

William J. McDermott · Richard E. A. Van Emmerik  
Joseph Hamill

## Running training and adaptive strategies of locomotor-respiratory coordination

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**Abstract** It has been suggested that stronger coupling between locomotory and breathing rhythms may occur as a result of training in the particular movement pattern and also may reduce the perceived workload or metabolic cost of the movement. Research findings on human locomotor-respiratory coordination are equivocal, due in part to the fact that assessment techniques range in sensitivity to important aspects of coordination (e.g. temporal ordering of patterns, half-integer couplings and changes in frequency and phase coupling). An additional aspect that has not received much attention is the adaptability of this coordination to changes in task constraints. The current study investigated the effect of running training on the locomotor-respiratory coordination and the adaptive strategies observed across a wide range of walking and running speeds. Locomotor-respiratory coordination was evaluated by the strength and variability of both frequency and phase coupling patterns that subjects displayed within and across the speed conditions. Male subjects (five runners, five non-runners) locomoted at seven different treadmill speeds. Group results indicated no differences between runners and non-runners with respect to breathing parameters, stride parameters, as well as the strength and variability of the coupling at each speed. Individual results, however, showed that grouping subjects masks large individual differences and strategies across speeds. Coupling strategies indicated that runners show more stable dominant couplings across locomotory speeds than non-runners do. These findings suggest that running training does not change the strength of locomotor-respiratory coupling but rather how these systems adapt to changing speeds.

**Keywords** Running and breathing rhythms · Locomotor-respiratory coordination

### Introduction

The coordination between locomotory and breathing rhythms has been described in many species of animals. Many display very tight coordination between limb rhythms and breathing rhythms due to mechanical constraints in the thoracic region. Horses, for example, have an almost fixed breathing to stride ratio of 1:1. This results from the constraints put on the thoracic region from the repeated impact loading when the forelimbs strike the ground (Alexander 1993; Bramble and Carrier 1983; Young et al. 1992). They are, however, able to change gait patterns as in an energetic ‘gearing’ mechanism. Another constraint on breathing during locomotion that has been proposed is a ‘visceral piston’ that is formed by the cyclical motion of the visceral mass being somewhat out of phase with the musculoskeletal frame. This may account for the tight 1:1 frequency coupling found in other animals such as the hopping wallaby (Baudinette et al. 1987). When two rhythmical components of a system interact in a way so that one (locomotory rhythm) imposes its rhythm on the other (respiration) the first is said to have entrained the other. Entrainment is defined as frequency and phase locking (Kelso 1995) and in the previous examples it is caused by mechanical constraints.

Mechanical constraints during locomotion do not always cause entrainment of the respiratory rhythm but sometimes disrupt it. Lizards, for example, breathe by contracting the intercostal muscles on both sides of the body at the same time. Their locomotion, however, is accomplished by means of a lateral undulating gait pattern, where the intercostal muscles of either side of the body must contract in an alternating fashion. This conflict is described as a speed-dependent axial constraint that results in inadequate lung ventilation during locomotion (Owerkowicz et al. 1999).

Besides mechanical constraints, interaction between locomotory and respiratory rhythms may have a neurogenic source. Evidence of this has come from animal

W. J. McDermott (✉) · R. E. A. Van Emmerik · J. Hamill  
Department of Exercise Science, University of Massachusetts,  
110 Totman Building, Amherst, MA 01003, USA  
E-mail: wm@exscsci.umass.edu

preparation studies. Coupling between central pattern generators for locomotory and respiratory rhythms has been identified at the level of the spinal cord in the rabbit (Viala 1986; Viala and Freton 1983; Viala and Vidal 1978). The extent to which these interactions appear in humans is unknown. Because of our upright posture and bipedal locomotion, however, we are not forced into 1:1 couplings and locomotion is normally not thought of as interfering with ventilation. In fact, a wide range of frequency couplings between movement and respiratory rhythms has been observed in humans, including coupling ratios of 1:1, 2:1, 3:1, 3:2, 4:1, and 5:2, with the 2:1 ratio being used most often (Bernasconi and Kohl 1993; Bramble and Carrier 1983; Paterson et al. 1986; Takano 1995). These coupling ratios often show as more variable than those observed in the animal literature.

Although humans appear to have greater variability in respiration during locomotion, there is still evidence of entrainment occurring to varying degrees. It has been suggested that tighter coordination between limb rhythms and respiration may reduce the metabolic cost of a movement (Bramble and Carrier 1983; Hill et al. 1988; Paterson et al. 1986), or at least the perception of the workload (Bonsignore et al. 1998). In light of this, several researchers have investigated the coordination between locomotory and respiratory rhythms to assess if entrainment increases the economy of movement (Bernasconi and Kohl 1993; Garlando et al. 1985; van Alphen and Duffin 1994) and whether it occurs more in experienced athletes than in novices (Bernasconi et al. 1995; Bramble and Carrier 1983; Kohl et al. 1981). Limb frequency and exercise workload have also been suggested as factors that affect entrainment (Bechbach and Duffin 1977; Bernasconi and Kohl 1993; Bernasconi et al. 1995; Jasinkas et al. 1980; Paterson et al. 1986). In this literature, however, one finds considerable disagreement in the extent to which these rhythms are coordinated and what factors affect the level of coordination. One possible reason for this is that definitions of entrainment and, therefore, the predefined criteria chosen to identify entrainment differ from study to study and vary in sensitivity from very sensitive to very crude.

An aspect that has not received much attention in the literature is the adaptability of the locomotory-respiratory coordination to changes in task constraints. Recent developments in nonlinear and complex systems approaches have led to an emphasis on variability and nonlinear qualitative changes in physiological patterns. This perspective has proven fruitful in understanding complex waveforms of rhythmic physiological systems in health and disease (Glass 2001; Mackey and Milton 1987) as well as the coordination between certain physiological rhythms necessary for homeostasis such as cardiovascular and respiratory rhythms.

In the area of motor control, the relative phase between oscillatory components in the system is used as a critical variable to address issues of stability and change in coordination (Schöner and Kelso 1988). Based on this approach, the observed qualitative behavior is

dependent on the cycling frequency of the components, the level of symmetry between the components, and the nature of the coupling between them. Symmetry refers to the similarity between the natural frequencies of each of the oscillators. Asymmetry is considered important in the emergence of multi-frequency couplings (so-called polyrhythms that are similar to those reported between locomotion and breathing) as well as for specific transitions from one state to another.

