# PREFERRED AND ENERGETICALLY OPTIMAL TRANSITION <br> SPEEDS DURING BACKWARD HUMAN LOCOMOTION 

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#### Abstract

Some aspects of backward locomotion are similar to forward locomotion, while other aspects are not related to their forward counterpart. The backward preferred transition speed (BPTS) has never been directly compared to the energetically optimal transition speed (EOTS), nor has it been compared to the preferred transition speed (PTS) during forward locomotion. The purpose of this study was to determine whether the BPTS occurs at the EOTS, and to examine the relationship between the backward and forward preferred gait transition speeds. The preferred backward and forward transition speeds of 12 healthy, young subjects ( 7 males, 5 females) were determined after subjects were familiarized with forward and backward treadmill locomotion. On a subsequent day, subjects walked backward at speeds of $70,80,90,100$, and $110 \%$ of the BPTS and ran backward at speeds of $60,75,90,100$, and $120 \%$ of the BPTS while $\mathrm{VO}_{2}$ and RPE data were collected. After subtracting standing $\mathrm{VO}_{2}$, exercise $\mathrm{VO}_{2}$ was normalized to body mass and speed. For each subject, energy-speed curves for walking and running were fit to the normalized data points. The intersection of these curves was defined as the EOTS which was compared to the BPTS using a paired t-test ( $\mathrm{p}<0.05$ ). RPE and $\mathrm{VO}_{2}$ at the BPTS were also compared between walking and running conditions, and the correlation between BPTS and PTS was calculated. The EOTS $\left(1.85 \pm 0.09 \mathrm{~m} \cdot \mathrm{~s}^{-1}\right)$ was significantly greater than the BPTS $\left(1.63 \pm 0.11 \mathrm{~m} \cdot \mathrm{~s}^{-1}\right)$. Even though RPE was equal for walking and running at the BPTS, $\mathrm{VO}_{2}$ was significantly greater when running. There was a strong correlation $(r=0.82)$ between the BPTS and the PTS. Similar to forward locomotion, the determinants of the BPTS must include factors other than metabolic energy. The gait transition during backward locomotion exhibits several similarities to its forward counterpart.


KEY WORDS: Running, walking, gait transition, preferred transition speed.

## INTRODUCTION

Although walking and running in the backward direction are relatively novel tasks for most people, there are several situations in which these movements are performed regularly. Various sports such as soccer, football, and basketball require the use of backward locomotion in a variety of situations. Backward locomotion is also commonly used in rehabilitation situations as a treatment
modality for injuries such as patellofemoral pain syndrome as a means of maintaining cardiorespiratory fitness while limiting the amount of stress placed on an injured structure (Clarkson et al., 1997; Flynn and Soutas-Little, 1991). For similar reasons, some individuals also employ backward locomotion as a regular exercise regimen.

While some aspects of backward locomotion have been found to be related to forward walking and running, other aspects of backward walking and
running are not similar to forward locomotion. Unlike reverse bicycle pedaling (Bressel et al., 1998) and reverse arm cranking (Langbein and Maki, 1995), in which the metabolic cost $\left(\mathrm{VO}_{2}\right)$ is similar to their forward counterparts, the $\mathrm{VO}_{2}$ of walking or running backward at a given speed has been reported to be significantly greater than the metabolic cost of walking or running forward at the same speed (Chaloupka et al., 1997; Flynn et al., 1994; Williford et al., 1998). Furthermore, it has been demonstrated (Flynn et al., 1994) that there is little correlation between a subject's metabolic energy consumption during forward and backward running. Schott and Decker (1998) determined that when walking backward, subjects choose a stride length/frequency combination that minimizes metabolic energy consumption. This is similar to observations made during forward walking, in which it has been reported (Cavagna and Kaneko, 1977; Minetti and Alexander, 1997) that the metabolic cost of walking a given distance reaches a minimum value at a speed of approximately $1.25 \mathrm{~m} \cdot \mathrm{~s}^{-1}$ and increases curvilinearly as speed is decreased or increased. At similar speeds, vertical ground reaction forces and vertical impulses have been reported to be lower during backward running than forward running (Threlkeld et al., 1989), while other kinetic variables (hip moment and power patterns) have been shown to be similar in magnitude, but opposite in direction to what has been reported during forward running (Devita and Stribling, 1991). One common kinematic variable, the relative stance/swing time has been shown to be similar between forward and backward running, but two other common kinematic variables, stride length and stride frequency, were found to differ considerably between forward and backward running (DeVita and Stribling, 1991; Threlkeld et al., 1989). Although some authors (van Deursen et al., 1998; Winter et al., 1989) have noted similarities in muscle activation patterns between forward and backward walking, others (Thorstensson, 1986; Vilensky et al., 1987) have concluded that muscle activation patterns between forward and backward walking vary distinctly.

