

# Factors influencing variation in locomotor-respiratory coupling in Standardbred Trotters in the field

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## Summary

**Reasons for performing study:** A close relationship between limb and respiratory rhythms has been shown in clinically healthy galloping horses due to mechanical constraints in the thoracic region. This synchronisation leads to a 1/1 ratio between stride frequency (SF) and respiratory frequency (RF) during galloping. Very little is known about locomotor-respiratory coupling (LRC) during fast trot.

**Objectives:** To investigate stride and respiratory rates during a standardised exercise test on the track in Standardbred Trotters.

**Methods:** Forty-four French Trotters age 2–10 years performed a standardised exercise test consisting of three 3 min steps at constant speeds. Speed (V) of exercise varied between 500 and 750 m/min. Variables measured during exercise: SF, heart rate, RF using a microphone between the nostrils, blood lactate concentration. Physiological variables V4 and V200 were calculated and race performance index recorded.

**Results:** There was no age-related difference in RF or in LRC. Two LRC strategies were found: around 1/1 ratio and 3/2 ratio between SF and RF, respectively. A relationship between SF/RF ratio and physiological parameters showed a higher LRC in good performers because of a lower RF during submaximal and maximal exercise.

**Conclusion:** RF is significantly lower and LRC significantly higher in good compared to poor performers.

**Potential relevance:** More investigations are needed to ensure that the breathing techniques of Trotters may be used in the selection process of race horses.

## Introduction

Because of the thoracic muscles involved in respiration and locomotion, anatomical and mechanical restraints produce a relationship between respiration and locomotion. Studying respiration during exercise, it was found that breathing often occurred at the same part of the locomotor cycle. The coordination between gait and respiratory rhythms have been documented in man (Bramble 1989; Lee and Banzett 1997; Siegmund *et al.* 1999; Villard *et al.* 2005) and in many animal species, such as rabbits (Simons 1999), dogs (Bramble 1989), sheep (Entin *et al.* 1999), birds (Funk *et al.* 1989; Nassar *et al.* 2001) and horses

(Attenburrow 1971, 1982; Bramble 1989; Butler *et al.* 1993; Lafortuna *et al.* 1996). In all of these studies, a phase-locked 1:1 coupling of breaths and strides has been shown during galloping. Three mechanisms have been postulated by Bramble and Carrier (1983) to explain how galloping motion dictates respiration: the compacted effect of the stress loading of the thorax, flexing and extension of the axial skeleton and then caudal motion of the pelvis and viscera, enhancing inspiration during back extension or a visceral piston mechanism. However, such body movements do not occur during trotting. Few data are available on trotting animals. Bramble (1989) and Carrier (1996) described a 1:1 and a 1:2 locomotor cycle to respiratory cycle ratios in, respectively, 3 and 4 trotting dogs. But the authors also observed numerous breathing patterns in which ventilation was not always synchronised with stride. In trotting horses, 4 studies have shown different breathing strategies. Attenburrow (1982) found no correlation between timing of the respiratory cycle and stride in 11 horses on the field. Bramble and Carrier (1983) observed a 1:1 ratio or an absence of strict phase locking in 4 gallopers at slow trot on a flat ground. A constant ratio of 2:1 was observed by Art *et al.* (1990) in 5 ponies during fast trotting on a treadmill. And no coupling at a slow trot, but a 1:1 coupling at a fast trot, in 2 French Trotters on a treadmill had been shown by Barrey (2000). These results led us to investigate the locomotor and respiratory coupling in a larger population of trotters while fast trotting on the field.

## Materials and methods

### Horses

A total of 44 French Trotters, in full training and clinically sound age 2–10 years were studied in this cross-sectional experiment. Ages were 2 years (n = 12), 3 years (n = 10), of 4 years (n = 7) 5 years (n = 7), and >5 years (n = 8). The 2-year-olds were not involved in competition, in contrast to older horses. All horses were exercised using a traditional training schedule.

