Effects of exercise modality on patterns of ventilation and respiratory timing

David M. Caretti, Patricia C. Szlyk and Ingrid V. Sils
Comparative Physiology Division, U.S. Army Research Institute of Environmental Medicine, Natick, MA, USA
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Abstract. Ventilatory patterns and respiratory timing were measured in 14 subjects during cycling (CYC) and treadmill exercise (TM) at similar leg frequencies (fLEG) to determine if mode of exercise affects patterns of ventilation and respiratory timing. Measurements of breathing frequency (fR), tidal volume (VT), expired ventilation (VE), and inspiratory (Ti) and expiratory (Te) time were obtained at fLEG of 50, 70, and 90 rev-min⁻¹ (rpm) for CYC and at similar incremental fLEG (strides-min⁻¹; spm) during TM achieved by increasing belt speed at 0% grade. CYC exercise intensity was ~50% Vo2max at all fLEG, whereas Ve increased progressively with TM. fR increased significantly (P<0.001) with increasing fLEG of TM (20.5±4.6, 25.4±5.8, and 36.3±7.6 breaths-min⁻¹; x±SD), but during CYC fR changed significantly (P<0.05) only between fLEG of 70 and 90 rpm (25.0±5.9 vs 28.5±6.9 breaths-min⁻¹). Both average breath Ti and Te obtained by grouping into incremental ranges of fR decreased significantly (P<0.05) with increasing fR up to 36 breaths-min⁻¹ and the relationships of Ti and Te to fR, Ti to Te, and central inspiratory drive (VT/Ti) to VE were the same for CYC and TM. Group average fR and fLEG were synchronized during TM, but individual subjects did not exhibit a high degree of entrainment. This study shows respiratory timing patterns to be independent of mode of exercise over the range of fR observed when describing patterns by grouping into incremental ranges of fR.

Control of breathing, pattern, exercise; Exercise, mode, pattern of breathing; Mammals, humans; Pattern of breathing, exercise modes

Breathing patterns and respiratory timing variables have been investigated during various types of exercise in both animals and humans to determine whether neurogenic influences, originating in the exercising limbs, contribute to exercise hyperpnea. Several investigators have observed synchronization of breathing frequency to leg frequency during rhythmic exercise, suggesting that the ventilatory response to exercise can be accounted for by limb reflexes (Bannister et al., 1954; Hey et al., 1966; Asmus sen, 1973; Bechbache and Duffin, 1977; Jasinskas et al., 1980; Bramble, 1983; Bramble and Carrier, 1983). Others have concluded that afferent input from muscle receptors is not a component of exercise ventilation (Sipple and Gilbert, 1966; Kelman and Watson, 1973; Kay et al., 1975a; Clark et al., 1983).

Correspondence to: D.M. Caretti, Commander, U.S. Army CRDEC. Attn: SMCCR-PPI David M. Caretti, Aberdeen Proving Ground, MD 21010-5423, USA.

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Measurements of tidal volume and durations of the inspiratory and expiratory phases of the ventilatory cycle correspond to variables that can be used to characterize the neural regulation of respiration. Specifically, the ratios of tidal volume to inspiratory time and of inspiratory time to total breath duration serve as indices of central inspiratory drive and respiratory timing, respectively (Milic-Emili and Grunstein, 1976). Evidence of whether these variables are affected by different modes of exercise is limited (Kay et al., 1975b; Clark et al., 1983). Furthermore, in order to determine if differences in breathing patterns occur between exercise modes, ventilatory patterns should be measured under the same conditions (i.e. environment, leg frequency) for each mode. However, these considerations have often been overlooked.

Therefore, the present study was undertaken to determine (1) the effects of three progressively increasing leg frequencies on ventilatory patterns and respiratory timing; and (2) the effects of two modes of exercise, cycle ergometry and treadmill exercise, on these variables.

