THE EFFECT OF LOCOMOTOR-RESPIRATORY COUPLING ON RUNNING ECONOMY AT SUB-LACTATE THRESHOLD RUNNING SPEEDS

by

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A THESIS

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Locomotor-respiratory coupling (LRC), the phase-locking of gait and respiratory cycles, has been heavily researched. Previous studies reported on the effects of LRC ratios and their variability on various biomechanical and physiological processes, but no study has explicitly examined the effect of increasing workload on LRC. The purpose of the study was to develop a more precise testing protocol and to document the relationship between average LRC ratio and LRC ratio variability on VO_2 and running economy at increasing workloads. Eight subjects completed a modified lactate threshold test wherein the timing of their gait and respiratory cycles were recorded as well as oxygen uptake. Results indicated a significant decrease in average LRC ratio with increasing workload ($p<0.001$), with average LRC ratios appearing at integer, half-integer, and non-integer values with increasing workload. There was no significant difference between root mean square error in LRC ratio variabilities at increasing workloads ($p=0.725$). Findings indicate recreational runners do not favor whole or half-integer LRC ratios, and instead LRC decreases with a linear trend with increasing workload.

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Introduction

Running is an important form of locomotion for many animals. Whether an animal runs to escape predators, catch prey, or migrate, the ability to run efficiently is critical to its survival. It is well established that locomotor-respiratory coupling is essential to effective running in a wide range of vertebrates, including horses, wallabies, and birds (Baudinette et al., 1987; Bramble et al., 1983; Boggs, 2002; Funk et al., 1993; Simons, 1999).

The term "locomotor-respiratory coupling" (LRC) refers to the phase-locking of footfall and breathing rhythms such that a constant number of respiratory cycles occur during successive gait cycles (Daley, 2013). In quadrupeds, LRC is facilitated by the inertial movement of soft-tissues and thoracic muscles. The tissue movement and thoracic muscle activation caused by running motions generate a "visceral piston" that alters intraabdominal and intrathoracic pressures in such a way that inspiration and expiration are virtually "locked" to certain phases of gait (Carrier, 1990; Carrier, 1991; Carrier, 1996; Codd et al., 2005; Deban and Carrier, 2002).

Though the vast majority of animals limit their runs to short sprints, some animals, like wolves, horses, and humans, regularly run long distances. Unlike most running animals that have a narrow range of sustainable running speeds, humans are extraordinarily adept endurance runners and can run great distances at a wide range of speeds. Numerous studies have attributed humanity's broad range of energetically sustainable running speeds to a unique combination of qualities, including bipedal locomotion and profuse sweating (Bramble and Carrier, 1983; Bramble and Lieberman, 2004; Carrier et al., 1984; Lieberman et al., 2009). These qualities distinguish human runners from other vertebrate runners.

A runner's ability is typically quantified in terms of their running economy. Running economy (RE) is a measure of the energy demand of a given sustainable running speed. It is calculated by measuring a person's steady-state oxygen consumption (VO_2) relative to their running speed. Though it has an explicit definition, running economy is an umbrella metric that is affected by many factors including: individual physiology, biomechanics, environment, training, and anthropometry (Saunders et al., 2004). Improved running economy translates to improved performance and has applications in everything from professional sports to military fitness assessment. Consequently, many studies have been done to determine how, by what means, and to what degree RE can be manipulated.

In their seminal study, Bramble et al. (1983) posited that humans, like other running animals, use LRC to reduce energy costs in running. Since that time, studies have been conducted on the incidence and effects of LRC in rowing, cycling, running, wheelchair propulsion, and finger and arm tracking (Amazeen et al., 2001; Bernasconi et al., 1995; Daffershofer et al., 2004; Daley et al., 2013; Ebert et al., 2000; Kohl et al., 1981; Mahler et al., 1991; Mahler et al., 1991; McDermott et al., 2003; Raßler et al., 1996; Siegmund et al., 1991; Stickford et al., 2015). One question that remains unanswered is whether using an LRC ratio during exercise reduces the energy cost of that exercise. Some studies suggest that LRC stability at sustainable speeds may reduce VO_2 and increase endurance capacity (Bernasconi et al., 1993; Bernasconi et al., 1995; Bonsignore et al., 1998; Bramble et al., 1983; Daffertshofer et al., 2004; Garlando et al., 1985; Hoffman et al., 2012; McDermott et al., 2003; O'Halloran et al., 2012). Others, however, claim the opposite (van Alphen and Duffin, 1994; Raßler et al., 1996; Stickford et al., 2015; Takano, 1994; Yonge and Peterson, 1983).

