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ANALYSIS OF CO-ORDINATION BETWEEN BREATHING AND EXERCISE RHYTHMS IN MAN

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SUMMARY

1. The purpose of the present study was to analyse the incidence and type of coordination between breathing rhythm and leg movements during running and to assess the effect of co-ordination on the running efficiency, as well as to compare the results with those found during cycling.

2. The experiments were carried out on thirty-four untrained volunteers exercising at two work loads (60 and 80% of subject's physical work capacity 170) on a treadmill. In addition nineteen of the subjects exercised at the same two work loads on a bicycle ergometer. The subjects were running at both work loads in three different modes in randomized order: with normal arm movements, without arm movements and with breathing paced by an acoustic signal which was triggered by the leg movement.

3. Respiratory variables, oxygen uptake and leg movements were continuously recorded and evaluated on-line. The degree of co-ordination was expressed as a percentage of inspirations and/or expirations starting in the same phase of the step or pedalling cycle.

4. The average degree of co-ordination was higher during running (up to 40%) than during cycling (about 20%) during both work loads. The difference in the degree of co-ordination between running and cycling is probably not due to the lack of arm movements during cycling since the degree of co-ordination during running with and without arm movements was the same.

5. The degree of co-ordination during running increased slightly but not significantly with increasing work load and could be increased significantly by paced breathing.

6. The co-ordination between breathing and running rhythms occurred in three different patterns: (a) breathing was co-ordinated all the time with the same phase of step, (b) co-ordination switched suddenly from one phase of step to another and (c) co-ordination ensued alternatively once on the right and once on the left leg movement. During cycling the pattern described in (a) occurred almost exclusively.

7. During running with a high degree of co-ordination, oxygen uptake for a given work load was slightly but significantly lower than during running with weak co-ordination.

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INTRODUCTION

There is general agreement about participation of a large number of stimuli in the control of breathing during exercise. Since Dejours summarized the early concepts about control of respiration in muscle exercise (Dejours, 1963), this topic has been repeatedly reviewed as new findings have occurred. One of the recent reviews by Whipp (1983) gives a detailed analysis of the respiratory drives discussed during exercise. Usually, the very fast initial phase of the adjustment of respiration to momentary requirements is supposed to be mediated by neural mechanisms, whereas in the subsequent slow component of the respiratory response and in the steady state humoral mechanisms (e.g. carbon dioxide, proton concentration, potassium, osmolarity, or catecholamines) are also thought to be involved. However, new aspects are turning up, especially regarding the relative role of individual stimuli. For example a recent study by Jeyaranjan, Goode & Duffin (1989) has seriously challenged the widely accepted concept about the role of lactic acid in the ventilatory response to heavy exercise. This study has shown that other factors, perhaps of neurogenic origin, must also be involved in regulation of breathing under these conditions.

The most important neural mechanisms capable of increasing ventilation are the feedback control from the moving limbs and the feedforward control from the locomotor areas of the central nervous system, both mechanisms being closely related to the motor action itself. Therefore, in the case of rhythmic movements, e.g. walking, running, or cycling, the question arises whether the rhythms of movement and breathing interact in some way. Although the majority of authors searching for a kind of co-ordination or coupling between exercise rhythm and rhythm of breathing found some relationship (e.g. Bechbache & Duffin, 1977; Jasinskas, Wilson & Hoare, 1980; Bramble & Carrier, 1983; Paterson, Wood, Morton & Henstridge, 1986; Paterson, Wood, Marshall, Morton & Harrison, 1987; Hill, Adams, Parker & Rochester, 1988), there are also reports that breathing and exercise rhythms are independent (Kelman & Watson, 1973; Kay, Petersen & Vejby-Christensen, 1975). The variety of the results may be explained by differences in experimental design, in the type of exercise and other experimental conditions and methods of evaluation which in turn make a quantitative comparison between the different studies more difficult. In two of our previous studies we found in the majority of the subjects a degree of co-ordination between limb movements and respiration during cycling (Kohl, Koller & Jäger, 1981; Garlando, Kohl, Koller & Pietsch, 1985). Moreover, we found a higher degree of co-ordination in experienced rather than unexperienced cyclists. Therefore, the question arises whether there is a higher degree of co-ordination during running than during cycling since running is a phylogenetically older and more widespread kind of locomotion which is used more often even by untrained individuals.

The purpose of the present study was to analyse, by methods comparable with our previous studies, the incidence and type of co-ordination between breathing rhythm and limb movement during running, as well as to compare the results with those found during cycling. The following questions should be answered. (1) How frequent is the spontaneous co-ordination between breathing and running if compared with cycling? (2) Is there an effect of work load level on the occurrence of co-ordination? (3) Is there an effect of arm movements during running on the occurrence of co-ordination between breathing and running rhythms? (4) What are the characteristics of co-ordination during running? (5) Is there an effect of co-ordination on running efficiency?