### Standardised field exercise test

Horses were involved in a standardised field exercise test as described previously by Demonceau and Auvinet (1992): after a 10 min warm-up at about 350 m/min, they performed three 3-min steps at increasing speeds. Speeds of each step are shown in

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**TABLE 1: Velocity and stride frequency in age-groups. All data are mean  $\pm$  s.d.**

Step	Velocity (m/min)					Stride frequency (stride/s)				
	2-year-olds n = 12	3-year-olds n = 10	4-year-olds n = 7	5-year-olds n = 7	6 and over n = 8	2-year-olds n = 12	3-year-olds n = 10	4-year-olds n = 7	5-year-olds n = 7	6 and over n = 8
1	506 $\pm$ 8	513 $\pm$ 17	513 $\pm$ 17	520 $\pm$ 10	521 $\pm$ 13	1.86 $\pm$ 0.07	1.83 $\pm$ 0.08	1.88 $\pm$ 0.07	1.87 $\pm$ 0.07	1.84 $\pm$ 0.06
2	564 $\pm$ 14	581 $\pm$ 11	576 $\pm$ 9	574 $\pm$ 13	580 $\pm$ 8	1.91 $\pm$ 0.09	1.90 $\pm$ 0.09	1.97 $\pm$ 0.05	1.94 $\pm$ 0.07	1.90 $\pm$ 0.12
3	647 $\pm$ 55	648 $\pm$ 15	654 $\pm$ 22	650 $\pm$ 21	645 $\pm$ 29	2.01 $\pm$ 0.10	1.99 $\pm$ 0.08	2.10 $\pm$ 0.09	2.05 $\pm$ 0.05	1.95 $\pm$ 0.08

NS between age groups

NS = not significant ( $P > 0.05$ ).

Table 1. These tests were performed on 2 almost identical race tracks. The reproducibility of the test under field conditions was described by Dubreucq *et al.* (1995).

### Physiological parameters

Speed was recorded during tests with a tachometer<sup>1</sup> on the sulky. The driver used information on the tachometer screen to keep the speed as constant as possible during each step. Electrodes<sup>2</sup> were put under the harness to record heart rate (HR). Venous blood samples were taken from the jugular vein at the end of each step in tubes containing fluoride and oxalate for the measurement of whole blood lactate concentration (La) by the Boehringer enzymatic method. Two physiological variables were calculated individually:  $V_4$ , velocity for a 4 mmol/l blood lactate concentration, and  $V_{200}$ , velocity for a 200 beats/min heart rate. Horses were equipped with a microphone between the nostrils and an analogue recorder (Aiwa, TP-VA300). The respiratory sound analysis allowed the respiratory frequency (FR) to be measured.

### Biomechanical parameter

The 3-dimensional accelerometric device used for the experiment was an Equimetrix 3D accelerometric transducer, connected to a small data logger<sup>3</sup>. The transducer consisted of 3 orthogonal accelerometers measuring accelerations at the sternum, along the dorso-ventral, longitudinal, and lateral axes of the horse. The accelerometric data analysis was realised by signal analysis procedures.

### Data analysis

The route taken by the horses on the track was recorded as a function of time, by a GPS Garmin 12<sup>4</sup> attached on the left shaft of the sulky. This system also measured the spontaneous speed every 2.5 secs. A custom-designed program was used to synchronise the acceleration, respiratory and GPS signals. The synchronisation was done at the end of each step when the horse was stopped briefly. Samples of 20.48 secs, at constant speed and

**TABLE 2: Age, index of trot (ITR) and physiological variables in both performance-groups. All data are mean  $\pm$  s.d.**

	Age	$V_4$ (m/min)	$V_{200}$ (m/min)	ITR
Good performers n = 16	4.4 $\pm$ 1.2	640 $\pm$ 28	613 $\pm$ 44	120 $\pm$ 14
Poor performers n = 9	4.5 $\pm$ 1.1	617 $\pm$ 18	623 $\pm$ 34	83 $\pm$ 15
	NS	$P < 0.05$	NS	$P < 0.05$

at least after the first min exercising of each step, in straight line of the race track, were analysed. The accelerometric data analysis was realised by signal analysis procedures, developed under a scientific software environment (Matlab 5)<sup>4</sup>. Finally, the respiratory sound analysis was performed consisting of counting the number of expirations in the same sample in order to determine FR. LCR was then calculated by the SF/RF ratio.

### Performance index

Horses were divided into 2 groups in accordance with their annual official index of performance, Index of Trot (ITR), as published by the French National Studbook. This criterion is computed annually for each French trotter on the basis of the natural logarithm of the average winnings per race every year. The mean  $\pm$  s.d. of the population is 100  $\pm$  20. This index has a normal distribution and it provides a linear scale to compare race performances of all French trotters.

