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CARDIO-PULMONARY FUNCTION VALUES IN DOUBLE-MUSCLED CATTLE DURING MUSCULAR EXERCISE

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ABSTRACT

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Eleven double-muscled calves of the Belgian White and Blue breed and eleven Friesian calves have been investigated at rest, during exercise on a treadmill (11% incline; speed 1.3 m.sec^{-1}) and 10 and 30 minutes after the end of this exercise. Blood gases and acid-base status were determined in mixed venous and arterial blood sampled from the pulmonary and the carotid artery respectively. Expired gases were collected in a balloon. The time of collection, volume of expired gases and fractional O_2 and CO_2 concentrations in expired gases were measured.

In double-muscled calves, inadequate oxygen intake and carbon dioxide elimination were demonstrated by the increase in the carbon dioxide tension ($PaCO_2$) and in the hydrogen ion concentration $[H^+]_a$ and the decrease in the oxygen tension (PaO_2) in arterial blood during exercise. In Friesian calves, an adequate increase in oxygen intake occurred and no acidosis was recorded. A metabolic acidosis explained by only a 1.5-fold increase in the cardiac output and by the small increase in haemoglobin concentration was recorded in double-muscled calves.

It was concluded that some aspects of the cardio-pulmonary and metabolic responses to exercise in double-muscled calves can be related to their inability to greatly increase their O_2 consumption.

INTRODUCTION

The cardio-pulmonary adjustments to exercise in calves have been investigated recently (Kuhlman *et al.*, 1985; Karas *et al.*, 1987). These authors concluded that the cardio-pulmonary metabolic responses were qualitatively similar to those observed in other species. However, quantitative differences which could be related to the low resistance of cattle to exercise have been observed.

It has been demonstrated that the sensitivity of double-muscled cattle to respiratory diseases is greater than that of other bovine breeds, especially after transport or when environmental conditions are bad (Dive, 1983; Holmes *et al.*, 1973; Halipré, 1973). However, only changes in the venous acidobasis status induced by exercise have so far been studied in double-muscled cattle (Monin & Boccard, 1974).

Therefore, it seemed to us that it would be interesting to compare the cardio-pulmonary and metabolic responses to severe exercise in double-muscled and normal calves.

MATERIALS AND METHODS

Animals

Holstein Friesian (F) calves (normal calves; n = 11) and Belgian White and Blue (BWB) calves (double-muscled calves; n = 11) were used. The mean body weights were 175 kg (range: 156–200 kg and 183.5 kg (range: 165–200 kg) respectively. All the animals

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were healthy on clinical examination and had no history of disease. The right carotid artery was deviated into the jugular groove one month before the experiment (Gustin *et al.*, 1988a). The animals were trained to run on a motor driven treadmill 3 times a week over 2 weeks.

Preparations and procedures

Before the experiment started, a flow-directed catheter (5 F, Vygon, Brussels, Belgium) was advanced through a jugular vein introducer into the pulmonary artery under pressure recording control (Sirecust, Siemens, Belgium). The day before the study, the carotid artery was catheterized with a 17 G catheter (Vygon, Brussel, Belgium). The pulmonary and carotid artery catheters were used for anaerobic collection of mixed venous and arterial blood samples respectively.

Heart rate (HR) was determined from an electrocardiogram recorded by telemetry on a polygraph (Gould E-S Electronic, Wauthier-Braine, Belgium).

A technique similar to that described by Kuhlman *et al.* (1985) was used to obtain ventilation and gas exchange data. Briefly, a nonrebreathing valve (Hans Rudolph) was used to separate the inspired and expired air. The valve was fixed to a tight-fitting face mask. The total dead space was about 400 ml. Expired gas was collected into a 135 L meterological balloon and the time of collection was measured. A tube (2 mm ED) was placed in the face mask near a nostril and the other end was connected to a transducer (Elema, Siemens, Brussels, Belgium) to allow the respiratory frequency (f) to be measured by recording the pressure changes on the polygraph.