METHODS

Subjects

The experiments were carried out on thirty-four healthy, not particularly trained volunteers, eleven females and twenty-three males. The subjects were informed about all methods and procedures used in the study, as well as about the experimental protocol and all subjects gave their consent to participating in the experiments. The mean age of the subjects was 26·0 ($\pm$6·5) years, body length 172·5 ($\pm$8·0) cm and body mass 66·5 ($\pm$10·5) kg. Their average physical work capacity 170 (PWC 170) measured according to Sjöstrand (1960) was 208 ($\pm$48) W, thus exceeding the normal values (167$\pm$32·5 W) given by Bühlmann (1965), and suggesting a good level of fitness in the majority of subjects.

Apparatus

An electrically braked bicycle ergometer (Monark, Sweden) was used for measuring PWC 170 as well as for cycling at two work loads equal to 60 and 80% of PWC 170. Running was accomplished on a treadmill ergometer (Woodway, Germany) with adjustable velocity and/or slope to provide the desired work loads (see *Experimental protocol*). Respiratory variables such as, for example, respiratory air flow, tidal volume, breathing frequency, oxygen uptake or concentrations of respiratory gases were continuously measured and calculated (computer PDP 11/34, USA) by an automatic breath-by-breath respiratory analysis system (Pietsch, 1984; Boutellier, Kündig, Gomez, Pietsch & Koller, 1987). In this respiratory analysis system air flow was measured by a Fleisch pneumotachograph (head No. 3). A piezoelectrical differential pressure transducer (Morgan, USA) was used in this study to avoid the effect of vibrations due to foot impact during running which might be present using a membrane pressure transducer. This vibration-insensitive pressure transducer was, in addition, fastened onto a stable desk, thus allowing an artifact-free recording of air flow. The good quality of air flow signals enabled further processing, i.e. computer calculation of tidal volume and minute ventilation as well as detection of respiratory phases for the evaluation of co-ordination between breathing and running rhythms. Real flow fluctuations amounting to about 1–2% tidal volume associated with stride during walking and running have been demonstrated by Banzett, Mead, Reid & Topulos (1992). These real flow fluctuations were in some cases greater than those shown in Fig. 1, but did not present a problem for integration to respiratory volume using our system (Boutellier *et al.* 1987); we have never observed any indication of errors in the calculation of ventilation or co-ordination. Respiratory gas concentrations were measured by a mass spectrometer (Varian MAT, Germany). All respiratory data were available at any time in digital form and served for general monitoring of respiration as well as for detection of the respiratory steady state. Leg movements were registered by mechanoelectrical goniometers developed and constructed in the department workshop. The goniometers were fixed on the hips and the processed signal from the goniometers (Fig. 1) was either 'one', indicating forwards movement of the left leg or 'zero', indicating forwards movement of the right leg during running or cycling. The whole step lasted from the beginning of a 'zero' signal to the beginning of the next zero signal. For paced breathing, acoustic signals were generated by a 'control unit' and were triggered by the goniometer signal, the number of steps per breath being adjustable from 1 to 9. Heart rate was measured and monitored by a Sporttester (PE 3000, Finland) as an additional indicator of steady state and of subjects' condition. All recorded data were stored on computer disks for further evaluation.

Experimental protocol

At the beginning of the experiments the control values at rest of all above-mentioned variables were recorded over 5 min. Thereafter the PWC 170 was measured on the bicycle ergometer and from the results the work loads L_1 (= 60% of PWC 170) and L_2 (= 80% of PWC 170) were assessed. Afterwards the treadmill velocity (v) and for fifteen subjects (see below) also the slope (S) necessary to provide work loads L_1 and L_2 for a given subject were calculated. The calculation was carried out according to Di Prampero (1985) and was based on oxygen uptake found at L_1 and at L_2 during measurement of PWC 170 and on the subject's body mass and body surface. Work loads