Although asymmetrical systems can, under certain conditions, show entrainment at frequency couplings other than 1:1, it is more often the case that there are systematic shifts in the relative phase (phase slippage) with attraction to certain phase relations as well as a loss of entrainment characterized by constant increasing or decreasing phase relations (phase wandering) (Kelso 1995; Kelso and Jeka 1992; Turvey et al. 1986). Intermittency is often observed in these systems where the behavior of the system jumps between multiple coordinative states. These observed behaviors are also dependent on the level of coupling between the oscillators. There are various mechanisms that underlie the coupling between components in a system. These mechanisms can be mechanical (Bramble and Carrier 1983), physiological (Pompe et al. 1998), neurological (Viala 1986), or informational (Schmidt et al. 1990) in nature. In general, strong coupling can result in entrainment or tendencies toward certain phase relations despite the effects of asymmetry.

The purpose of this study is to employ methods derived from dynamical systems principles to assess stability and change in the coordination between locomotory and respiratory rhythms. This stability and change in coordination will be examined by manipulating subject constraints in the form of running training level and task constraints in the form of locomotory pattern (walking vs running) and locomotory speed. The method used in this study goes beyond many of the previous studies on locomotory-respiratory coordination, in that it includes: (1) an investigation of entrainment based on frequency and phase information that is not obtained independently; (2) temporal changes in coupling patterns rather than overall phase histograms; and (3) an analysis of coordination properties without pre-set criteria for entrainment.

At the basis of our method is the relative phase between each breath and stride cycle. The frequency coupling between these rhythms is determined geometrically by plotting the relative phase time series against itself with different time lags in the form of so-called return maps (Kelso and Jeka 1992). Assessing frequency coupling in this manner allows the identification of different coordinative modes, the strength and variability of these modes as well as transitions between modes. The level of phase attraction within these modes is determined by the dispersion of points from the line of identity in the appropriately lagged maps. As most of the research indicates that experience results in an increase in economy and that stronger coordination may increase

running economy (Bernasconi and Kohl 1993; Garlando et al. 1985), it was hypothesized that a higher level of running experience would lead to stronger coordination between these rhythms during both walking and running. In addition to coupling strength, we also investigated how the coordination between respiration and locomotion adapts to different locomotion patterns and speeds as a result of running experience.

## Methods

### Subjects

Ten male volunteers whose ages ranged between 20 and 31 years were divided into two groups, one with and one without running training experience. The runner group ( $n = 5$ ) ran an average of  $41.2 (32.2) [\text{mean (SD)}] \text{ km week}^{-1}$  over the previous 6 months with a range of  $16\text{--}97 \text{ km week}^{-1}$ . All of the non-runners ( $n = 5$ ) participated in recreational physical activity such as cycling and basketball. All subjects gave informed consent prior to testing according to University policy.

### Apparatus

Subjects walked and ran on a motorized treadmill. Heart rate was monitored using a wireless heart rate monitor (Polar CIC, Mass., model Vantage XL). Breath cycle events (end-inspiration, EI) were obtained using ribcage plethysmography. The changes in the circumference of the subject's chest wall were measured by a device consisting of a strain gauge mounted on spring steel fixed snugly around the chest just under the arms by an adjustable strap. The strain gauge was powered and amplified by a preamplifier (Grass Instrument, model 7P1 K) and an amplifier (Grass Instrument, model 7DAF). The timing of heel strike (HS) was acquired by a force-sensing resistor (Interlink Electronic, model 406) placed on the outside of the right shoe under the heel. Leg and arm movements were recorded by uniaxial accelerometers (Coulbourn T45-10 amplified by a Coulbourn S72-25 transducer coupler) placed on the styloid process of the ulna and the distal aspect of the tibia. Breath, HS, and accelerometer signals were sampled at 200 Hz by a 12-bit analog-to-digital converter (ComputerBoards, Mass.), interfaced with a microcomputer. Data were collected and stored using a custom written software program in DasyLab data acquisition software (Dasytec). Analysis of data was performed using custom written software in Matlab (The Math Works, Mass.).

### Procedure

After being instrumented, the subject stood quietly for approximately 1 min while his heart rate was recorded. This was used as a baseline measure for rest between conditions. The subject then warmed up by running on the treadmill for 5–10 min at a comfortable, self-selected pace. Upon completion of the warm-up, the next step was determining the preferred walking speed. This was done by first instructing the subject to find a comfortable pace at which he would walk for 5–10 min. He then began walking on the treadmill at a pace selected by the experimenter and signaled the experimenter to either increase or decrease the speed until the preferred pace was found. The treadmill was stopped and the process was repeated at least three times until he was able to identify the same speed (within  $0.2 \text{ km h}^{-1}$ ) on successive trials. The last three speed values were then averaged and used in the experiment. Preferred running speed was determined similarly with the instructions to find a comfortable running pace.

The preferred transition speed (PTS) was then determined as the average of the walk–run and run–walk transition speeds. The walk–run transition speed was determined first. The subject was instructed to utilize the gait that felt most comfortable and the treadmill was started at a speed at which the subject could easily walk. The speed was increased by  $0.2 \text{ km h}^{-1}$  every 10 s and the speed at which the subject switched from a walk to a run and remained running was recorded. The run–walk transition speed was determined in a similar manner, except the treadmill was started at an easy running speed and the speed was decreased by  $0.2 \text{ km h}^{-1}$  every 10 s.

Next, each of the following test conditions was administered in a random order: (1) walking at 40% below preferred walking speed (PW–40%); (2) walking at 20% below preferred walking speed (PW–20%); (3) walking at preferred walking speed (PW); (4) walking at preferred transition speed (W–PTS); (5) running at preferred transition speed (R–PTS); (6) running at preferred running speed (PR); and (7) running at 20% above preferred running speed (PR + 20%). Before beginning each test condition, subjects rested in a seated position until their heart rate was at or below the baseline value. The conditions began when the subject was on the treadmill at the determined speed and lasted 5 min. Data were collected for the entire duration of each condition.

