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The entrainment of ventilation frequency to exercise rhythm

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Summary. To investigate whether ventilation frequency could be entrained to a sub-harmonic of the exercise rhythm, 19 experimentally naive male volunteers were tested during steady state bicycle ergometry and arm cranking under conditions of constant applied workload. Each exercise was performed at two separate ventilatory loads, one within the linear range and the other in the curvilinear range of ventilatory response to exercise. A preferred exercise rhythm was initially adopted (4 min.) followed by forced incremented and decremented rhythm changes each lasting 3 min during a 12 min exercise period. Ventilation, pedal pulse train and heart rate were sampled at 17 Hz on a PDP 11/23 computer. Ratios of limb frequency to dominant respiratory frequency were determined following Fourier analysis of these signals. Data that lay within ±0.05 of an integer and half-integer ratio were accepted as indices of entrainment, provided that the observed entrained scores were statistically significant. Ventilation frequency showed a clear, but intermittent tendency to entrain with limb frequency. This tendency was greater during bicycle ergometry, possibly as a consequence of task familiarisation, although both exercise entrainments were independent of workload. No difference between preferred versus varied exercise rhythm was evident, but more entrainment ($p < 0.01$) was observed during a decremental change in exercise rhythm. These responses do not appear to support an appreciable role for limb-based afferents in the control of entrainment. The results of this study provide evidence that exercise rhythm has some regulatory role in the control of breathing during moderate rhythmical laboratory-based exercise ergometry.

Key words: Entrainment — Bicycle ergometry — Exercise hyperpnea — Arm cranking — Ventilatory control

Introduction

Breathing patterns during moderate steady state exercise are, in part, influenced by neural input from working limbs (Kao 1963). Proprioceptive afferents may even regulate the endogenous frequency of ventilation by forcing it to adopt a frequency of oscillation that is a sub-harmonic of the exercise rhythm, i. e. entrainment may occur. Limb frequency could then be seen as playing a regulatory role in the control of exercise hyperpnea (Iscoe and Polosa 1976). However, due to difficulties in quantifying entrainment, many studies reporting a coupling during bicycle ergometry and treadmill running remain anecdotal in nature (Bannister et al. 1954; Asmussen 1965; Hey et al. 1966). Few controlled experiments have reported entrainment (Bechbache and Duffin 1977; Jasinskas et al. 1980; Kohl et al. 1981), while others find not evidence for the phenomenon (Kelman and Watson 1973; Kay et al. 1975). Indeed recent research suggests that the intermittent nature of entrainment can be predominantly influenced by a metronome used to set the exercise rhythm during bicycle ergometry (Yonge and Petersen 1983; Painter and Yonge 1984).

These conflicting findings appear to be a consequence of research design and analysis. Lack of subject naivete, poor control of the subjects' physiological state, enforced pedal rhythms, invasive breathing transducers and the employment of time domain measures to analyse entrainment

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have all made the interpretation of data difficult. The purpose of the present study was to re-examine the relationship between ventilation frequency (f) and exercise rhythm during bicycle ergometry and arm cranking under conditions where the power output remained constant but the limb frequency was varied, during two separate workloads that produced different ventilatory responses.

Methods

Nineteen experimentally naive male volunteers aged between 19 and 30 years, who had no history of cardiovascular disease and who responded normally to a series of lung function tests (FVC and $FEV_{1\%}$) participated in the study. First, subjects underwent a continuous incremental work test on a Siemens Elema 380B electromagnetically braked bicycle ergometer, (which could be modified for arm cranking), to determine maximum oxygen consumption ($\dot{V}_{O_{2max}}$). The break-point analysis method described by Wasserman et al. (1973) was used to determine the respiratory compensation threshold (RCT; Simon et al. 1983) from ventilatory gas exchange variables. From the $\dot{V}_{O_{2max}}$ and RCT data, the workloads to be used in the entrainment experiments were calculated. A low workload, within the linear phase of ventilation response to exercise (30% $\dot{V}_{O_{2max}}$ for arms and 40% $\dot{V}_{O_{2max}}$ for legs) and a high workload, in the curvilinear phase (80% RCT for both exercises; Dejours 1963) were determined for each subject. To test the accuracy of the assigned workloads, a sample of expired gas was taken from all subjects during a preliminary testing session. Each workload was found to produce acceptable ventilation responses. Heart rate was also monitored to assess workload accuracy. All equipment was calibrated prior to each test.

