EFFECTS OF CARBON DIOXIDE AND UBA-LIKE BREATHING RESISTANCE ON EXERCISE ENDURANCE

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Technical Report
FROM June 2008 TO Dec 2009
2010 April15
32

ABSTRACT: Effects of inspired CO₂ and of resistance on exercise endurance were tested dry at sea level. Resistance R was designed to mimic that of the MK 16 underwater breathing apparatus (UBA) at 50 feet of seawater. The MK 16 UBA has turbulent inspiratory and laminar expiratory pressure drops. At the design flow, expiratory pressure was twice inspiratory pressure. Endurance was assessed as duration of exercise on a bicycle ergometer at 85% peak oxygen consumption. Ventilatory parameters and end tidal CO₂ also were measured. Three groups of twelve subjects participated: one breathing air with 0%, 2%, or 3% CO₂ without R; one breathing air against moderate, high, or no R without CO₂ and against moderate R with 1% or 2% CO₂; and one breathing O₂ with or without 2% CO₂, once with moderate and once with no R. Endurance in air was reduced by 20% or more relative to that with neither R nor CO₂ in: 2 of 10 subjects breathing against moderate R, 3 of 10 subjects breathing against high R, 3 of 10 subjects breathing against moderate R, 5 of 9 subjects breathing against moderate R with 2% CO₂, and 6 of 9 subjects with 3% CO₂, 3 of 10 subjects breathing against moderate R with 1% CO₂, and 5 of 10 subjects breathing against moderate R with 2% CO₂. Among 10 subjects breathing O₂, endurance was reduced similarly in 2 subjects breathing against moderate R, 3 with 2% CO₂, and 2 breathing against moderate R with 2% CO₂. When CO₂ was added without R, minute ventilation increased relative to that with air alone without R, but when R was present, minute ventilation decreased with or without inspired CO₂. Average end tidal CO₂ remained normal during air breathing without CO₂ but increased in all other cases. A few subjects reached alarmingly high end tidal CO₂ with combinations of R and CO₂ or with 3% CO₂ in air. We conclude that to allow inspired CO₂ in the MK 16 or other UBAs with similar pressure-flow characteristics would be hazardous.
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INTRODUCTION

Each model of rebreather underwater breathing apparatus (UBA) has its own pressure-flow (resistance) characteristics that depend on laminar and turbulent pressure drops within the apparatus. These characteristics determine the work of breathing (WOB) for the UBA. Testing for acceptable WOB assumes normal ventilatory requirements based on a diver’s external workload. However, if the CO₂ in the inspiratory gas is allowed to climb to 2% rather than 0.5% surface equivalent value (SEV) before the scrubber is considered to be expended, divers may need to increase respiratory minute ventilation (VE). Conversely, the UBA’s resistance characteristics may reduce ventilatory sensitivity to CO₂ and thus increase CO₂ retention. The effects of inhaling CO₂ while breathing against typical rebreather UBA resistance must be known before any consideration is given to relaxing the criteria for scrubber lifetime.

Subjects who inhale gas containing CO₂ when the resistance of their breathing circuit is minimal increase VE both at rest and during mild to moderate (below ventilatory threshold) exercise. However, when CO₂ is inhaled during heavy or maximal exercise, VE does not increase over that without CO₂, and, aerobic capacity decreases — probably because the metabolic acidosis of heavy exercise cannot be cleared.

During mild exercise the increases in VE with exercise and from CO₂ inhalation are more than additive. Absent any impediment to breathing, inspired CO₂ causes subjects to increase VE by the factor $\frac{P_{aCO₂}}{P_{aCO₂} - P_{inCO₂}}$, where $P_{aCO₂}$ is arterial and $P_{inCO₂}$ is inspired CO₂ partial pressure. For example, for a subject to maintain $P_{aCO₂}$ at 45 mm Hg (6% SEV) when inhaling with 2% instead of 0% CO₂, the subject will increase VE by 50%.

Breathing resistance in the absence of inhaled CO₂ can reduce exercise endurance and maximum oxygen uptake, because VE is reduced relative to that without breathing resistance, although not so much that WOB remains constant. The reduced VE leads to CO₂ retention; during exercise with a resistive breathing circuit, $P_{aCO₂}$ as indicated by end tidal PCO₂ ($P_{ETCO₂}$) increases.

Subjects who inhale gas containing CO₂ when the resistance of their breathing circuits is more than minimal show a much smaller increase in VE with inhaled CO₂ than without it both at rest and during exercise. Inspiratory WOB in subjects at rest with elevated inspired CO₂ has been reported to remain constant for a given $P_{ETCO₂}$ across a range of resistances. During exercise with elevated inspired CO₂, VE is lower when an inspiratory resistance is present than when it is not, a result suggesting a trade-off between increased effort and increased CO₂.
Rebreather UBAs have both inspiratory and expiratory resistance to breathing. If the inspiratory resistance is partially turbulent, pressure for flow increases as the square of the flow, and inspiratory WOB increases precipitously for high flows. However, the strategy of increasing inspiratory time to decrease flow may be limited by the need to overcome expiratory resistance. Although 2% SEV CO₂ may not be problematic for a short period of light to moderate exercise against minimal breathing resistance,¹ a UBA’s resistance is not minimal. Naval Sea Systems Command (NAVSEA) Task 08-06 initiated an exploration of the effects of CO₂ and UBA breathing resistance, first with background air and then with background O₂, with PO₂ of approximately 1 atmosphere (atm).¹⁸ Navy Experimental Diving Unit (NEDU) measured ventilatory and metabolic values and exercise endurance for subjects who exercised on a cycle ergometer in a dry environment at atmospheric pressure, where work is safer, faster, and less expensive than that in water at depth.

METHODS

GENERAL

The Institutional Review Board at NEDU approved the protocol. Military subjects from NEDU, its neighboring commands, and NEDU Reserve Unit Great Lakes gave written informed consent. Only those whose risk of a cardiovascular event in the next 10 years was less than 5% as estimated from parameters of the Framingham study,¹⁰ participated in this study. Twelve subjects completed each phase.

Exercise was imposed with a bicycle ergometer. Heart rate, Vₑ, and end tidal CO₂ fraction (FₑTCO₂) were recorded on a breath-by-breath basis. Compressed breathing gas was regulated to low pressure and fed into a reservoir, a 120 L spirometer, at atmospheric pressure. The subject breathed from that reservoir through wide-bore tubing and a system of one-way valves attached to an oronasal mask (Hans Rudolph; Kansas City, MO). Expired gas passed through a turbine flow meter, past a gas sampling port (Cosmed USA; Chicago, IL), and then through a wide-bore expiratory hose. For CO₂ in air, CO₂ was added with a system designed for this experiment (Fig. 1) and described below (equipment and instrumentation, Gas Mixing System). For CO₂ in O₂, premixed gas was used.