Good performers (GP) should have an ITR equal to or higher than 100 and poor performers (PP) would have an ITR lower than 100. Only 25 of the horses had obtained an ITR at the time of this study (the 2-year-olds and some 3-year-olds had not run more than 5 races and at least 5 races are necessary to calculate ITR). There were 16 good performers (age 4.4  $\pm$  1.2 years, 8 females and 8 males including geldings), and 9 poor performers (age 4.5  $\pm$  1.1 years, 5 females and 4 males including geldings). Table 2 shows the characteristics (average age and performance index) of the population studied.

### Statistical analysis

The values of  $V_4$  and  $V_{200}$ , RF, SF and ITR were calculated and a 2 way analysis of variance was calculated in order to assess the effect of speed age throughout the test. Then, a 2 way analysis of variance testing effect of speed and effect of performance level was calculated. Duncan's *post hoc* tests were calculated if differences appeared. A level of significance of  $P < 0.05$  was used throughout this study for all the tests.

### Results

The velocity was similar in both groups; therefore physiological and biomechanical variables can be compared (Table 1).

### Speed and age/training-related changes

As shown in Table 4, stride frequency changed significantly with speed and was age-related. Respiratory frequency (Tables 3 and 4) appeared not to be related to age, but to speed. The RF was

**Table 3: Respiratory frequency and locomotor-respiratory coupling in age-groups. All data are mean ± s.d.**

Age (years)	RF (respiration/sec)					LRC				
	2	3	4	5	≥6	2	3	4	5	≥6
Step	n = 12	n = 10	n = 7	n = 7	n = 8	n = 12	n = 10	n = 7	n = 7	n = 8
1	1.66 ± 0.16	1.53 ± 0.30	1.51 ± 0.30	1.61 ± 0.30	1.46 ± 0.29	1.13 ± 0.14	1.25 ± 0.32	1.28 ± 0.24	1.12 ± 0.21	1.30 ± 0.28
2	1.77 ± 0.21	1.67 ± 0.24	1.57 ± 0.36	1.60 ± 0.33	1.65 ± 0.15	1.10 ± 0.16	1.16 ± 0.21	1.32 ± 0.31	1.26 ± 0.26	1.16 ± 1.12
3	1.80 ± 0.23	1.70 ± 0.26	1.88 ± 0.33	1.69 ± 0.35	1.62 ± 0.25	1.15 ± 0.19	1.20 ± 0.21	1.16 ± 0.23	1.26 ± 0.26	1.24 ± 0.20

**Table 4: Results of the 2 way analysis of variance testing the effect of age**

	Effect of speed	Effect of age	Interaction
Velocity (m/min)	P<0.001	NS	NS
SF (stride/sec)	P<0.001	P<0.001	NS
RF (respiration/sec)	P = 0.02	NS	NS
LRC	NS	NS	NS

NS = not significant (P>0.05).

significantly lower during the first step than during the third one. Locomotor-respiratory coupling (Tables 3 and 4) was not significantly altered by speed or age.

*Effect of performance*

Mean age was similar in the 2 performance groups (Table 2). As expected, ITR and V4 were significantly higher in GP (Table 2).

Statistical analysis showed a significant effect of the level of performance on respiratory frequency: considering each step good performers had a lower respiratory frequency than poor performers (Fig 1). The speed was the same in both groups and stride frequency was not different (Fig 2). Consequently, LRC ratio was significantly higher in good than in poor performers (Fig 3).

**Discussion**

Although the horse respiratory system is known to be the first limit to maximal exercising, very few data are available concerning respiratory frequency (RF) and locomotor-respiratory coupling (LRC) in Standardbred trotters exercising on the field.

*Methodological background*

The standardised field exercise test has been described and validated previously (Demonceau and Auvinet 1992; Dubreucq *et al.*

*al.* 1995). Validation and reproducibility of the accelerometric measurements with Equimetrix has also been described previously in trotter racehorses (Barrey *et al.* 1995; Leleu *et al.* 2002, 2004). This method allows a reliable quantification of stride frequency. With respiratory frequency calculation, the initial studies aimed to record respiratory sounds were described by Attenburrow (1978; Attenburrow *et al.* 1983). This author showed that inspiratory and expiratory phases could be recognised and easily identified in the sound signal. Other studies demonstrated the use of a unidirectional microphone placed in close proximity to the nostrils (Barnes *et al.* 1979; Derksen 2001; Franklin *et al.* 2003). This method has been used in our study and respiratory sound samples were visualised in order to count the number of respiratory cycle and to define RF. As described previously RF was calculated on 20 secs samples and swallowing was sometimes found, which is why RF calculation was considered with a 5% error.