Just after the collection of expired gas was completed, the balloon was connected to a Fleisch head (Nr 3). Expired air was blown through the Fleisch pneumotachograph (Gould) and the volume was recorded on a polygraph (Gould). Fractional concentrations of O_2 and CO_2 in a mixed expired air sample were determined by infrared analysis (Medisoft, Dinant, Belgium).

Minute volume ($\dot{V}_E$) and tidal volume (V_T) were calculated from these data.

Arterial and mixed venous blood sampled at the end of the expired air collection period was immediately analyzed for blood gases (AVL, Louvain, Belgium) and pH at 37°C. Blood gas tensions were corrected for temperature (Kelman & Nunn, 1986; Gustin *et al.*, 1988b). The oxygen content (CaO_2) and oxygen saturation of the haemoglobin (Sat_aO_2) were also calculated for arterial blood (Gustin *et al.*, 1987b). The haemoglobin concentration was measured by the Drabkin method. Bicarbonate concentration and base excess (BE) were computed from these parameters.

Plasma samples were used for the determination of lactate, glucose, albumin and K^+. Lactate concentrations were determined by enzymatic methods (Monotest Lactate, Boehringer). Other blood chemical determinations were measured with an Auto Analyzer I (Technicon).

O_2 consumption ($\dot{M}O_2$) and CO_2 production ($\dot{M}CO_2$) were calculated taking into account the values of $\dot{V}_E$ and the fractional concentrations of O_2 and CO_2 in the expired gas and room air. Physiological dead space (V_D) was calculated using the Bohr equation and alveolar ventilation ($\dot{V}_A$) was determined by subtracting ($f.V_D$) from $\dot{V}_E$. Cardiac output ($\dot{Q}$) was calculated by the Fick equation. The ratio of $\dot{Q}$ with HR gave values for stroke volume (SV).

Experimental protocol

The animals were led to the treadmill set at an 11% incline. Fifteen minutes after the

animal had been installed and prepared, all measurements were performed. Then the exercise began (speed: 1.3 $m.s^{-1}$) and continued for 5 minutes. All measurements were repeated during the last minute of exercise. The exercise was then stopped and the measurements were repeated 10 and 30 minutes after the end of exercise.

Statistical analysis

Individual values were analyzed by two-way analysis of variance to determine if significant differences exist between the mean values obtained in BWB and F calves and between mean values obtained during the different stages of exercise. Contrasts were used to compare the individual values (BMDP, 1987).

RESULTS

The body temperature of the normal calves was higher than that of the BWB calves (+0.5°C). Exercise induced a similar increase of this parameter in both breeds (+0.5°C).

O_2 consumption and CO_2 production increased during exercise in both F and BWB calves. The increase in these parameters tended to be greater in F calves ($p<0.10$). The respiratory exchange ratio (R) was increased during exercise and 10 minutes after the end of exercise in BWB calves. A decrease in this ratio was recorded in F calves during exercise (Table I).

Values reported in Table I show that exercise induced a significant increase of $\dot{V}_E$, $\dot{V}_A$, V_T and V_D. In BWB calves, the increase of $\dot{V}_E$ and $\dot{V}_A$ tended to be smaller than in F animals ($p<0.1$) and values of V_T, $\dot{V}_E$ and $\dot{V}_A$ recorded ten minutes after exercise were higher than the resting values. The ratio V_D/V_T decreased during exercise in BWB and F calves and remained small ten minutes after the end of exercise in BWB calves. A decrease of $\dot{V}_E/\dot{M}O_2$ and $\dot{V}_E/\dot{M}CO_2$ was observed in both breeds during exercise. Return to resting values of $\dot{V}_E/\dot{M}CO_2$ was slower in BWB than in F calves. Ratios $\dot{V}_A/\dot{M}O_2$ and $\dot{V}_A/\dot{M}CO_2$ were not modified by exercise.