Graded incremental exercise to peak exercise capacity was used to determine the exercise level for later tests in each phase. During remaining testing, the ergometer was set to 80–85% of that at termination. Each subject then performed constant-load exercise to termination — that is, an endurance test under each different testing condition. Endurance test conditions were imposed in pseudorandom order.

Resting ventilatory sensitivity to CO₂ was measured separately, as described in procedures, Ventilatory Sensitivity to CO₂.
EXPERIMENTAL DESIGN AND ANALYSIS

Variables recorded continuously as functions of time included, in Phases 1 and 2, partial pressures of oxygen and carbon dioxide in the mask, tidal volume, respiratory frequency, $V_E$, and heart rate; in Phase 3, mask pressure, but not partial pressure of oxygen, which was exceeded the range of the analyzer. Exercise endurance time also was recorded for all phases. Within each phase of the study, conditions were presented to different subjects in different orders, and the subject was not told which gas or resistance was used.

To study effects of the experimental conditions on endurance and respiratory variables, NEDU compared subjects to themselves in repeated measures designs for each phase of the protocol. Because not all subjects participated in all phases, group responses were compared across phases.

Phase 1 (CO$_2$ only): Endurance was measured with
- air only,
- air plus 2% CO$_2$, and
- air plus 3% CO$_2$.

Resistance elements for Phases 2 and 3 were constructed to mimic the pressure-flow characteristics of the MK 16 UBA at 50 feet of seawater (fsw), as is described below (EQUIPMENT AND INSTRUMENTATION, Choice of Resistance Elements). High resistance was then defined as an element that would produce the maximum acceptable WOB per tidal volume (WOB/VT) at the median exercise $V_E$ with air alone, and moderate resistance as one that would produce that WOB/VT at the median $V_E$ for 2% CO$_2$ in air.

Phase 2 (Resistance and CO$_2$): Endurance was measured with
- air only;
- air and just the resistance of the valve and tube assembly;
- air and moderate inspiratory resistance and the expiratory resistance;
- air and high inspiratory resistance and the expiratory resistance;
- 1% CO$_2$ in air, with moderate inspiratory resistance and the expiratory resistance; and
- 2% CO$_2$ in air, with moderate inspiratory resistance and the expiratory resistance.

Phase 3 (Resistance and CO$_2$ in O$_2$): Endurance was measured with
- air and just the resistance of the valve and tube assembly;
- O$_2$ and just the resistance of the valve and tube assembly;
- O$_2$ with moderate inspiratory and expiratory resistance;
- 2% CO$_2$ in O$_2$, with just the resistance of the valve and tube assembly; and
- 2% CO$_2$ in O$_2$, with moderate inspiratory and expiratory resistance.
EQUIPMENT AND INSTRUMENTATION

We measured breath-by-breath gas concentration and flow during exercise with the COSMED k2b4 (Cosmed USA; Chicago, IL). Flow was measured with a turbine flow meter (range 0–20 L/s, resolution 4 mL, and accuracy ±1%) and gases with fast response (<120 ms for 90% full scale) analyzers. The nondispersive infrared sensor CO2 has a reported range of 0–8% but agreed with a mass spectrometer to just above 10%. The galvanic fuel cell to measure O2 has a range of 7–24%. To measure mask pressure in Phase 3 we used a solid-state differential pressure transducer (Honeywell, DC020NDR5; Freeport, IL; range, ±20 inches of water).

For all of Phases 1 and 2 and for some subjects in Phase 3, we used a cycle ergometer built at NEDU — a successor to the Collins Pedal Mate ergometer, a device no longer available. A pedal shaft drives the shaft of a hysteresis brake (Magtrol, HB210; Buffalo, NY) through a gear train with an overall gear ratio of 1:19.2. The torque necessary to turn the brake is regulated by the electric current supplied to the brake. Because of hysteresis in the brake rotor (in addition to that which causes braking), torque at a given setting is higher if the current is decreased to the value than if it is increased. A constant (regulated) current power supply was used to provide a stable load. Subjects, who watched their pedal cadence on an analog meter connected to an electronic pickup, pedaled at 60 revolutions per minute (rpm) to maintain a constant power output.

For some subjects in Phase 3, we used a Monarch (Vansbro, Sweden) Ergomedic 839E cycle ergometer. This mechanically-braked ergometer adjusts torque for changes in cadence to maintain a constant power output. The Monarch ergometer is more comfortable to ride than the ergometer built at NEDU because both seat and handlebars adjust. It is also much quieter. We would have used it for all of Phase 3, but its arrival was delayed. Results from the Monarch and the calibrated, hysteresis brake ergometer are entirely comparable; one subject performed Phase 1 exercise with the hysteresis brake and Phase 3 exercise with the Monarch, and the relation between oxygen consumption and ergometer workload were superimposable.

Subjects wore a silicone rubber oronasal nonrebreathing face mask with a T-shaped valve (Hans Rudolph 8920 [large], 8930 [medium], or 8940 [small]; Kansas City, MO). The mask was held to the head by a mesh headpiece and Velcro straps. The T-piece that contains the one-way valves has dimensions of 28.6 mm i.d. and 35 mm o.d., over which we slid large-bore respiratory tubing. The tubing on the inspiratory side connected to the spirometer, and that on the expiratory side held the turbine flow meter and the expiratory resistance element when resistance was added. The inspiratory resistance element, when used, was inserted inside the end of the T-piece. To keep the T-piece dry, expiratory resistance was kept as far as possible from exhaled moisture.
Figure 1. Apparatus to provide air with adjustable CO₂ concentration. The subject breathed from the system at point (A). Compressed air from a storage tank (B) was delivered at whatever flow was required to maintain a suitable volume in the 120 L spirometer (C), and that flow was controlled manually with a needle valve (D). The flow was measured with a mass flow meter (E), which provided an input to the control box (F), where the desired CO₂ concentration was set manually. The control box (F) caused the CO₂ mass flow regulator (G) to deliver CO₂ from a tank (H). A two-channel CO₂ analyzer (not shown) monitored the gas compositions entering the spirometer and being delivered (A) to the subject (not pictured).