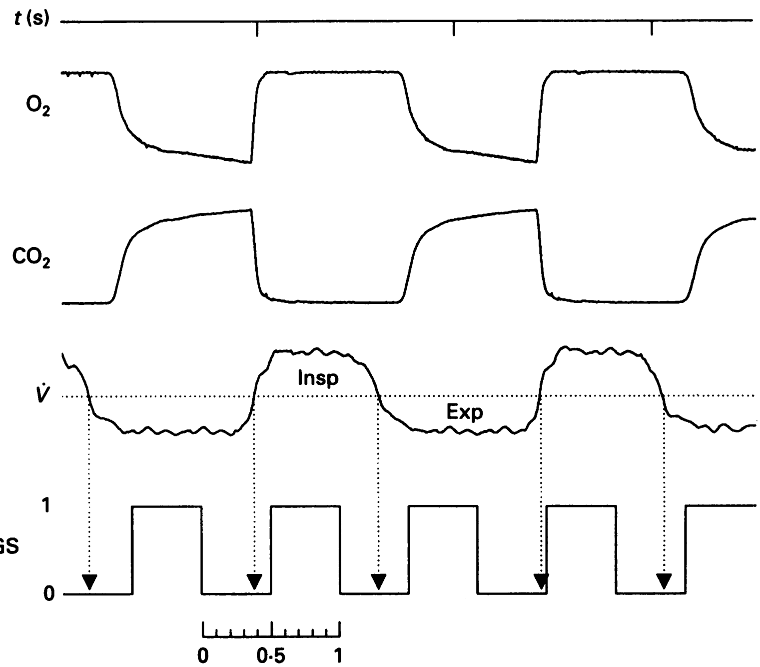

Fig. 1. Computer print out of respiratory and leg movement signals. From top to bottom: time (t), oxygen (O_2) and carbon dioxide (CO_2) concentration in respired air, synchronized with respiratory flow ($\dot{V}$), and goniometer signal (GS), with an example of evaluation of co-ordination between breathing and exercise rhythms (scale 0–1 = division of one step into ten phases).

of 60 and 80 % of PWC 170 were chosen on the assumption that both of them were in the aerobic range for our subjects who had quite high level of fitness as measured by PWC 170 (see above). The work loads could thus be carried out within 5 min in steady state. This assumption was based on the fact that according Bühlmann & Gattiker (1964) PWC 170 represents a work load of about 80 % of maximum oxygen consumption ($\dot{V}_{O_2,max}$) so that 80 % of PWC 170 equals 64 % of $\dot{V}_{O_2,max}$. This relationship between PCW 170 and $\dot{V}_{O_2,max}$ was confirmed by the findings of Boutellier & Piwko (1992) in sedentary subjects. With the same method, anaerobic threshold was found to be 77 % of $\dot{V}_{O_2,max}$ in fit subjects (Boutellier, Büchel, Kundert & Spengler, 1992).

To keep the total demand on each subject as well as the eventual effect of fatigue as low as possible, the main experiment was carried out in two groups of subjects undergoing two slightly different protocols. In one group (group I, 15 subjects) the effect of the type of increasing load (velocity *vs.* slope) on the degree of co-ordination was tested, whereas in the other (group II, 19 subjects) the comparison between running and cycling was carried out.

The main experiment in group I consisted in the following seven experimental runs each of them lasting 5 min (the symbols used for each run in Figs 3 and 4 and in Table 1 are given in parentheses):

(1) running with velocity v_1 at L_1 and with normal arm movements (v_1, +A),

(2) running with v_1 at L_1 without arm movements, i.e. with hands loosely holding the treadmill hand-rail (v_1, −A),

(3) running with v_1 at L_1 with paced breathing and normal arm movements (v_1, PB),