Methods

Fourteen healthy male subjects (age 28.4 ± 7.1 years; X ± SD) volunteered for this study. The study was approved by the U.S. Army Research Institute of Environmental Medicine in accordance with Army Regulation 70-25 for the use of human volunteers. After informed consent was obtained, subjects completed a health and physical activity questionnaire and measurements of height and body weight were taken. One day before testing each subject performed a maximal oxygen consumption (\(V'\text{O}_2,\text{max}\)) test on a cycle ergometer. Briefly, subjects pedaled continuously at 60 rev·min\(^{-1}\) (rpm) while workload was increased 50 Watts every 3 min until exhaustion or until pedal frequency could not be maintained. One day before testing each subject performed a maximal oxygen consumption (\(V'\text{O}_2,\text{max}\)) test on a cycle ergometer. Briefly, subjects pedaled continuously at 60 rev·min\(^{-1}\) (rpm) while workload was increased 50 Watts every 3 min until exhaustion or until pedal frequency could not be maintained. Following a 5-min rest period, subjects exercised again starting at a workload 50 Watts lower than the highest workload that they had obtained. After 3 min, intensity was increased by 50 Watts and subjects continued to exercise to exhaustion. It was determined that \(V'\text{O}_2,\text{max}\) had been obtained if oxygen consumption (\(V'\text{O}_2\)) during this second maximal exercise bout did not exceed peak values from the first exhaustive test. \(V'\text{O}_2,\text{max}\) values were used for determination of relative oxygen consumption during subsequent testing. Subjects had relatively wide ranges of body weights (57.97–110.52 kg) and physical fitness levels (\(V'\text{O}_2,\text{max}\): 38.77–61.60 ml·kg\(^{-1}\)·min\(^{-1}\)).

This investigation involved 4 separate days of testing. Subjects randomly performed one exercise session on a cycle ergometer (Collins Pedalmate) and a treadmill on either of the first 2 testing days. During cycle ergometry, subjects exercised continuously at an estimated intensity of 50% \(V'\text{O}_2,\text{max}\) at leg frequencies (\(f_{\text{LEG}}\)) of 50, 70, and 90 rpm for 15 min each. Subjects maintained leg frequencies by watching a speedometer and were individually monitored by technical personnel to assure sustainment of the respective frequency. Also, \(f_{\text{LEG}}\) were measured in conjunction with sequential breath measurements during the last 5 min of exercise at each frequency interval by counting the number of pedal revolutions for a given amount of time.
During treadmill trials, subjects walked, or jogged, at zero percent grade at three treadmill speeds adjusted to elicit /fLEG of 50, 70, and 90 strides min⁻¹ (spm), similar to the frequencies of cycling. Leg frequencies were measured as during cycling but by counting the number of strides for a given amount of time. For both modes of exercise subjects were unaware that these measurements were being taken. Each /fLEG involved 15 min of total exercise. Six days later subjects repeated both the cycling and treadmill regimens on 2 separate days. Speeds selected on each subject’s initial treadmill exercise session were duplicated for the final bout of treadmill exercise.

Heart rate (HR), /fLEG, breathing patterns, and expired gases were monitored using the same procedures for both cycling and treadmill trials. Heart rate was monitored continuously from 3-channel ECG leads using a Hewlett-Packard telemetry system. A semi-automated system consisting of a Hewlett-Packard 85B computer and digital voltmeter interfaced with a gas meter (Parkinson-Cowan), oxygen analyzer (Applied Electrochemistry S3A), and carbon dioxide analyzer (Beckman LB2) was used to collect and analyze expired gases from the expiratory side of a Collins J-valve. Expired gases were collected on-line during the last 5 min of exercise at each /fLEG. Sustained levels of VO₂ for 4–5 min signified that a steady-state of exercise had been obtained.

Patterns of ventilation and respiratory timing were measured concurrently with expired gases. A pneumotachometer (Hans Rudolph), connected to a pressure transducer (Validyne MP45), carrier demodulator (Validyne CD15), and a polygraph (Western Graphitech), was affixed to the inspiratory side of a Collins J-valve to measure inspiratory air flow. After subjects inserted the mouthpiece connected to the Collins J-valve into their mouth, a noseclip was put in place and recordings of ventilatory flow were monitored on the polygraph. Once the subject felt comfortable with the mouthpiece and breathing apparatus, based on steady polygraph readings and visual observation, measurements of expired gases and breathing patterns began. Measurements of breathing frequency (/fR), tidal volume (VT), expired ventilation (VE), and inspiratory (Ti) and expiratory (Te) time were obtained on 3 separate occasions during the last 5 min of each /fLEG interval. Measurements were averaged for each incremental leg frequency. Average ratios of pedaling or stepping frequencies to breathing frequency were calculated to test for synchronization of breathing frequency to leg frequency.