Air and CO₂ were mixed using a system designed and built for this experiment and detailed in Figure 1. Breathing gas, either air or air mixed with CO₂, was available for the subjects to breathe at ambient pressure from a volume tank, a 120 L spirometer (Collins; Braintree, MA). We set the flow manually (Valve D, Fig. 1,) to accommodate Vₑ and a mass flow meter (E in Fig. 1; Omega Engineering, model FMA1843, serial number 205587-1; range, 0–200 L/min standard temperature pressure, dry [STPD]) provided the measured value to a control box (F, Fig. 1) that had been built in-house for
this experiment. On that control box, we set the desired CO₂ concentration. The box
provided the resultant output from the two inputs, namely measured Vₑ and selected
CO₂ concentration, to a mass flow controller for CO₂ (G, Fig.1; Matheson Gas Products,
model 8272-0414, serial number A735124327; range, 0–10 L/min STPD), which
allowed an appropriate flow of CO₂ into the inlet line to the spirometer. Gas could
continue to mix inside the spirometer tank (C, Fig. 1). We used a two-channel CO₂
analyzer (Rosemont MLT, Rosemount Analytical Inc.; Solon, OH), to monitored the
composition of the gas entering the spirometer and of that leaving the spirometer to the
subject (at A, Fig. 1).

Choice of Resistance Elements

We wanted to match the pressure-volume characteristics of the MK 16 and its ratio of
inspiratory to expiratory WOB/Vₑ. The target was to provide the maximum tolerable
WOB/Vₑ if subjects maintained Vₑ as measured without resistance. Maximum tolerable
WOB/Vₑ varies with water depth, but at the surface it is 2.99 J/L.¹⁹

When Phase 1 subjects breathed room air, their median exercise Vₑ measured 80
L/min, and that with 2% CO₂ was 100 L/min. Those rates were used as the design Vₑ
levels for high and moderate resistance, respectively. In other words, the high
resistance caused WOB/Vₑ = 3 J/L at 80 L/min, and moderate resistance caused
WOB/Vₑ = 3 J/L at 100 L/min.

Pressure-volume loops from unmanned testing of the MK 16 were analyzed for
inspiratory and expiratory WOB, and the ratios were calculated for data from three
depths (0, 50, and 100 fsw) and four Vₑ (22.5–90 L/min) per depth. At 100 fsw the WOB
was too high when flow was 90 L/min, but the average ratio of expiratory to inspiratory
WOB/Vₑ was 1.9 across the other tests (SD = 0.29, n = 11). This became our target
ratio. In other words, we chose to partition the WOB/Vₑ into approximately 1 J/L on
inspiration and 2 J/L on expiration at the target Vₑ of 80 L/min for high resistance and
100 J/L for moderate resistance.

We selected the pressure-volume and pressure-flow data from the MK 16 at 50 fsw as
our pattern. From these data we found resistive pressure drops by subtracting the static
and elastic components of pressure — that is, the line connecting end inspiration and
dexpiration, including offset. The remaining resistive pressure-flow data were then
split into inspiratory and expiratory components, and polynomials were fitted to each
segment. Expiratory pressure was nearly linear with flow (laminar) and inspiratory
resistance was quadratic with flow (turbulent); the fitted equations were

$$\Delta P_{res, insp} = C_{x2} \cdot Q^2, \quad C_{x2} = 0.0618, \quad r^2 = 0.69, \text{linear term insignificant},$$
\[ \Delta P_{\text{res, exp}} = C_x \cdot Q, \quad C_x = 0.413, \quad r^2 = 0.82, \text{ quadratic term insignificant}, \]

where \( Q \) is volumetric flow in L/s and \( C_x \) and \( C_{x2} \) are the fitted coefficients of linear and quadratic terms, respectively.

With numerically simulated sinusoidal flow, these values gave \( \text{WOB/VT} = 2.8 \) and \( \text{WOB/VT} = 1.7 \) J/L at 100 L/min and 80 L/min, respectively. However, a 5% increase in the coefficients increased \( \text{WOB/VT} \) to 2.97 J/L at 100 L/min, and an 8% increase brought \( \text{WOB/VT} \) to 2.98 J/L at 80 L/min.

Turbulent pressure drops can be generated by flow through orifices. Flow through a straight-holed orifice relates to its cross-sectional area and \( \Delta P \) as

\[ Q = 0.62 \cdot A \cdot \left(2 \cdot \frac{\Delta P}{\rho}\right)^{0.5}, \]

where \( \rho \) is density of the fluid.

But

\[ \Delta P = C_{x2} \cdot Q^2, \text{ or} \]

\[ A = \left[\rho \cdot \left(2 \cdot 0.62^2 \cdot C_{x2}\right)^{-1}\right]^{0.5}, \]

from which the orifice diameter can be calculated. Design orifice diameters were 14.1 mm (0.56 in) and 12.3 mm (0.48 in) for moderate and high resistance, respectively. The machine shop provided us with a series of plugs with holes of 11.2, 12.2, 13.2, 14.2, and 15.2 mm (0.44, 0.48, 0.52, 0.56, and 0.60 inches). For laminar elements we used jersey knit cloth stretched over the end of the expiratory hose. We measured the pressure drop across the cloth for a number of flows.

To confirm our calculations, we measured \( \text{WOB/VT} \) with our resistive elements on a breathing simulator. A mask with a T-piece like the one used with the subjects was attached to the breathing simulator head, and the simulator was run with all the plugs, one at a time, on the inspiratory side. Resistance elements (two, four, six, or eight layers of cloth) were attached to the expiratory side. Inspiratory and expiratory loads were tested in combination and separately, and \( \text{WOB/VT} \) was determined by the standard software in NEDU’s Testing and Evaluation Department. The measurements confirmed that even though the inspiratory elements were long plugs rather than orifice disks, the hole diameters of 0.56 and 0.48 inches gave the desired inspiratory \( \text{WOB/VT} \). Corresponding expiratory resistances required four and seven layers of cloth, respectively. However, early during exercise testing we found the expiratory resistance to be unworkably high, and we used three layers of cloth for all resistive runs.
PROCEDURES

Testing was conducted at ambient room temperature. A large fan provided extra cooling for the subjects when they wanted it. Subjects who used the hysteresis brake were required to maintain a cadence of 60 rpm, at which the ergometer had been calibrated, while those riding the Monarch ergometer were free to alter cadence during the test. Once the graded test was complete, experimental conditions were presented in varying order for each subject. No individual performed more than one test on any day.

Graded testing began at 25 W, and loading continued in increments of 50 W — or 25 W, when we deemed that a subject was nearing peak power capacity — to voluntary termination or termination necessitated by the apparatus: the hysteresis brake we used began to overheat at settings >250 W, but the Monarch ergometer was not so limited. Each load lasted for three minutes.