There are two main possibilities for the disagreement surrounding the significance of the effect of LRC on VO_2. The first reason is a lack of precision in measurement. The aforementioned studies frequently present VO_2 as an average value for a collection period (a timespan of anywhere from 20 seconds to a number of minutes) (Bernasconi et al., 1995; Daffershofer et al., 2004; Hoffman et al., 2012; Stickford et al., 2015). However, VO_2 changes with each inspiration, and even a collection period of 20 seconds can contain multiple respiratory cycles. Thus, averaging VO_2 by collection period may excessively smooth the metric and limit true comparisons between VO_2 and other parameters. In addition to the potential over-smoothing of VO_2, if VO_2 changes on a breath-to-breath level, it follows that locomotor-respiratory coupling may as well. If LRC changes with each breath, reporting an average or the most common LRC ratio for a collection period (van Alphen and Duffin, 1994; Bramble and Carrier, 1983; Dafferstshofer et al., 2004; Daley et al., 2013; O'Halloran et al., 2010) may over-smooth the metric in much the same way as VO_2. As with over-smoothing of VO_2, over-smoothing LRC may hide important nuances of the metric.

The second possible reason for confusion over the significance of the effect of LRC on VO_2 is that many studies neglect to discuss the variability of LRC ratios within a collection period. Most studies searched only for LRC ratios in integer (eg, 1:1, 2:1, 3:1, etc.) and half integer (3:2, 5:2, etc.) increments and categorized other, non-integer ratios as "non-coupled" or ignored them entirely (van Alphen and Duffin, 1994;

Bernasconi and Kohl, 1993; Daley et al., 2013; McDermott et al., 2003; Hoffman et al., 2012; O'Halloran et al., 2012; Paterson et al., 1986; Perségol et al., 1990; Stickford et al., 2015; Takano, 1994). In addition, only a small number of studies have addressed the variability of average LRC ratio within a collection period.

The purpose of this study was to develop a novel protocol for the analysis of LRC at increasing workloads in order to (1) document the variability of LRC ratios at sub-lactate threshold workloads, (2) establish whole-stage LRC ratios relative to increasing workload, and (3) present whole-stage LRC ratios relative to VO_2 and running economy.

It was hypothesized that with this novel technique (1) LRC ratio variability will decrease with increasing workload (2) whole-stage LRC ratios will decrease with increasing workload, and (3) VO_2 and running economy will increase with decreased LRC ratio.

Methods

Eight healthy, recreational runners (4M/4F) who habitually run 10-25 miles each week were recruited for this study. Subjects averaged 28±9 years of age, 172±6 centimeters in height, and 68±9 kilograms in body mass. Subjects ran an average of 18±5 miles over the span of 4±0.5 days per week. All subjects had experience running on a treadmill, were non-smokers, and were free of chronic and acute respiratory, cardiovascular, and orthopedic conditions that would affect exercise performance or running gait.

The protocol for this study was approved by the Institutional Review Board of the University of Oregon. All subjects gave informed consent prior to participation in accordance with University policy. Data for this study were collected during a modified lactate threshold test. The initial protocol for the lactate threshold test was developed for use in the Bowerman Sports Science Clinic at the University of Oregon. The protocol utilized in this study is illustrated in Fig. 1.

Subjects were equipped with in-shoe FootSwitch pads (Noraxon DTS FootSwitch, Noraxon U.S.A. Inc., Scottsdale, Arizona, USA), a heart rate monitor (Polar H2 Heart Rate Sensor, Polar Electro Inc., Lake Success, New York, USA), nose clip, and headgear with an attached mouthpiece (Parvo Medics TrueOne 2400 system, Parvo Medics Inc., Sandy, Utah, USA). After donning collection equipment subjects were instructed to stand on the treadmill belt (Woodway Desmo Evo, Woodway USA Inc, Waukesha, Wisconsin, USA) for a five minute rest stage prior to the lactate test. Data regarding heart rate, respiratory exchange ratio, VO_2, time of inspiration (T_I), time of expiration (T_E), and total time were collected from the beginning of the rest phase through the end of the test (Parvo Medics' TrueOne 2400). Resting heart rate and blood lactate values were collected three minutes into the rest period (Lactate Plus Analyzer, Sports Resource Group Inc., Hawthorne, New York, USA). If subjects chose to warm up prior to testing, resting heart rate and lactate values were collected prior to the five minute warm up period. At the end of the rest stage the treadmill was turned on and the belt grade was increased to +1%. Subjects sped up along with the belt and continued running once the belt was up to speed. The stage speeds for the protocol were dependent on the subjects' stated 5-kilometer run pace. The subjects' Stage 1 pace was 2 km/h slower than their pre-determined 5k pace. Pace was increased by 1 km/h per stage, so that the subjects were running at their stated 5k pace during Stage 3. Stages lasted five minutes and were immediately preceded and followed by 30-second inter-stage periods during which subjects straddled the treadmill belt. Blood lactate concentration was measured with a hand-held lactate reader and treadmill speed increased during each inter-stage period. Onset and duration of right foot strikes were collected between minutes 3:30 and 4:30 of each stage (MyoResearch XP Master, Noraxon, Arizona, USA). Stride frequency (in gait cycles per minute) was measured for 30 seconds between 4:00 and 4:30 of each stage. Though subjects were asked to run for as long as possible, to the protocol was stopped if their blood lactate concentrations exceeded 10 mmol/L. Subjects generally completed between five and seven stages.