Next, subjects were randomly assigned to first undertake either arm or leg exercise. Each subject exercise session was separated by a period of three days and all exercise testing took place at the same time of day. The ergometer was set in the constant power mode to ensure a uniform work rate despite fluctuations in pedal rate. The low workload was administered first, followed by a 30 min rest in the recumbent position to reduce possible fatigue effects before the high workload commenced. For each exercise and corresponding workload the subjects were gradually warmed-up over a nine minute period before the start of data sampling. Each subject was instructed to initially adopt a constant pedal rhythm of preferred frequency with no frequency feedback being given. Following the warm-up period, data were gathered every minute for 12 min, the first four minutes of which were at the preferred pedal rate. An anlogue speedometer was then revealed to the subject who was instructed to augment his preferred rhythm by five rpm at the beginning of each subsequent minute for a period of 3 min. The required rhythm was thereafter decremented in a similar fashion during a further period of three minutes. The speedometer was finally removed to enable a final two minutes of data gathering at the preferred frequency.

Ventilation frequency was determined by a non-invasive thermistor mounted into a cone (15 cm diameter) that was placed two centimeters from the mouth. No nose clip was used. A half-bridge resistance circuit was coupled to the sensor, with the output passing to an active bandpass filter (20 dB down at 0.16 & 16 Hz and roll-off 20 dB/decade) and amplifier. Exercise rhythm was determined from a TTL pulse train that was generated by a magnetic sensor, one pulse being produced with every revolution when the right pedal arm was 90° to the horizon. Three ECG electrodes were also placed on the anterior chest wall using the CM_5 configuration (Blackburn et al. 1967). The ECG signal was amplified (Grass RPS 107 amplifier), bandpass filtered (6 dB down at 0.1 & 10 Hz) and displayed on an oscilloscope. A Schmidt trigger was used to detect every R spike of the ECG signal, and the resulting pulse train was used to determine cardiac frequency. All three signals were connected to the analogue input of a laboratory computer (PDP 11/23). Prior to data collection a series of known signals was run through the data collection and post-processing programs. Each signal was within the expected physiological range of f, heart rate (HR) and pedal frequency. The signals were varied during the calibration test in a similar manner to that expected during the exercise test. An ECG wave simulator was used to ensure correct triggering from the R spike.

Each of the three analogue signals was sampled at 60 ms intervals for a one minute period using routines from the DAOS software package (Laboratory Software Associates, Melbourne, Australia). On attaining steady state (preferred frequency), data gathering was triggered by a switch held by the experimenter. While anlogue to digital conversion occurred, the ventilation signal was continuously diplayed on a VT105 visual diplay unit. At the end of a sampling period the data were written to disk and the trigger was re-enabled for the next data capturing period. The program was terminated at the end of the twelfth data collection period. The digitized signals were subsequently analysed by a post-processing program that took each data gathering period (1.024 min) and analysed each period as four separate epochs (256 data points) in order to increase the sensitivity of the analysis to changes in f. However, each epoch was extended to series of length 1024 by adding zeros in order to increase the resolution of the frequency analysis. A power spectrum was then derived for each epoch using a fast Fourier transform (FFT) algorithm with the mean of the signal being first subtracted to remove any DC offset. The resulting periodiogram was smoothed using a three point moving average. The dominant frequency of ventilation and pedal pulse train for each time interval were identified, and ratio scores (pedal frequency:ventilation frequency) of paired frequencies were computed using a time series analysis package (Henstridge 1982) to ascertain the percentage of data that lay on an integer or half-integer multiple.

Insofar as entrainment is often mathematically described as close integer multiples (Minorsky 1962), confidence limits of ±0.05 of the integer and half-integer multiple ratio were designated as the boundaries for identifying entrained points. However, the probability of a random coincidence of ratios on either an integer or half-integer multiple, would theoretically represent, on average 20% of all coupled data. In order to statistically model this random occurrence, all possible coupling combinations (48^2) were computed for each trial to determine the more accurate estimate of chance entrainment. A paired '*t*-test' was used to ascertain if instances of entrainment were greater than that expected by chance.

The complete data acquisition and processing system is shown schematically in Fig. 1.