Blood gases, acid-base equilibrium data, bicarbonate concentrations and BE are shown in Table I and in Figure 1. Exercise induced a significant decrease in PaO_2 in BWB calves. Ten minutes after exercise PaO_2 increased significantly and returned to rest values 30 minutes after exercise. No changes were observed in F calves. $PaCO_2$ decreased in F calves during exercise and increased in BWB calves. In the latter, a significant decrease in $PaCO_2$ was recorded 10 minutes after exercise. Hydrogen ion concentration ($[H^+]_a$) in arterial blood increased during exercise in BWB calves. In both breeds, $P\bar{v}O_2$ decreased and $P\bar{v}CO_2$ and $[H^+]_{\bar{v}}$ increased during exercise. The changes in these parameters was more marked in BWB calves. Moreover the $[H^+]_{\bar{v}}$ value remained high ten minutes after the end of the exercise in the latter.

Changes in PaO_2 explain the evolution of Sat_aO_2 shown in Figure 1. The increase in CaO_2 and haemoglobin concentration (Hb) observed during exercise was smaller in BWB calves than in F calves.

Figure 2 shows the evolution of HR, $\dot{Q}$ and SV. The smaller increase in $\dot{Q}$and the decrease in SV observed in BWB cattle during exercise are the main differences as compared to F calves.

In double-muscled calves, the increase in lactate concentration was greater and the recovery was slower than in F calves. In the latter, a small but significant decrease in glucose concentration during exercise was observed. In BWB calves, the glucose concentration increased during exercise and remained high ten minutes afterwards. Serum albumin concentrations and K^+ concentrations increased during exercise in both breeds.

TABLE I
Evolution of some ventilatory parameters, of arterial bicarbonate concentration and base excess, of O_2 and CO_2 tension and hydrogen ion concentration in mixed venous blood and of some serum metabolites and electrolytes at rest, during exercise (E) and ten minutes (10) and thirty minutes (30) after exercise in Belgian White and Blue (BWB) and Friesian calves (F).

Parameters	Breed	Rest	E	10	30	p
V_T	BWB	7.5	15.6***	8.7*	7.7	
($ml.kg^{-1}$)		±1.5	±4.1	±2.3	±1.6	NS
	F	8.6	17.0***	8.1	8.3	
		±2.0	±4.7	±1.3	±1.0	
V_D	BWB	4.5	6.8**	4.3	4.5	
($ml.kg^{-1}$)		+ 0.8	±1.7	±0.7	±0.8	NS
	F	4.9	6.9**	4.8	4.7	
		±1.2	±1.6	±0.7	±0.8	
$\dot{V}_E$	BWB	0.21	0.73***	0.27*	0.22	
($L.min^{-1}.kg^{-1}$)		±0.05	±0.21	±0.10	±0.08	NS
	F	0.24	0.87***	0.24	0.21	(p<0.1)
		±0.05	±0.20	±0.04	±0.04	
$\dot{V}_A$	BWB	0.09	0.41***	0.15*	0.09	
($L.min^{-1}.kg^{-1}$)		±0.02	±0.16	±0.08	±0.03	NS
	F	0.09	0.51***	0.10	0.10	(p<0.1)
		±0.02	±0.18	±0.02	±0.01	
$\dot{M}O_2$	BWB	0.23	1.07***	0.27	0.21	
($mM.min^{-1}.kg^{-1}$)		±0.05	±0.30	±0.11	±0.05	NS
	F	0.24	1.32***	0.24	0.24	(p<0.1)
		±0.04	±0.37	±0.04	±0.03	
$\dot{M}CO_2$	BWB	0.18	0.93***	0.27*	0.19	
($mM.min^{-1}.kg^{-1}$)		±0.04	±0.30	±0.11	±0.05	NS
	F	0.20	1.12***	0.21	0.20	
		±0.05	±0.39	±0.05	±0.02	
R	BWB	0.83	0.88	1.00***	0.87	
(-)		±0.09	±0.15	±0.08	±0.06	NS
	F	0.92	0.82*	0.90	0.83	(p<0.1)
		±0.11	±0.15	±0.11	±0.15	
V_D/V_T	BWB	0.60	0.45**	0.48**	0.58	
(-)		±0.04	±0.10	±0.07	±0.06	S
	F	0.60	0.41**	0.59	0.56	
		±0.04	±0.10	±0.08	±0.07	
$\dot{V}_E/\dot{M}O_2$	BWB	0.97	0.70**	1.00	1.00	
($L.mMol.^{-1}$)		±0.10	±0.10	±0.10	±0.10	NS
	F	1.00	0.65**	1.00	0.88	
		±0.15	±0.06	±0.20	±0.13	
$\dot{V}_E/\dot{M}CO_2$	BWB	1.19	0.83**	1.00**	1.10	
($L.mMol^{-1}$)		±0.17	±0.17	±0.09	±0.20	S
	F	1.12	0.83**	1.15	1.08	
		±0.11	±0.08	±0.25	±0.16	
$\dot{V}_A/\dot{M}O_2$	BWB	0.38	0.38	0.52^{Δ}**	0.40	
($L.mMol^{-1}$)		±0.04	±0.10	±0.07	±0.05	SS
	F	0.40	0.37	0.38	0.38	
		±0.06	±0.06	±0.06	±0.07	
$\dot{V}_A/\dot{M}CO_2$	BWB	0.47	0.43	0.52	0.46	
($L.mMol^{-1}$)		±0.03	±0.07	±0.07	±0.05	NS
	F	0.44	0.45	0.44	0.45	
		±0.03	±0.08	±0.04	±0.03	