### Data analysis

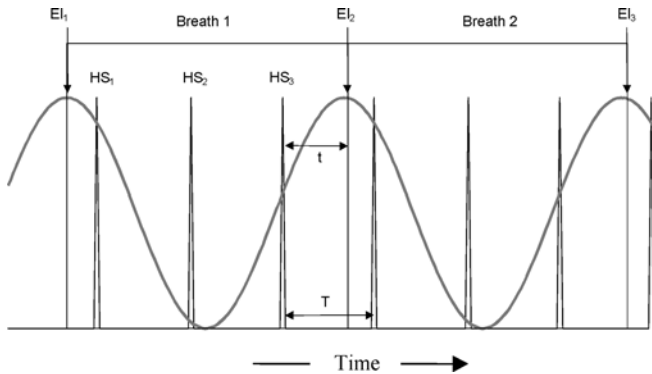
The last 2.5 min of each 5-min trial was used in the data analysis. HS was determined based on the foot switch. Before breath cycles were examined, the influences of arm movement and vertical accelerations on the strain gauge apparatus that occurred during locomotion had to be removed. Frequency components of the breath signal, arm accelerometer, and leg accelerometer signals were compared using amplitude spectra estimated through a fast Fourier transformation (FFT) algorithm. The signals were smoothed using a Hanning window (Press et al. 1990). Based on the amplitude spectra, it was assumed that the arm movements occurred at frequencies equal to or greater than the leg frequency (i.e. stride frequency) and that the breathing frequencies were always lower than those of the stride frequency. Therefore, the extraneous signals in the breathing signal were removed by setting all frequencies that were equal to and greater than the stride frequency to zero amplitude. The breath signal was then reconstructed using an inverse FFT with unwinding. Breath cycles were then determined by choosing peaks corresponding to EI of each breath. Relative phase was calculated between the breathing rhythm and HS. Using the time series of relative phase, it was possible to identify specific frequency couplings. Frequency couplings were defined as ratios of HS per breath occurring in more than one consecutive cycle.

### Calculation of relative phase

Discrete relative phase (RP) was calculated between each right HS within a breath cycle and EI as follows:

$$\text{RP} = \frac{t + nT}{T} \times 360^\circ, \quad (1)$$

where  $n$  is the number of complete stride cycles between each HS and the subsequent EI,  $T$  is the time duration of the stride in which EI occurred, and  $t$  is the time lag from the beginning of the stride in which EI occurred to the subsequent EI. To illustrate this calculation of relative phase, simulated breath and HS signals are plotted in Fig. 1. The HS signal in this example is a pulse wave with a period of 100 ms and breath signal in this example is a sine wave with a period of 300 ms with a 75-ms shift. To calculate RP for each HS in breath 1,  $T$  is equal to 100 ms,  $t$  is 75 ms, and  $n$  is equal to 2, 1, and 0 for HS<sub>1</sub>, HS<sub>2</sub>, and HS<sub>3</sub> respectively. The resulting RP values are therefore  $990^\circ$ ,  $630^\circ$ , and  $270^\circ$  respectively. Note that if there are three HS within one breath as in this example, the RP value of each HS will fall within the specific ranges:



**Fig. 1** Simulated breath signal (sinusoid) and heel strike (HS) signal (pulse). One-breath ranges from end-inspiration (EI) to the next EI.  $T$  is the period of the stride in which EI occurred, and  $t$  is the time lag from the beginning of the stride in which EI occurred and the subsequent EI

$$\begin{aligned} 1080^\circ &\geq \text{RP}_1 > 720^\circ \\ 720^\circ &\geq \text{RP}_2 > 360^\circ \\ 360^\circ &\geq \text{RP}_3 > 0^\circ \end{aligned} \quad (2)$$

According to this relationship, the relative phase value of the first HS ( $\text{RP}_1$ ) in the breath cycle will fall in the highest range and the last ( $\text{RP}_3$  in this example) will fall in the lowest range (between  $0^\circ$  and  $360^\circ$ ). Example time series of RP from three subjects during the PR + 20% condition are plotted in Fig. 2. R1 was a recreational runner averaging 16 km week<sup>-1</sup>, R4 was a competitive runner training about 97 km week<sup>-1</sup> and NR1 was a non-runner. These data were chosen to illustrate different degrees of locomotor-respiratory coupling that were observed within and between the groups.

#### Identification of frequency couplings

The following specific frequency couplings were identified using the present method: 6:1, 5:1, 5:2, 4:1, 3:1, 3:2, 2:1, and 1:1. As per our definition, each coupling comprises at least two consecutively occurring frequency ratios that have a specific number of HS per breath and repeat with a specific periodicity. These criteria were assessed by constructing return maps of the RP data with lags ranging from 1 to 6 and identifying the appropriate two-dimensional ranges within the maps that identify each frequency coupling (Eq. 2). In Fig. 3A is series of return maps constructed from the example RP data depicted in Fig. 2. R1 (Fig. 3A, left panel)

displays two groupings of points that converge to the line of identity when plotted with a lag of 2 or 4, indicating a rhythm of period 2 or 4. R4 (Fig. 3A, middle panel) displays a tendency for a period 2 rhythm because of the convergence of points to the line of identity with a lag of 2. There is, however, no distinct grouping of points along the line of identity as seen in R1. NR1 (Fig. 3A, right panel) shows no convergence to the line of identity with any of the lags used, indicating that either there is no periodicity in the relative phase data or that it is made up of several different rhythms.

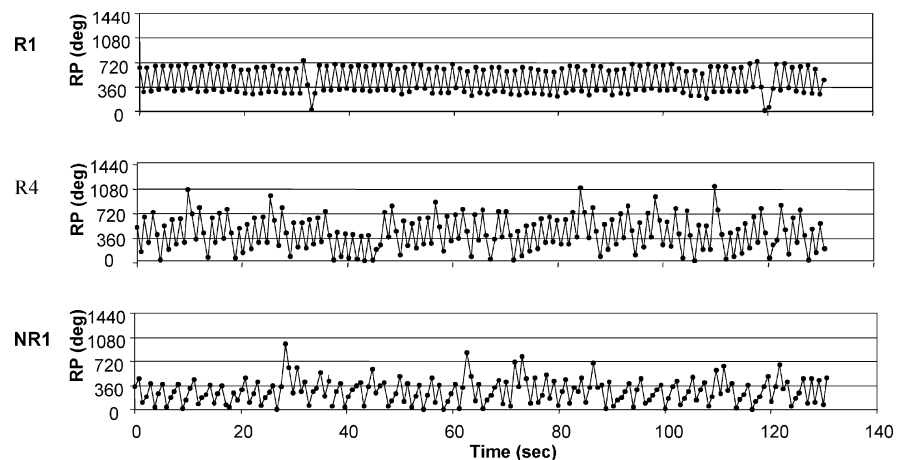
The integer and half-integer couplings were identified in the present study by their unique range and lag combinations by which each frequency coupling was identified. The integer couplings (1:1, 2:1, 3:1, 4:1, 5:1, 6:1) were identified by the integer lag and the range corresponding to the integer multiple of 360. Other couplings (3:2 and 5:2) comprise multiple ratios that repeat in an alternating fashion and therefore are identified by the same lags as integer couplings but different ranges. For example, a 3:2 coupling is made up of alternating 2:1 and 1:1 ratios. In this case, the range of RP of the first HS of the 2:1 component used to identify this coupling is  $360\text{--}720^\circ$  and will repeat every third HS (lag of 3). In contrast, a 3:1 coupling would be identified by RP in the range of  $720\text{--}1080^\circ$ , also with a lag of 3. The return maps ensured that frequency couplings were identified as ratios that occurred at least twice in consecutive cycles.