Results

The results of this study indicate that entrainment is a physiological reality. Ventilation frequency

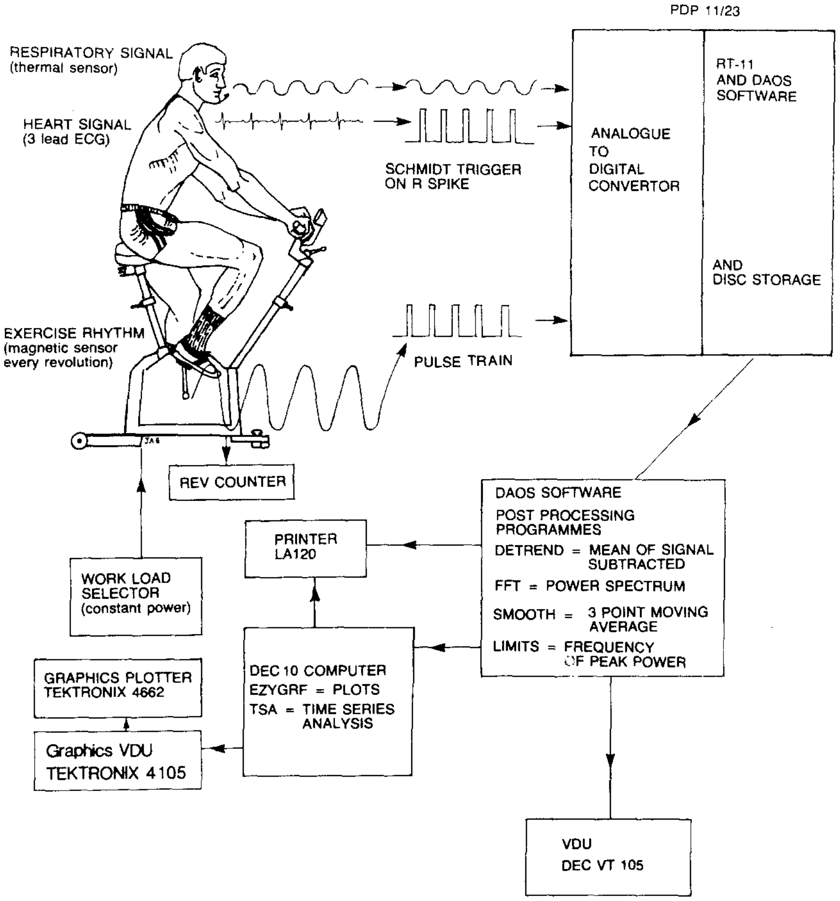

Fig. 1. Summary of data acquisiton and processing system

displayed a clear, but intermittent tendency to correspond to a multiple of the exercise rhythm, at both low or high workloads, and during both arm or leg exercise. Over all trials, mean incidence of entrainment was statistically greater ($p < 0.001$) than that which would be expected by chance (Table 1).

The occurrence of entrainment ranged from 13 to 62 percent of the total experimental period, with an average value of approximately 25% over all conditions. Periods of non-entrainment were clearly distinguishable from entrained data. Figure 2 illustrates the dominant frequencies of ventilation and exercise rhythm plotted against experimental time for one subject during preferred, incremented, decremented and again preferred exercise rhythms. The corresponding integer-multiple couplings of ventilation frequency to pedal frequency are shown in the second part of Fig. 2. Interestingly, a number of different coupling ra-

Table 1. Observed and expected entrainment over each of the four conditions (entrainment expressed as a percentage of total work time)

Type of exercise and work load:	Leg-low	Leg-high	Arm-low	Arm-high
Range of time entrained (% of total)	21—42%	13—62%	15—37%	13—35%
Expected ouctome (% of total)	12.6 ± 2.66	11.8 ± 2.78	12.2 ± 2.16	11.4 ± 1.83
Mean ± SD of entrainment time (% of total)	27.4% ± 4.98	25.2% ± 10.31	24.0% ± 6.67	24.1% ± 6.00

Table 2. Breakdown of mean entrainment data (expressed as a percentage of total time) for preferred versus varied exercise rhythms

Type of exercise		Arms		Legs	
	Time period	Preferred pedal frequency	Varied pedal frequency	Preferred pedal frequency	Varied pedal frequency
Work load	LOW $\bar{X}$(%)±SD	23.6±9.01	20.9±8.43	26.9±8.32	27.5±9.08
	HIGH $\bar{X}$(%)±SD	24.3±5.77	20.5±6.20	22.0±11.06	27.3±11.54