TABLE I (Continued)

Parameters	Breed	Rest	E	10	30	p
HCO_{3a} (mM.L-1)	BWB	24.5 ±2.4	$19.8^{\Delta**}$ ±4.0	21.2** ±5.0	24.8 ±3.8	
	F	26.0 ±3.3	23.0* ±2.6	25.2 ±2.4	25.4 ±2.4	
BEa (mM.L-1)	BWB	0.7 ±2.9	$-6.1^{\Delta***}$ ±5.3	−2.4** ±5.6	0.0 ±3.8	SSS
	F	1.4 ±3.7	−1.4* ±3.6	0.7 ±3.2	1.3 ±3.2	
$P_{\bar{v}}O_2$ (kPa)	BWB	5.47 ±0.41	3.50* ±0.73	5.53 ±0.93	5.50 ±0.62	NS
	F	5.43 ±0.57	3.97* ±0.79	5.49 ±0.75	5.50 ±0.63	(p<0.1)
$P_{\bar{v}}CO_2$ (kPa)	BWB	6.79 ±0.53	$8.41^{\Delta**}$ ±0.35	6.67 ±0.61	6.39 ±0.39	SSS
	F	6.83 ±0.29	7.55* ±0.57	6.67 ±0.26	6.66 ±0.37	
$[H^+]_{\bar{v}}$ (nM/L)	BWB	46.8 ±3.7	$66.7^{\Delta**}$ ±12.0	$52.4^{\Delta*}$ ±8.1	46.8 ±3.8	SSS
	F	45.6 ±3.5	52.4* ±7.0	46.5 ±3.2	45.2 ±2.7	
Lactate (mg.dl-1)	BWB	16.6 ±7.6	$82.2^{\Delta\Delta\Delta***}$ ±31.0	$65.1^{\Delta**}$ ±35.0	$43.7^{\Delta*}$ ±26.0	SSS
	F	16.0 ±6.1	34.5* ±17.0	24.0 ±11.0	18.0 ±6.0	
Glucose (mg.dl-1)	BWB	73.2 ±2.2	108.0** ±27.0	94.7* ±19.0	85.0 ±18.0	SSS
	F	85.9 ±8.0	80.0* ±6.0	83.0 ±5.4	85.5 ±5.4	
Albumin (g.dl-1)	BWB	4.7 ±0.6	5.1* ±0.6	4.7 ±0.7	4.6 ±0.7	NS
	F	5.0 ±0.7	5.4* ±0.7	5.0 ±0.7	5.0 ±0.6	
K^+ (meq.L-1)	BWB	4.3 ±0.3	4.5* ±0.3	4.0* ±0.2	4.0* ±0.3	S
	F	4.0 ±0.3	4.3* ±0.2	4.1 ±0.3	3.9 ±0.2	