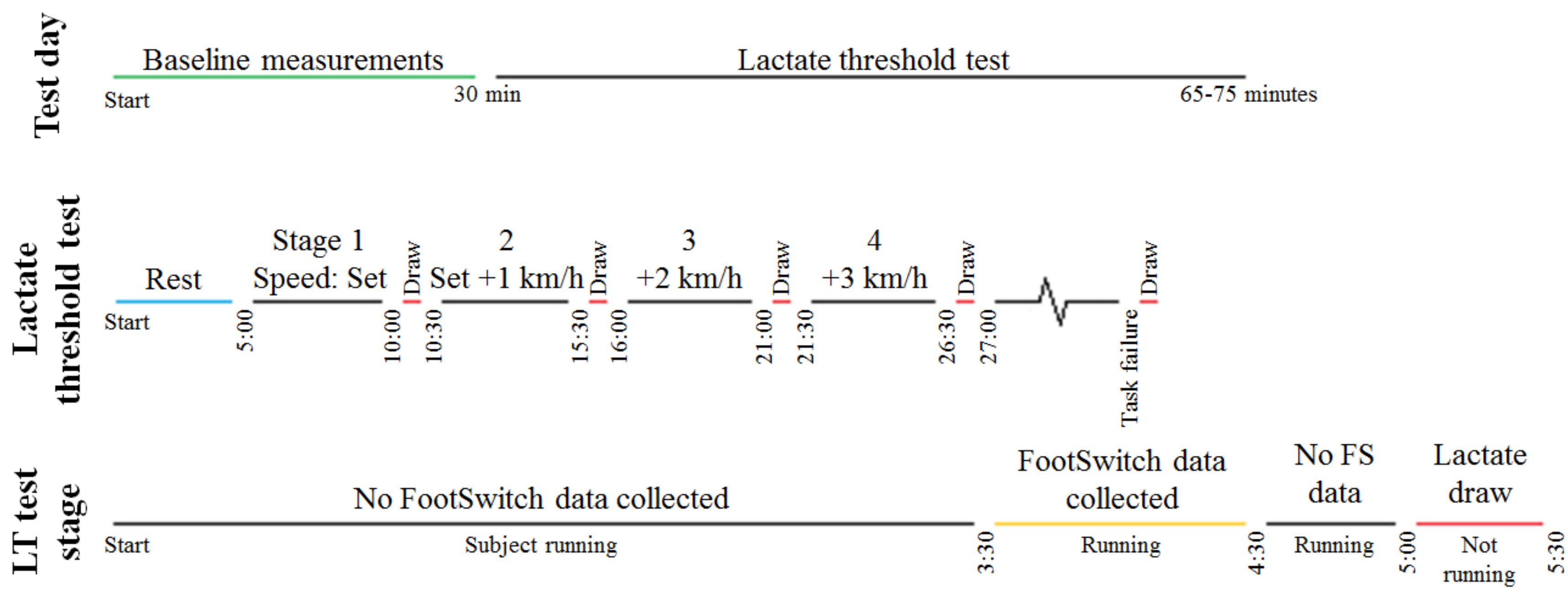

Fig. 1 Timeline depicting progression of the entire test day, the lactate threshold test, and one lactate threshold stage

Locomotor-respiratory coupling ratios and respiratory data were assessed for the one-minute segments of the lactate threshold test during which FootSwitch data were collected. Though data exist for all stages of the lactate test, the only data segments analyzed were those collected before the subjects' blood lactate levels surpassed their lowest unsustainable workload, or second lactate threshold (LT2). Each subjects' LT2 pace was determined post hoc using methods developed by the Bowerman Sports Science Clinic.

An in-house MATLAB code was developed to align FootSwitch trials with the appropriate MetCart time periods and respiratory data (MATLAB version R2015a, MathWorks, Inc., Natick, Massachusetts, USA). The same custom code determined the absolute duration of each respiratory cycle (here defined as onset of inspiration to onset of inspiration) within each one-minute collection period, as well as the number of gait cycles (as a percentage) that occurred in each respiratory cycle. A gait cycle percentage could, for example be expressed as 200%. A gait cycle percentage of 200% would indicate that two complete gait cycles fit in that respiratory cycle.

All recorded metrics, including VO_2, LRC ratios, and RE were submitted to a two-tailed, one-way repeated measures analysis of variance (ANOVA) to evaluate between-stage variations in the parameters. Additionally, bivariate correlations between LRC ratio and VO_2, LRC ratio and RE, and LRC ratio and workload were calculated to observe significant relationships between running characteristics.

Furthermore, root mean square errors of LRC ratios were calculated to evaluate the comparative variability, more specifically the deviation from the mean, for each subject's running pattern, unique to varying workloads. These values were subsequently submitted to a one-way ANOVA to observe statistically significant changes in variability across workloads. Statistical tests on root mean square error were performed for one to four stages pre-LT2. Five stages prior did not have enough data points for analysis because only one subject completed five stages prior to hitting LT2. All statistical analyses were performed using SPSS software version 21.0 (SPSS, Chicago, IL, USA) with α levels set to 0.05.