Type of exercise		Arms		Legs	
	Time Period	Incremental pedal frequency	Decremental pedal frequency	Incremental pedal frequency	Decremental pedal frequency
Work load	LOW $\bar{X}$(%)±SD	9.5±4.95	11.4±5.90	14.3±6.70	13.2±7.64
	HIGH $\bar{X}$(%)±SD	9.26±5.64	11.2±6.89	12.7±7.84	14.5±8.54

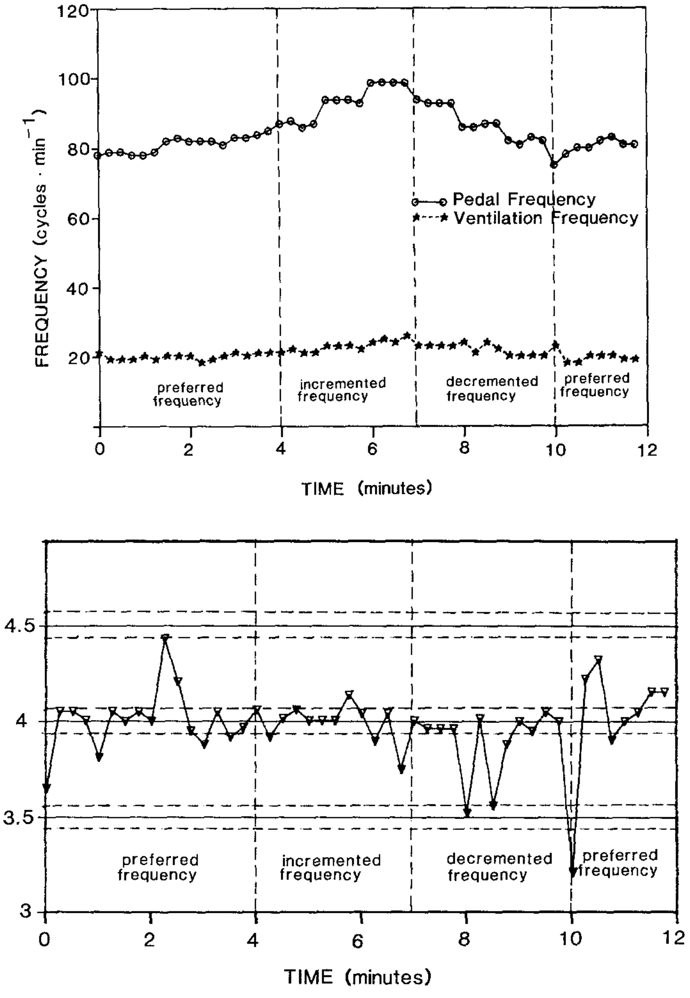

Fig. 2a. Dominant frequencies of pedalling and ventilation during a 12 min exercise period for one subject during a constant power exercise. The incidence of entrained data in this subject can be ascertained from plate **b**. **b** Ratio of pedal to ventilation frequency during a 12 min exercise period for one subject. Entrainment is indicated by data that fall within ±0.05 of an integer or half-integer ratio. Each data point represents a 15 s period of data capture. This subject was entrained for 62% of the total experimental time. Note the coupling shifts and intermittent nature of entrainment

tios was observed over all conditions during the constant power exercise. These couplings (e.g., 2:1, 3:1, 3:2, 4:1, 5:2) appear to have occurred in a non-systematic manner. Subjects, when later asked, were unaware of any coupling or coupling shift.

Table 2 illustrates the breakdown of mean entrainment scores for each condition. To test for experimental effects on the dependent variable (incidence of entrainment), four comparisons (leg v arm, low v high, preferred v varied, increment v decrement) as well as interactional effects were analysed multivariately (MANOVA) in a $2 \times 2 \times 3$ factorial design with repeated measured based on one and nine degrees of freedom (Bock 1975). A significant multivariate F ($F = 21.6$; $p < 0.001$) and significant main effects difference ($p < 0.04$) was observed between bicycle ergometry (26%) and arm cranking (22%). No differences were apparent between workloads or preferred versus varied exercise rhythms. However, a greater degree of entrainment ($p < 0.01$) was observed during decremental rhythm changes (12.6%) when compared to incremental pedal frequency variations (11.4%). This finding applied to all conditions except low work with the legs.

Predicted heart rate data, used to ascertain workload reliability were not different from recorded heart rates associated with exercise rhythms of preferred frequency. However, heart rates during exercise that were associated with incremental frequency changes were significantly higher ($p < 0.01$). These heart rates decreased ($p < 0.01$) when the exercise rhythm was decremented to preferred movement frequencies.