Endurance testing began with a two-minute warm-up at 50 W and was followed by a steady load of 80–85% of the peak load achieved. In general, 85% was chosen if the subject completed most of a three-minute increment, and 80% if the duration at the peak load was short, with the same load used for all endurance tests. Testing continued until the subject stopped cycling or could not maintain cadence. To prevent subjects from setting specific time goals for themselves, they were told neither how long they had cycled nor which condition had been presented in any test until the series ended, and they were not permitted to wear watches or to have a clock visible. They were permitted to listen to music.

**Ventilatory Sensitivity to CO₂**

Each subject sat in a chair and held an oronasal mask to his or her face. The COSMED unit was connected to the mask and, through the adaptor used for this study, to the wide-bore respiratory tubing and to the spirometer. The spirometer contained 8 to 10 L of 7% CO₂ in O₂. Subjects were instructed to exhale to residual volume and then signal, after which the valve to the spirometer was opened and the subjects rebreathed the CO₂-rich gas. Inspired and end tidal CO₂ and respiratory variables were recorded, while the computer screen displayed VE as a function of end tidal CO₂ in real time. Rebreathing continued for no more than six minutes and until end tidal PCO₂ reached 70 Torr — or until a clear relationship could be seen between ventilation and end tidal CO₂. Although no subject felt a need to end the test early, early termination could have been accomplished simply by removing the mask. Ventilatory sensitivity to CO₂ was measured as the slope of the line relating VE to end tidal CO₂ and, when there was an offset, as the end tidal CO₂ at which ventilation first began to increase.
RESULTS

Twelve subjects completed each phase. Seven subjects completed both Phases 1 and 2; three, both Phases 1 and 3; and two, both Phases 2 and 3. (The two subjects who completed Phases 2 and 3 in fact completed all three phases). Several subjects began phases of testing but were unable to complete them, and their data are not included.

Data from Phase 1 generally are reported for ten subjects, but endurance values are reported only for nine. We excluded all data except end tidal CO₂ from one subject (for whom we had set the workload inconsistently) and all data from one for whom we had had great difficulty maintaining a face seal. We include all but endurance data for a third subject who cycled under each condition without evidence of fatigue for one hour, after which we stopped him.

Data for Phase 2 also are reported for only ten of the twelve subjects. We disregarded all but end tidal CO₂ data from one subject because he frequently reported to the laboratory a short time after performing exhaustive leg exercise although the protocol proscribed it. We also excluded all data from the subject for whom a good face seal was difficult.

Endurance data from Phase 3 are reported for only ten subjects, because we stopped two subjects while they could have continued. One was stopped after 60 min with each of two test conditions (100% O₂ without resistance and 2% CO₂ in O₂ with moderate resistance), and then at 30 min on each of his subsequent tests. We stopped the other when we exhausted the gas supply after 35 min of 2% CO₂ in O₂ with moderate resistance. However, all other data from those two subjects have been considered.

We measured variables breath-by-breath, but values averaged over the last 1.5 to 2 minutes of endurance cycling were considered to represent each subject. Cross-subject means of those average values are reported.

Table 1. Subject characteristics. Median values, with minimum to maximum in parentheses.

<table>
<thead>
<tr>
<th></th>
<th>Phase 1</th>
<th>Phase 2</th>
<th>Phase 3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10 men, 2 women</td>
<td>10 men, 2 women</td>
<td>12 men, 0 women</td>
</tr>
<tr>
<td>Age (years)</td>
<td>35.5 (27–40)</td>
<td>38.5 (32–47)</td>
<td>37.5 (20–40)</td>
</tr>
<tr>
<td>Height (cm)</td>
<td>175 (160–190)</td>
<td>173 (160–185)</td>
<td>183 (169–193)</td>
</tr>
<tr>
<td>Body mass (kg)</td>
<td>82 (73–107)</td>
<td>81 (62–107)</td>
<td>87 (70–114)</td>
</tr>
<tr>
<td>Ergometer settings (W)</td>
<td>185 (90–210)</td>
<td>160 (100–250)</td>
<td>185 (160–250)</td>
</tr>
</tbody>
</table>
Table 2. Average baseline values, by phase.

<table>
<thead>
<tr>
<th>n</th>
<th>Endurance time [min]</th>
<th>Mean</th>
<th>SD</th>
<th>Median</th>
<th>Max</th>
<th>Min</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><strong>Phase 1: CO2 in air, no Resistance</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Endurance time [min]</td>
<td>9</td>
<td>17.0</td>
<td>8.6</td>
<td>14.7</td>
<td>33.5</td>
</tr>
<tr>
<td></td>
<td>VE [L/min]</td>
<td>10</td>
<td>86</td>
<td>20</td>
<td>88</td>
<td>116</td>
</tr>
<tr>
<td></td>
<td>VT [L]</td>
<td>10</td>
<td>2.3</td>
<td>0.6</td>
<td>2.5</td>
<td>2.8</td>
</tr>
<tr>
<td></td>
<td>f [breaths/min]</td>
<td>10</td>
<td>37</td>
<td>5</td>
<td>37</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>T[i] [s]</td>
<td>10</td>
<td>0.63</td>
<td>0.10</td>
<td>0.63</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>T[E] [s]</td>
<td>10</td>
<td>0.96</td>
<td>0.11</td>
<td>1.00</td>
<td>1.09</td>
</tr>
<tr>
<td></td>
<td>T[i]/Ttot</td>
<td>10</td>
<td>0.40</td>
<td>0.05</td>
<td>0.40</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>FETCO2 [%]</td>
<td>10</td>
<td>5.5</td>
<td>0.7</td>
<td>5.6</td>
<td>6.8</td>
</tr>
<tr>
<td></td>
<td><strong>Phase 2: Resistance with or without CO2 in air</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Endurance time [min]</td>
<td>10</td>
<td>17.5</td>
<td>12</td>
<td>13.5</td>
<td>49.8</td>
</tr>
<tr>
<td></td>
<td>VE [L/min]</td>
<td>10</td>
<td>93</td>
<td>27</td>
<td>91</td>
<td>153</td>
</tr>
<tr>
<td></td>
<td>VT [L]</td>
<td>10</td>
<td>2.3</td>
<td>0.6</td>
<td>2.5</td>
<td>3.0</td>
</tr>
<tr>
<td></td>
<td>f [breaths/min]</td>
<td>10</td>
<td>42.4</td>
<td>8.9</td>
<td>42.0</td>
<td>56.3</td>
</tr>
<tr>
<td></td>
<td>T[i] [s]</td>
<td>10</td>
<td>0.63</td>
<td>0.11</td>
<td>0.62</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>T[E] [s]</td>
<td>10</td>
<td>0.80</td>
<td>0.13</td>
<td>0.81</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>T[i]/Ttot</td>
<td>10</td>
<td>0.46</td>
<td>0.04</td>
<td>0.47</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>FETCO2 [%]</td>
<td>10</td>
<td>4.9</td>
<td>0.9</td>
<td>4.6</td>
<td>7.3</td>
</tr>
<tr>
<td></td>
<td><strong>Phase 3: Resistance with or without CO2 in O2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Endurance time [min]</td>
<td>10</td>
<td>19.2</td>
<td>9.2</td>
<td>18.1</td>
<td>38.0</td>
</tr>
<tr>
<td></td>
<td>VE [L/min]</td>
<td>12</td>
<td>81</td>
<td>11</td>
<td>81</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>VT [L]</td>
<td>12</td>
<td>2.2</td>
<td>0.5</td>
<td>2.3</td>
<td>1.1</td>
</tr>
<tr>
<td></td>
<td>f [breaths/min]</td>
<td>12</td>
<td>39</td>
<td>9</td>
<td>35</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>T[i] [s]</td>
<td>12</td>
<td>0.63</td>
<td>0.17</td>
<td>0.64</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td>T[E] [s]</td>
<td>12</td>
<td>0.97</td>
<td>0.19</td>
<td>0.97</td>
<td>1.31</td>
</tr>
<tr>
<td></td>
<td>T[i]/Ttot</td>
<td>12</td>
<td>0.39</td>
<td>0.03</td>
<td>0.38</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>FETCO2 [%]</td>
<td>12</td>
<td>5.4</td>
<td>0.7</td>
<td>5.5</td>
<td>4.1</td>
</tr>
</tbody>
</table>
Mean endurance time was not affected by resistance alone or with 1% or 2% CO₂, or by 2% CO₂ alone. Endurance time was reduced (p<0.03) by 3% CO₂ (Fig. 2a). None of the other conditions was different from baseline by repeated measures ANOVA and testing of difference contrasts.