Over level ground (and on a treadmill), the speed of locomotion generally determines the gait that is chosen, with running being the gait of choice at higher speeds. During forward locomotion, humans change gaits over a relatively narrow range of speeds, as demonstrated in a number of studies (Beuter and Lefebvre, 1988; Brisswalter and Mottet, 1996; Diedrich and Warren, 1995; 1998; Hreljac, 1993; 1995; Kram et al., 1997; Mercier et al., 1994; Minetti et al., 1994; Thorstensson and Roberthson, 1987; Turvey et al., 1999) that have reported the preferred transition speed (PTS) to be between 1.89 $\mathrm{m} \cdot \mathrm{s}^{-1}$ and $2.16 \mathrm{~m} \cdot \mathrm{~s}^{-1}$. Although not verified
experimentally, several researchers (Alexander, 1989; Cavagna and Franzetti, 1986; Grillner et al., 1979; Heglund and Taylor, 1988; Hoyt and Taylor, 1981; McMahon, 1985) have suggested that the gait transition during human forward locomotion is an energy saving mechanism, making the unsubstantiated assumption that gait changes occur spontaneously at the energetically optimal transition speed (EOTS). Others (Thorstensson and Roberthson, 1987; Mercier et al., 1994) have suggested that it is doubtful that the choice of transition speed during human locomotion is based upon energy considerations since energetic demands cannot be sensed by subjects in acute situations. The available experimental evidence appears to agree that factors other than metabolic energy effectuate the gait transition. It has been demonstrated in several studies (Brisswalter et al., 1996; Hreljac, 1993; Hreljac et al., 2002; Minetti et al., 1994; Raynor et al., 2002) that the gait transition during forward locomotion actually occurs at speeds that are significantly lower than the EOTS, even though subjects perceive walking at the PTS to be more difficult than running at the PTS (Hreljac, 1993), as measured by a rating of perceived exertion (Borg, 1973).

It is unclear whether the gait transition in the backward direction occurs for similar reasons as have been hypothesized during forward locomotion. In a recent study (Kram, 1999), it was suggested that the gait transition during backward locomotion may be an energy saving mechanism as originally speculated for forward locomotion, but the evidence supporting this speculation is inconclusive. The primary purpose of this study was to test the hypothesis that the gait transition during backward locomotion is an energy saving mechanism. It was hypothesized that the intersection of the energyspeed curves for walking and running backward (definition of EOTS) would occur at a significantly greater speed than the backward preferred transition speed (BPTS), as observed during forward locomotion. A secondary purpose of this study was to determine whether there is a correlation between the forward and backward preferred transition speeds.

## METHODS

Participants in this study were 12 (seven males, five females) young, healthy college students (age $=26.2$ $\pm$ SD 4.1 yr ), who were free from musculoskeletal injury or disease at the time of the study. Prior to participation, subjects signed informed consent forms, reiterating the basic procedures and intent of the study, as well as warning of any potential risks involved as a result of participation. On the first of
two testing sessions, the backward preferred transition speed (BPTS) and the preferred transition speed (PTS) in the forward direction were determined. This session occurred on a day prior to the collection of metabolic data to ensure that fatigue was not a factor during metabolic data collection. During each testing session, subjects wore their own running footwear. Subjects who were unfamiliar with forward or backward treadmill locomotion were habituated prior to the first testing session by walking and running forward and backward at a variety of speeds on the treadmill for a period of approximately 15 minutes (more if requested). Previous researchers (Charteris and Taves, 1978; Schieb, 1986; Wall and Charteris, 1980) have shown that 15 minutes of treadmill accommodation is sufficient to reduce the variability in kinematic variables.