V_T: tidal volume; V_D: dead space; $\dot{V}_E$: minute volume; $\dot{V}_A$: alveolar ventilation; $\dot{M}O_2$: O_2 consumption; $\dot{M}CO_2$: CO_2 production; R: respiratory exchange ratio; HCO_3: bicarbonate concentration; BE: base excess; $p_{\bar{v}}O_2$ and $p_{\bar{v}}CO_2$: oxygen and carbon dioxide tension in mixed venous blood; $[H^+]_{\bar{v}}$: hydrogen ion concentration in mixed venous blood; significantly different from value measured before exercise (* : p<0.05;**: ** : p< 0.01:*** : p<0.001); Δ: significantly different from the corresponding value measured in Friesian calves (Δ: p<0.05; ΔΔ: p<0.01; ΔΔΔ: p<0.001); p: p value of the interaction of breed with responses associated with exercise (NS: not significant; S: p<0.05; SS: p<0.01; SSS: p<0.001). Values are means ± SD.

Albumin concentrations returned to resting values 10 minutes after exercise. In BWB calves, K^+ concentrations fell below the resting values after exercise. The changes in these parameters are indicated in Table I.

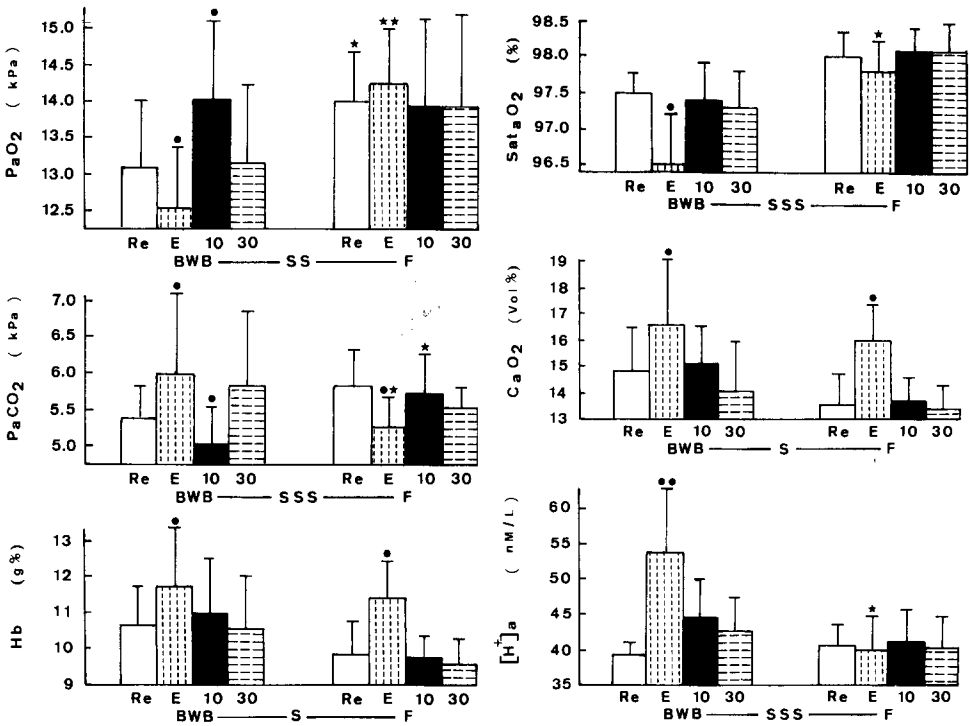

Figure 1. Oxygen tension (PaO_2), carbon dioxide tension ($PaCO_2$), hydrogen ion concentration ($[H^+]_a$) in arterial blood, haemoglobin concentration (Hb), arterial saturation of haemoglobin (Sat_aO_2) and arterial blood oxygen content (CaO_2) at rest (R_e), during exercise (E) and ten minutes (10) and thirty minutes (30) after exercise in Belgian White and Blue (BWB) and Friesian (F) calves (n = 11 in both groups).
●: significantly different from resting values (●: $p<0.05$; ●●: $p<0.01$; ●●●: $p<0.001$); ⋆: significantly different from corresponding values measured in BWB calves (⋆: $p<0.05$; ⋆⋆: p: $p<0.01$; ⋆⋆⋆: $p<0.001$). The p values of the interaction of breed with responses associated to exercise are also indicated (NS: not significant; S: $p<0.05$; SS: $p<0.01$; SSS: $p<0.001$). Values are means +SD.

