoT, and muscle activity, respectively. Our observations suggest that physiological responses during running were influenced by the amount of BWS provided; however, physiological responses during running decreased with increasing BWS in less than direct proportion to BWS provided, regardless of stride frequency and running direction.

Our observations of the decreased lower extremity muscle activity and similar stride frequency during running with increasing BWS suggest that the vertical impulse may have been influenced by the BWS during running. For example, the predicted vertical active peak of ground reaction force value during forward running at 50% BWS (1.5 body weight) was lower than that of running forward at 0% BWS (2.4 body

weight) (Grabowski and Kram 2008). Future biomechanical studies to investigate the external (e.g., ground reaction forces) and internal (e.g., joint compressive forces) forces during backward and forward running with BWS may be helpful in understanding our observations of the non-proportional decrease in physiological responses during backward and forward running with increasing BWS.

We observed that RPE during backward and forward running decreased with increasing BWS within a relatively narrow range (e.g., an average of 0.9 decrease in RPE ranking for a 20% increase in BWS), which is in general agreement with the previous observations (Masumoto et al. 2019). These observations suggest that BWS may have a greater influence on physiological responses than on perceptual responses during backward and forward running.

Influence of running direction on running mechanics

We observed that $\dot{V}O_2$ and HR during backward running were 14–23% and 9–17% lower than when running forward, respectively. Additionally, gastrocnemius muscle activity and preferred speed during backward running were 7–25% and 48–55% lower than when running forward, respectively. During running with BWS at the individual's preferred pace, backward running produced similar metabolic costs to that of forward running (Masumoto et al. 2019). However, preferred speed during backward running was 29–42% lower than when running forward in the previous study (Masumoto et al. 2019). The difference in the relative reduction in the preferred speed account for the different observations of metabolic costs between our study and the previous study (Masumoto et al. 2019).

We observed that changes in stride frequency and BWS during backward and forward running had minimal influence on muscle activity patterns, however, a change in running direction influenced muscle activity patterns during running. For example, a change in running direction influenced biceps femoris muscle activation patterns. In fact, we observed that the biceps femoris produced two peaks (i.e., 50% and 90% of gait cycle) during forward running, although it produced only one peak during backward running at 100% of gait cycle (Fig. 2b).

However, we observed that the rectus femoris muscle activity pattern was unaffected by the change in running direction. In this study, the rectus femoris produced a peak during early stance phase of backward and forward running (Fig. 2a). Nevertheless, the knee flexion during early stance phase of forward running was absent during backward running (Fig. 3). Therefore, we suggest that muscle action of the rectus femoris during stance phase of backward running may possibly be isometric and concentric muscle contractions, although muscle action during forward running may

possibly be eccentric and concentric muscle contractions, regardless of BWS and stride frequency.

To emphasize the coordination pattern between muscles, we plotted rectus femoris versus biceps femoris during running at different running direction, BWS, and stride frequency conditions (Fig. 6). Using these plots, we observed that a change in running direction influenced the biceps femoris and rectus femoris muscle coordination patterns (Fig. 6). Recently, Masumoto et al. (2017) reported that the biceps femoris and rectus femoris muscle coordination patterns during backward and forward running may be different, regardless of BWS (0–80% BWS). These observations of the different biceps femoris and rectus femoris muscle coordination patterns between running directions suggest that backward running may provide a new locomotor stimulus during running.

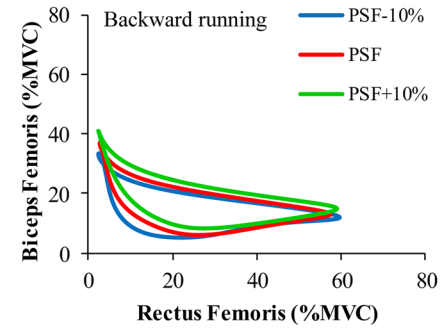
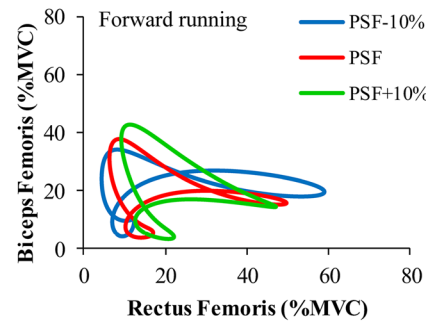
Furthermore, in this study, CoT indicated backward running to be more metabolically costly per unit distance than that of forward running only when running at 0% BWS. Our observations suggest that BWS may attenuate the difference in the metabolic costs per unit distance between backward and forward running, although biceps femoris and rectus femoris muscle coordination patterns may be different between backward and forward running with increasing BWS.