Discussion

The entrainment of f to exercise rhythm during moderate aerobic activity was thought to be a regular occurrence, although few studies support the relationship. In this study, breathing patterns showed a distinct tendency to intermittently entrain with limb frequency over all experimental conditions. Entrainment was however, highly variable between subjects and treatment conditions.

During bicycle ergometry, the degree of entrainment was not as great as previous reports suggested. This study observed that during both workloads entrainment occurred during approximately 25% of the total experimental period. In contrast, Jasinskas et al. (1980) reported that under similar workloads and preferred pedal frequencies, all 16 subjects were entrained for both workloads during a three minute data collection period. It is noteworthy, though, that their use of Fourier analysis on cross correlated data might be invalid, as the analysis involved a duplication of breath counts at displacements equal to the pedal period (Yonge 1982). Furthermore, the Type B histograms used to signify entrainment could be generated by random numbers. Bechbache and Duffin (1977) also observed a high degree of entrainment during bicycle ergometry, but Yonge (1982) suggested that the cross correlation technique used by those workers does not adequately discriminate between the synchronisation of breath signals to the same phase of the pedal period in consecutive breaths. However, Kohl and co-workers (1981) have observed in the majority of subjects that pedalling and breathing rhythms were often synchronised in integer ratios.

Yonge and Petersen (1983), as well as Painter and Yonge (1984) observed that entrainment was uncommon during cycling, and when present, was predominately influenced by the subjects' attention to a metronome. Entrainment was observed in the present study without external stimuli, although significantly more ($p < 0.01$) entrainment was seen during exercise at both low and high workloads when the frequencies were deliberately decremented. On first appraisal, the greater degree of entrainment during decremented exercise rhythms could be attributed to the subject's attention to the cycle speedometer. But it would seem unlikely that direct monitoring of the analogue speedometer would act as an entraining stimuli, since there was no associated auditory or beat/rhythm. Alternatively, the effect of time can not be dismissed in partial explanation of an increased incidence of entrainment. This factor may have facilitated a greater experimental familiarisation, thus minimising the conscious control.

The relatively intermittent nature of entrainment during the ergometry exercises when compared to the higher incidence that was reported during treadmill running (Bechbache and Duffin 1977) and unrestrained running (Bramble 1983; also observed in our laboratory), may be explained by a greater involvement of active muscles and the piston-like action of the visceral mass that could enforce a rhythmicity on the respiratory system. Further, a cycling action of the legs or arms would not be regarded as an ecologically natural movement for a bipedal mammal, since the biomechanical system was constrained by the mechanical structure of the ergometer. Studies on birds (Butler et al. 1977, 1980) and some mammals

(Bramble and Carrier 1983) conclusively demonstrate the entrainment of f during flight and locomotion, and suggest that the phenomenon was evolutionally related to the species' ability to efficiently undertake aerobic activity. A cycling action of the arms and legs was therefore less likely to act as a strong entraining rhythm on f when compared to walking and running. Interestingly, a higher degree of entrainment during bicycle ergometry might also support the hypothesis of task familiarisation, since cycling was a common mode of exercise that was regularly undertaken by all subjects.

Bechbache and Duffin (1977) speculated that entrainment may be associated with a reduction in aerobic fitness. No significant linear relationship ($r = 0.62$; $p > 0.05$) to verify this was apparent from the results of the present study. Bramble and Carrier, 1983) did, however, note that inexperienced runners showed little or no entrainment, irrespective of physical condition. The subjects who demonstrated a high degree of entrainment during both exercises in this study did cycle or swim regularly. Thus, entrainment may be enhanced by a high degree of subject habituation. Task familiarisation could thus increase the possibility of entrainment by reducing the disabling effect of conscious control. This suggestion is further supported by Kohl et al. (1981) who reported that trained cyclists showed a greater tendency for coupling than non-cyclists.