DISCUSSION

Although the calves of both the BWB and F breeds were submitted to the same exercise, the cardio-pulmonary responses were quantitatively very different.

During a preliminary study, BWB calves were trained to run at different speeds. At speeds higher than 1.3 $m.s^{-1}$, they refused to run and sometimes fell down after the first two minutes. This fact and the marked increased in $[H^+]_a$, $[H^+]_{\bar{v}}$ and in lactate concentration, the decrease in PaO_2 and the increase in $PaCO_2$ recorded in BWB calves during exercise suggest that their O_2 consumption was near the maximum $\dot{M}O_2$ (Kuhlman *et al.*, 1985). The 4.5-fold increase in $\dot{M}O_2$ over resting values recorded in our BWB calves is small compared with the increase observed in the Hereford calves, dogs or horses, for

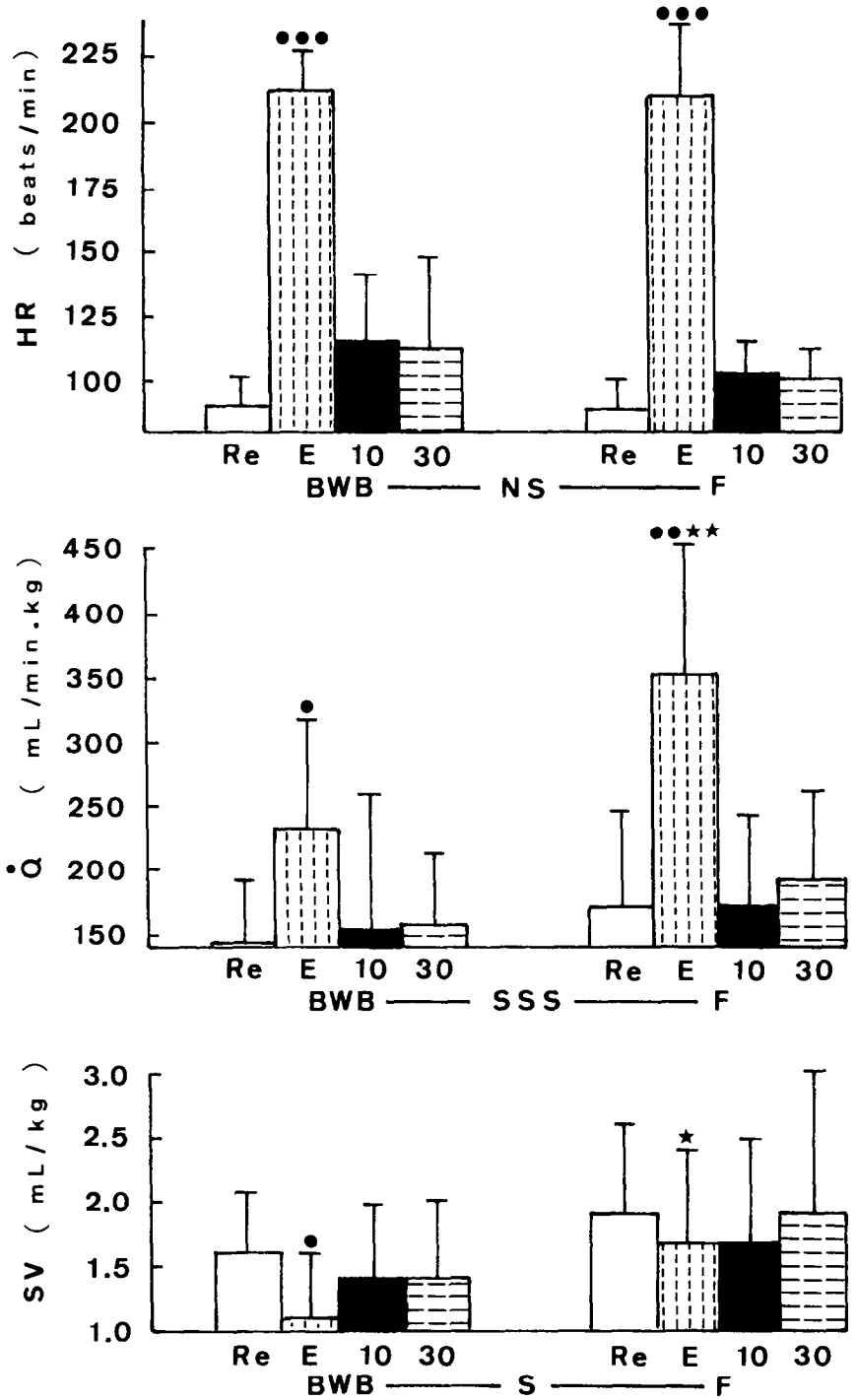

Figure 2. Heart rate (HR), cardiac output ($\dot{Q}$) and stroke volume (SV) at rest (R_e), during exercise (E) and ten minutes (10) and thirty minutes (30) after exercise in Belgian White and Blue (BWB) and Friesian (F) calves (n = 11 in both groups). For statistical significance levels see Fig. 1.

which 8-fold, 15-fold and 30-fold increases in $\dot{M}O_2$ have been reported respectively during maximum exercise (Thomas & Fregin, 1981; Kuhlman *et al.*, 1985; Musch *et al.*, 1986).