#### Assessment of frequency coupling

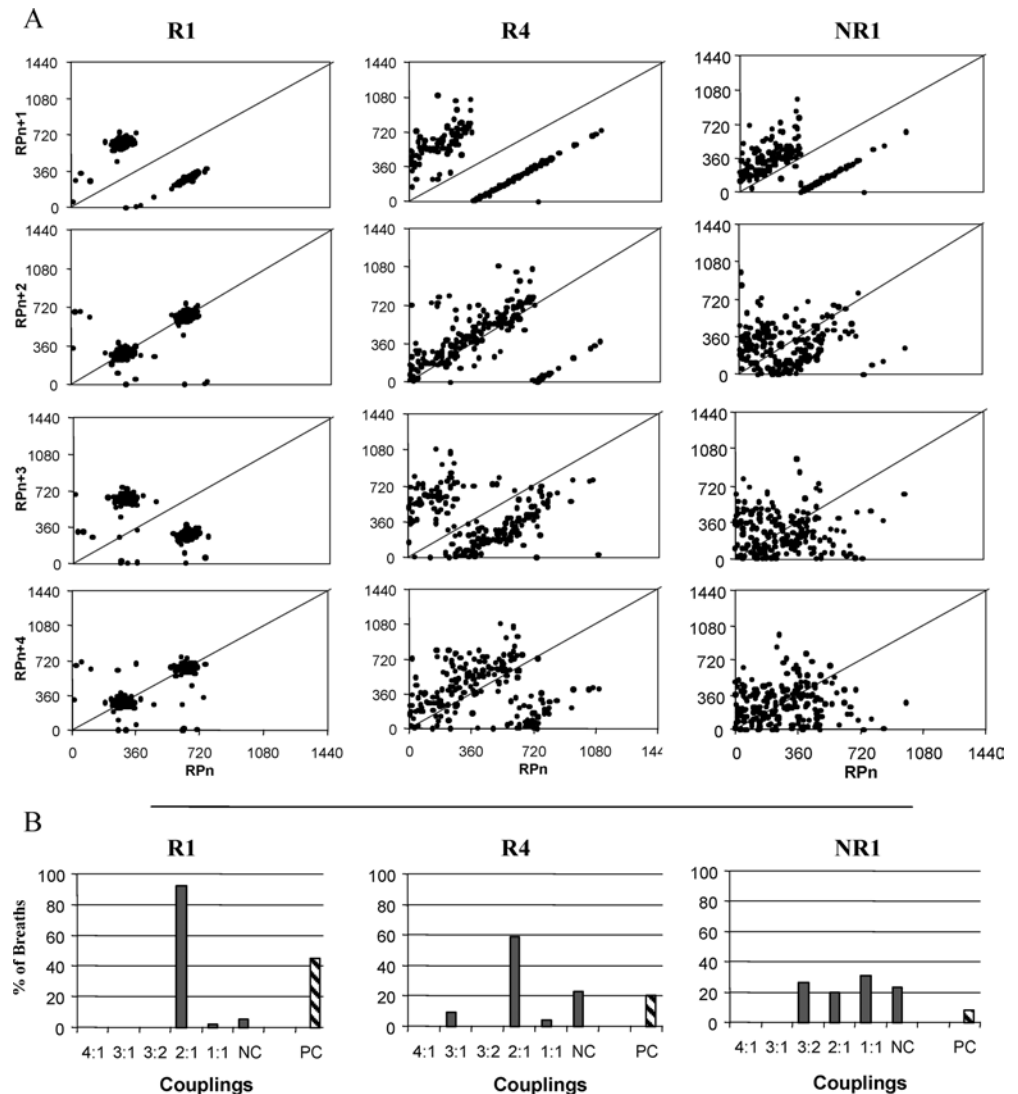
Each frequency coupling identified was quantified by the percentage of total breath cycles in which it occurred. Those breath cycles that did not have consecutive integer or half-integer ratios were designated non-couplings (NC). Figure 3B shows the extent of each of the frequency couplings that were identified in the series of return maps for each subject. R1 shows a very strong 2:1 coupling, R4 used 2:1 as the dominant coupling as well, but to a lesser extent, and NR1 showed the weakest coupling, utilizing 1:1 as the dominant coupling. Variability in coupling for these subjects is seen by the occurrences of NC and couplings other than the dominant. Although coupling variability can be attributed primarily to the occurrence of NC in all three of these subjects, the non-runner (NR1) shows a significant contribution of the second dominant coupling to the variability. Additionally, the higher mileage runner (R4) showed less strength in coupling than the less-trained runner (R1).

Three variables obtained from these figures were used to quantify the frequency coupling in each condition: (1) the percentage of breaths occurring with the dominant frequency coupling (DC) was used as a measure of the strength of coupling; variability in coupling was measured by (2) the percentage of breaths occurring with the second dominant coupling (SC) (i.e. the ratio with the second highest occurrence); and (3) the percentage of breaths occurring with NC.