![Graph showing endurance times](image)

**Figure 2.** Endurance time, change from baseline, mean and standard errors. Baseline (valve system without resistance or CO₂) values are listed in Table 2. “R” means resistance; “mod” is moderate. Only mean endurance with 3% CO₂ in air is different from baseline.

Median relative endurance times, the lowest relative time seen in each group, and the number of subjects with endurance less than 80% of baseline are shown in Table 3.
Table 3. Endurance times relative to baseline.

<table>
<thead>
<tr>
<th>Phase (gas)</th>
<th>Condition</th>
<th>Median</th>
<th>n</th>
<th>≥10%</th>
<th>≥20%</th>
<th>≥30%</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 (air)</td>
<td>Mod R, 0% CO2</td>
<td>0.94</td>
<td>10</td>
<td>4</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>2 (air)</td>
<td>High R, 0% CO2</td>
<td>0.89</td>
<td>10</td>
<td>6</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>1 (air)</td>
<td>No R, 2% CO2</td>
<td>0.90</td>
<td>9</td>
<td>4</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>1 (air)</td>
<td>No R, 3% CO2</td>
<td>0.72</td>
<td>9</td>
<td>7</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>2 (air)</td>
<td>Mod R, 1% CO2</td>
<td>0.96</td>
<td>10</td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>2 (air)</td>
<td>Mod R, 2% CO2</td>
<td>0.78</td>
<td>10</td>
<td>6</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>3 (O2)</td>
<td>Mod R, no CO2</td>
<td>1.06</td>
<td>10</td>
<td>3</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>3 (O2)</td>
<td>No R, 2% CO2</td>
<td>1.07</td>
<td>10</td>
<td>3</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>3 (O2)</td>
<td>Mod R, 2% CO2</td>
<td>1.12</td>
<td>10</td>
<td>3</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>

Subjective reports — Reasons for stopping exercise

Subjects stopped exercise sometimes because of generalized fatigue, leg fatigue, or achy knees. Sometimes they stopped because breathing was too difficult, sometimes for other reasons, and sometimes for a combination of reasons. Some subjects stopped because of symptoms likely resulting from elevated FETCO2. In Table 4 the “breathing” heading includes complaints of air hunger and inability to exhale fast enough. Not included in Table 4 is the report from one Phase 2 subject that he was nauseated initially but felt better as he continued to exercise; he maintained FETCO2 of approximately 7% throughout.

In Phases 1 and 2 all but one of the reports of nausea, headache, or tunnel vision (Table 4) corresponded to FETCO2 >7%, but not all occasions of elevated FETCO2 were accompanied by symptoms. With 3% inhaled CO2 in Phase 1, subjects reported no symptoms connected with seven incidences of FETCO2 >7%, but they reported symptoms connected to three others. In Phase 2 the association of symptoms and an elevated FETCO2 was no different from that expected if symptoms were independent of FETCO2. In Phase 3 two reports (Table 4) of headache occurred with a normal FETCO2, and irritability was reported once with a FETCO2 of 6.8%. The other reports of headache, irritability, and feeling “zoney” corresponded to a FETCO2 >7%. Additionally, four of the exercise terminations in Phase 3 because of general fatigue (Table 4) corresponded to a FETCO2 >7%.
Table 4. Reasons for stopping exercise. Some subjects reported multiple reasons, and some of the listings under “Other” were symptom reports given following exercise but not stated as reasons that the subject had stopped.

<table>
<thead>
<tr>
<th>Phase 1 — Air</th>
<th>Legs, fatigue</th>
<th>Breathing</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>No CO₂</td>
<td>10</td>
<td>0</td>
<td>1 headache</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1 stopped at 1 hr</td>
</tr>
<tr>
<td>2% CO₂</td>
<td>9</td>
<td>2</td>
<td>2 headaches</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1 vertigo</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1 stopped at 1 hr</td>
</tr>
<tr>
<td>3% CO₂</td>
<td>5</td>
<td>5</td>
<td>1 headache</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1 headache, red tunnel vision</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1 nausea</td>
</tr>
</tbody>
</table>

Phase 2 — Air

| No R, 0% CO₂ | 12            | 0         | 0 |
| Mod R, 0% CO₂| 6             | 5         | 1 not recorded |
| High R, 0% CO₂| 7             | 5         | 1 not recorded |
| Mod R, 1% CO₂| 5             | 5         | 2 not recorded |
|               |               |           | 1 nausea |
| Mod R, 2% CO₂| 3             | 9         | 1 nausea |
|               |               |           | 1 headache |
|               |               |           | 1 headache and tunnel vision |

Phase 3 — O₂

| No R, 0% CO₂ | 7             | 0         | 4 not recorded |
| Mod R, 0% CO₂| 7             | 1         | 4 not recorded |
| No R, 2% CO₂ | 6             | 1         | 1 “stich in the side” |
|               |               |           | 3 not recorded |
|               |               |           | 1 stopped |
|               |               |           | 1 headache |
|               |               |           | 1 felt irritable but continued |
| Mod R, 2% CO₂| 6             | 1         | 2 stopped |
|               |               |           | 1 felt “zoney” |
|               |               |           | 3 headaches |
|               |               |           | 1 felt irritable but continued |
Figure 3. VE change from baseline, means and standard errors. Baseline (valve system without resistance or CO₂) values are listed in Table 2. “R” means resistance, “mod” is moderate.