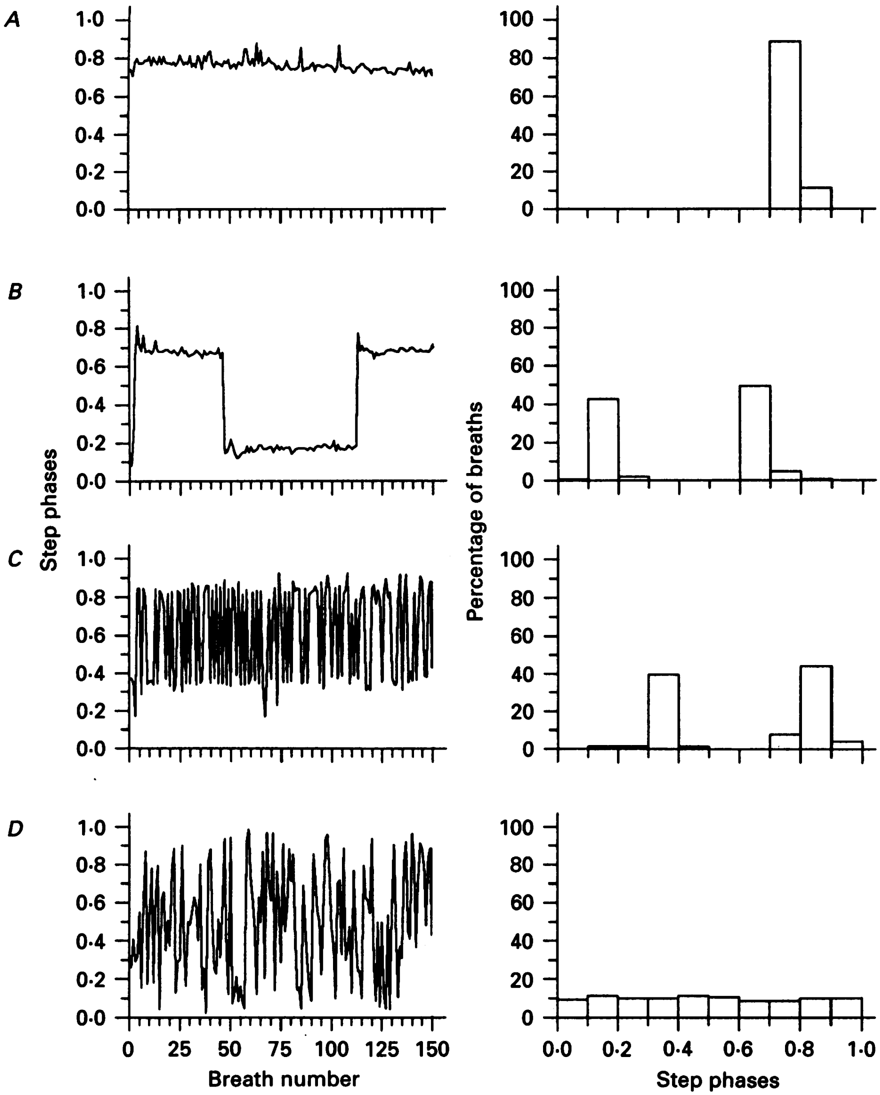

Fig. 2. Patterns of co-ordination between breathing and running rhythms. From top to bottom: *A*, co-ordination of breathing with the same phase of step during the whole run; *B*, switch of co-ordination from one phase of step to another; *C*, alternate co-ordination of breathing once with the right, once with the left leg; *D*, no co-ordination between breathing and running. Left breath-by-breath records of the step phase coinciding with the beginning of inspiration. Right, number of breaths (as a percentage of all evaluated breaths) starting in the same phase of step.

(4) running at L_2 whereby the increase of work load was achieved by increasing treadmill velocity to v_2 (v_2, +A),

(5) running with v_2 at L_2 without arm movements (v_2, −A),

(6) running with v_1 at L_2 and normal arm movements, the increase of work loading being achieved by increase of treadmill slope (v_1, +A, S),

(7) running at the same conditions as in run (6) but without arm movements (v_1, −A, S).

In group II the main experiment consisted of the following eight experimental runs, each of them lasting 5 min:

(1) running with v_1 at L_1 with normal arm movements (v_1, +A),

(2) running with v_1 at L_1 without arm movements (v_1, −A),

(3) running with v_1 at L_1 with paced breathing and with normal arm movements (v_1, PB),

(4) cycling at L_1 (c_1),

(5) running with v_2 at L_2 with normal arm movements (v_2, +A),

(6) running with v_2 at L_2 without arm movements (v_2, −A),

(7) running with v_2 at L_2 with paced breathing and with normal arm movements (v_2, PB),

(8) cycling at L_2 (c_2).

In both groups the sequence of all experimental runs was randomized. Recovery periods between runs lasted 5 min each.

Evaluation

For assessment of co-ordination between breathing and exercise rhythms the whole-step and/or the whole-pedal cycle was divided into ten equal phases (Fig. 1) whereby during the first five phases the right leg and during the second five phases the left leg was moving forwards. The phase of movement in which inspiration and expiration started was continuously – breath-by-breath – assessed and displayed (Fig. 2, left part) by computer. At the end of each experimental run the distribution of the beginning and expiration of all recorded breaths in respiratory steady state (mostly about 150) was available as histogram (Fig. 2, right part). To quantify the occurrence of co-ordination we used the term 'degree of co-ordination' which was defined as the number of inspirations or expirations starting in the same phase of leg movement and expressed as a percentage of the total number of breaths recorded in a given run (e.g. the degree of co-ordination in Fig. 2*A* is 89%). An accumulation $\geqslant 15\%$ of recorded breaths in one phase of step was considered significant ($P = 0{\cdot}05$, χ^2 test). The highest columns of the histograms were used for calculation of mean values and standard errors for the whole group in each experimental run. In cases of co-ordination of types B and C (see Results), the two relevant columns were added together (Fig. 2*B* and *C*). Significance of differences between experimental runs was tested by the Wilcoxon test for paired differences. The minimal accepted level of probability was $P = 0{\cdot}05$.