**Fig. 2** Time series of relative phase (RP) for three subjects during the running at 20% above preferred running speed (PR + 20%) condition. R1 and R4 are runners and NR1 is a non-runner



**Fig. 3** **A** Example return maps for the relative phase data presented in Fig. 2. For each map, each relative phase value ( $RP_n$ ) is plotted versus the relative phase value with the appropriate time lag ( $RP_{n+1}$ ,  $RP_{n+2}$ ,  $RP_{n+3}$ ,  $RP_{n+4}$ ). The data for each of the three subjects (left, middle, right panels) is plotted with time lags of 1–4 (rows). **B** Solid bars percentage of breaths occurring at each frequency coupling and non-coupling (NC) based on lag and range criteria; hatched bars strength of phase coupling (PC)



#### Assessment of phase coupling

Phase coupling (PC) between EI and the preceding HS was assessed by the dispersion of points from the line of identity in the lowest range of each of the return maps (between 0 and 360). These data were all identified as frequency couplings (NC were not included). Perfect PC (no variability) would be evident if all points were lying on the line of identity and variability in PC would be shown as deviations from this line. Therefore, PC was quantified by first calculating the Euclidian distance of each point ( $d_n$ ) from the line of identity and then summing the weighted distances (wd):

$$wd_n = \begin{cases} 1 - \frac{|d_n|}{40 \cos(45^\circ)}, & d_n \leq 40 \\ 0, & d_n > 40 \end{cases} \quad (3)$$

$$PC = \frac{\sum_{n=1}^m wd_n}{m} \times 100, \quad (4)$$

where  $m$  is the number of points in the lowest range of each of the return maps. This measure essentially weights points with distances from the line of identity that are greater than or equal to 40° by zero and those with distances less than 40° according to their distance and expresses their sum as a percentage of highest possible sum. Perfect PC would therefore result in a PC = 100% of breaths and the amount of variability in the PC is proportional to the decrements from 100%. The resulting PC values for the example data are also plotted in Fig. 3B.

#### Statistical analysis

Statistical analysis was performed by means of a repeated measures analysis of variance. Comparisons during walking were made with one between subject factor (group, runners vs non-runners) and one within subject factor (speed, with four levels: PW-40%, PW-20%, PW, W-PTS). Comparisons during running were made with one between subject factor (group, runners vs non-runners) and one within subject factor (speed, with three levels: R-PTS, PR, PR+20%). Comparisons were made on the following dependent variables: mean breath period and mean stride period, and the extent of the DC, SC, NC, and PC. The criterion alpha level was set at 0.05. Significant effects were evaluated using Tukey's post hoc analysis.

## Results

### Speed, breath, and stride parameters

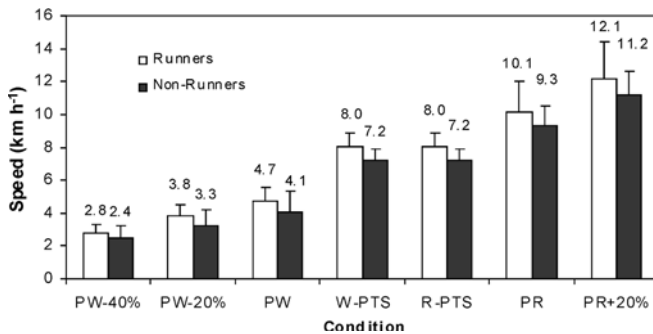
The mean PTS for the runner group was 8.0 (0.8) km h<sup>-1</sup>. The non-runner group had a mean PTS of 7.2 (0.7) km h<sup>-1</sup>. The mean PW were 4.7 (0.8) and 4.1 (1.2) km h<sup>-1</sup> and the mean PR were 10.1 (1.9) and 9.3 (1.21) km h<sup>-1</sup> for the runner and non-runner groups,

respectively. Figure 4 depicts the resulting average treadmill speeds used for the seven experimental conditions.

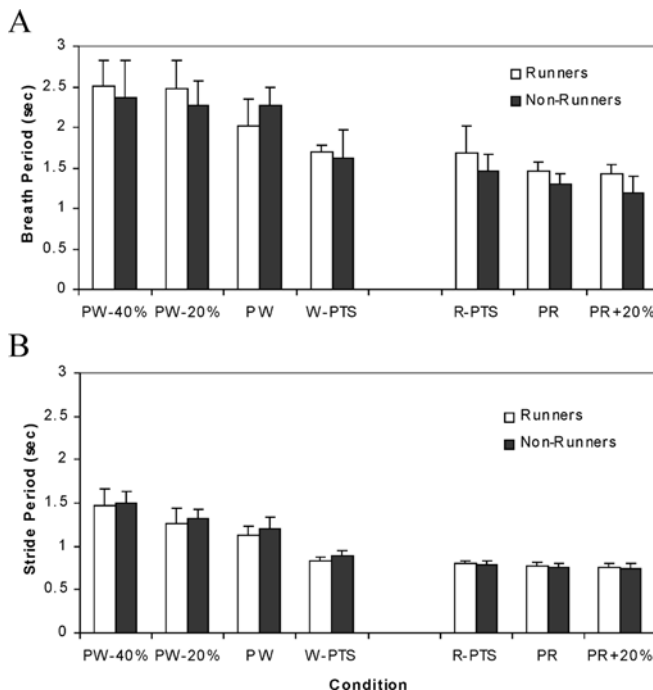
Mean breath periods calculated from EI intervals and stride periods calculated from HS intervals are plotted in Fig. 5. For both variables, there were no significant group or speed effects during either walking or running ( $P > 0.5$ ).

### Frequency coupling

Across all subjects and conditions, a frequency coupling of 2:1 was the dominant coupling during 71.1% of the



**Fig. 4** Average speeds within each group used for all seven conditions. *PW* is preferred walking speed; *PW-20%* and *PW-40%* are walking at 20% and 40% below preferred walking speeds, respectively; *W-PTS* is walking at the preferred walk-run transition speed; *R-PTS* is running at the preferred walk-run transition speed; *PR* is preferred running speed; and *PR+20%* is running at 20% above the preferred running speed. Error bars represent one standard deviation of the group mean