Results

Overall, we observed that as workload increased, average LRC ratio decreased. Additionally, we observed that average LRC ratio also decreased with increasing VO_2 and running economy. Table 1 shows the average workload (km/h), locomotor-respiratory coupling ratio (%), VO_2 (ml/kg/min), and RE for each subject at each of their sub-LT2 workloads. Also denoted in Table 1 are the average workload, LRC ratio, VO_2, and running economy per stage for all subjects and the relative sample sizes for those stages. Subjects 1 and 7 were removed from the analysis due to a lack of complete data. Data collected during testing for Subject 1 were lost, and Subject 7 had to stop exercise prior to hitting LT2 because they felt faint. Raw VO_2 and LRC values were significantly different between stages (p<0.001). A Tukey post hoc test revealed significant differences in these parameters between all combinations of stages except for between Stages 3 and 5, and 4 and 5 regarding VO_2 (p=0.087 and p>0.999) and between Stages 3 and 4, and Stages 4 and 5 for LRC (p=0.071 and p=0.171, respectively). No significant differences between stages were observed regarding running economy values (p=0.201).

Subject	Stages Prior to LT2	Workload (km/h)	LRC ratio (%)		VO_2 (ml/kg/min)		RE (ml/kg/km)		
			Mean	SD	Mean	SD	Mean	SD	
2	3	11.10	223.91	33.98	40.56	5.38	219.91	29.22	
	2	12.07	213.96	32.90	43.72	5.23	218.04	25.34	
	1	13.04	189.89	23.43	45.50	4.49	210.55	20.34	
3	5	9.66	280.95	35.43	32.29	3.95	200.89	24.62	
	4	10.62	253.56	25.19	35.00	5.05	198.44	29.44	
	3	11.59	227.64	23.18	38.22	3.99	198.42	20.58	
	2	12.55	220.19	42.17	42.28	5.89	201.66	27.38	
	1	13.52	207.40	32.94	45.04	5.27	199.86	22.13	
4	4	8.85	300.11	13.24	26.37	1.35	179.22	9.51	
	3	9.82	313.58	38.84	30.37	5.25	185.76	31.22	
	2	10.78	198.88	18.87	32.52	3.88	181.50	21.44	
	1	11.75	201.55	15.40	36.26	3.62	185.80	18.81	
5	3	9.17	202.18	34.22	39.84	7.23	249.84	45.80	
	2	10.14	204.99	31.22	42.77	5.10	250.84	30.85	
	1	11.10	167.94	27.00	45.92	5.58	245.14	29.65	
6	2	10.94	227.05	50.61	36.78	5.50	202.08	29.91	
	1	11.91	193.26	34.73	41.63	6.12	211.08	31.41	
8	4	9.33	199.64	12.84	31.28	3.00	202.18	19.61	
	3	10.30	198.30	16.80	32.94	3.23	197.25	27.43	
	2	11.27	185.76	21.37	34.39	5.15	183.48	26.94	
	1	12.23	188.00	42.64	35.71	5.09	174.99	25.13	
9	4	8.85	334.09	46.75	35.93	3.98	244.61	26.88	
	3	9.82	287.67	28.14	38.12	2.62	234.87	16.24	
	2	10.62	266.91	23.30	41.80	3.41	237.83	19.87	
	1	11.59	237.41	22.86	46.06	4.60	239.40	23.72	
10	3	8.85	281.03	43.20	27.34	3.27	185.81	22.57	
	2	9.82	243.54	28.57	31.01	4.78	190.28	29.35	
	1	10.78	204.14	15.98	34.32	2.52	190.98	14.06	
Average	5	9.66	280.95	35.43	32.29	3.95	200.89	24.62	n=1
	4	9.41	271.85	24.51	32.15	3.35	206.11	21.36	n=4
	3	10.09	247.76	31.19	35.34	4.42	210.27	27.58	n=7
	2	11.02	220.16	31.13	38.16	4.87	208.21	26.39	n=8
	1	11.99	198.70	26.87	41.31	4.66	207.22	23.16	n=8

Table 1 Individual averages of LRC ratios, VO_2, and economy relative to increasing sub-lactate threshold stage

Increased workload was correlated with increased VO_2 (p<0.001; r^2=0.514). Decreased running economy (p=0.002; r^2= -0.099), and decreased average LRC ratio (p<0.001; r^2= -0.359) were also correlated with increased workload. Additionally, increased LRC ratio was correlated with decreased VO_2 (p<0.001; r^2= -0.372; Figure 4) and decreased running economy (p<0.001; r^2= -0.186).