In our F calves, the increase in $\dot{M}O_2$ was only 5.5 fold, the changes in $[H^+]_v$ and lactate concentration were not important, PaO_2 $[H^+]_a$ were not modified and $PaCO_2$ decreased during exercise. During the preliminary study, these animals were able to run at speeds higher than 1.3 $m.s^{-1}$. These observations indicate that F calves were not exercised maximally. The maximum values of O_2 consumption and CO_2 production reported by Kuhlman *et al.* (1985) in Hereford calves averaged 1.70 $mMol.min^{-1}.kg^{-1}$ and 1.85 $mMol.min^{-1}.kg^{-1}$ respectively. If our values of $\dot{M}O_2$ and $\dot{M}CO_2$ are compared to these data, it can be seen that the level of effort in our F calves corresponded to approximately 70% of the maximum effort that such calves could produce under our experimental conditions.

In a previous study, Kuhlman *et al.* (1985) demonstrated that Hereford calves are able to efficiently ventilate their lungs during heavy exercise. Moreover these animals develop a special ventilatory pattern which allows them to increase their ventilatory efficiency. Indeed a decrease in $\dot{V}_E/\dot{M}O_2$ and $\dot{V}_E/\dot{M}CO_2$ due to the decrease in V_D/V_T was observed while $\dot{V}_A/\dot{M}O_2$ and $\dot{V}_A/\dot{M}CO_2$ remained unchanged during exercise in these calves. In man, an increase in $\dot{V}_A/\dot{M}O_2$ has been reported during high work loads (Farrel & Ivy, 1987).

An increase in the ventilatory efficiency was also observed in our calves during exercise. However, it seems that these adaptive mechanisms are not sufficient to assure efficient gas exchange in BWB calves as indicated by the relative arterial hypoxaemia, hypercapnoea and acidaemia.