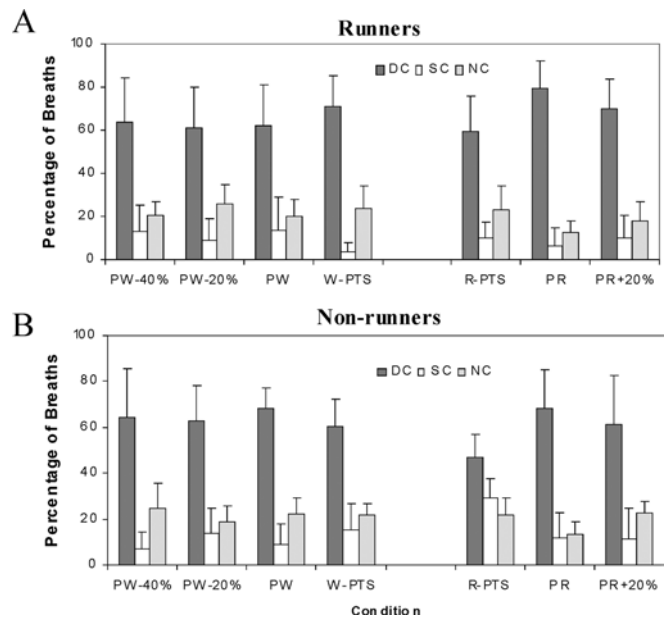
**Fig. 5** Averages across subjects of breath period (A) and stride period (B) in each group during the last 2.5 min of each condition. Error bars represent one standard deviation of the group mean

trials followed by 3:2 at 17.1% and 1:1 at 10%. The only other coupling observed was 5:2 which was a second dominant coupling in 5.7% of the trials.

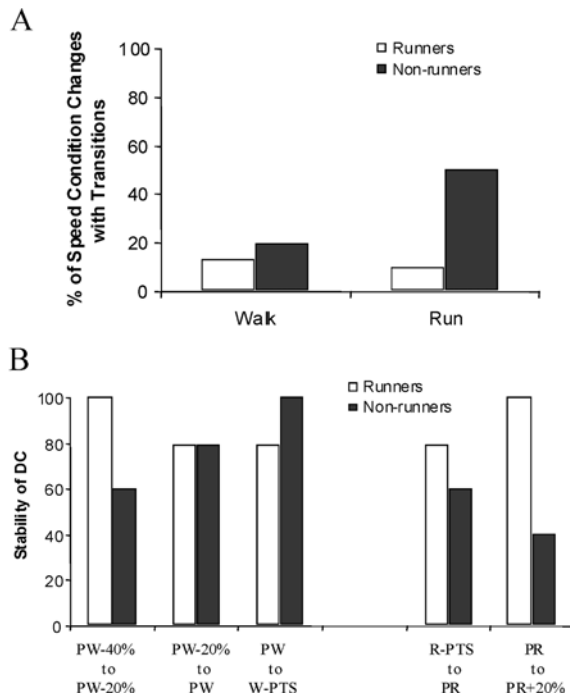
Group averages of strength of coupling (independent of the coupling ratio) as well as the contributions of SC and NC are plotted in Fig. 6. There were no group differences found in any of the frequency coupling measures during walking and running, indicating that frequency coupling strength and variability were unaffected by running training level ( $P > 0.05$ ). There were also no significant speed effects on the strength and variability of frequency coupling during walking ( $P > 0.05$ ). During running, however, there were significant effects of speed ( $P < 0.04$ ) in all three frequency coupling measures. Post hoc analysis indicated that the frequency coupling during the R-PTS was less strong than during the other two running speeds, with a greater variability in coupling.

### Stability of couplings

Because the strength and variability of frequency coupling measures are independent of the frequency coupling being used, we further examined the individual subject's frequency coupling response across the walking and running conditions. The stability of the frequency couplings was inferred from the transitions (or lack thereof) in the DC between speed conditions. A transition was identified each time there was a different DC utilized between two consecutive speed conditions. Figure 7A illustrates the differences between the runner and non-runner groups in terms of the percentage of speed condition changes that had transitions for walking



**Fig. 6** Contributions (in percentage of breaths) of dominant frequency coupling (DC), second dominant coupling (SC), and non-couplings (NC) during each of the conditions for the runners (A) and non-runners (B)



**Fig. 7A** Percentage of speed condition changes for each group that had transitions in the DC. **B** Average stability of DC determined by the percentage of subjects that maintained the DC across each condition change

and running. These data are the result of the total number of transitions that each group had divided by the total number of speed condition changes. The number of condition changes being 15 for the walking conditions (5 subjects  $\times$  3 condition changes) and ten for the running conditions (5 subjects  $\times$  2 condition changes). On average, the runners show fewer transitions in the DC, particularly during running. We also calculated a measure of the stability of the DC for each condition as the percentage of subjects within each group that maintained the DC. This is plotted in Fig. 7B. Besides further illustrating the greater stability of the runners' DC during running, this figure indicates that the non-runners show the most stable couplings while walking at the fastest speeds and the least stable couplings at the fastest running speeds. The runners, on the other hand, show the most stable couplings at the slowest walking and fastest running speeds.

The nature of these transitions is more apparent upon the examination of the individual subjects' frequency coupling responses to the speed conditions. In Fig. 8, the percentage of each frequency coupling and NC is plotted as a function of walking and running speed for the runners (left panel) and non-runners (right panel). The frequency couplings show two distinct patterns in response to locomotory speed: the first was a stable DC where no transitions were observed over the walking or running conditions. This was seen in four of the runners (R1, R2, R3, R4) and three of the non-runners (NR2, NR3, NR5) during the walking conditions and four of the runners (R2, R3, R4, R5) and two of the

non-runners (NR3, NR4) during the running conditions. During these conditions, variability in frequency coupling was primarily due to the presence of NC. The second pattern observed was a gradual transition in the DC as a function of increasing locomotory speed that indicates less stable frequency coupling. This transition in almost all cases occurred over several conditions and when present during walking (R5, NR1, NR4) was characterized by the DC changing from 1:1 to 2:1 using an intermediate 3:2 coupling. When present during running (NR1, NR2, NR5), it was characterized by a 2:1 changing to a 1:1 again using a 3:2 intermediate. In these cases, additional variability in coupling was due to a greater contribution of the SC. The SC also became the DC in the next greater speed condition.

