Immediate CO₂ Storage Capacity at the Onset of Exercise

Tokuo YANO*

Tokyo College of Wellness Science, Shinagawa-ku, Tokyo, 140 Japan

Abstract The purpose of the present study was to obtain the immediate CO₂ storage capacity at the onset of exercise. The CO₂ stores at the onset of the exercise were calculated from the difference between the respiratory gas exchange ratio (R) and the metabolic gas exchange ratio (RQ ; R obtained at 5.5 min of exercise). The CO₂ stores per body weight (CO₂ stores/ w) were linearly related to the CO₂ pressure ($P'\bar{v}_{\text{CO}_2}$) determined by the CO₂ rebreathing method ($r=0.713$, $p<0.001$), the slope being 0.330 ml/(mmHg · kg). The CO₂ stores were then corrected for change in O₂ stores with exercise, that defined as total CO₂ stores. $P'\bar{v}_{\text{CO}_2}$ was also corrected for the effect of lung-bag volume shrinkage and Haldane effect during CO₂ rebreathing, that defined as true $P\bar{v}_{\text{CO}_2}$. The total CO₂ stores/ w were also related linearly to the true $P\bar{v}_{\text{CO}_2}$ ($r=0.725$, $p<0.001$), the slope of the regression line defined as the immediate CO₂ storage capacity being 0.650 ml/(mmHg · kg).

Key words: respiratory gas exchange ratio, mixed venous CO₂ pressure, immediate CO₂ storage capacity, onset of exercise.

At the steady state in light exercise, it is often assumed that metabolic CO₂ production is equal to the CO₂ output, but this assumption is invalid at the onset of exercise (YANO *et al.*, 1984a; HUGHSON and INMAN, 1985). While metabolically produced CO₂ is partially exhaled from the airway, the rest is stored at the onset of exercise. The increase of body CO₂ storage results in the increase of mixed venous CO₂ pressure (CERRETELLI *et al.*, 1966; YANO *et al.*, 1984a). In the heavy exercise, lactate is produced and causes the excessive CO₂ elimination (ISSEKUTZ and RODAHL, 1961; YANO *et al.*, 1984a), thus CO₂ stores are diminished. As the increases in lactate and mixed venous CO₂ pressure were observed in heavy exercise (YANO *et al.*, 1984a; HUGHSON and INMAN, 1985), both effects on CO₂ stores should be taken into consideration.

CLODE and CAMPBELL (1969) proposed a quantitative approach to distinguish the effects of lactate and mixed venous CO₂ pressure on CO₂ stores. In their model,

Received for publication September 17, 1986

* Present address: Faculty of Education, Hokkaido University, Sapporo, 060 Japan.

the slope of the whole body CO_2 dissociation curve (body CO_2 slope) was assumed to be $1 \text{ ml}/(\text{mmHg} \cdot \text{kg})$ and 1 mol increase in blood lactate was assumed to correspond to 1 mol decrease in CO_2 stores. At the same time, metabolic CO_2 production was estimated from oxygen uptake by assuming a constant metabolic gas exchange ratio and the difference between metabolic CO_2 production and measured CO_2 output was assumed to be derived from the change in body CO_2 storage. As this estimate cannot accurately evaluate the independent effects of both lactate and CO_2 pressure, it is defined as gross change of CO_2 stores. CLODE and CAMPBELL (1969) reported that this estimated gross change of CO_2 stores was consistent with the amount of change in CO_2 stores estimated by their approach mentioned above.

In the incremental exercise, it is known that blood lactate is produced above a given level of exercise intensity, and CO_2 simultaneously begins to be excessively exhaled (WASSERMAN *et al.*, 1973). Since this excessive CO_2 elimination can be a tool to estimate change in CO_2 stores due to lactate production, YANO *et al.* (1984a) employed this incremental exercise to examine Clode's assumption on lactate- CO_2 stores relation, and suggested that CLODE and CAMPBELL (1969) may have overestimated the net decrease of CO_2 stores due to lactate production. Nevertheless, when assuming CLODE and CAMPBELL (1969) obtained a good approximation of gross change of CO_2 stores, it can be inferred that the net increase of CO_2 stores due to CO_2 pressure change was also overestimated and, as a result, these two overestimations might have been canceled by each other.