Breath-by-breath analyses of respiratory timing were taken from the 3 data collection periods during the last 5 min of exercise for each /fLEG. Up to ten sequential breaths (maximum of 30 breaths from each steady-state) were analyzed for Ti, Te, and total breath duration (TTOT). Instantaneous breath frequency (/fR) (60/TTOT) and respiratory timing (Ti and Te) were calculated. For analysis, individual breath data for each mode of exercise were grouped into incremental ranges of breath frequency (3 breaths·min⁻¹ intervals).

With a Complete Statistical System (CSS) software package (StatSoft 1987), data were analyzed within and between exercise modes using ANOVA and Scheffe’s post-hoc analyses. The null hypothesis was rejected at the P<0.05 level. All values represent mean ± SD.
Results

No differences existed between each cycling and each treadmill trial. Therefore, data from both cycling trials were pooled and analyzed as one data set vs the pooled treadmill data.

Exercise intensity
Expressed as percent $\dot{V}_{O_2,\text{max}}$, the average intensity of exercise during cycling was not significantly different at the three different pedal frequencies (Table 1). For treadmill exercise, subjects utilized a significantly ($P<0.001$) greater percentage of $\dot{V}_{O_2,\text{max}}$ with each increase in stride frequency. The $\dot{V}_{O_2}$ during cycling was significantly ($P<0.05$) different from treadmill exercise at all leg frequencies. Heart rate responses differed significantly ($P<0.001$) between modes at the lowest and highest $f_{\text{LEG}}$, and increased significantly ($P<0.001$) with progressively increasing $f_{\text{LEG}}$ during treadmill exercise (Table 1).

Ventilatory and respiratory timing patterns
Average values of $f_R$, $V_T$, $V_E$, and $T_i$ and $T_e$ at each $f_{\text{LEG}}$ are presented in Table 2. No significant changes in $V_T$ or $V_E$ occurred with increasing $f_{\text{LEG}}$ during cycling. Treadmill exercise elicited a significant ($P < 0.001$) increase in $V_T$ when stride frequency increased from 70 to 90 spm, and $V_E$ increased significantly ($P<0.005$) with each $f_{\text{LEG}}$ increase.

For both modes, as $f_{\text{LEG}}$ increased, $f_R$ increased progressively. With incremental $f_{\text{LEG}}$, elevations in $f_R$ during cycling were less than the corresponding increases during treadmill exercise. Increases in $f_R$ at each incremental $f_{\text{LEG}}$ were significant ($P < 0.001$) during treadmill exercise, but during cycling increases in $f_R$ were significant ($P < 0.05$) only when subjects progressed from 70 to 90 rpm. At the highest $f_{\text{LEG}}$, $f_R$ was significantly ($P<0.001$) greater for treadmill vs cycling exercise. As $f_R$ increased with

<table>
<thead>
<tr>
<th>Measure</th>
<th>Cycling (rpm)</th>
<th>Treadmill (rpm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\dot{V}_{O_2,\text{max}}$</td>
<td>46.4 (10.6)</td>
<td>20.7 (7.2)</td>
</tr>
<tr>
<td>$V_T$</td>
<td>47.1 (13.1)</td>
<td>35.8 (12.8)</td>
</tr>
<tr>
<td>$V_E$</td>
<td>53.3 (14.5)</td>
<td>(14.5)</td>
</tr>
<tr>
<td>HR</td>
<td>114.7 (17.0)</td>
<td>123.1 (22.5)</td>
</tr>
</tbody>
</table>

Values are means (± SD) of measures taken at each leg frequency interval ($n = 28$). $\dot{V}_{O_2,\text{max}} = \%$ of maximal oxygen consumption; HR = heart rate (beats·min⁻¹). $^a$ Significant difference between modes of exercise. $^b$ Significant difference between sequential leg frequency intervals.
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TABLE 2
Average ventilatory and respiratory timing patterns