Similar changes in arterial blood gases was observed in horses (Bayly *et al.*, 1983) but not in Hereford calves (Kuhlman *et al.*, 1985) or in dogs (Wathen *et al.*, 1962) during strenuous exercise. The decrease in PaO_2 recorded in our BWB calves is small compared with the hypoxaemia found in horses and does not significantly affect the oxygen carrying capacity of blood. In this respect, the limitation imposed by the small increase in haemoglobin concentration in BWB calves (+11 g/l) is certainly more important. During severe exercise, the haemoglobin concentration increased by 35 g/l in Hereford calves (Kuhlman *et al.* 1985) and by 75 g/l in ponies (Park & Manohar, 1984). Since the increase in haemoglobin concentration contributes largely to the increase in the arterio-venous difference in blood oxygen content (Karas *et al.*, 1987), it can be concluded that the oxygen carrying capacity of blood is a limiting factor for exercise in BWB calves compared with other bovine breeds and other species.

Arterial hypocapnoea was observed in dogs (Wathen *et al.*, 1962), ponies (Park & Manohar, 1984) and Hereford calves (Kuhlman *et al.*, 1985) during severe exercise. In our BWB calves, hypercapnoea similar to that recorded in horses (Bayly *et al.*, 1983) was found. This increase in $PaCO_2$ can reduce the efficiency of muscle metabolism by exacerbating the metabolic acidaemia (Bayly *et al.*, 1983).

Ventilation-perfusion inequalities, decrease in the diffusion capacity and inadequate ventilation could explain the hypoxaemia and the hypercapnoea recorded in BWB calves. In man, the two first mechanisms do not seem to play an important role in blood gas and acid-base changes during strenuous exercise (Dempsey *et al.*, 1982). Accordingly, it is unlikely that this does occur in double-muscled calves. Concerning ventilation, $\dot{V}_E$ $\dot{V}_A$ tended to be smaller in BWB than in F calves but these results were not significant ($p<0.1$). Nevertheless, this does not imply that a relative hypoventilation did not exist in the double-muscled calves. It was mentioned above that the BWB calves were near their maximum O_2 consumption and that the exercise performed by normal calves was submaximal. The decrease in $PaCO_2$ and the constancy of PaO_2 and $[H^+]_a$ recorded in the latter calves show that their ventilation was adapted to their essentially aerobic muscular

metabolism. The arterial blood-gases and arterial acid-base status changes observed in BWB calves suggest that their ventilation, while only slightly smaller than that recorded in the F calves, is not adapted to their muscular metabolism, which is largely anaerobic. These functional peculiarities of BWB calves may be related to their higher pulmonary resistance (Gustin *et al.*, 1987a; Gustin *et al.*, 1987b) and their smaller ratio of lung weight to body weight than in F calves (Hanset, 1984).

Differences in these two breeds regarding their regulation of ventilation may also occur but nothing is known about this point.

In normal calves submitted to exercise, the chronotropic effect is approximately the same as in other species but the stroke volume does not increase (Kuhlman *et al.*, 1985). Our results obtained in normal calves are in good agreement with these findings. The increase in the stroke volume recorded in horses during exercise explains why the increase in cardiac output is greater in horses than in calves (Fregin & Thomas, 1983; Karas *et al.*, 1987). Kuhlman *et al.* (1985) suggested that the large increase in serum K^+ concentration observed in calves during exercise may limit the contractility of the myocardium. However, great changes in K^+ concentration were not recorded in our calves.

In BWB calves, the increase in the cardiac output was smaller than that in Hereford calves submitted to strenuous exercise (Kuhlman *et al.*, 1985) and that in our F calves. This explains their inability to greatly increase their oxygen consumption. This small increase in the cardiac output was due to the decrease in their stroke volume from resting values. Possibly because of their large muscle mass and their low ratio of blood volume to muscle weight (Monin & Boccard, 1974), the double-muscled calves may have a circulating blood volume which is insufficient to assure a good venous return during strenuous exercise.

Changes in the albumin concentrations recorded in F and BWB calves show that a haemoconcentration occurs during exercise. This may explain the increase in serum K^+ concentration. The increase in the haemoglobin concentration is induced by haemoconcentration and probably by contraction of the spleen (Judson *et al.*, 1983).

The small increase in plasma lactate recorded in F calves during exercise and its rapid return to resting values demonstrate that muscular metabolism was essentially aerobic in these animals. In BWB calves, muscular metabolism was clearly anaerobic.

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