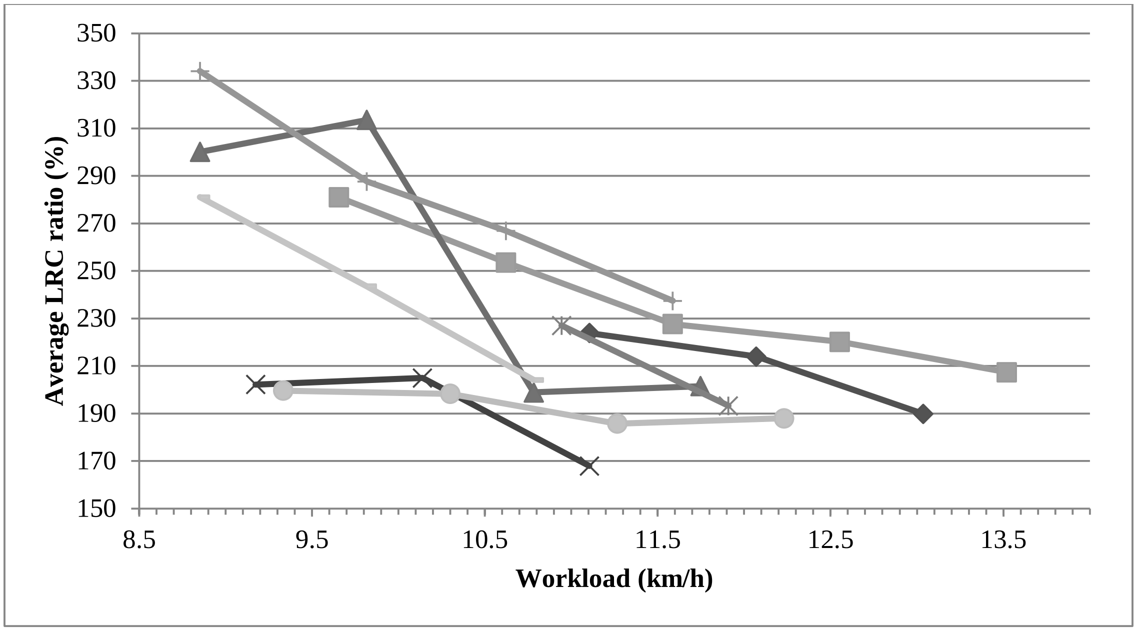

Fig. 2 Individual average LRC ratios (%) for each subject by workload (km/h)

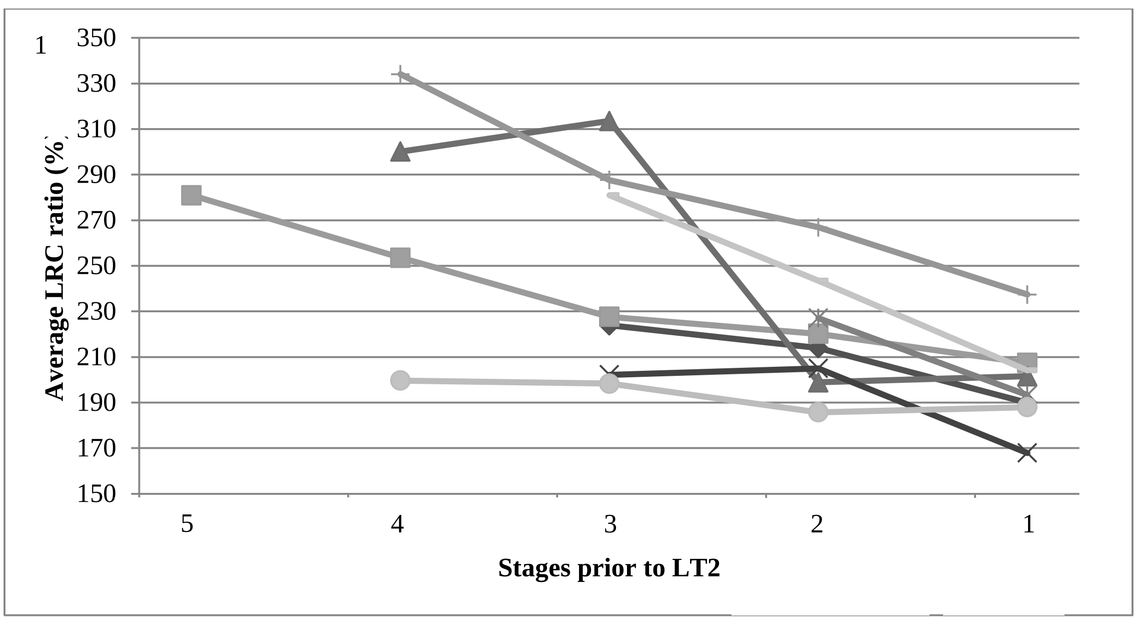

Fig. 3 Individual average LRC ratios (%) for each subject by sub-lactate threshold stage

Individual average LRC ratios (%) showed a decreasing trend relative to absolute workload (km/h; Figure 2) and relative workload (Figure 3). Relative workload is organized such that each subjects' highest, sub-LT2 stage is on the far right, denoted as 1 stage prior to LT2). Average LRC ratios decreased with increasing workload for all subjects (p<0.001, r^2 = -0.359), though some subjects' average LRC ratio increased non-significantly between non-consecutive stages. Subjects completed an average of 3.63 ± 0.92 stages before meeting or surpassing the workload at which they reached their LT2.