To determine the BPTS of each subject, the treadmill was initially set to a speed at which subjects would be able to walk backward comfortably (approximately $1.0 \mathrm{~m} \cdot \mathrm{~s}^{-1}$ ). Subjects were instructed to mount the treadmill and utilize the gait which felt most natural. After a decision period of approximately 30 s , the treadmill was stopped and the subject dismounted. If the subject indicated that walking was the preferred gait at that speed, the treadmill speed was increased by about $0.1-0.2 \mathrm{~m} \cdot \mathrm{~s}^{-1}$ before the subject remounted. Again, subjects were instructed to determine the gait which felt most natural at the new speed. This process continued until a speed was reached at which the subject indicated that running was the most natural gait at that particular speed. That speed was defined as the backward walk to run transition speed. By starting the treadmill at a high enough speed to ensure that subjects ran ( $>2.0 \mathrm{~m} \cdot \mathrm{~s}^{-1}$ ), then decreasing the treadmill speed incrementally (as described earlier), the backward run to walk transition speed was determined. The entire process was repeated three times in random order. In order to obtain a single value, the average of the backward walk to run and run to walk transition speeds was defined as the BPTS. The PTS was found in an identical manner while subjects walked or ran in the forward direction, with slightly greater initial speeds than in the backward direction. A similar procedure has been utilized in several earlier studies (Hreljac, 1993; 1995; Hreljac et al., 2001; Raynor et al., 2002).

During the second testing session, subjects ran at speeds of $60 \%, 75 \%, 90 \%, 100 \%$, and $120 \%$ of the BPTS, and walked at speeds of $70 \%, 80 \%, 90 \%$, $100 \%$, and $110 \%$ of the BPTS while $\mathrm{VO}_{2}$ data were collected. For each of the 10 separate experimental conditions, which were randomly ordered, an indirect calorimetry method was utilized to quantify
the rate of oxygen consumed $\left(\mathrm{VO}_{2}\right)$ and energy expenditure during the experimental conditions. A metabolic cart, equipped with a pneumotach, paramagnetic oxygen analyzer and infrared carbon dioxide analyzer was used to quantify the volume of oxygen expired and consumed, and the volume of carbon dioxide produced (TrueMax 2400 Metabolic Measurement System, Parvo Medics, Consentius Technologies, Utah). Prior to testing, oxygen and carbon dioxide analyzers were calibrated using medically certified oxygen and carbon dioxide gas concentrations. The volume of inspired air was measured with a Ventilation Measurement Module calibrated prior to each test using a 3 L calibration syringe. Each subject was outfitted with a two way low resistance breathing valve connected by large bore tubing to a 4 L mixing chamber for the determination of expired volume and gas concentrations.

Average $\mathrm{VO}_{2}$ data were acquired in 30 second intervals until one minute after steady state was reached. Steady state was defined as the point at which a "leveling off" of the $\mathrm{VO}_{2}$ value occurred, identified by three consecutive 30 second readings within approximately $5 \%$ of each other. A single value of $\mathrm{VO}_{2}$ was calculated for each condition by averaging the last three readings obtained during a trial. Between trials, subjects were allowed as much rest as desired. A value of "standing" $\mathrm{VO}_{2}$ was obtained prior to any of the exercise trials by monitoring oxygen consumption during four minutes of quiet standing. The "exercise" $\mathrm{VO}_{2}$ for each condition was found by subtracting the standing, V $\mathrm{O}_{2}$ from the gross $\mathrm{VO}_{2}$ value obtained during the trial. The actual value utilized for all subsequent analyses was the exercise $\mathrm{VO}_{2}$.

A rating of perceived exertion (RPE) score was determined after two minutes of each condition. A printed 15 point graded category scale of perceived exertion (Borg, 1973), mounted on a cardboard background was exhibited to subjects after two minutes of each of these conditions. Subjects were instructed to point to the number on the scale that most accurately corresponded to their overall sense of effort.