In the present study, therefore, Clode's quantitative assumption on CO_2 pressure- CO_2 stores relation was examined in light exercise in which no lactate would be produced (YANO, 1985). Since it is pointed out that the CO_2 rebreathing method which was often used to determine mixed venous CO_2 pressure in the study of body CO_2 slope, needs the corrections to give the true mixed venous CO_2 pressure (LUNDIN and THOMSON, 1965; JONES *et al.*, 1969; YANO *et al.*, 1984b), the corrections were made on the theoretical basis. Furthermore, since O_2 uptake measured by the Douglas bag method does not include the consumption of O_2 stores, this correction was tried in the present study.

SUBJECTS AND METHODS

Maximal O_2 uptake ($\dot{V}_{\text{O}_{2\text{max}}}$) and physical characteristics of the subjects are shown in Table 1. The subjects were students majoring in physical education and participating in the regular training. They were requested not to do any exercise or work before the experiments so as to maintain a resting state. They were all familiar with the experimental apparatuses.

Ten min after the subjects showed up at the laboratory, the measurement at rest was conducted for 5 min in the sitting position. Then the subjects exercised on a bicycle ergometer (Monark) for 6 min. The exercise was repeated 5 times (Exercise 1 to 5) with a given work rate. More than 6 min were allowed to elapse before the

Table 1. Physical and physiological characteristics of the subjects.

Subj.	Age (year)	Height (cm)	Weight (kg)	$\dot{V}_{O_2 \max}$ (l/min)	HR _{max} (beats/min)
SA	23	168	68	3.20	186
HB	21	165	60	3.19	204
SC	23	166	58	2.97	191
MD	26	164	57	2.99	187
GE	23	175	76	3.88	163
$\bar{X}$	23	168	64	3.25	186
S.D.	1.6	3.9	7.2	0.331	13.3

$\dot{V}_{O_2 \max}$: maximal O₂ uptake; HR_{max}: maximal heart rate.

subsequent run to let the respiratory gas exchange ratio (R) recover to the resting level (see LINNARSSON, 1974; WHIPP *et al.*, 1980). The work loads used in the present experiment were 300, 450, and 600 kpm/min with 50 rpm. The O₂ uptake ($\dot{V}_{O_2}$) and CO₂ output ($\dot{V}_{CO_2}$) were determined for 5 min at rest, and every 1 min at Exercise 3 by the Douglas bag method. The CO₂ rebreathing (DEFARES *et al.*, 1961) was performed at rest, 1.5 min of Exercise 1, 0.5 min of Exercise 2, 3.5 min of Exercise 4, and 5.5 min of Exercise 5. End-tidal P_{CO_2} was recorded at rest and during Exercise 3, and heart rate was measured throughout the experiment.

The rebreathing bag volume ranged from 2 to 2.5 l dependent on the body size of the subjects. The O₂ and CO₂ concentrations in the Douglas bags and in the rebreathing air during CO₂ rebreathing were analyzed with a mass spectrometer (Perkin Elma MGA-1100). Minute ventilation was measured with a dry gas meter sucking in at a constant flow rate. Tidal volume was calculated by dividing minute ventilation by respiratory rate.

It was assumed that the metabolic gas exchange ratio (RQ) during exercise remained constant from the start of exercise to the steady state. Accordingly, the difference between R and RQ at the onset of exercise was assumed to be due to the change in CO₂ storage in the body. In the present study, the RQ was considered to be equal to the R obtained at 5.5 min in exercise. The CO₂ stores until a given time was estimated from the following equation:

$$CO_2 \text{ stores} = \sum (RQ - R) \cdot \dot{V}_{O_2} = \sum (RQ \cdot \dot{V}_{O_2} - \dot{V}_{CO_2}) \quad (1)$$

The oxygen uptake determined by the Douglas bag method does not include the consumption of O₂ stores. If the O₂ stores is obtained, Eq. (1) can be rearranged as follows:

$$\text{Total } CO_2 \text{ stores} = RQ \cdot (O_2 \text{ stores} + \sum \dot{V}_{O_2}) - \sum \dot{V}_{CO_2} \quad (2)$$