### Phase coupling

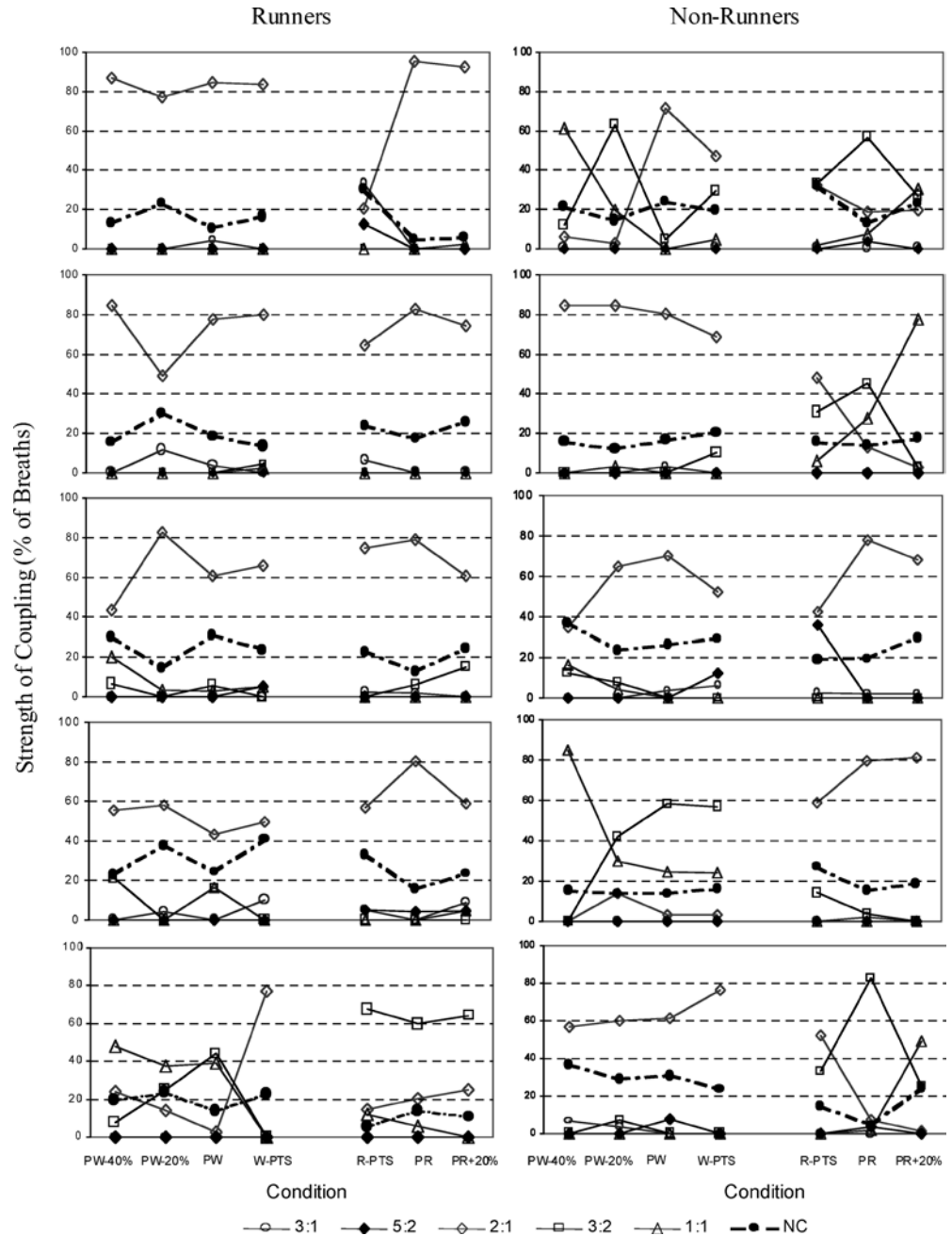
Group averages of PC are plotted in Fig. 9. Despite several subjects showing high strength of frequency coupling values, the overall PC for both groups was quite low. PC values averaged around 20% across both groups and all conditions and ranged from 1.2% to 46.3%. There were no significant group or speed effects during walking or running. There was, however, a significant group by speed interaction during walking ( $P < 0.02$ ). The runners had greater PC at the lower and higher walking speeds compared with the preferred speed whereas the non-runners had lower PC at these speeds compared with preferred speeds.

### Discussion

The analysis technique used in the present study identified the frequency and phase coupling behavior between locomotory and respiratory rhythms in which multiple frequency couplings are present. Quantification of the coordination was accomplished by calculating the extent to which specific couplings or NC occur within a condition and to what extent the phase relation varies. The analysis is not on predefined states of coordination (i.e. entrainment) but assesses the coordination by focusing on the systems' dynamics within and across conditions.

The focus of this experiment was on elucidating changes in frequency and phase coupling strength and variability between locomotory and respiratory rhythms as a function of running training. Contrary to the hypothesis, the group results suggest that there is little difference in terms of strength of coupling and variability in coupling between runners and non-runners. In fact, both groups tended to maintain a DC for about 60% of the breath cycles and maintained about 20% PC across conditions. This aspect of the results support those of Bernasconi et al. (1995), who reported that running experience had no influence on the degree of coupling (as measured by the extent to which the same phase relation occurred) while running below the

**Fig. 8** Percentage of breaths occurring at each frequency coupling for all subjects (subjects 1–5 are plotted from top to bottom). A stable DC was observed in 4/5 runners and 3/5 non-Runners during walking and 4/5 runners and 2/5 non-runners during running. Where the gradual transitions were observed, the DC changed from 1:1 to 3:2 to 2:1 during walking, and 2:1 to 3:2 to 1:1 during running

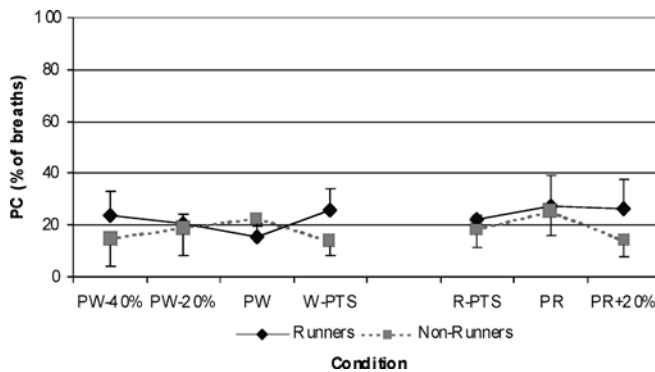


anaerobic threshold. Results from Bramble and Carrier (1983) suggested that coordination between breathing and stride rhythms increases as a function of running training or experience level and Kohl et al. (1981) suggest the same for cycling. Although an explanation for this may be that cycling imposes different constraints on the coordination of these rhythms than running does, it is more likely that the differences in findings between the present study and those of Bramble and Carrier (1983) and Kohl et al. (1981) are the result of differences in the methods used. Kohl et al. (1981) were concerned with entrainment only, which was defined as ratios of pedal cycles to breath cycles that were within  $0.1^\circ \text{ breath}^{-1}$  of an integer ratio and occurred in at least six breaths.