<table>
<thead>
<tr>
<th>Measure</th>
<th>Cycling (rpm)</th>
<th>Treadmill (spm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>50</td>
<td>70</td>
</tr>
<tr>
<td>VT</td>
<td>1.67</td>
<td>1.64</td>
</tr>
<tr>
<td></td>
<td>(0.49)</td>
<td>(0.41)</td>
</tr>
<tr>
<td>VE</td>
<td>37.9</td>
<td>39.5</td>
</tr>
<tr>
<td></td>
<td>(7.9)</td>
<td>(7.6)</td>
</tr>
<tr>
<td>fR</td>
<td>23.2</td>
<td>25.0</td>
</tr>
<tr>
<td></td>
<td>(5.6)</td>
<td>(5.9)</td>
</tr>
<tr>
<td>Ti</td>
<td>1.17</td>
<td>1.11</td>
</tr>
<tr>
<td></td>
<td>(0.36)</td>
<td>(0.32)</td>
</tr>
<tr>
<td>TE</td>
<td>1.57</td>
<td>1.44</td>
</tr>
<tr>
<td></td>
<td>(0.48)</td>
<td>(0.34)</td>
</tr>
</tbody>
</table>

Values are means (± SD) of measures taken at each leg frequency interval (n = 28). VT = tidal volume (L); VE = expired ventilation (L·min⁻¹); fR = breathing frequency (breaths·min⁻¹); Ti = inspiratory time (sec); TE = expiratory time (sec).

* Significant difference between modes of exercise.

b Significant difference between sequential leg frequency intervals.

progressively increasing leg frequencies during treadmill exercise, both average breath Ti and TE decreased significantly (P < 0.05). Average breath Ti and TE decreased with increasing fLEG during cycling, but changes were not significant. In addition, average breath TE was greater than Ti at all three leg frequencies. This relationship was not different between modes of exercise.

Average group values of the breath-by-breath relationship of Ti and TE to fR obtained by binning into incremental ranges for both modes of exercise can be seen in Fig. 1. For the 14 subjects a total of 3744 breaths, 1538 during cycling and 2206 during treadmill exercise, were measured. The relationships of Ti and TE to fR were similar between modes of exercise. Average Ti and TE decreased significantly (P < 0.05) with increasing fR up to approximately 36 breaths·min⁻¹ and the absolute change in TE was greater than that for Ti. At fR greater than 36 breaths·min⁻¹ average Ti did not change significantly, whereas TE continued to decrease significantly. Only between fR of 36–39 breaths·min⁻¹ during cycling was the change in TE not significant. Average duration of Ti was significantly (P < 0.05) less than TE at all fR below 39 breaths·min⁻¹.

The relationships of Ti and TE to fR were quantitatively similar between cycling and treadmill modes of exercise at fR above 12 breaths·min⁻¹. However, at the single fR bin below 12 breaths·min⁻¹ average TE during treadmill exercise was significantly greater compared to cycling.

Average durations of TE vs Ti obtained from the same binned incremental fR are plotted in Fig. 2 against isolines of the proportion of total breath duration spent in inspiration (Ti/TTOT) for both modes of exercise. As breath Ti and TE decreased with
increasing $f_R$, $T_l/T_{TOT}$ was reduced and the ratio approached 0.50. This relationship was the same for both modes of exercise.

Respiratory drive

Central inspiratory drive ($VT/T_l$), an index of inspiratory motor input, was plotted against $VE$ in Fig. 3 for both modes of exercise. During both cycling ($r = 0.97; P < 0.001$)
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3.8 3.8-
3.4 3.4-
3.0 3.0-
2.6 2.6-
2.2 2.2-
1.8 1.8-
1.4 1.4-
1.0 1.0-

Fig. 3. Central inspiratory drive (VTi/Ti) plotted against \( \dot{V}E \) for both modes of exercise. Data represent average values of VTi/Ti and \( \dot{V}E \) obtained during each of the 3 leg frequency intervals.

and treadmill exercise \((r = 0.98; P < 0.001)\) central inspiratory drive was positively correlated to \( \dot{V}E \), and no differences were found between exercise modes.

Influence of limb movement on breathing frequency
To evaluate the possibility of synchronization of \( f_R \) to leg frequency \((f_{LEG})\), or entrainment, calculations of the ratio of \( f_{LEG} \) to \( f_R \) \((f_{LEG}/f_R)\) were made. Ratios of \( f_{LEG}/f_R \) were identical for the subject group at each leg frequency \((2.6 \pm 0.8, 2.7 \pm 0.6, \text{and} 2.6 \pm 0.7)\) during treadmill exercise. Average group ratios of \( f_{LEG}/f_R \) increased significantly \((P < 0.001)\) for the group with increasing leg frequencies during cycling \((2.3 \pm 0.7, 2.9 \pm 0.6, \text{and} 3.4 \pm 0.9)\).