The O₂ stores consist of those in the muscle, venous and the arterial blood. The O₂

stores in the muscle and the arterial blood were assumed to remain constant from rest to exercise. The change of O₂ stores in venous blood was calculated from the product of venous blood volume and the changed value in mixed venous O₂ contents from rest ($C\bar{v}_{O_2 \text{ rest}}$) to exercise ($C\bar{v}_{O_2 \text{ ex}}$). The venous blood volume was assumed to be 5% of body weight (w).

$$\Delta O_2 \text{ stores} = 0.05w \cdot (C\bar{v}_{O_2 \text{ rest}} - C\bar{v}_{O_2 \text{ ex}}) \quad (3)$$

The change in mixed venous O₂ content from rest to exercise can be calculated from the change of arteriovenous O₂ content differences by assuming the constant arterial O₂ content.

$$C\bar{v}_{O_2 \text{ rest}} - C\bar{v}_{O_2 \text{ ex}} = (\dot{V}_{O_2}/\dot{Q})_{\text{rest}} - (\dot{V}_{O_2}/\dot{Q})_{\text{ex}} \quad (4)$$

where $\dot{Q}$ is cardiac output. YANO *et al.* (1984b) proposed an equation to estimate cardiac output by the CO₂ rebreathing method (DEFARES *et al.*, 1961) with a correction for lung-bag volume shrinkage during rebreathing, since LUNDIN and THOMSON (1965) and YANO *et al.* (1984b) observed the lung-bag volume shrinkage during rebreathing which causes the underestimation in cardiac output.

$$\dot{Q} = \frac{\dot{V}_{CO_2}}{(C'\bar{v}_{CO_2} - Ca_{CO_2})} + \frac{\dot{V}_{O_2} \cdot P'\bar{v}_{CO_2}}{(C'\bar{v}_{CO_2} - Ca_{CO_2})(P_B - 47 - P'\bar{v}_{CO_2})} \quad (5)$$

where $C'\bar{v}_{CO_2}$ = CO₂ content corresponding to $P'\bar{v}_{CO_2}$, Ca_{CO_2} = arterial CO₂ content corresponding to arterial P_{CO_2} (Pa_{CO_2}), P_B = barometric pressure, $P'\bar{v}_{CO_2}$ = the value determined by the CO₂ rebreathing method (YANO *et al.*, 1984b). Pa_{CO_2} was estimated from the end-tidal P_{CO_2} and tidal volume at Exercise 3 based on a multiple regression equation (JONES *et al.*, 1979). Ca_{CO_2} and $C'\bar{v}_{CO_2}$ were estimated from Pa_{CO_2} and $P'\bar{v}_{CO_2}$ using a standard CO₂ dissociation curve for oxygenated blood (ROOT, 1958), respectively.

The procedure for obtaining mixed venous CO₂ pressure (true $P\bar{v}_{CO_2}$) is as follows: FARHI *et al.* (1976) proposed an equation to evaluate the effect of lung-bag volume shrinkage during rebreathing.

$$\dot{Q}(C'\bar{v}_{CO_2} - C\bar{v}_{CO_2}) = (\dot{V}_{O_2} \cdot P'\bar{v}_{CO_2}) / (P_B - 47 - P'\bar{v}_{CO_2}) \quad (6)$$

where $C\bar{v}_{CO_2}$ is mixed venous CO₂ content. KIM *et al.* (1966) suggested that instant gas exchange ratio during rebreathing becomes 0.32 when arterial P_{CO_2} during rebreathing reaches the level of mixed venous P_{CO_2} (true $P\bar{v}_{CO_2}$). Nevertheless, the CO₂ content in the arterial blood ($C'a_{CO_2}$) is still lower than the mixed venous CO₂ content due to the Haldane effect. The difference is given by the following equation:

$$0.32\dot{V}_{O_2} = \dot{Q} \cdot (C\bar{v}_{CO_2} - C'a_{CO_2}) \quad (7)$$

Combining Eqs. (6) and (7) to eliminate $C\bar{v}_{CO_2}$, we obtain the following equation,

$$C'a_{CO_2} = C'\bar{v}_{CO_2} - \frac{\dot{V}_{O_2}}{\dot{Q}} \left(\frac{P'\bar{v}_{CO_2}}{P_B - 47 - P'\bar{v}_{CO_2}} + 0.32 \right) \quad (8)$$

The $C'a_{\text{CO}_2}$ was converted to true $P\bar{v}_{\text{CO}_2}$ with a standard CO₂ dissociation curve for oxygenated blood (ROOT, 1958).