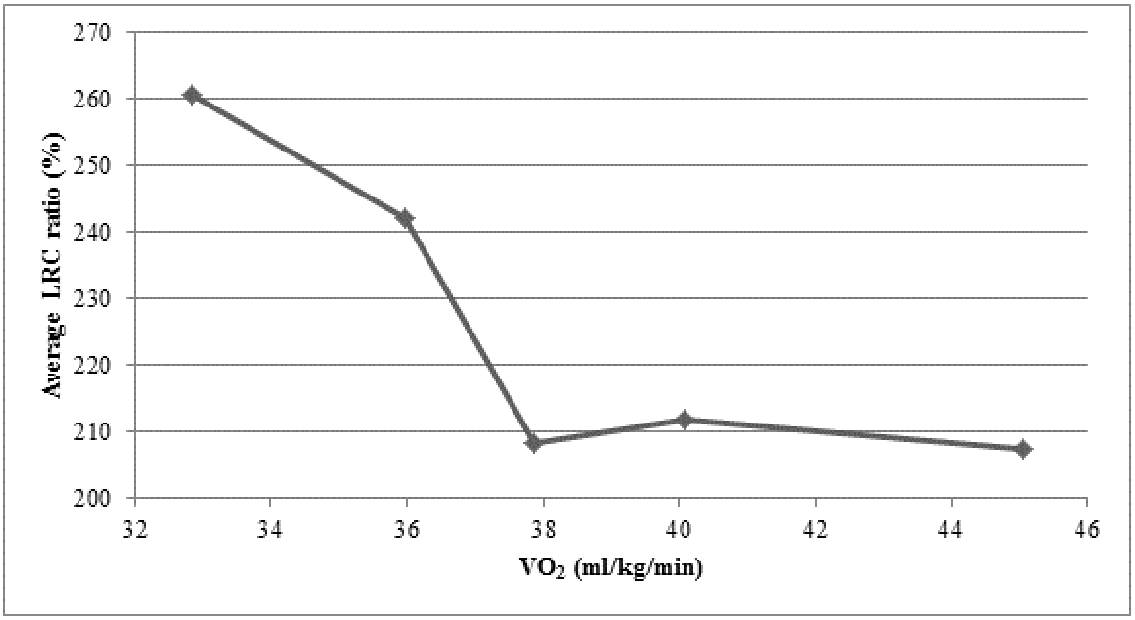

Fig. 4 Average LRC ratio (%) relative to VO_2 (ml/kg/min)

Figure 4 shows the relationship between average LRC ratio (%) and VO_2 (ml/kg/min). Average LRC ratio decreased with increasing VO_2 (p<0.001; r^2=-0.372). Related to VO_2 but not shown in the above figure is the relationship between average LRC ratio and running economy. It was also found that average LRC ratio decreased with increased running economy (p<0.001; r^2=-0.186).

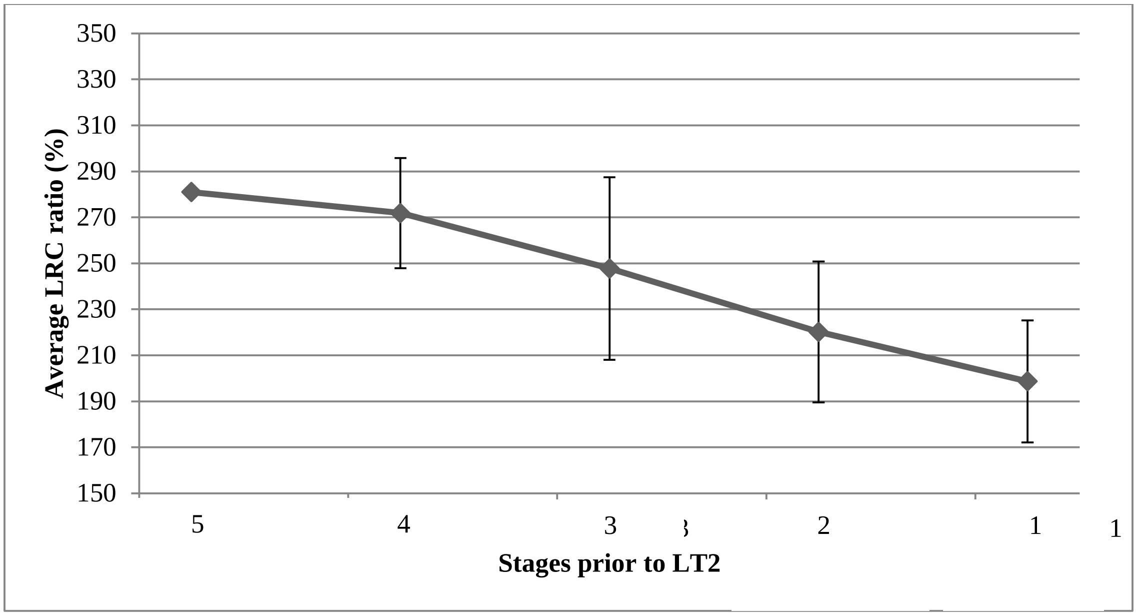

Fig. 5 Average LRC ratio (%) with root mean square error relative to sub-lactate threshold stage