VE changed under most conditions (Fig. 3). The addition of CO₂ without resistance increased VE (p<0.01 in air or O₂) without dose response. When resistive elements were present, VE decreased (p<0.01 in air and O₂), with no difference when CO₂ was added to inspired air. When 2% CO₂ was added to O₂, VE remained no different from baseline. VE was lower (p<0.02) with high resistance than with moderate resistance.
End tidal CO2 Fraction
Background Air

Baseline (valve system without resistance or CO2) values are listed in Table 2. "R" means resistance; "mod" is moderate. Elevation above baseline with moderate and high resistance in air is not significant, but all other changes are. Each of the conditions with background O2 is different from all the others.

Despite reduced $V_E$, mean $F_{ET}CO_2$ was unchanged with moderate resistance and no added CO2 in air (Fig. 4), but it increased with moderate resistance ($p<0.01$) during O2 breathing. With inspired CO2, mean $F_{ET}CO_2$ was elevated above baseline ($p<0.01$) to 6.4% with 2% inspired CO2 in air, to 6.8% with 2% inspired CO2 in O2 (in different subjects), and to 7.2% with 3% inspired CO2 in air (Fig. 4). Note that 1% inspired CO2 in air with moderate resistance is similar to 2% inspired CO2 in air without resistance, and 2% inspired CO2 in air with moderate resistance is similar to 3% inspired CO2 in air without resistance.

$F_{ET}CO_2$ in the final 90 to 120 s of each exercise condition is shown for each subject in Figure 5.
Figure 5. F_{ET}CO_2 for all subjects and all conditions. Lines join values for the same individual, but the same symbol on two panels does not indicate the same subject in both cases. “R” indicates resistance, “mod” means moderate, and percentages are those of inhaled CO_2. Maximum limits refer to those for manned acceptance testing of diving gear.\(^{20}\)
Figure 6 shows part of the time course of $F_{ET}CO_2$ for one subject, the one with the highest recorded end tidal CO$_2$ in this study. Note that the peak $F_{ET}CO_2$ for each recording was reached at about five minutes, about three minutes after the end of the warm-up period. At about 10 minutes, $F_{ET}CO_2$ was somewhat decreased again.

This subject reached dangerously high $F_{ET}CO_2$ with the combination of 2% inhaled CO$_2$ and moderate resistance in air, but when breathing air without resistance, he exercised with normal end tidal values.

Figure 6. $F_{ET}CO_2$ for the subject with the highest values recorded in this study. Five experimental conditions are given. Several of the endurance measurements continued longer than the 20 minutes shown.
Figure 7. Breathing frequency \( f \), percentage change from baseline, means and standard errors. Baseline (valve system without resistance or CO\(_2\)) values are listed in Table 2. "R" means resistance; "mod" is moderate. The \( f \) was lower than baseline with R (\( p<0.01 \)) but not different from baseline with different R, breathing gas, or CO\(_2\) fraction. It was higher than baseline (\( p<0.03 \)) only with 2% CO\(_2\) in air.
Figure 8. VT, percentage change from baseline, means and standard errors. Baseline (valve system without resistance or CO₂) values are listed in Table 2. “R” means resistance; “mod” is moderate. VT differed from baseline (p<0.03) only for 2% CO₂ in O₂.

Changes in VE were caused only by changes in f during air breathing and in f or VT during O₂ breathing (Figs. 7 and 8).

Figure 9. Respiratory duty cycle, percentage change from baseline, means and standard errors. Baseline (valve system without resistance of CO₂) values are listed in Table 2. “R” means resistance; “mod” is moderate. None of the differences from baseline was significant.
Respiratory duty cycle ($T_i/T_{tot}$) was not changed by any of the conditions of this experiment (Fig. 9). However, duty cycle is difficult to interpret when, as in these measurements, $f$ varies so much across measurements.

![Inspiratory and Expiratory Times](image)

**Figure 10.** Inspiratory and expiratory times, percentage change from baseline, means and standard errors. Baseline (valve system without resistance or CO$_2$) values are listed in Table 2. “R” means resistance; “mod” is moderate. With background air, $T_E$ increased (p<0.02) when resistance was present, and $T_I$ decreased with 2% CO$_2$. With background O$_2$, $T_I$ increased when resistance was present. No other difference from baseline was significant.

In the presence of resistance with or without CO$_2$, $T_E$ increased (p<0.02) with air as the background gas, and $T_I$ increased with O$_2$ as background gas (p<0.01; Fig. 10). With 2% inspired CO$_2$ in air but no added resistance, $T_I$ decreased (p<0.03). None of the other changes was significant (Fig. 10).

We did not measure mask pressure or instantaneous flow in Phases 1 and 2. In Phase 3, water at the pressure tap sometimes compromised the measurement of mask pressure, and only expiratory flow profiles were available. However, we measured expiratory pressures ranging from 5.0 to 13.8 cm H$_2$O.

The valve system alone had no significant effect; in Phase 2 we conducted a second control measurement, valve and tubing system versus oronasal mask only, and measured no difference in any parameter considered. The pressure drop of the one-way valves is nominally 1.1 cm H$_2$O for inspiration and 1.0 cm H$_2$O for expiration at 100
L/min, and 3.0 cm H_2O for inspiration and 2.8 cm H_2O for expiration at 300 L/min.\textsuperscript{22} In Phase 3 we measured sample expiratory pressures of 2.7 cm H_2O at 194 L/min and 4.3 cm H_2O at 356 L/min.