RESULTS

Occurrence of co-ordination

The degree of inspiratory and expiratory co-ordination in group I for all experimental runs is given in Fig. 3. Except for the significant difference ($P < 0{\cdot}05$) between run 1 (v_1, +A) and run 3 (v_1, PB) in inspiratory co-ordination, the other differences in the degree of co-ordination between experimental runs in group I were insignificant. In other words, the degree of co-ordination during running did not significantly change with arm movements or with the work load level, whether the latter was changed by treadmill velocity or treadmill slope. However, the degree of co-ordination was significantly increased by paced breathing.

Figure 4 summarizes the results of group II. For a better overview, the statistical significance of the differences between experimental runs in group II is given separately in Table 1. The degree of both inspiratory and expiratory co-ordination during running was significantly higher in all experimental runs than during cycling. The degree of expiratory co-ordination increased significantly with paced breathing at both work levels, whereas the increase of inspiratory co-ordination was only

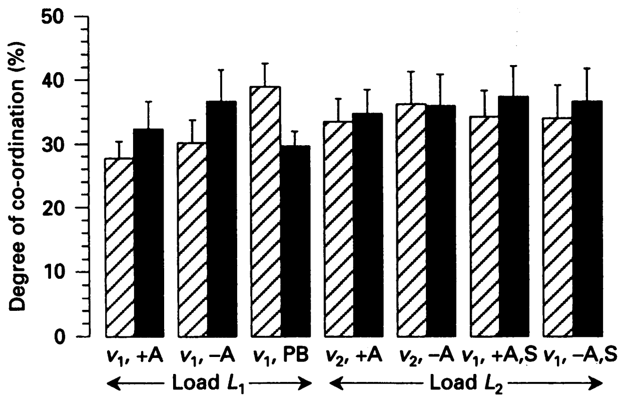

Fig. 3. Degree of inspiratory (hatched columns) and expiratory (filled columns) co-ordination in 15 subjects (group I) in seven experimental runs (mean values and standard errors), (v, velocity; A, arm movement; PB, paced breathing; S, treadmill slope).

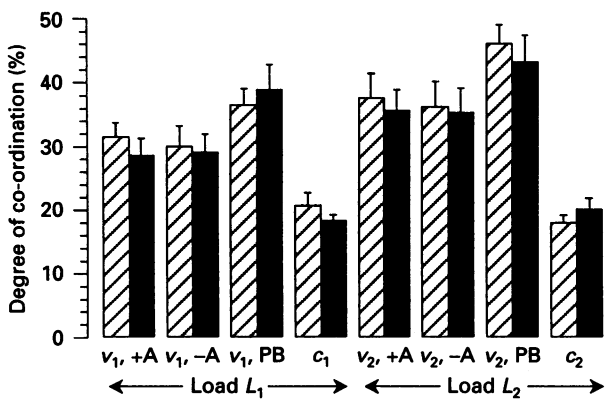

Fig. 4. Degree of inspiratory (hatched column) and expiratory (filled columns) co-ordination in 19 subjects (group II) in eight experimental runs (mean values and standard errors), (v, velocity; A, arm movement; PB, paced breathing; c, cycling).

TABLE 1. Significance of the differences in the degree of co-ordination between experimental runs in group II

Run	v_1, +A	v_1, −A	v_1, PB	c_1	v_2, +A	v_2, −A	v_2, PB	c_2
v_1, +A	—	n.s.	n.s.	*	n.s.	n.s.	*	**
v_1, −A	n.s.	—	n.s.	*	n.s.	n.s.	*	**
v_1, PB	*	n.s.	—	**	n.s.	n.s.	*	**
c_1	*	*	**	—	**	*	**	n.s.
v_2, +A	n.s.	n.s.	n.s.	**	—	n.s.	*	**
v_2, −A	n.s.	n.s.	n.s.	**	n.s.	—	*	**
v_2, PB	*	*	n.s.	**	n.s.	*	—	**
c_2	*	*	**	n.s.	**	**	**	—

The differences in inspiratory co-ordination are given in the right upper part, the differences in expiratory co-ordination in the left lower part (* $P < 0.05$, ** $P < 0.01$; n.s. non significant).

significant at L_2. Arm movements had no effect on the degree of co-ordination. There was no significant difference in the degree of co-ordination between the two submaximal work loads, except a higher inspiratory co-ordination during PB at L_2 than during PB at L_1.