Figure 5 shows the relationship between average LRC ratio (%) and sub-LT2 workload. The error bars represent the root mean square error (%) of the average LRC ratio at each workload. The root mean square errors are 34.79, 23.99±15.41, 39.65±28.36, 30.68±10.67, 26.54±9.36, for Stages 5, 4, 3, 2, and 1, respectively. N values for those stages are 1, 4, 7, 8, and 8, which is why the Stage 5 root mean square error does not include a standard deviation. The root mean square errors are not significantly different for different workloads (p=.725). LRC ratios were averaged across all subjects and are 281, 272, 247, 220, and 199% for Stages 5 through 1.

Discussion

The goal of this study was to develop a new protocol for the analysis of LRC ratios at increasing workloads and to use that protocol to document the variability of LRC ratios at sub-LT2 workloads and establish whole-stage LRC ratios relative to VO_2, RE, and increasing workload. This study measured the timing of right footed heel strike and toe-off, in addition to T_I, T_E, VO_2, and RER at increasing sub-lactate threshold running speeds. Respiratory metrics were collected on a breath-to-breath basis such that the nature and physiologic effects of LRC could be measured on a more precise scale than has been used in previous studies.

Protocol: Adjustments in assessment

The rolling method of LRC ratio assessment used in this study allowed for a more discrete means of LRC analysis than the decile method (Bernasconi and Kohl, 1993; Stickford et al., 2015) or degree method (Daffertshofer et al., 2004; Daley et al., 2013; Hoffman et al., 2012; O'Halloran et al., 2012) because it allows for greater freedom of pattern recognition. Previous study methods either "bin" their results based on the location of respiratory events relative to gait cycle stage or use other methods to detect "coupled", whole and half-integer ratios and "non-coupled", non-integer ratios (van Alphen and Duffin, 1994; Bernasconi and Kohl, 1993; Daley et al., 2013; McDermott et al., 2003; Hoffman et al., 2012; O'Halloran et al., 2012; Paterson et al., 1986; Perségol et al., 1990; Stickford et al., 2015; Takano, 1994). Unlike binning methods and coupling methods, the rolling method does not depend on assessing where in a gait cycle a respiratory event occurs. Instead, it counts the number of gait cycles that occur in a respiratory.

There are several advantages to using the gait cycle as a basic counting unit. The entire purpose of LRC ratio measurement is to determine if the gait and respiratory cycles synch. If the cycles synch, then the same number of gait cycles will consistently fit in the same number of respiratory cycles, regardless of where in a gait cycle a respiratory event occurs. Additionally, the rolling method of LRC ratio assessment opens the door for assessment of LRC ratios considered by other studies to be "non-coupled" (McDermott et al., 2003). Non-coupled patterns are those that do not fit into whole integer (eg 2:1) and half integer (eg, 5:2) ratios. Thus, one of the advantages of the rolling method employed by this study is that it allows for use of other, non-integer ratios to be considered coupled.

LRC variability relative to workload

Although some studies claim that coupling does not occur at non-integer ratios, the data collected in this study do not support that claim, nor do they support the hypothesized idea that LRC ratio variability decreases with increasing workload. As seen in Fig. 5, only two of the five average LRC ratios (247% at Stage 3 and 199% at Stage 1) manifest as integer or half integer ratios. While it is tempting to dismiss the remaining stages as non-coupled, the root mean square error of the data do not vary significantly between stages, suggesting that subjects are just as consistently choosing the "non-coupled" ratios compared to the coupled ratios at any sub-LT2 workload. These data also support the work of other studies that found no significant correlation between LRC ratio stability and workload (Paterson, 1986; Raßler, 1996; Stickford, 2015; Takano, 1994; van Alphen, 1994; Yonge, 1983). The data suggest that LRC is not an instinctual response to increased workload. If LRC were an instinctual response to increased workload, we would expect to see increases in incidence and stability of LRC with increasing workload.

Whole-stage LRC ratio relative to workload

The study found support for its hypothesis that as workload increases toward LT2, the average LRC ratio value decreases (Figs. 2, 3, and 5). This finding is in agreement with the findings of Bramble and Carrier (1983) and Takano (1995).

Logic also supports the finding that LRC ratio decreases with increasing workload. The current definition of LRC ratio is essentially the fraction of gait cycles within a respiratory cycle. Although both respiratory rate and stride frequency increase with increasing workload, respiratory rate increased more than twice as fast as stride frequency in the present study. Due to the fact that respiratory rate increases more rapidly than stride frequency for the same increase in workload, it makes sense that LRC ratio, or the number of respiratory cycles per gait cycle, would decrease with increasing workload.