*Respiratory frequency during exercise*

In this study, RF was significantly different as speed of trotting increased (P = 0.02). Yet it is well known that ventilation increases when speed of running increases. In fact, ventilation

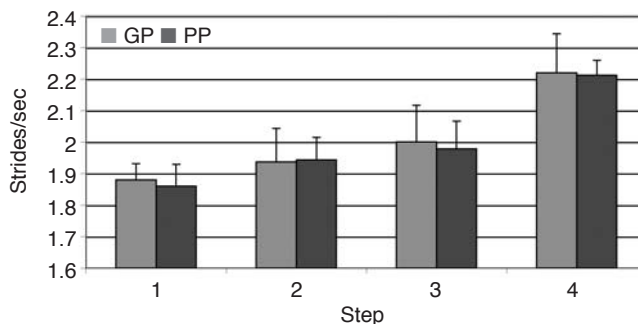


Fig 2: Stride frequency in good (n = 16) and poor (n = 9) performers.

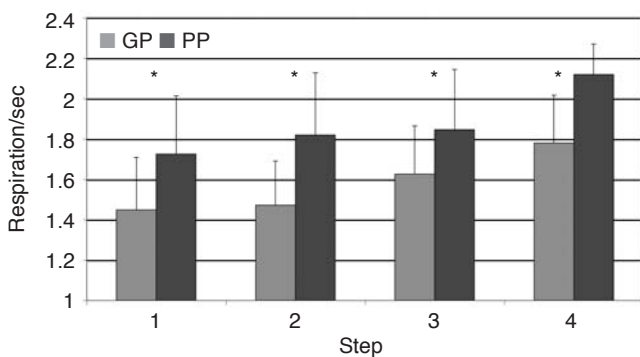


Fig 1: Respiratory frequency in good (n = 16) and poor (n = 9) performers. \* = significant difference.

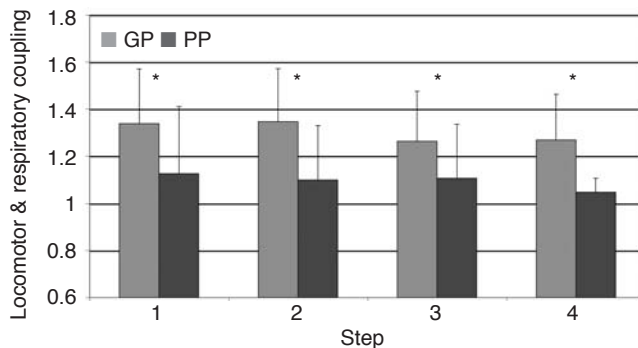


Fig 3: Locomotor and respiratory coupling (SF/RF) in good (n = 16) and poor (n = 9) performers. \* = significant difference

can be increased by increasing RF, tidal volume or both. Marlin (2002) described, in Thoroughbreds, the relationships between RF, tidal volume, minute ventilation and speed of running: when exercising at low speed, the horses increased ventilation largely by increasing RF, with only a small increase in tidal volume. During canter and gallop RF is related to SF on a one for one ratio, and any increase in ventilation is therefore due largely to increases in tidal volume, with only small increases in RF. Marlin (2002) showed that RF increases quicker at low speeds than at fast speeds which is in accordance with our results as a poor increase in RF was found at high speed.

#### *Locomotor and respiratory coupling when trotting*

Previous studies suggested that LRC did not exist during the trot in riding saddle horses (Hörnigke *et al.* 1983) or at least that it was nonconstant and not a general rule (Attenburrow 1982, 1983; Bramble and Carrier 1983). Some authors found, on the contrary, an LRC constant at a fast trot in French Trotters (Barrey, 2000). However, none of these authors has investigated an important population of horses. In the present cross-sectional study, the LRC ratio was studied in 44 horses during a 4-steps-exercise test.