Prior to statistical analyses, all $\mathrm{VO}_{2}$ data were normalized to body mass and speed of locomotion to obtain a metabolic cost of transport in units of $\mathrm{ml} \cdot \mathrm{kg}^{-}$ ${ }^{1} \cdot \mathrm{~km}^{-1}$. Curves for individual subjects as well as average curves of all subjects combined were fit to the five normalized data points for both walking and running with speed along the abscissa of the curve and metabolic energy consumption $\left(\mathrm{VO}_{2}\right)$ values along the ordinate. Both linear and quadratic models were tested for each condition, using a least squares regression method. The model which fit the data points better was utilized in each case. The

Table 1. Mean ( $\pm \mathrm{SD}$ ) of $\mathrm{VO}_{2}$ and RPE for walking and running at the BPTS.

|  | Condition |  |  |
| :--- | :---: | :---: | :---: |
| Variables | Walking | Running | Effect Size |
| VO $_{\mathbf{2}}\left(\mathbf{m l}^{-\mathbf{k g}^{-1}} \mathbf{k m ~}^{-1}\right.$ ) | $180.3(36.0)$ | $233.6(25.8)^{*}$ | 1.72 |
| RPE (Borg Scale) | $12.7(2.3)$ | $12.7(2.8)$ | 0.0 |

* value is significantly greater than value for walking condition ( $\mathrm{p}<0.05$ ).
intersection of the fitted walking and running curves was defined as the EOTS for each subject.

Using paired t-tests, three comparisons were made. The calculated EOTS was compared to the BPTS to examine whether subjects changed gaits at the metabolically optimal speed; normalized $\mathrm{VO}_{2}$ values were compared between walking and running at the BPTS to determine which gait required more metabolic energy at the BPTS; and RPE values were compared between walking and running at the BPTS to determine which gait was perceived to be more difficult at the BPTS. For each comparison, an effect size (ES) was calculated. The ES is a standardized estimate of the magnitude of the differences between groups, and is considered to be a "useful way to describe the meaningfulness of findings" (Thomas et al., 1991, p. 344). The ES for each comparison was calculated using the equation for ES presented by Cohen (1988, p. 20). In mathematical terms, this equation states:

$$
\begin{equation*}
E S=\left(M_{1}-M_{2}\right) / S D \tag{1}
\end{equation*}
$$

where $M_{1}$ and $M_{2}$ are the mean values of the variables being compared, and SD is a pooled standard deviation. In addition to these comparisons, the Pearson correlation coefficient (r) between the BPTS and the PTS was determined.

## RESULTS

The average BPTS of the 12 subjects was $1.58 \pm$ $0.16 \mathrm{~m} \cdot \mathrm{~s}^{-1}$, while the average PTS was $1.99 \pm 0.20$ $\mathrm{m} \cdot \mathrm{s}^{-1}$. The BPTS and the PTS were fairly strongly correlated to each other, with a Pearson correlation coefficient (r) of 0.82 calculated between these two variables.

The metabolic cost of running at the BPTS was significantly greater than the $\mathrm{VO}_{2}$ while walking at the BPTS, even though there was no difference between the RPE while walking at the BPTS and running at the BPTS (Table 1). Figure 1 reveals that the RPE was lower during walking than running at speeds less than the BPTS, but greater during walking than running at speeds higher than the BPTS.

For both backward walking and running conditions, a quadratic model was found to fit all individual $\mathrm{VO}_{2}$-speed data sets better than a linear model, although there were two subjects for which neither model fit well. For all other subjects, the quadratic model was a good fit, with the coefficient of determination $\left(\mathrm{r}^{2}\right)$ being greater than 0.88 in all cases. For the average data of all 12 subjects, a quadratic model was an excellent fit for both walking and running, with an $\mathrm{r}^{2}$ value of 0.99 calculated for both conditions (Figure 2). The minimum value for the average walking curve occurred at a speed of approximately $1.00 \mathrm{~m} \cdot \mathrm{~s}^{-1}$ ( $63 \%$ of BPTS), while the minimum value of the average running curve occurred at a speed of approximately $1.98 \mathrm{~m} \cdot \mathrm{~s}^{-1}$ ( $125 \%$ of BPTS ).


Figure 1. Average RPE values at each speed and gait.


Figure 2. Fitted energy-speed curves for walking and running.