Discussion

Ventilatory patterns and respiratory timing and drive
Changes in \( f_R \) have generally been attributed to changes in \( T_E \) rather than \( T_i \), in both resting animals and humans (Newsom-Davis and Stagg, 1975; Sullivan et al., 1978). Kay et al. (1975b) and Clark et al. (1983) also reported this relationship during exercise in man. However, Iscoe et al. (1983) and Jennings and Szlyk (1985) reported that both \( T_i \) and \( T_E \) change as \( f_R \) spontaneously changes for dogs and cats, respectively, while breathing room air. Rather than using consecutive breaths with varying \( f_R \) to average timing, these latter investigators grouped \( T_i \) and \( T_E \) by individual breath \( f_R \). This unique approach enabled comparisons of \( T_i \) and \( T_E \) at a given \( f_R \) in response to a stimulus with timing at the same \( f_R \) under control conditions. By averaging timing from consecutive breaths with variable \( f_R \), previous investigators masked not only the differences in timing related to \( f_R \) but also the considerable amount of variability found.
in breathing patterns (Kay et al., 1975b; Newsom-Davis and Stagg, 1975; Sullivan et al., 1978; Clark et al., 1983). Kay et al. (1975b) further restricted interpretation of their data by eliminating any breath if VT was greater than one and a half times the mean or if Ti was two times greater than the mean, and by eliminating the two breaths immediately following any mis-recorded breath. Clark et al. (1983) averaged timing patterns for each minute of an exercise session rather than for fR, thus failing to actually compare timing at a given breath fR.

In our data analysis we employed the technique of grouping Ti and Te by individual fR and found that the relationship of respiratory timing and fR during submaximal exercise in man was qualitatively similar to that of resting, awake cats and dogs (Iscoe et al., 1983; Jennings and Szlyk, 1985). As fR increased up to approximately 36 breaths·min⁻¹, both Ti and Te decreased significantly (Fig. 1). Above this fR, average Ti was relatively fixed, whereas Te continued to decrease significantly. Average Ti was less than Te at fR below 39 breaths·min⁻¹, but as fR increased above this frequency the durations of Ti and Te became equal. This relationship of Ti and Te to fR was similar for both treadmill exercise and cycling, and for a given fR there was a predictable Ti and Te.

At a given fR above 12 breaths·min⁻¹, the Ti and Te for treadmill exercise were indistinguishable from the Ti and Te for cycling (Fig. 1). Significantly longer average Te was observed at fR less than 12 breaths·min⁻¹ during treadmill compared to cycling exercise. This difference resulted from the greater variability of Te measured at the lowest fR interval during cycling (3.55 ± 1.06 sec; n = 12) compared to treadmill exercise (4.02 ± 0.85 sec; n = 15). Sequential breath measurements also showed a large degree of variability in Ti and Te below fR of 18 breaths·min⁻¹. As breath fR increased above 18 breaths·min⁻¹, respiratory timing decreased and varied less at a given fR.

It has been reported that during maximal exercise average Te becomes slightly less than Ti at an average fR of 62 breaths·min⁻¹ (Clark et al., 1983). In the present study, with the greater decrease in Te than Ti with increasing fR, the amount of time spent in inspiration (Ti/TTOT) increased from approximately 0.40 to 0.50 for both exercise modes. At the highest recorded fR during cycling and treadmill exercise, average durations of Ti essentially equalled those of Te. However, during cycling the duration of Ti was longer (not significantly) than Te, and a slight 'cross-over' of Te and Ti was observed at a fR of approximately 45–50 breaths·min⁻¹. Our inability to see a sustained 'cross-over' of Te and Ti during exercise probably is due to the lower fR of our subjects compared to those reported during maximal exercise. Numerous reports suggest that central hypothalamic mechanisms probably regulate breathing when Ti/TTOT exceeds 0.50 (Jennings and Szlyk, 1985; Szlyk and Jennings, 1987).