RESULTS

The $\dot{V}_{\text{O}_2}$ and R at 5.5 min in exercise (Table 2) increased with increasing exercise intensity. The $\dot{V}_{\text{O}_2}$ was all below 50% of $\dot{V}_{\text{O}_{2\text{max}}}$. R at the onset of exercise temporarily decreased and then showed the steady state about 3 min after the start of the exercise.

CO₂ stores/ w continued to increase until 3.5 min and reached a steady state (Fig. 1). At 0.5 min, the CO₂ stores/ w with 300 kpm/min were not significantly lower than those with 450 kpm/min but significantly less than those with 600 kpm/min ($p < 0.05$). The CO₂ stores/ w at the steady state became larger in proportion to the increase in exercise intensity. The O₂ stores at steady state increased with increasing exercise intensity (Table 2). The total CO₂ stores/ w that was obtained after the correction for the O₂ stores, became larger than CO₂ stores/ w , but the tendency along the time course of exercise and the interrelationships among the three work loads were unchanged (Fig. 1).

$P'\bar{v}_{\text{CO}_2}$ increased until 1.5 min and remained stable (Fig. 2). At 0.5 min, $P'\bar{v}_{\text{CO}_2}$ with 300 kpm/min was not significantly lower than that with 450 kpm/min but significantly less than that with 600 kpm/min ($p < 0.05$). With 600 kpm/min, $P'\bar{v}_{\text{CO}_2}$ at 5.5 min significantly decreased from that at 3.5 min ($p < 0.05$) although CO₂ stores/ w did not show any changes during the period of 3.5 to 5.5 min. The $P'\bar{v}_{\text{CO}_2}$ increased more than the true $P\bar{v}_{\text{CO}_2}$ from the rest to the exercise. The difference between $P'\bar{v}_{\text{CO}_2}$ and true $P\bar{v}_{\text{CO}_2}$ at the steady state increased with the increase in exercise intensity (Table 2). True $P\bar{v}_{\text{CO}_2}$ showed almost the same time profile as $P'\bar{v}_{\text{CO}_2}$ for each work rate. Although the true $P\bar{v}_{\text{CO}_2}$ with 300 and 450 kpm/min showed a tendency to increase after 3 min, the differences were not significant.

A significant correlation between $P'\bar{v}_{\text{CO}_2}$ and CO₂ stores/ w which were taken at

Table 2. The respiratory data measured or estimated at 5.5 min in exercise and at rest.

		$\dot{V}_{\text{O}_2}$ (l/min)	$\dot{V}_{\text{CO}_2}$ (l/min)	R	O ₂ stores (ml)	$P'\bar{v}_{\text{CO}_2}$ - true $P\bar{v}_{\text{CO}_2}$ (mmHg)
Rest	$\bar{X}$	0.28	0.22	0.81	—	7.3
	S.D.	0.042	0.033	0.056		1.16
300 kpm/min	$\bar{X}$	0.89	0.76	0.85	116	11.6
	S.D.	0.057	0.046	0.026	22.8	0.92
450 kpm/min	$\bar{X}$	1.16	1.00	0.86	133	12.3
	S.D.	0.052	0.060	0.025	63.5	1.01
600 kpm/min	$\bar{X}$	1.48	1.32	0.89	147	12.9
	S.D.	0.091	0.070	0.033	57.2	1.69

Fig. 1. CO₂ stores and total CO₂ stores plotted against time following the onset of exercise. ● 300, ○ 450, × 600 kpm/min.