Each LRC ratio value could not be associated to an integral ratio but 2 strategies have been shown: a ratio close to 1, i.e. LRC 1:1, and also about 1.5, i.e. LRC 3:2; each horse coupling at the same ratio during the 4 steps of the test. Our results are consistent with Attenburrow (1982) who described a SF/RF ratio of 1.35 when observing a Thoroughbred at trot. No information was known in this study about the timing of the 2 cycles, but the observed constant ratio throughout the test meant there is a tight relationship between respiration and locomotion. A particularity of the trot is that the major muscles associated with both locomotion and respiration contract and relax unilaterally. Moreover, extension and flexion of the back and lumbar sacral joint during a stride at trot is not as important as during gallop. As a result, it cannot be said that respiration is forced by locomotion during the trot. However, our results showed that some trotters displayed a 1:1 LRC throughout the test and this agrees with Barrey (2000). That study also found a 1:1 LRC in Standardbred trotters exercising at fast trot on a treadmill. Besides, it has been demonstrated in 38 human subjects, walking on a treadmill, that the majority showed some evidence of breathing entrainment while walking; and that the walking cadence provides a persuasive, but not dominant, input to the central breathing pattern generator even if mechanical constraints are not obvious (Hill *et al.* 1988). Another study is required to describe the timing relationship between respiration and locomotion at a fast trot.

#### *Effect of age/training status*

There was a significant effect of exercising speed on SF, this parameter being very speed-dependent as previously described (Leleu *et al.* 2004). Also SF differed significantly among the age-groups: we found a decrease in SF. An explanation for such results could be the phenomenon of growth, the same results were found by others in, respectively, 4 Standardbred trotters on the track at age 4 years and again 3 years later (Drevemo *et al.* 1980) and in 143 French Trotters on the track age 2–7 years (Leleu *et al.* 2004). In our experiment, there was no effect of age/training on RF. The same results were found in exercising Thoroughbreds by Roberts *et al.* (1999). In that study, 6 Thoroughbred horses performed a

standardised treadmill exercise test prior and after 16 weeks training. Respiratory frequency was not significantly altered by training. Moreover, in man, such results were reported by Lucia *et al.* (2001) in a longitudinal study to clarify changes induced by endurance training on breathing pattern of 13 professional cyclists during a 7 month training season. They found no changes in breathing patterns despite significant changes in training loads. These findings suggest that endurance conditioning did not alter breathing pattern of trained subjects during an incremental exercise test. In a recent study, 5 runners with a history of, at least, 6 months running training (40 km/week) have been compared to 5 nonrunners. The conclusion was that there was no difference between runners and nonrunners with respect to breathing parameters, stride parameters, as well as the strength and variability of the coupling at each speed of the test. These findings suggested that running training does not change the strength of LRC (McDermott *et al.* 2003) and our results are in accordance.

#### *Effect of performance*

Respiratory frequency was found lower in good compared to poor performers. In man, Eastwood *et al.* (2001) found that during exercise 6 elite marathon runners breathed with a lower frequency, but a higher tidal volume, and longer inspiratory and expiratory time than sedentary subjects. In our study, poor performers had a shorter respiratory cycle because of very rapid respiratory rhythms. As their gas exchange was probably decreased during exercise, it is possible they reached a higher level of hypercapnoea and hypoxaemia during the same exercise than good performers. Overall, the lower RF resulted in a higher LRC ratio in good performers, as the SF did not change. These results led to the belief that a high ratio between stride frequency and respiratory frequency could be more efficient for middle distance runners i.e. trot racers.

#### *Conclusions*

Different patterns of breathing are employed during locomotion. The respiratory frequency increases with increased speeds, as well as the stride frequency. As a result, no change in locomotor-respiratory coupling has been found during the incremental test. An age-related change was found concerning SF, but no change was observed for RF and LRC. During the investigation of the level of race performance, a different breathing strategy was found to exist: good performers had a lower RF and a higher LRC than poor performers at the same trotting speed. Subsequently, a tendency to reach a 1:1 locomotor and respiratory coupling has been described at high speed. More investigations are required on a larger scale to prove the difference in breathing strategy according to race performance level.

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#### **Manufacturers' addresses**

<sup>1</sup>Schoberer Rad Meßtechnik, Jülich, Germany.

<sup>2</sup>Polar Oy, Kempele, Finland.

<sup>3</sup>Centaure Metrix, Fontainebleau, France.

<sup>4</sup>Garmin Corporation, Olathe, Kansas, USA.

<sup>5</sup>The MathWorks Inc, Natick, Massachusetts, USA.