For two subjects for whom neither model fit well, an EOTS could not be determined since the fitted curves for walking and running did not intersect. For the remaining 10 subjects, the average BPTS $\left(1.63 \pm 0.11 \mathrm{~m} \cdot \mathrm{~s}^{-1}\right)$ was significantly less than the average EOTS $\left(1.85 \pm 0.09 \mathrm{~m} \cdot \mathrm{~s}^{-1}\right)$ as determined by the intersection of the individual walking and running $\mathrm{VO}_{2}$-speed curves. In relative terms, the EOTS of these 10 subjects occurred at a speed that was $13 \%$ greater than their BPTS. In the average curve (Figure 2), which included data from all 12 subjects, the EOTS was $1.83 \mathrm{~m} \cdot \mathrm{~s}^{-1}$ which is $16 \%$ greater than the average BPTS of all 12 subjects $\left(1.58 \pm 0.16 \mathrm{~m} \cdot \mathrm{~s}^{-1}\right)$. The effect size (ES) calculated from the differences between these variables (BPTS and EOTS) was 2.2. Previous researchers (Cohen, 1988; Thomas et al., 1991) have defined an ES of greater than 0.8 to be a large ES.

## DISCUSSION

The speed variables reported in this study were generally in agreement with similar variables reported in earlier studies. The BPTS of subjects in the current study was comparable to the BPTS found in the only study (Kram, 1999) which had previously calculated this value ( $1.58 \mathrm{~m} \cdot \mathrm{~s}^{-1}$ vs. $1.56 \mathrm{~m} \cdot \mathrm{~s}^{-1}$ ). The EOTS reported by Terblanche et al. (2003) was similar to that found in the current study. These researchers (Terblanche et al., 2003) reported an EOTS of between 6.4 and $6.7 \mathrm{~km} \cdot \mathrm{~h}^{-1}$ ( 1.77 to 1.86 $\mathrm{m} \cdot \mathrm{s}^{-1}$ ), while the average EOTS in the current study was $1.83 \mathrm{~m} \cdot \mathrm{~s}^{-1}$. The PTS of subjects in the current study $\left(1.99 \pm 0.20 \mathrm{~m} \cdot \mathrm{~s}^{-1}\right)$ was in the mid-range of values which have been reported previously (from $1.89 \mathrm{~m} \cdot \mathrm{~s}^{-1}$ to $2.16 \mathrm{~m} \cdot \mathrm{~s}^{-1}$ ) by other researchers (Beuter
and Lefebvre, 1988; Brisswalter and Mottet, 1996; Diedrich and Warren, 1995; 1998; Hreljac, 1993, 1995; Kram et al., 1997; Mercier et al., 1994; Minetti et al., 1994; Thorstensson and Roberthson, 1987; Turvey et al., 1999). Even though backward locomotion was a relatively novel task for all subjects, there was a fairly strong correlation ( $\mathrm{r}=$ 0.82 ) found between the BPTS and the PTS. This may be an indication that the transition speeds in both directions are influenced by related factors.

In many aspects, the results of this study have demonstrated that backward locomotion is similar to forward locomotion. In addition to a strong correlation between the BPTS and the PTS, the quadratic relationship found in the $\mathrm{VO}_{2}$-speed curve for backward walking was similar to the corresponding curve reported for walking forward (Hreljac et al., 2002). In the current study, the minimum value of the curve occurred at a speed of approximately $63 \%$ of the BPTS (see Figure 2). In the forward walking study (Hreljac et al., 2002), the minimum of the $\mathrm{VO}_{2}$-speed curve was found to occur at a speed of approximately $62 \%$ of the PTS. It is not surprising that the energy-speed curves for walking forward and backward could both be best represented by quadratic functions, but it is interesting to note that the metabolic cost of backward walking follows an almost identical (but offset) pattern as forward walking when speed is expressed relative to the transition speed. Gait transitions have often been referenced as a point of comparison between animals of various sizes since gait transitions are considered to be a physiologically similar event (Alexander, 1989; Biewener and Taylor, 1986; Heglund and Taylor, 1988; Rubin and Lanyon, 1982) in animals. The
results of the current study may indicate that the gait transition during human backward locomotion is a physiologically similar event to the gait transition during forward locomotion.

The quadratic relationship found in the fitted $\mathrm{VO}_{2}$-speed curve (Figure 2) for running appears to be different from the linear relationship that has generally been reported between these variables during forward running (Brisswalter and Mottet, 1996; Cavagna et al., 1976; Hreljac, 1993; Minetti et al., 1994). All of these studies, however, based their results on the examination of a wide range of running speeds. In a recent investigation (Hreljac et al., 2002) which examined the $\mathrm{VO}_{2}$-speed relationship during low running speeds (comparable to the backward running speeds tested in the current study), it was found that a quadratic relationship also existed, although the minimum $\mathrm{VO}_{2}$ of the energyspeed curve for forward running was found to occur at a speed of approximately $96 \%$ of the PTS. In the present study, the minimum value of the fitted $\mathrm{VO}_{2^{-}}$ speed curve for backward running occurred at a speed of approximately $125 \%$ of the BPTS, and the fitted energy-speed curve sloped upward much more steeply than the corresponding curve in forward locomotion. From the perspective of energy-speed curves, it appears that there are greater differences between forward and backward running compared to forward and backward walking, as observed by Devita and Stribling (1991) when comparing kinematic variables.