0.5, 1.5, 3.5, and 5.5 min during exercise (Fig. 3) was obtained as follows:

$$\text{CO}_2 \text{ stores/w} = -20.9 + 0.330 P\bar{v}_{\text{CO}_2} \quad (r=0.713, n=59, p<0.001)$$

Also a significant correlation between true $P\bar{v}_{\text{CO}_2}$ and total CO₂ stores/w (Fig. 4) was obtained as:

$$\text{Total CO}_2 \text{ stores/w} = -33.2 + 0.650 \text{ true } P\bar{v}_{\text{CO}_2} \\ (r=0.725, n=59, p<0.001)$$

DISCUSSION

In the present study, $P\bar{v}_{\text{CO}_2}$ was determined by the CO₂ rebreathing method and this measurement was repeated at each intended time in the exercise. Although there was an unexpected decrease in the $P\bar{v}_{\text{CO}_2}$ at 600 kpm/min at 5.5 min, this decrease was within the reported range of reproducibility of the CO₂ rebreathing method (AUCHINCLOSS *et al.*, 1980). Therefore, it appeared that the change in the

Fig. 2. $P'\bar{v}_{CO_2}$ and true $P'\bar{v}_{CO_2}$ plotted against time following the onset of exercise. Symbols are the same as those in Fig. 1.

$P'\bar{v}_{CO_2}$ in time course of exercise was almost parallel with the change in CO₂ stores. Actually, the CO₂ stores/*w* were linearly related to the $P'\bar{v}_{CO_2}$ ($r=0.713$) and the slope of the regression line was 0.330 ml/(mmHg·kg) (body CO₂ slope).

The CO₂ rebreathing technique which can determine $P'\bar{v}_{CO_2}$ is generally performed immediately after expiratory gas collection because the $P'\bar{v}_{CO_2}$ during gas collection is necessary for solving the Fick principle for CO₂. If the $P'\bar{v}_{CO_2}$ is equal to that after the gas collection, cardiac output will be estimated by the Fick principle. In the present study, cardiac output determination was necessary for obtaining true $P'\bar{v}_{CO_2}$. However, as $P'\bar{v}_{CO_2}$ especially at the onset of exercise was changing, the conventional procedure for cardiac output determination mentioned above was not feasible. Then, the expiratory gas collection and $P'\bar{v}_{CO_2}$ determination were separately performed at the corresponding time.

HUGHSON and INMAN (1985) assumed *RQ* kinetics at the onset of exercise in

Fig. 3. Relationship between CO_2 stores per weight and $P'\bar{v}\text{CO}_2$. Symbols are the same as those in Fig. 1.

Fig. 4. Relationship between total CO_2 stores per weight and true $P'\bar{v}\text{CO}_2$. Symbols are the same as those in Fig. 1.

three models to estimate CO₂ stores as follows. (1) RQ increased in an exponential manner from the pre-onset RQ to the new steady level RQ with a time constant 45 s (i.e. steady state in approximately 3–4 min). (2) RQ changed as a square wave from the pre-onset RQ to the steady level RQ of exercise. (3) RQ increased instantly to 1.0 then declined with a time constant of 45 s to the exercise steady level RQ . In the present study, model (2) which provides an alternative to the two extremes of model (1) and (3), was employed. The increase of CO₂ stores obtained under this assumption should result in the increase of $P'\bar{V}_{CO_2}$ (YANO *et al.*, 1984a). The CO₂ stores in the present study corresponded to the $P'\bar{V}_{CO_2}$ not only at the steady state of exercise but also at the onset of exercise.

The R in steady state can usually be attained 3–4 min after start of exercise, and in the present study the R at 5.5 min was used as RQ in exercise.

Muscle myoglobin and blood hemoglobin can combine and release oxygen. This causes the change in body O₂ stores. While venous blood O₂ stores were estimated in the present study, arterial blood O₂ stores were assumed to remain constant. This assumption can be invalidated by an increase in hemoglobin and O₂ pressure but the direct measurement indicated little difference between arterial O₂ contents at rest and in exercise (ÅSTRAND *et al.*, 1964). Muscle O₂ stores cannot accurately be estimated because there are no available data of muscle O₂ pressure in exercise. In the oxygen dissociation curve of myoglobin, O₂ saturation increases until 30 mmHg of O₂ pressure and then shows fairly stable state (ROUGHTON, 1964). It may, therefore, be supposed that O₂ stores obtained in the present study must be estimated less if muscle tissue O₂ pressure falls below 30 mmHg. Under these assumptions, O₂ stores were estimated and were added to the oxygen uptake to give the total CO₂ stores.