Our target peak expiratory pressure was twice the peak inspiratory pressure, and we achieved that ratio. From seven Phase 3 measurements with moderate resistance where we have flow and pressure drops for all conditions, the mean ratio of expiratory to inspiratory pressures was 1.75, with a range from 1.4 to 2.3. Overall results are summarized in Table 5.

**Table 5.** Summary of changes on the average.

<table>
<thead>
<tr>
<th>Background Air:</th>
<th>Endurance</th>
<th>V_E</th>
<th>f</th>
<th>V_T</th>
<th>T_I</th>
<th>T_E</th>
<th>P_{ETCO2}</th>
</tr>
</thead>
<tbody>
<tr>
<td>CO_2</td>
<td>↓</td>
<td>↑</td>
<td>↑</td>
<td>↔</td>
<td>↓</td>
<td>↔</td>
<td>↑</td>
</tr>
<tr>
<td>Resistance</td>
<td>↔</td>
<td>↓</td>
<td>↓</td>
<td>↔</td>
<td>↔</td>
<td>↑</td>
<td>↔</td>
</tr>
<tr>
<td>Both</td>
<td>↔</td>
<td>↓</td>
<td>↓</td>
<td>↔</td>
<td>↔</td>
<td>↑</td>
<td>↑</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Background O_2:</th>
<th>Endurance</th>
<th>V_E</th>
<th>f</th>
<th>V_T</th>
<th>T_I</th>
<th>T_E</th>
<th>P_{ETCO2}</th>
</tr>
</thead>
<tbody>
<tr>
<td>CO_2</td>
<td>↔</td>
<td>↑</td>
<td>↔</td>
<td>↑</td>
<td>↔</td>
<td>↔</td>
<td>↑</td>
</tr>
<tr>
<td>Resistance</td>
<td>↔</td>
<td>↓</td>
<td>↓</td>
<td>↔</td>
<td>↑</td>
<td>↔</td>
<td>↑</td>
</tr>
<tr>
<td>Both</td>
<td>↔</td>
<td>↔</td>
<td>↓</td>
<td>↔</td>
<td>↑</td>
<td>↔</td>
<td>↑</td>
</tr>
</tbody>
</table>

Key: ↓ = decrease, ↔ = no change, ↑ = increase.

**Phase 3: O_2 breathing versus air breathing**

We measured Phase 3 subjects under both air- and O_2-breathing baseline conditions. On the average, V_E with O_2 was lower than that with air (mean, 13%; standard error, 4%; p<0.01 by paired t-test), and T_I increased (mean, 14%; standard error, 5%; p<0.02). None of the other differences between air- and O_2-breathing was significant. Changes in endurance times ranged from –45% to +229%; those in F_ETCO_2, from –10% to +17%; those in f, from –24% to +17%; those in V_T, from –44% to +42%; those in duty cycle, from –8% to +11%; and those in expiratory time, from –16% to +39%.

**Ventilatory Sensitivity to CO_2**

Ventilatory sensitivity to CO_2 was not measured in three subjects: two who became unavailable for testing, and one who declined to be tested because the CO_2 exposure during testing had triggered debilitating headaches. Results from another three subjects could not be interpreted, perhaps because of technical flaws. The distribution of values for all other subjects from all three experimental phases is summarized in Figure 11.
Generally, $P_{ETCO_2}$ increased without change in ventilation when the subject first began to breathe from the reservoir of 7% CO$_2$, 93% O$_2$; then ventilation began to increase steeply. When the increase of VE with $P_{ETCO_2}$ seemed to have two components, the second, longer-lasting linear segment was used, and its slope was considered to be the ventilatory sensitivity to CO$_2$.

**Figure 11.** Histogram of ventilatory sensitivity to CO$_2$ at rest, rebreathing method, 19 subjects from all three phases. Note that four subjects were insensitive to CO$_2$, and four were hypersensitive.

Ventilatory sensitivity to CO$_2$ measured at rest did not correlate with end tidal CO$_2$ during exercise.

**DISCUSSION**

The average values presented in Figure 2 suggest that subjects breathing air or O$_2$ and exercising at 80 to 85% of peak aerobic capacity were able to compensate for 2% inspired CO$_2$ and for inspiratory and expiratory resistance patterned on that of the MK
Of the conditions tested, only 3% CO₂ in air decreased mean endurance time relative to that for subjects breathing unimpeded.

Individual results suggest a very different conclusion: neither can a dive be planned nor can equipment be designed for the population average. Rather, the individual who is most impaired is the one who must be accommodated. The effects on group endurance are thus better portrayed in Table 3 than in Figure 2. With background air, moderate resistance patterned after the MK 16 at 50 fsw reduced endurance time by 10% or more in four of ten subjects. That resistance, accompanied by 2% CO₂, reduced endurance time by at least 30% in four of ten subjects. With oxygen as background gas, the reduction in endurance affected fewer subjects, but even then the combination of CO₂ and UBA-like resistance impaired performance for some. Further, some subjects continued to exercise when they probably should have stopped because of CO₂ accumulation (Figs. 5 and 6, and Table 4).

The risk of elevated, inhaled CO₂ is real: exercising, air-breathing subjects have been seen to become confused and irrational with FETO₂ of 8.5% and higher23 — a CO₂ level matched or exceeded by the two of our subjects who reported tunnel vision, and almost matched by one who reported a sense of altered mental status (feeling "zoney"). These subjects did not have to cope with increases in internal WOB like those that result from submersion. Further, elevated arterial CO₂ increases the risk of central nervous system (CNS) oxygen toxicity even at oxygen partial pressures that are otherwise considered to be safe, either in rats in dry studies24 or in human divers using rebreather UBAs at PO₂ as low as 1.2 atm.25 In divers, CNS toxicity at shallow depths has included loss of consciousness. In four cases where divers lost consciousness and the UBAs were tested, inspired CO₂ measured from the rig after the accident was between 2.5% and 8%.14

According criteria used for acceptance of dive gear,21 two air-breathing subjects showed that a diving rig with the resistance we called moderate and 2% inspired CO₂ is unsafe: they exceeded the limit of end tidal CO₂ allowed for outliers from the group. Using the same criteria, the mean of O₂-breathing subjects at the end of exercise came close to the group limit that would declare that combination to be unsafe. Early in exercise, the group mean may have crossed that threshold; Figure 6 indicates the usual pattern of a FETO₂ increase that occurs early in exercise and is moderated after about 10 minutes.