Backward gait training improved forward running performance by approximately 3% (Ordway et al. 2016) and by 30% (Terblanche et al. 2005) in trained runners and in habitually active individuals, respectively. Hoogkamer et al. (2014) hypothesized that the transfer characteristics may be either related to common gains in cardiovascular fitness (or in musculoskeletal properties) or caused by common neural structures. However, there are still remaining question on the actual underlying mechanisms for the transfer of the improvements. Our observations of the (1) greater metabolic costs per distance during backward running than when running forward and (2) different muscle coordination patterns between backward and forward running may contribute to better understand why backward gait training improves forward running performance (e.g., Ordway et al. 2016; Terblanche et al. 2005).

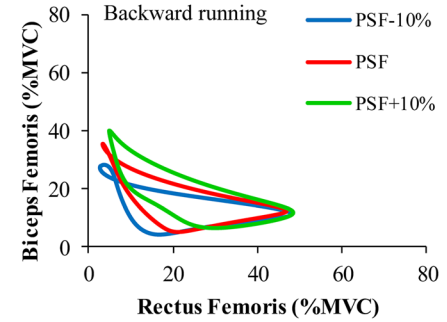
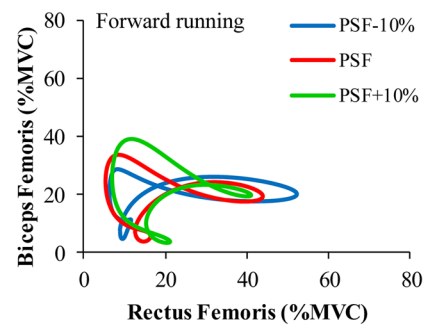
It is not clear how familiarization of stride frequency, running direction, and BWS influence physiological and perceptual responses during running at the individual's preferred pace. For example, time required for metabolic accommodation to forward running with BWS was longer for greater BWS levels (McNeill et al. 2015). However, Masumoto et al. (2019) reported that metabolic costs, RPE, PSF, and preferred speed during backward running and forward running with BWS at the individual's preferred pace were consistent between 4 days. Clarification of the definitive contribution of the task familiarity to these different conditions on preferred running patterns may require additional long-term research.

Fig. 6 Muscle coordination patterns between the rectus femoris and biceps femoris during backward and forward running at different body weight support conditions at various stride frequencies. %MVC average muscle activity as a percentage of that observed during maximal voluntary contraction, *FR* forward running, *BR* backward running, *BWS* body weight support, *PSF* preferred stride frequency

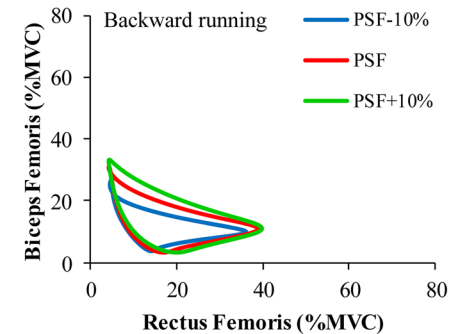
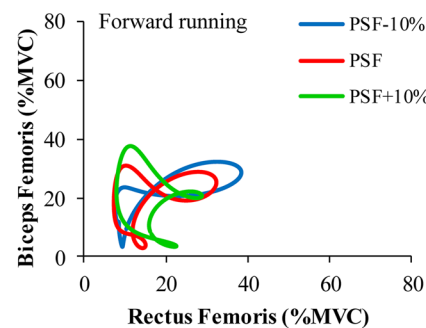
a Running at 0%BWS



b Running at 20%BWS



c Running at 50%BWS



Conclusions

Manipulation of stride frequency during running may have a greater influence on physiological responses than on perceptual responses at a given speed, regardless of running direction and BWS. Individuals who need to increase their physiological demands during running may benefit from a 10% increase in stride frequency from the PSF at a given speed, regardless of BWS and running direction.

Author contributions KM and JAM conceived and designed the research. KM, DD, ACJ, and JAM conducted the experiments. KM and JAM analyzed the data. KM and JAM wrote the manuscript. All authors read and approved the final version of manuscript.

Funding This study was supported by a Grant-in-Aid for Scientific Research (C) from the Japan Society for the Promotion of Science (JSPS KAKENHI Grant Number JP16K01663).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional research committee (University Institutional Review Board of the University of Nevada, Las Vegas, United States, code:1104369-4) and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent Written informed consent was obtained from all individual participants included in the study.

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