## References

- Alexander, R.McN. (1993) Breathing while trotting. *Science* **262**, 196-197.
- Art, T., Desmecht, D., Amory, H. and Lekeux, P. (1990) Synchronisation of locomotion and respiration in trotting ponies. *J. vet. Med.* **A37**, 95-103.
- Attenburrow, D.P. (1978) Respiratory sounds recorded by radio-stethoscope from normal horses at exercise. *Equine vet. J.* **10**, 176-179.
- Attenburrow, D.P. (1982) Time relationship between the respiratory cycle and limb cycle in the horse. *Equine vet. J.* **14**, 69-72.
- Attenburrow, D.P. (1983) Respiration and locomotion. In: *Equine Exercise Physiology I*. Eds: D.H. Snow, S.G.B. Persson, R.J. Rose, Cambridge, Granta Editions. pp 17-22.
- Attenburrow, D.P., Flack, F.C., Hörnicke, H., Meixner, R. and Pollman, U. (1983) Respiratory airflow and sound intensity. In: *Equine Exercise Physiology I*. Eds: D.H. Snow, S.G.B. Persson, R.J. Rose, Cambridge, Granta Editions. pp 23-26.
- Attenburrow, D.P. and Goss, V.A. (1994) The mechanical coupling of lung ventilation to locomotion in the horse. *Med. Eng. Phys.* **16**, 188-192.
- Barnes, G.R., Brennan, M., Goulden, B.E. and Kirkland J. (1979) Sound spectrography in the diagnosis of equine respiratory disorders: a preliminary report. *N. Z. Vet. J.* **27**, 145-146.
- Barrey, E., Couroucé, A., d'Orsetti, H., Evans, D., Roberts, C. and Rose, J.R. (2000) Couplage de la ventilation respiratoire avec la locomotion du cheval de course. *Equathlon*. **30**, 32-35.
- Bechbache, R.R. and Duffin, J. (1977) The entrainment of breathing frequency by exercise rhythm. *J. Physiol.* **272**, 553-561.
- Boggs, D.F. (2002) Interactions between locomotion and ventilation in tetrapods. *Comp. Biochem. Physiol. A* **133**, 269-288.
- Bramble, D.M. and Carrier, D.R. (1983) Running and breathing in mammals. *Science* **219**, 251-256.
- Bramble, D.M. and Jenkins, F.A. (1993) Mammalian locomotor-respiratory integration: implications for diaphragmatic and pulmonary design. *Science* **262**, 235-240.
- Butler, P.J., Woakes, A.J., Smale, K., Roberts, C.A., Hillidge, C.J., Snow, D.H. and Marlin D.J. (1993) Respiratory and cardiovascular adjustments during exercise of increasing intensity and during recovery in Thoroughbred racehorses. *J. expt. Biol.* **179**, 159-180.
- Carrier, D.R. (1996) Function of the intercostals muscles in trotting dogs: ventilation or locomotion? *J. expt. Biol.* **199**, 1455-1465.
- Demonceau, T. and Auvinet, B. (1992) Test d'effort de terrain pour trotteurs à l'entraînement : réalisation pratique et premiers résultats. In: *Compte-rendu de la 18ème Journée d'Etude*, CEREOPA. pp 120-132.
- Derksen, F.J., Holcombe, S.J., Hartmann, W., Robinson, N.E. and Stick, J.A. (2001) Spectrum analysis of respiratory sounds in exercising horses with experimentally induced laryngeal hemiplegia or dorsal displacement of the soft palate. *Am. J. vet. Res.* **62**, 659-664.
- Drevemo, S., Dalin, G., Fredricson, I. and Bjorne, K. (1980) Equine locomotion: 3. The reproducibility of gait in Standardbred Trotters. *Equine vet. J.* **12**, 71-73.
- Dubreucq, C., Chatard, J.C., Couroucé, A. and Auvinet, B. (1995) Reproducibility of standardized exercise test for Standardbred trotters under field conditions. *Equine vet. J., Suppl.* **18**, 108-112.
- Eastwood, P.R., Hillman, D.R. and Finucane K.E. (2001) Inspiratory performance in endurance athletes and sedentary subjects. *Respirology* **6**, 95-104.
- Entin, P.L., Robertshaw, D. and Rawson, R.E. (1999) Effect of locomotor respiratory coupling on respiratory evaporative heat loss in the sheep. *J. appl. Physiol.* **87**, 1887-1893.