Subjects who inhaled CO₂ in air without added resistance generally increased Vₑ enough to moderate but not to prevent CO₂ buildup, while those breathing CO₂ in O₂ allowed more CO₂ accumulation (Figs. 3, 4). Subjects who breathed air without added CO₂ against resistance decreased Vₑ without significant increase in CO₂. However, those breathing O₂ without added CO₂ against resistance decreased Vₑ enough to accumulate CO₂ (Figs. 3, 4). These results are consistent with others that show that the body will accept some accumulation of CO₂ to moderate the increase in WOB and some increase in WOB to moderate the accumulation of CO₂.17 However, subjects who
breathed air against moderate resistance failed to respond to inspired CO\textsubscript{2} (Fig. 3), and F\textsubscript{ETCO2} became considerably higher than baseline (Fig. 4). Some subjects reached very high F\textsubscript{ETCO2} (Fig. 5). Subjects who breathed O\textsubscript{2} against moderate resistance had higher V\textsubscript{E} with inspired CO\textsubscript{2} than they had without it. But V\textsubscript{E} did not approach that level for the same inspired CO\textsubscript{2} without resistance (Fig. 3), and F\textsubscript{ETCO2} was elevated above baseline (Fig. 4). Because these different levels of V\textsubscript{E} seen across conditions were supporting similar external work and thus similar metabolic CO\textsubscript{2} production, they represent different ventilatory responses to exercise and V\textsubscript{E}/V\textsubscript{CO2} for different breathing conditions.

For Phase 2, in the absence of pressure measurements we used the measured pressure-flow characteristics of the resistance elements to estimate mask pressures. Although we recognize this to be a first approximation only, we modeled flow as a sinusoid with the measured tidal volume and frequency. Mean estimated pressures were similar with or without inhaled CO\textsubscript{2}, because mean V\textsubscript{E} and f were similar across all conditions with resistance present (Figs. 3 and 7). The mean of estimated peak inspiratory pressures for moderate resistance was 11 (SD, 3) cm H\textsubscript{2}O, and that for high resistance was 22 (SD, 10) cm H\textsubscript{2}O. If we accept the sinusoidal approximation for inspiration, the estimated inspiratory WOB/V\textsubscript{T} in Phase 2 was 1.1 (SD, 0.4) J/L for moderate resistance on inspiration and 2.1 (SD, 0.8) J/L with high resistance, independent of inspired CO\textsubscript{2}. The ratio of pressure drops measured in Phase 3 indicates expiratory work of about 2 J/L.

In addition to reducing f, subjects faced with inspiratory resistance often increase duty cycle to prolong inspiratory time and thus to reduce peak inspiratory pressure and flow. However, unlike many devices that introduce an impediment to breathing, the MK 16 and other rebreather UBAs have higher expiratory than inspiratory resistance, because the diver must force gas through the scrubber. Duty cycle did not change significantly in these measurements (Fig. 9), and, for air breathing, expiratory time increased more than inspiratory time when f slowed (Fig. 10).

Because the expiratory resistance was laminar, expiratory pressure was directly proportional to flow, or for the same V\textsubscript{T}, it was almost inversely proportional to expiratory time. That is, any change in pressure resulted in a proportional change in flow, independent of flow magnitude. However, because the inspiratory resistance was turbulent, the inspiratory pressure drop changed rapidly as flow changed. The change in inspiratory pressure was proportional to the change in the square of flow: a small decrease in a previously high inspiratory flow rewarded the subject with a large decrease in inspiratory pressure. Subjects unconsciously had to balance the inspiratory and expiratory pressure demands, as well as the penalty of CO\textsubscript{2} accumulation if the minute ventilation became too low. The balance intriguingly appears to be subtly different when the background gas is O\textsubscript{2} rather than air.

Baseline exercise V\textsubscript{E} was lower during O\textsubscript{2} breathing than during air breathing in the same subjects and at the same ergometer settings, but with unchanged F\textsubscript{ETCO2}. We
speculate that this unchanged $F_{ETCO2}$ with lower $V_E$ may be a result of hyperoxic pulmonary vasodilation: CO$_2$ elimination in the lungs is perfusion limited.

Other investigators have shown that breathing 100% oxygen reduces the ventilatory response to exercise.$^{26}$ Because higher oxygen fractions are unlikely to improve hemoglobin saturation in healthy subjects and dissolved oxygen at atmospheric pressure contributes little to total oxygen transport, anaerobic threshold and oxygen delivery to tissues will not be affected by the change of breathing gas. More likely, the O$_2$ affects chemoreceptors involved in the control of breathing. Hyperoxia at rest has been shown to decrease the CO$_2$ sensitivity of the central chemoreceptors by 15% and to blunt that of the peripheral receptors by 70%.$^{27}$ This result may explain the greater rise of $F_{ETCO2}$ from baseline during O$_2$ breathing than during air breathing, both with 2% inspired CO$_2$ and no resistance (Fig. 4).

We saw no correlation between the ventilatory sensitivity to CO$_2$ at rest and $F_{ETCO2}$ at end exercise. This lack of correlation may imply that, for some individuals, the hierarchy of physiological importance in balancing WOB, CO$_2$ accumulation, maximum pressure swings, and any other factors placed CO$_2$ lower than other factors. It may imply that the CO$_2$ accumulation was unavoidable for some subjects if exercise was to continue. Certainly, others have seen a lack of correlation between an exercise ventilatory response during unencumbered breathing and ventilatory sensitivity to CO$_2$ measured as we did.$^{26}$

CONCLUSIONS

Other authors have suggested that subjects may be able to compensate for 2% inspired CO$_2$ in a low-resistance circuit,$^{28}$ and on the average this might be true. However, no one is “the average.” Even with the low resistance conditions in this study, endurance for some subjects was limited by inability to breathe enough, and two subjects complained of headache and one of vertigo after the trials. However, with resistance like that of the MK 16 UBA at 50 fsw in the circuit, the maximum $V_E$ attained by subjects was reduced, probably by high expiratory pressures, and even the presence of inhaled CO$_2$ did not drive subjects to increase their breathing. When CO$_2$ was present, many subjects had endurance limited by difficulty in breathing, and symptoms of CO$_2$ retention became increasingly common. The apparent reduction in this phenomenon when O$_2$ was the background gas is false: although subjects felt less limited by the breathing impediment, this was likely because their breathing and other corrective responses were less sensitive to CO$_2$ when O$_2$ was the background gas than when they breathed air, and not because consequences of CO$_2$ retention were any less with high O$_2$ than with air. The mean $F_{ETCO2}$ with moderate resistance and 2% CO$_2$ in O$_2$ reached 7.2%, 30% above control. For diver safety with the MK 16 and other rebreather UBAs with similar pressure-flow characteristics, inspired CO$_2$ should be maintained as close to 0% as possible.
REFERENCES