When respiratory timing data was analyzed by averaging timing from sequential breaths of different frequencies we found that average duration of Te was longer than Ti at each of the three leg frequency intervals (Table 2). This was true for both modes of exercise. However, this analysis suggests that changes in Ti and Te did not contribute significantly to increasing fR during cycling. In contrast, grouping Ti and Te by individual fR showed that both Ti and Te decreased significantly with increasing
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fR during cycling. This analysis supports the concept that averaging timing from sequential breaths obscures the differences of timing related to individual fR. Furthermore, averaging sequential fR at each /fLEG also obscured measures of individual fR. Averaging timing from sequential breaths showed that Ti and TE between exercise modes were significantly shorter during treadmill exercise at the highest leg frequency. The higher fR exhibited at this leg frequency level during treadmill exercise would account for these observed differences. This greater fR, in turn, probably resulted from the greater oxygen consumption observed between treadmill vs cycling modes at the highest leg frequencies.

Clark et al. (1983) reported two linear relationships of TE to Ti, one during walking and the second while running. One relationship had a shallow slope that included all values of respiratory timing obtained during exercise and Ti/TTOT was approximately 0.50. The second, obtained during walking and when at rest, displayed a steeper slope, and TE was longer than Ti. We did not observe two distinct linear relationships when comparing breath-by-breath durations of TE and Ti during either cycling or treadmill exercise at the three different leg frequencies. However, no rest or recovery data were included in our analysis.

As shown in Fig. 3, mean inspiratory flow rate (VT/Ti) increased linearly as VE increased during cycling and treadmill exercise. Thus, VT/Ti appeared to be an index of central inspiratory drive as previously reported (Milic-Emili and Grunstein, 1976). Also, Milic-Emili and Grunstein (1976) and Clark et al. (1983) have stated that the relationship of VT/Ti to VE will be linear as long as Ti/TTOT remains constant. In our experiments Ti/TTOT varied from approximately 0.40 to 0.53 during cycling and from 0.38 to 0.53 during treadmill exercise as VE increased. This finding indicates that central inspiratory drive is linearly related to VE independent of respiratory timing or modes of exercise. Similar results have been observed for air and CO₂ inhalation in cats (Jennings and Szlyk, 1985; Szlyk and Jennings, 1987).

The relationships of TE and Ti (Fig. 2) and VT/Ti and VE (Fig. 3) were indistinguishable between cycling and treadmill exercise. The drive for ventilation, therefore, was the same for the three leg frequency levels during both modes of exercise. This observation indicates that these relationships are not influenced by exercise mode.

Entrainment

The possibility of entrainment, or synchronization of breathing frequency to exercise rhythm, has long been recognized, but has been difficult to detect (Bannister et al., 1954; Hey et al., 1966; Kay et al., 1975a; Bechbache and Duffin, 1977; Jasinskas et al., 1980; Bramble and Carrier, 1983; Clark et al., 1983). The results of the present study showed average ratios of fLEG/fR to be constant with progressive increases in leg frequency during treadmill exercise, but not during cycling. However, based on average fLEG/fR ratios for each individual subject, only 64% of the subjects had constant ratios at all leg frequencies during treadmill exercise.

It has been suggested that exercise intensity may influence entrainment (Bechbache and Duffin, 1977; Jasinskas et al., 1980; McMurray and Ahlborn, 1982). In the present
study, no entrainment was observed when exercise intensity remained unchanged while cycling. During treadmill exercise, intensity increased significantly with increasing /LEG and 64° of the subjects appeared to entrain /R to /LEG. These findings tend to support that metabolic rate may determine the degree of subject entrainment. Also, since timing patterns of ventilation and central inspiratory drive did not differ between exercise modes, the relationship of respiratory timing to /R appeared not to be influenced by entrainment. However, since our subject population did not exhibit a high degree of entrainment, no definite conclusions could be made about the effects of exercise intensity on entrainment, or the influence of entrainment on timing patterns and inspiratory drive.

Thus, the quantitative description of the variability of ventilation on a breath-by-breath basis in this study shows that decreases in the duration of both expiratory and inspiratory time contribute significantly to increases in breathing frequency. Also, the relationship of timing patterns to breathing frequency is independent of mode of exercise, and intensity, over the range of leg and breathing frequencies observed. Qualitatively, our data indicate that the relationship between breath timing and breathing frequency in man is similar to that of cats and dogs. Establishment of this fundamental relationship between species may allow for stronger comparisons between species when evaluating the effects of various stimuli on respiratory timing.

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References

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