Thus, in spite of the above mentioned limitation, the total CO₂ stores per body weight were linearly related to the true $P'\bar{V}_{CO_2}$ ($r=0.725$) and the slope of the regression line was 0.650 ml/(mmHg·kg), which was defined as the immediate CO₂ storage capacity in the present study.

The body CO₂ slopes have been determined with various methods. A body CO₂ slope obtained at the onset of light exercise was reported to be 0.33–0.38 ml/(mmHg·kg) (HUGHSON and INMAN, 1985), which was consistent with the present one. The body CO₂ storage can be changed by exhaling CO₂ with hyperventilation. This is another method to determine the body CO₂ slope. However, the only body CO₂ slope obtained in performing hyperventilation for short durations would be available as the comparative data with the present one because hyperventilation lasting 5 or more is known to produce blood lactate (HONDA *et al.*, 1975) which can affect the body CO₂ slope. The hyperventilation data satisfying this condition and on human in exercise was reported by CLODE *et al.* (1967). This value was 1 ml/(mmHg·kg), which was considerably higher than the present one.

Oxygen uptake and $P'\bar{V}_{CO_2}$ were the basis for estimating body CO₂ slope in the present study. However, the oxygen uptake determined by the Douglas bag method does not include the consumption of O₂ stores. When the utilization of O₂ stores is

neglected, the CO_2 stores are underestimated. Furthermore, although the change in tissue CO_2 pressure is assumed to be equal to that in true $P\bar{V}_{\text{CO}_2}$, the $P'\bar{V}_{\text{CO}_2}$ determined by the CO_2 rebreathing method which was often used on the study of body CO_2 slope, was not such that it corrected for the lung-bag volume shrinkage (LUNDIN and THOMSON, 1965; YANO *et al.*, 1984b) and Haldane effect (JONES *et al.*, 1969) during rebreathing. The degrees of Haldane effect and lung-bag volume shrinkage effect during rebreathing and O_2 stores effect were enlarged by increasing the exercise intensity (Table 2). The corrections for these effects would, therefore, be essential in the study involving transit condition from rest to exercise. On the other hand, these corrections were not included in the previous study. Although there is no direct information about these effects in hyperventilation during a steady state of exercise, as indicated in the method, O_2 stores and Haldane effects can be changed by the changes of $\dot{V}_{\text{O}_2}$ and $\dot{Q}$. Since $\dot{V}_{\text{O}_2}$ and $\dot{Q}$ can remain fairly constant during hyperventilation (HONDA *et al.*, 1975), it may be unnecessary to correct the above mentioned effects.

In the present study, the immediate CO_2 storage capacity obtained after the corrections above mentioned was $0.650 \text{ ml}/(\text{mmHg} \cdot \text{kg})$ which was still lower than $1 \text{ ml}/(\text{mmHg} \cdot \text{kg})$ reported in hyperventilation study. Hyperventilation causes the decrease of P_{aCO_2} which can make the change in whole body CO_2 storage. In contrast, P_{aCO_2} remained constant in light exercise (HUGHSON and INMAN, 1985) so that CO_2 storage in tissues except working muscle may be unaffected. Since various body tissues have different CO_2 slopes and muscle has rather lower CO_2 slope (CHERNIACK *et al.*, 1972), it may be possible that the immediate CO_2 storage capacity becomes lower at the onset of exercise.

The constant body CO_2 slope was observed in the present study while some studies with hyperventilation and at the onset of exercise have indicated a decrease of body CO_2 slopes accompanying an increase of $P'\bar{V}_{\text{CO}_2}$ within approximately the same range in $P'\bar{V}_{\text{CO}_2}$ (JONES and JURKOWSKI, 1979; HUGHSON and INMAN, 1985). This contrast may be related to the lactate production. The change in body CO_2 stores is not only related to $P'\bar{V}_{\text{CO}_2}$ increase, but also to lactic acid accumulation. Therefore, for the given change in $P'\bar{V}_{\text{CO}_2}$, the gross change in CO_2 stores can be distorted with the degree of lactate production. In fact, HUGHSON and INMAN (1985) recognized that the decrease of body CO_2 slope accompanied the increase of blood lactate.