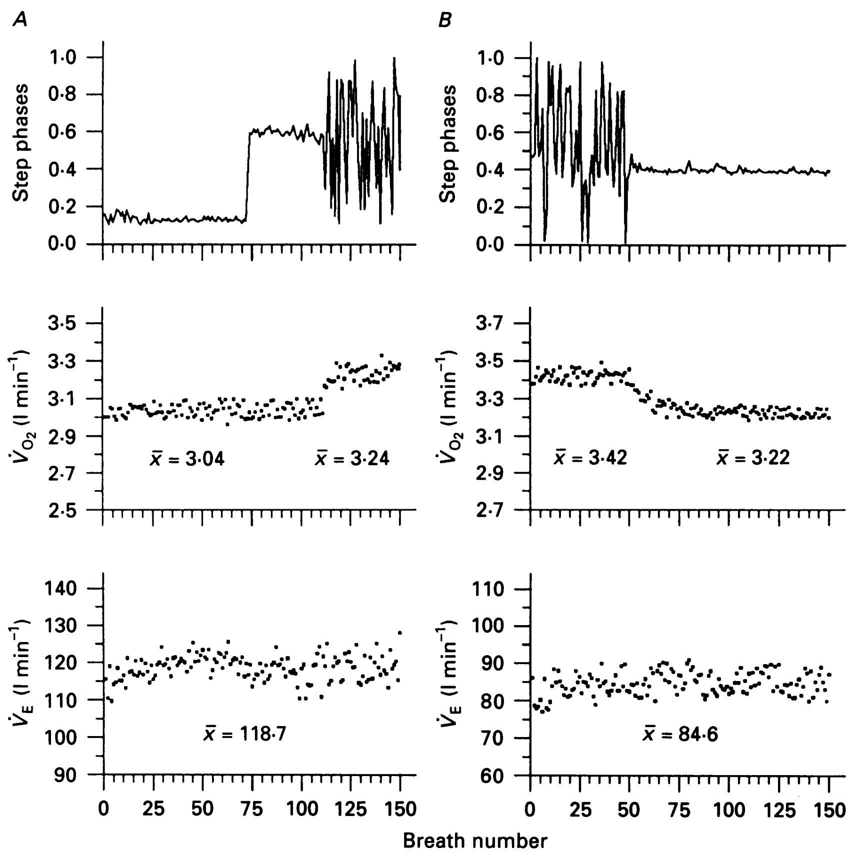

Fig. 5. Two examples (*A* and *B*) of a change in the degree of co-ordination within one experimental run, accompanied by a change in oxygen uptake, whereas the minute ventilation remained constant. Upper panels: breath-by-breath record of step phase in which inspirations started, i.e. in the example *A* a period of high co-ordination (breath Nos. 1–120) was followed by a low one, and vice versa, in the example in *B* low co-ordination at first (breath Nos. 1–50) was followed by high co-ordination. Middle panels: breath-by-breath record of oxygen uptake ($\bar{x}$, mean values in a steady state). Lower panels: breath-by-breath record of minute ventilation.

Types of co-ordination

From the breath-by-breath records of phases of the step in which inspiration and/or expiration started it was obvious that there were three different types of co-ordination between breathing and running (Fig. 2): (a) the subject started to inspire and/or to expire in the same phase of step during the whole experimental run (co-ordination type A, Fig. 2*A*), (b) there was a change from one phase to another within one experimental run (co-ordination type B, Fig. 2*B*) and (c) the subject started to inspire and/or to expire alternately on the left and right leg forwards movement (co-ordination type C, Fig. 2*C*). Type C was, moreover, characterized by a ratio of number of steps to number of breaths of 5:2. Types A and B were associated with ratios of 2:1, 3:1 and 4:1. A single subject often used all three types

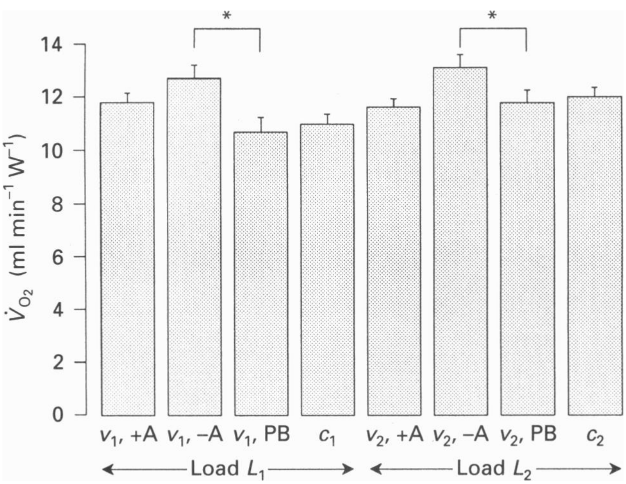

Fig. 6. Oxygen uptake ($\dot{V}_{O_2}$) per W (net values after subtraction of the uptake at rest) in 19 subjects (group II) in eight experimental runs (mean values and standard errors), (v, velocity; A, arm movement; PB, paced breathing; c, cycling; $*P < 0{\cdot}05$).