Besides the limitation of identifying only a narrow range of behavior, their method is insensitive to ratios other than integer ratios. The present study shows the importance of non-integer ratios (e.g. 3:2) and their role in transitions in coordination. Bramble and Carrier (1983), on the other hand, presented ratios of mean strides per minute to mean breaths per minute calculated over 45–65 strides, which provides only global assessments of the coordination.

The method in the present study focused on the relative behavior of these systems over breath-by-breath time scales using a phase resolution of  $360^\circ$ . The various frequency and phase coupling found within and across the conditions provide additional insight into the pref-





**Fig. 9** Group averages of PC strength expressed as a percentage of breaths. Error bars represent one standard deviation of the group mean

erential states of coordination of these systems. Although the group averages indicated no differences between the groups with respect to the strength of coupling, the individual data presented suggest that grouping subjects according to running training masks marked individual differences. The time series of relative phase presented in Fig. 2 shows behaviors consistent with phase locking and phase slipping which, in turn, result in varying degrees of frequency coupling. The example data for subjects R1 and R4 during the PR+20% condition indicate further that, in fact, running training in terms of weekly kilometers or competition is not an indicator of the strength of coupling. This aspect of the individual subject data, therefore, supports our overall group findings.

The results from the walking conditions indicated that frequency coupling is unaffected by changes in speed. Despite a difference in measures, this is in general agreement with van Alphen and Duffin (1994) who reported no difference in the extent that stepping events occurred within 0.1 s of consecutive breath events over two walking workloads. Contrary to the present findings, Raßler and Kohl (1996) reported a significant increase in the degree of coordination with increasing treadmill speeds over similar walking speeds. There are two possible explanations for this discrepancy. The first is based on methodological differences. Measurement of respiration in the present study was indirect through ribcage plethysmography and did not include the contribution of the abdomen to breathing. It seems unlikely that this would alter our results greatly, because we compared EI from the ribcage with EI recorded from a differential pressure transducer connected to a facemask worn during the same run for one subject. The number of cycles identified from the ribcage was only marginally lower than the number identified from the facemask and slightly time lagged by a consistent amount. A more likely explanation is the differences in the assessment of coordination. Raßler and Kohl (1996) based their coordination measure on the distribution of the relative phase between HS and EI and HS and end-expiration. The degree of coordination was quantified by the sum of specific bins of the distribution and expressed relative to

the total number of observations. Although the calculations of relative phase in the current study were different, the difference in results may be explained by the temporal constraint that the two-dimensional return maps place on the assessment of coupling. PC in the current study is a function of the variations of pairs of relative phase points from the line of identity in the return maps. These points are paired based on the periodicities of the data identified within the return maps. Therefore, the variations from this line in the appropriately lagged map represent variability across consecutive breath cycles. Histograms of relative phase reveal how often a value of relative phase is observed during a trial but not the temporal ordering of the values. Therefore, an interpretation of the combined results of Raßler and Kohl (1996) and the present study is that certain phase relations are observed more often with increasing treadmill speed while walking but that the temporal ordering of these phase relations remains unaffected.

A switch of the focus from the strength of coupling to the frequency coupling response within and across these conditions reveals distinct patterns and indicates differences between the groups based on the stability of the DC. This stability is inferred from the nature of transitions (or lack thereof) in the coordination between these rhythms. The *no transition* response was observed mostly in the runner group, particularly during running, thus indicating that the dominant frequency coupling was stable for these subjects across the range of speeds. The *gradual transition* was observed mostly in the non-runner group, where each different condition had a systematic effect on the strength of the DC. From lower to higher running speeds the 2:1 coupling decreased in strength, giving way to the 3:2 coupling followed by the 1:1 coupling. During walking, the transition occurred from 1:1 to 3:2 to 2:1. The larger influence of speed on the frequency coupling during these conditions indicates that the frequency coupling was less stable for these subjects. The role of the SC seems to be that of a second preferred or competing state and is mostly related to potential transitions in the DC. The role of the NC in these data is not associated with the stability of the DC. This is indicated by the relatively constant level of NC across all subjects compared with the SC. NC are probably associated with shorter duration fluctuations in the stride frequency due to transient instabilities or short duration variability in breathing frequency due to respiratory drive variability.

The difference in stability of the frequency coupling between the runners and non-runners reflects differences in the adaptive strategies of the locomotory and respiratory systems of these subjects. For example, as the treadmill speed was increased the subjects' stride length and/or frequency must adapt in order to remain on the treadmill. Since the metabolic demand also changes with treadmill speed, breathing frequency and tidal volume must adapt to meet the ventilatory requirements. Stable DC reflect strategies characterized by concomitant changes (or lack of changes) in both breathing and stride

frequencies. Gradual transitions in the DC reflect strategies where the frequency of one component is affected to a different extent than the other component. If the adaptive strategy that results in a stable DC across speed conditions is optimal (because it was observed more often in the runner group) then it can be beneficial for training or rehabilitation programs where movement efficiency is an important factor.

In addition to utilizing a novel method for identifying various coordination patterns within each condition, the present study focused on the changing or lack of changing of these patterns across the locomotory speeds. The importance of this approach in studying the coordination between breathing and movement is also illustrated by Ebert et al. (2000), who investigated the coordination between breathing and forearm movements while subjects tracked a sinusoidal target at various frequencies. Entrainment bands (ranges of tracking frequencies) were identified for different frequency ratios. The width of these entrainment bands in conjunction with the strength of coordination within each tracking frequency discriminated between 'good coordinators' and 'poor coordinators'.

In conclusion, group data suggest that running training affects neither the frequency coupling nor the phase coupling strength between locomotory and breathing rhythms during short bouts of treadmill locomotion. Individual data, however, indicate that the lack of statistically significant differences between the groups is not due to a uniform response by both groups but due to marked individual responses. Additionally, the coupling responses across conditions suggest that a difference between the groups lies in the stability of the DC. This difference in stability may reflect a greater level of adaptability of the locomotor and/or respiratory systems to changing speed and metabolic demands and this adaptability comes about as a result of training.

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