In the present study, it was a prerequisite that the two effects of lactate and CO_2 pressure on CO_2 stores can be distinguished. Accordingly, MIYAMURA and HONDA (1978) observed that the blood CO_2 dissociation curve was shifted downward by the existence of lactate without changing its slope. If this result can be applied to the whole body CO_2 dissociation curve, the effect of $P'\bar{V}_{\text{CO}_2}$ may be expressed as the value changed along its slope, and the effect of lactate may be evaluated as the magnitude to cause parallel shift, respectively. Actually, CLODE and CAMPBELL (1969) tried to obtain the net change of CO_2 stores from the quantitative relations in lactate- CO_2 stores and $P'\bar{V}_{\text{CO}_2}$ - CO_2 stores.

Recently, YANO *et al.* (1984a) indicated that the lactate-CO₂ stores relation assumed by CLODE and CAMPBELL (1969) was quantitatively incorrect. Therefore, in the present study, the better quantitative relation on CO₂ pressure-CO₂ stores was explored. In the present study, $P'\bar{V}_{\text{CO}_2}$ changed more than true $P\bar{V}_{\text{CO}_2}$ from rest to exercise. That is, $\Delta P'\bar{V}_{\text{CO}_2} > \Delta \text{true } P\bar{V}_{\text{CO}_2}$. When the relationship of $\Delta \text{true } P\bar{V}_{\text{CO}_2} > 0.65\Delta \text{true } P\bar{V}_{\text{CO}_2}$ is applied to the above inequality equation,

$$\Delta P'\bar{V}_{\text{CO}_2} > \Delta \text{true } P\bar{V}_{\text{CO}_2} > 0.65\Delta \text{true } P\bar{V}_{\text{CO}_2}$$

In this equation, $0.65\Delta \text{true } P\bar{V}_{\text{CO}_2}$ is equivalent to the changed value in total CO₂ stores. $\Delta P'\bar{V}_{\text{CO}_2}$ was the CLODE and CAMPBELL (1969) estimate of CO₂ stores, since they measured the $P'\bar{V}_{\text{CO}_2}$ and used 1 ml/(mmHg·kg) as body CO₂ slope. Therefore, the present study indicated that CLODE and CAMPBELL (1969) overestimated the change of CO₂ stores due to the CO₂ pressure change.

The author would like to thank Drs. K. Asano and H. Ikegami (University of Tsukuba) for their critical reading of the manuscript.

REFERENCES

- ÅSTRAND, P. O., CUDDY, T. E., SALTIN, B., and STENBERG, J. (1964) Cardiac output during submaximal and maximal work. *J. Appl. Physiol.*, **19**: 268–274.
- AUCHINCLOSS, J. H., GILBERT, R., KUPPINGER, M., and PEPPI, D. (1980) Mixed venous CO₂ tension during exercise. *J. Appl. Physiol.: Respir. Environ. Exercise Physiol.*, **48**: 933–938.
- CERRETELLI, P., SIKAND, R., and FARHI, L. E. (1966) Readjustments in cardiac output and gas exchange during onset of exercise and recovery. *J. Appl. Physiol.*, **21**: 1345–1350.
- CHERNIACK, N. S., TUTEUR, P. G., EDELMAN, N. H., and FISHMAN, A. P. (1972) Serial changes in CO₂ storage in tissues. *Respir. Physiol.*, **16**: 127–141.
- CLODE, M. and CAMPBELL, E. J. M. (1969) The relationship between gas exchange and changes in blood lactate concentrations during exercise. *Clin. Sci.*, **37**: 263–272.
- CLODE, M., CLARK, T. J. H., and CAMPBELL, E. J. M. (1967) The immediate CO₂ storage capacity of the body during exercise. *Clin. Sci.*, **32**: 161–165.
- DEFARES, J. G., WISE, M. E., and DUYFF, J. W. (1961) New indirect Fick procedure for the determination of cardiac output. *Nature*, **192**: 760–761.
- FARHI, L. E., NESARAJAH, M. S., OLSZOWKA, A. J., METILDI, L. A., and ELLIS, A. K. (1976) Cardiac output determination by simple one-step rebreathing technique. *Respir. Physiol.*, **28**: 141–159.
- HONDA, Y., MIYAMURA, M., and NAKANO, E. (1975) Serial observations of arterial and mixed-venous blood gases after step change in ventilation. *Pflügers Arch.*, **353**: 123–138.
- HUGHSON, R. L. and INMAN, M. D. (1985) Gas exchange analysis of immediate CO₂ storage at onset of exercise. *Respir. Physiol.*, **59**: 265–278.
- ISSEKUTZ, B. and RODAHL, K. (1961) Respiratory quotient during exercise. *J. Appl. Physiol.*, **16**: 606–610.
- JONES, N. L., CAMPBELL, E. J. M., EDWARDS, R. H. T., and WILKOWFF, W. G.