Similar to what has been reported during forward locomotion (Brisswalter et al., 1996; Hreljac, 1993; Hreljac et al., 2002; Minetti et al., 1994; Raynor et al., 2002), the average EOTS during backward locomotion was found to be significantly greater than the average BPTS, with a large effect size noted between the variables. Unlike forward locomotion, however, the RPE when walking and running at the BPTS did not differ from each other. At speeds of less than the BPTS, the RPE of backward walking was lower than the RPE of backward running (Figure 1). Terblanche et al. (2003) reported similar speeds $\left(<6.0 \mathrm{~km} \cdot \mathrm{~h}^{-1}\right.$ or 1.67 $\mathrm{m} \cdot \mathrm{s}^{-1}$ ) to those found in the current study at which the RPE of walking backward was less than the RPE of running backward. It should be noted that Terblanche et al. (2003) examined speeds in 0.5 $\mathrm{km} \cdot \mathrm{h}^{-1}$ intervals. In forward locomotion (Hreljac, 1993), the RPE when walking at the PTS was found to be significantly greater than the RPE when running at the PTS despite the fact that the energetic cost of running at the PTS was significantly greater than the energetic cost of walking at the PTS.

During forward locomotion, the PTS has been hypothesized (Hreljac, 1995; Hreljac et al., 2001) to be triggered primarily by localized fatigue in the
relatively small dorsiflexor muscles as walking speed increases. It has been suggested (Hreljac, 1995) that the localized muscular stress as subjects walk at speeds near the PTS is responsible for the higher RPE values during walking than running at the PTS. The RPE has been shown (Ekblom and Goldbarg, 1971; Noble et al., 1973) to be influenced by two factors, a "local" factor related to the feeling of strain in the working muscles, and a "central" factor involving the perception of ventilatory and circulatory stress. Since several larger muscles were shown to increase their activity as gait was changed to a run while maintaining a relatively low activation level (Hreljac et al., 2001), the energetic cost could easily increase while the perception of effort decreases. In backward locomotion, the sense of effort appears to be directly related to the gait transition, as the "cross-over" point in RPE between walking and running corresponds exactly with the BPTS (Figure 1). This suggests that there may also be a "local" factor that influences the RPE during fast backward walking. Since the EOTS is considerably greater than the BPTS during backward locomotion, it is possible that local discomfort or fatigue in a relatively small muscle group when walking backward at speeds near the BPTS may trigger a gait change to a run, thereby reducing the stress in the smaller muscle group, but placing more stress on larger (and thus more metabolically active) muscles. If these larger muscles are not activated to a level near maximum when running backward, then it is possible that the perception of effort may not increase as rapidly as the increase in metabolic energy consumption. The most likely muscle group that would be fatigued during fast backward walking, and thus lead to a gait change, would be the dorsiflexors, but the results of this study could not verify this speculation.

## CONCLUSIONS

It can be concluded that the gait transition during backward locomotion is not an energy saving mechanism. Although subjects perceived that walking and running at the BPTS were equally strenuous, considerably less metabolic energy was used during backward walking than running at the BPTS. Factors other than metabolic energy must be considered as possible determinants of the gait transition during backward locomotion.

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## KEY POINTS

- The backward preferred transition speed $\left(1.63 \pm 0.11 \mathrm{~m} \cdot \mathrm{~s}^{-1}\right)$ was significantly less than the energetically optimal transition speed $\left(1.85 \pm 0.09 \mathrm{~m} \cdot \mathrm{~s}^{-1}\right)$, similar to what is observed during forward locomotion.
- RPE was equal for walking and running at the backward preferred transition speed.
- There was a strong correlation $(\mathrm{r}=0.82)$ between the backward and forward preferred transition speeds.
- Similar to forward locomotion, the determinants of the BPTS must include factors other than metabolic energy.


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