Although our data gives no direct indication as to the mechanisms involved in entrainment, or its significance in ventilatory control, it now seems apparent that in man limb frequency may have a regulatory role in breathing control during moderately intensive rhythmical exercise. The relative importance of a peripheral, rather than a central control mechanism is difficult to ascertain. The higher degree of entrainment observed in this study during the decremental rhythm change appears to negate the hypothesis that an increase in limb frequency will increase entrainment during bicycle ergometry and arm cranking. Thus, neural pathways from limb-based afferents to the pontomedullary centre (Asmussen et al. 1965; Kalia et al. 1972; McCloskey and Mitchell 1972) or ergoreceptors (Kao 1963) may form only part of the entrainment control system. Bramble (1983) has suggested that even though the on and off setpoints for respiratory half-cycles usually have a constant temporal relationship to footfall during running, it was possible that the relationship could be sustained by a direct central coupling of the locomotive and respiratory programs. The likelihood of such an alternative was supported by claims that the sub-thalamic area can act as a feedforward mechanism to the respiratory and locomotor muscles in the absence of afferent feedback (Eldridge et al. 1981; Di Marco et al. 1983; Eldridge et al. 1985). Viala et al., 1979) also reported that spinal stimulation was capable of producing synchronized outputs to respiratory and locomotive musculature. Consequently these endogenous mechanisms activated in association with limb movements could also contribute to entrainment and breathing control.

Changes in coupling ratios are an extremely intesting phenomenon. In this study coupling ratios of 2:1, 3:1, 4:1, 3:2 and 5:2 were observed, which were similar to the values reported by Iscoe and Polsa (1976) and Bramble and Carrier (1983). Bramble (1983) suggested that the varying of coupling ratios during running may be geared to the control of respiratory efficiency, as there presumably exists a specific rate and depth of breathing that optimises ventilation.

Since there appeared to be no conscious change in the motor program during coupling shifts in this study, one could speculate that the entrainment shift from one frequency combination to another may be explained with reference to non-linear limit cycle oscillators (Solleberger 1965). In order to find the optimal frequency for the respiratory system, the entrained oscillator may jump from one oscillation frequency to another. Bramble (1983) hypothesized that when f is entrained, and the demand on the respiratory system increases, the driving action that might shift the ratio or determine the threshold of the limit cycle may be related to an upper limit tidal volume (V_T) threshold. When the V_T reaches its upper limit, the coupling ratio shifts and abruptly adjusts the f. These 'jumps' might indicate a greater economy of effort for the pulmonary and locomotor systems. There is of course strong teleological appeal for entrainment and associated coupling shifts to be based upon principles of minimal effort, although there is no evidence to suggest that these 'jumps' in ratios are related to the control of respiratory efficiency. However, one recent study did observe that the metabolic cost of entrained cycling was significantly decreased when compared to non-entrained cycling (Garlando et al. 1985).

Casaburi et al. (1978) report that mechanical calibration of an electromagnetically braked bicycle ergometer set in the constant power mode exhibits fluctuations in power output when the pedalling rate changes. These fluctuations suggest that a change in work may have caused metabolic changes over varying exercise rhythms. The findings of this study, which linked increases in HR to changes in exercise rhythm, could be used to support such claims. Alternatively, the higher HR changes could also be influenced by an increased afferent input into the cardiovascular centre (Mitchell et al. 1977) when cycling rhythms were increased. Heart rates in this study returned to values associated with preferred movement frequencies when the cycling rhythm was decremented, and yet a higher degree of entrainment was observed during the decremented frequency. Further, the MANOVA showed no significant difference in entrainment between the two workloads, indicating that factors contributing to the control of f in the entrained state were independent of the workload. Therefore the metabolic state of the muscle may not be important in the control of entrainment, since the high workloads were related to the curvilinear aspects of ventilation response to work (Dejours 1963), where blood lactate levels are reported to gradually increase until RCT is reached. Kohl et al. (1981) did note, however, that the coupling occurrence decreased during increases in workload. They concluded that this was a consequence of a decreased neural influence and an increased effect from metabolic factors that would appear to adjust the breathing pattern.

We conclude from these data that the forcing frequency induced by the exercise rhythm periodically entrains the endogenous frequency of ventilation. This infrequency appears to be influenced by the specific movement of arm cranking and bicycle ergometry and the subjects degree of task familiarization. Despite the intermittent nature of entrainment, the observed couplings do provide some evidence for a regulatory role of limb frequency in the control of breathing during steady state exercise. Our data gives no direct indication as to the control mechanism of entrainment. However, it is hypothesised that the sensory input(s) to the pontomedullary centre that excite respiratory motorneurons to follow the rhythm of exercise, may not be completely governed by a prioproceptive action from working limbs. The slow feedforward neural rhythmicity from spinal and sub-cortical centres may also act as alternative or collective drives for entrainment.

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