in different experimental runs or two different types within one run. In a few cases co-ordination between breathing and running was completely absent, i.e. inspiration and/or expiration started randomly in all phases of the step (Fig. 2*D*). The total number of experimental runs in thirty-four subjects was 219. Inspiratory co-ordination of type A occurred in 38 (7·6%), type B in 23 (10·5%), type C in 32 (14·5%), two different types in 83 (37·8%) and no co-ordination in 43 (19·6%) out of 219 (100%) experimental runs. Expiratory co-ordination of type A occurred in 35 (16·1%), type B in 22 (10·0%), type C in 38 (17·2%), two different types in 88 (40·2%), and no co-ordination in 36 (16·5%) out of 219 (100%) experimental runs. During cycling type A co-ordination was observed almost exclusively, but the periods of co-ordination were shorter and the degree of co-ordination was therefore significantly lower than during running.

Oxygen uptake

Figure 5 gives two examples of a change in oxygen uptake coinciding with a change in the degree of co-ordination within one experimental run during running: in Fig. 5*A* a high degree of co-ordination was followed by a low one; in Fig. 5*B* vice versa. In both cases, during higher co-ordination oxygen uptake was lower. The total minute ventilation, however, remained the same throughout the whole run. The results of oxygen uptake during running and cycling at two work loads are summarized in Fig. 6. During paced breathing (characterized by the highest degree of co-ordination; Fig. 4) oxygen uptake was significantly lower ($P < 0{\cdot}05$) than during running without arm movements at both work loads. The other differences in oxygen uptake were statistically insignificant. It should be pointed out that all our subjects reached steady state at both work loads: after an initial increase, minute ventilation showed only the usual scatter around a mean value (Fig. 5) but no continuous increase during the whole 5 min run.

DISCUSSION

Incidence of co-ordination

A great majority of the studies dealing with the phenomenon of co-ordination between breathing and exercise rhythms have found a more-or-less tight relationship between these two rhythms (e.g. Bechbache & Duffin, 1977; Jasinskas *et al.* 1980; Bramble & Carrier, 1983; Paterson *et al.* 1986, 1987; Hill *et al.* 1988). To our knowledge, there are only two studies showing that these two rhythms are independent (Kelman & Watson, 1973; Kay *et al.* 1975). Therefore, the general tendency to co-ordination between breathing and exercise rhythms can be taken for granted. However, the occurrence and the degree of co-ordination obviously depends on a large number of factors in experimental design as well as on the method of evaluation. There are also great differences in the definition of co-ordination between different authors. Therefore, it is difficult to compare quantitatively the results of all relevant studies. However, the results of the present study and of our previous studies (Kohl *et al.* 1981; Garlando *et al.* 1985) are at least partially comparable, as in all of them we concentrated on the so called relative co-ordination (von Holst, 1939), characterized by significant relationships between the individual phases of both rhythms.

Our present results show better co-ordination between breathing and movement during running than during cycling. The possibility that during running the arm movements contribute to locking between the two rhythms and so increase the degree of co-ordination can clearly be excluded. The degree of co-ordination during running was not reduced by deliberate exclusion of arm movements. Any influence of upper thorax rotation on the degree of co-ordination is unlikely as with hands holding the treadmill handrail the thorax rotation was largely prevented. We suggest rather that the frequency of repetition of a given type of exercise increases the degree of co-ordination and this might be responsible for the differences between running and cycling. In a previous study (Kohl *et al.* 1981) we found a higher degree of co-ordination in racing cyclists than in non-cyclists, and Bramble & Carrier (1983) reported a higher degree of co-ordination in experienced runners than in inexperienced runners. In the present study none of the subjects was specially trained in either type of exercise, but they were generally more familiar with running than with cycling as the former is a natural and instantly available type of locomotion. Physical fitness alone has no influence on the degree of co-ordination (Garlando *et al.* 1985).

The attempt to increase the degree of co-ordination by paced breathing was undertaken in order to assess the effect of co-ordination on oxygen uptake. In the majority of the subjects the degree of co-ordination was increased by paced breathing, although there were great interindividual differences. Some subjects felt annoyed by paced breathing and the degree of co-ordination was even reduced by it.

However, a higher degree of co-ordination, no matter whether spontaneous or due to paced breathing, was, with a few exceptions, associated with a lower oxygen uptake. Surprisingly, the increase of co-ordination due to paced breathing was significantly higher at the higher work load. In runs without paced breathing the spontaneous incidence of co-ordination was also slightly higher at the higher work load, but these differences were just below the 0·05 level of significance.

Different patterns of co-ordination observed during running are probably all equally beneficial, as there was no change in oxygen uptake when a single subject switched within one run or between runs from one pattern to another. However, a more detailed analysis of the effect of co-ordination on work efficiency during running will be carried out in a further study (see below).