- (1969) Alveolar-to-blood P_{CO_2} difference during rebreathing in exercise. *J. Appl. Physiol.*, **27**: 811–815.
- JONES, N. L. and JURKOWSKI, J. E. (1979) Body carbon dioxide storage capacity in exercise. *J. Appl. Physiol.: Respir. Environ. Exercise Physiol.*, **46**: 811–815.
- JONES, N. L., ROBERTSON, D. G., and KANE, J. W. (1979) Difference between end-tidal and arterial P_{CO_2} in exercise. *J. Appl. Physiol.: Respir. Environ. Exercise Physiol.*, **47**: 954–960.
- KIM, T. S., RAHN, H., and FARHI, L. E. (1966) Estimation of true venous and arterial P_{CO_2} by gas analysis of a single breath. *J. Appl. Physiol.*, **21**: 1338–1344.
- LINNARSSON, D. (1974) Dynamics of pulmonary gas exchange and heart rate changes at start and end of exercise. *Acta Physiol. Scand. Suppl.*, **415**: 1–68.
- LUNDIN, G. and THOMSON, D. (1965) Determination of the mixed venous CO_2 pressure with a rebreathing method. Correction for volume changes of the lung-bag system. *Acta Physiol. Scand.*, **64**: 448–452.
- MIYAMURA, M. and HONDA, Y. (1978) CO_2 dissociation curves of oxygenated whole blood obtained at rest and in exercise. *Eur. J. Appl. Physiol.*, **39**: 37–45.
- ROUGHTON, F. J. W. (1964) Transport of oxygen and carbon dioxide. In: Handbook of Physiology, Section 3, Respiration, ed. by FENN, W. O. and RAHN, H., Am. Physiol. Soc., Washington, D.C., Vol. 1, pp. 767–826.
- ROOT, R. W. (1958) Blood CO_2 absorption as function of CO_2 pressure. In: Handbook of Respiration, ed. by DITTER, D. S. and GREBE, W. B., Saunders Co., Philadelphia and London, p. 65.
- WASSERMAN, K., WHIPP, B. J., KOYAL, S. N., and BEAVER, W. L. (1973) Anaerobic threshold and respiratory gas exchange during exercise. *J. Appl. Physiol.*, **35**: 236–243.
- WHIPP, B. J., WASSERMAN, K., DAVIS, J. A., LAMARRA, N., and WARD, S. A. (1980) Determinants of O_2 and CO_2 kinetics during exercise in man. In: Exercise Bioenergetics and Gas Exchange, ed. by CERRETELLI, P. and WHIPP, B. J., Elsevier/North-Holland Biomedical Press, Amsterdam, New York, and Oxford, pp. 175–185.
- YANO, T. (1985) Anaerobic threshold, O_2 deficit and response time of O_2 uptake in long, middle and short distance runners. *J. Phys. Fitness Jpn.*, **34**: 176–182.
- YANO, T., ASANO, K., NOMURA, T., MATSUZAKA, A., and HIRAKOBA, K. (1984a) Kinetics of V_{CO_2} during incremental exercise. *J. Phys. Fitness Jpn.*, **33**: 201–210.
- YANO, T., NORSK, P., and BONDE-PETERSEN, F. (1984b) Cardiac output determined by the CO_2 rebreathing method with correction of lung-bag volume shrinkage. *Jpn. J. Physiol.*, **34**: 883–891.