- Evans, D.L. and Rose R.J. (1988) Dynamics of cardiorespiratory function in standardbred horses during different intensities of constant-load exercise. *J. comp. Physiol. B.* **157**, 791-799.
- Evans, D.L., Silverman, E.B., Hodgson, D.R., Eaton, M.D. and Rose, R.J. (1994) Gait and respiration in Standardbred horses when pacing and galloping. *Res. vet. Sci.* **57**, 233-239.
- Franklin, S.H., Usmar, S G., Lane, J.G., Shuttleworth, J. and Burn J.F. (2003) Spectral analysis of respiratory noise in horses with upper airway disorders. *Equine vet. J.* **35**, 264-268.
- Funk, G.D., Valenzuela, I.J. and Milson W.K. (1997) Energetic consequences of coordinating wingbeat and respiratory rhythms in birds. *J. expt. Biol.* **200**, 915-920.
- Harms, C.A., Wetter, T.J., Croix, C.M., Pegelow, D.F. and Dempsey J.A. (2000) Effects of respiratory muscle work on exercise performance. *J. appl. Physiol.* **89**, 131-138.
- Hill, A.R., Adams, J.M., Parker, B.E. and Rochester D.F. (1988) Short-term entrainment of ventilation to the walking cycle in humans. *J. appl. Physiol.* **65**, 570-578.
- Hörnicke, H., Meixner, R. and Pollmann U. (1983) Respiration in exercising horses. In: *Equine Exercise Physiology I*. Eds: D.H. Snow, S.G.B. Persson and R.J. Rose R.J., Cambridge, Granta Editions, pp 7-16.
- Lafortuna, C.L., Reinach, E. and Saibene F. (1996) The effects of locomotor-respiratory coupling on the pattern of breathing horses. *J. Physiol.* **492**, 587-596.
- Lee, H. and Banzett, R. (1997) Mechanical links between locomotion and breathing: can you breathe with your legs? *News Physiol. Sci.* **12**, 273-278.
- Leleu, C., Gloria, E., Renault, G., and Barrey, E. (2002) Analysis of trotter gait on the track by accelerometry and image analysis. *Equine vet. J., Suppl.* **34**, 344-348.
- Leleu, C., Bariller, F., Cotrel, C. and Barrey, E. (2004) Reproducibility of a locomotor test for trotter horses. *Vet. J.* **168**, 160-166.
- Lucia, A., Hoyos, J., Pardo, J. and Chicharro, J. (2001) Effects of endurance training on the breathing pattern of professional cyclists. *Jap. J. Physiol.* **51**, 133-141.
- Marlin, D. and Nankervis K. (2002) *Equine Exercise Physiology*. Blackwell Science, Oxford. pp .
- Nassar, P.N., Jackson, A.C. and Carrier D.R. (2001) Entraining the natural frequencies of running and breathing in Guinea Fowl (*Numida meleagris*). *J. expt. Biol.* **204**, 1641-1651.
- Persegol, L., Jordan, M. and Viala, D. (1991) Evidence for the entrainment of breathing by locomotor pattern in human. *J. Physiol. Paris*, **85**, 38-43.
- Roberts, C.A., Marlin, D.J. and Lekeux, P. (1999) The effects of training on ventilation and blood gases in exercising thoroughbreds. *Equine vet. J., Suppl.* **30**, 57-61.
- Saunders, S.W., Rath, D. and Hodges, P.W. (2004) Postural and respiratory activation of the trunk muscles changes with mode and speed of locomotion. *Gait Posture* **20**, 280-290.
- Siegmund, G.P., Edwards, M.R., Moore, K.S., Tiessen, D.A., Sanderson, D.J. and McKenzie, D.C. (1999) Ventilation and locomotion coupling in varsity male rowers. *J. appl. Physiol.* **87**, 233-242.
- Viala, D. (1997) Coordination of locomotion and respiration. In: *Neural Control of Respiratory Muscles*, Eds: A.D. Miller, A.L. Bianchi, B.P. Bishop. CRC Press, New York, pp 285-296.
- Villard, S., Casties, J.F. and Mottet, D. (2005) Dynamic stability of locomotor respiratory coupling during cycling in humans. *Neurosci. Lett.* **383**, 333-8.