Perhaps even more intriguing is the finding relating to the average LRC ratios for those increasing workloads. Prior studies of LRC have referred to non-integer ratio frequencies as “non-coupled”, if they refer to those ratios at all (van Alphen and Duffin, 1994; Bernasconi and Kohl, 1993; Daley et al., 2013; McDermott et al., 2003; Hoffman et al., 2012; O’Halloran et al., 2012; Paterson et al., 1986; Perségol et al., 1990;

Stickford et al., 2015; Takano, 1994). Past studies appear to operate under the assumption that respiratory and gait synchrony will occur at integer and half-integer ratios only. They neglect two important possibilities. First, that respiratory and gait cycles may synch at a different ratio than integer or half-integer, and second, that locomotor respiratory coupling does not exist. Both assertions can be supported but the fact that average LRC ratio, but not average LRC ratio variability, decreases with increasing workload (Figs. 2, 3, and 5), as discussed in “LRC variability relative to workload” above.

Support for the idea that locomotor respiratory coupling may not exist beyond the bounds of chance can also be found in the data presented in Fig. 5. Figures 2, 3, and 5 show that average LRC ratio decreases with a linear trend as workload increases in recreational runners. Figure 5 also shows that the root mean square values of the LRC ratio are not significantly different with increasing workload and range from 24 to 35% variability around the mean. The minimum level of variability (24%) is large enough to ensure that a runner will employ a whole or half-integer ratio at a given sub-LT2 workload. The maximum level of variability is large enough that, if the average LRC ratio lies between integer and half-integer ratios, a runner could use both in a single workload. Given that coupling strength does not change significantly for any LRC ratio, as indicated by RMSE values between workloads, it seems likely that pure locomotor respiratory coupling may not actually occur in humans for any sub-maximal running speed.

Whole-stage LRC ratio relative to VO_2 and running economy

The present study found that average LRC ratio decreased with increasing VO_2 ($p<0.001$; see Fig. 4). Furthermore, this study found that average LRC ratio decreased with increased running economy ($p<0.001$). These findings support the hypotheses made earlier in this study. Further, it makes sense that both VO_2 and running economy would respond in the same way relative to average LRC ratio because running economy is calculated from, and directly proportional to, VO_2.

More important than the revelation that VO_2 and running economy are inversely proportional to LRC ratio is the orientation of these results relative to those of past studies. Though previous studies have discussed VO_2 relative to increasing workload and LRC relative to VO_2, this is the first study to examine the relationship between LRC and VO_2 at increasing workload. As shown in Fig. 4, as VO_2 increases with increasing workload, the average LRC ratio decreases ($p<0.001$). The likely cause of this correlation can be inferred from the observation that LRC ratio decreases with increasing workload (as discussed previously in "Whole-stage LRC ratio relative to workload") and VO_2 increases with increasing workload.

Limitations to the study

This study was not without limitations. The execution of protocol included slight variations between subjects that may have affected the subjects' locomotion or respiration. For example, one subject held on to the treadmill with at least one hand for all stages of the lactate threshold test. Given that passive arm swing is used to stabilize the trunk during running and activation of abdominal muscles (which counteracts trunk motion) has been correlated with LRC incidence, such a safety measure may have impacted that subject's data (Bramble and Carrier 1983; Lee and Banzett 1997; Pontzer et al., 2009). In addition to variations within subjects, separate software systems were used to record gait and respiratory data and had to be hand-synchronized for each stage. Precision in signal-synchronization was not as high as the 1500 Hz sampling frequency employed by the MyoElectric FootSwitch software. Due to the limits of hand-synching, gait and respiratory data may have been offset slightly due to the reaction time needed to translate a visual cue into a physical response. This problem may be corrected in future studies by tracking gait and respiration on the same software system. One possible method can be found in McDermott et al., 2003.

Applications for the data presented in this study include fitness programs for elite athletes, those looking to improve their overall health, and the military. All such groups routinely look to research to improve their training methods, and any information regarding breathing patterns and performance can be useful.

It would be worthwhile in future work to address the issue of lag between decreased LRC variability and change in VO_2 on a breath-to-breath basis. This could be important in determining a causal relationship between LRC and VO_2 and provide support for claims made in past studies.

It would also be useful to determine if people that participate in highly coupled sports, such as rowing and cycling, are more likely to couple when running. These data would be useful for subject exclusion criteria and the elimination of confounds in future studies.

Conclusion

Locomotor-respiratory coupling has been previously demonstrated in a wide range of human activities, including running, but it has never at increasing, sub-LT2 workloads. This study used a novel approach to data collection and analysis that allowed for increased freedom of LRC ratio detection and assessment. Using this novel approach revealed that average LRC ratio decreases as VO_2 increases, and that there is no significant difference between the variability of LRC ratio usage at whole and half-integer increments and intermediate ratios, contrary to the assumptions of previous studies. Further research needs to be done to ascertain the existence and duration of the lag between decreased LRC ratio variability and change in VO_2 on a breath-to-breath basis. Practical applications can be found in adjustments of respiratory training methods in the military, and elite and recreational athletics.

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