Possible mechanisms of co-ordination

Several mechanisms have been suggested as a neurophysiological basis for the co-ordination between movement and respiration and these have been partially confirmed, at least in animal experiments. There is much evidence for both central neurogenic and peripheral reflex influences. Eldridge, Millhorn & Waldrop (1981) and Eldridge, Millhorn, Kiley & Waldrop (1985) found a parallel activation of respiration and locomotion from the hypothalamus in cat. The findings of Di Marco, Romanuk, von Euler & Yamamoto (1983) suggest that 'the motor pathway to both the spinal locomotor pattern generator and the pattern controlling mechanisms for respiration are driven in parallel to provide a quantitative relationship between respiratory motor output and locomotor activity'. Viala & Freton (1983) and Viala (1986) reported direct interactions between the respiratory and the locomotor rhythm generators at the spinal cord level in rabbits. Iscoe & Polosa (1976) found a mechanism in cats capable of locking respiratory frequency to that of a periodic somatic afferent input. Biomechanical factors are probably also involved, e.g. the piston-like movements of abdominal organs during running can influence respiration (Bramble & Carrier, 1983).

Possible meaning of co-ordination

The question arises whether the co-ordination between breathing and exercise rhythms may in some way influence performance. Coleman (1921), one of the earliest authors dealing with the phenomenon of co-ordination between rhythms, suggested a beneficial effect; he found that energy can be saved and fatigue postponed when two or more periodic activities are in accordance. Our previous study (Garlando *et al.* 1985) revealed a significant reduction of oxygen uptake for a given work load in experimental runs with high degree of co-ordination during cycling. In the present experiments with running the reduction in oxygen consumption due to co-ordination, although present, was less pronounced than during cycling. Running itself is already a very efficient type of exercise (Di Prampero, 1985), so that a further increase of efficiency may be more difficult to achieve. Generally, we expect that a moderate degree of co-ordination, or even changing from one pattern of co-ordination to another is better than very tight co-ordination, the latter probably reducing the flexibility of respiratory responses to changing demands during exercise. Our suggestion is in agreement with the experience of competitive cyclists who, although co-ordinating breathing and leg movements more than non-cyclists, try to keep their breathing rhythm partly independent of the rhythm of cycling in order to be able to change easily from one gearing ratio to another (Garlando *et al.* 1985). Our suggestion is, furthermore, in agreement with the recent recognition of 'healthy chaos' *vs.* strong regularity of heart rate (Golberger, 1991), a new concept which is probably relevant to all physiological functions.

Possible mechanisms of reduced oxygen uptake

Although the analysis of the mechanisms which might reduce oxygen uptake during co-ordination exceeds the goals of this study, some possible explanations might be considered. In our opinion, the periods of co-ordination are associated with a lowering of sympathetic tone and thus with a reduction of metabolic rate. The reduction of oxygen uptake during periods of higher co-ordination due to the changing cost of ventilation is rather unlikely as neither the minute ventilation (Fig. 5) nor the tidal volume and breathing frequency differed between runs or periods with high and with low degrees of co-ordination. An increased anaerobic contribution to the total energy expenditure during co-ordination can certainly be ruled out at work load L_1, and probably also at L_2, as all our subjects reached steady state in minute ventilation at L_2 both in runs with low and with high degrees of co-ordination. The possibility that running style itself might be more efficient during co-ordination is very unlikely, as both the treadmill speed and the stride frequency during high and low degrees of co-ordination were the same. We suggest that the reduction of sympathetic tone might reduce oxygen uptake during periods of high co-ordination. This suggestion will be tested in a further study.

Conclusions

Co-ordination between breathing rhythm and exercise rhythm is more frequent during running than during cycling. This difference cannot be explained by a lack of arm movements during cycling as the degree of co-ordination during running with and without arm movements was the same. The degree of co-ordination slightly increased with increasing work load and in some subjects could be further increased by paced breathing. The pattern of co-ordination between breathing and running rhythms was not always the same; we observed three different types of co-ordination. During running with paced breathing and with the highest degree of co-ordination the oxygen uptake for a given work load was lowest.

This paper is dedicated to Professor Erwin A. Koller, Zurich, on the occasion of his sixtieth birthday. We would like to express our thanks to Mr Martin Gähwiler and Mr Kilian Schuster for construction of goniometers, Dr Urs Boutellier for his helpful comments on the manuscript and also to Mr Daniel Britschgi for his assistance during the experiments. The financial support of the Swiss National Foundation, grant no. 32-28983.90 and the Hermann Klaus-Stiftung zur Förderung der Medizinschen Forschung an der Universität Zürich is gratefully acknowledged.

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