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THE RELATIONSHIP BETWEEN VENTILATION AND OXYGEN CONSUMPTION IN MAN IS THE SAME DURING BOTH MODERATE EXERCISE AND SHIVERING

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SUMMARY

1. Four naïve subjects clothed in protective suits were immersed up to the neck in water on twenty-two occasions, the minimum skin temperature was 20 °C and the average skin temperature 26 °C. Subjects at first rested, initially demonstrating an increase in thermal muscular tone which did not lead to perceptible limb movements. Later, while resting, visible shivering with small unco-ordinated limb movements supervened. The subjects then exercised while still immersed by stationary cycling.

2. Steady-state minute oxygen consumption ($\dot{V}_{O_2}$) and minute ventilation ($\dot{V}_E$) were measured on 152 occasions by timed collection of expired air.

3. The first collection was made at least 5 min after initial immersion. Hyperventilation due to recent immersion in cold water was not demonstrated.

4. The same linear relationship between $\dot{V}_E$ and $\dot{V}_{O_2}$ was demonstrated whether the increased oxygen consumption was due to shivering alone or to a combination of shivering and exercise.

5. $\dot{V}_E$ was matched to $\dot{V}_{O_2}$ in spite of an increase in the work of breathing as well as any ventilation–perfusion mismatching as a consequence of head-out water immersion.

6. Minute ventilation was not influenced by the large co-ordinated limb movements which only occurred during exercise. These results reinforce previous findings which have shown that in conscious man $\dot{V}_E$ can be closely matched to $\dot{V}_{O_2}$ below the anaerobic threshold despite large variations in the type and intensity of limb movements.

7. When $\dot{V}_{O_2}$ is increased by thermal muscular tone $\dot{V}_E$ is increased in direct proportion in a situation when the limbs are not perceptibly moving at all.

INTRODUCTION

The steady-state ventilatory response to exercise in normal man is uninfluenced by either variations in the rate of limb movements, or different patterns of limb movements (Kay, Strange Petersen & Vejby-Christensen, 1975; Casaburi, Whipp, Wasserman & Koyal, 1978). Passive exercise will lead to an increase in ventilation,

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which however increases only in proportion to the increase in metabolic rate (e.g. Lloyd & Patrick, 1962). $\dot{V}_E$ is proportional to $\dot{V}_{O_2}$ in exercising man if the level of work performed is below the 'anaerobic threshold' (e.g. Wasserman, Van Kessel & Burton, 1967). Different patterns of limb movement such as cycling, running or passive cycling involve considerable appendicular skeletal movement, capable of stimulating joint and muscle proprioceptors. In contrast, when man is exposed to the cold, there is at first an irregular unco-ordinated activity of motor units contracting out of phase (known as 'thermal muscular tone') which does not result in perceptible limb movement. Later the activity becomes regular and phasic as shivering occurs. If co-ordinated limb movements provide a proportion of the ventilatory drive during steady-state exercise, that proportion ought to be absent both during the phase of thermal muscular tone and while the subjects were shivering but not exercising. In the experiments reported here $\dot{V}_E$ and $\dot{V}_{O_2}$ were measured during head-out water immersion while subjects either rested, during which they exhibited muscular thermogenesis, or exercised by stationary cycling.

METHODS

Four male subjects (age range 21–35 years) participated in the experiments which involved immersion on twenty-two separate occasions in stirred water up to the neck wearing a variety of protective neoprene 'wet suits'. The suits ranged from 4 to 7 mm in thickness and covered the limbs, trunk and head; separate neoprene gloves and boots were worn. The head was irrigated by a shower of water at the temperature of the water in which the subjects were immersed. The water temperature ranged from 5 to 35 °C. The protocol of the twenty-two experiments reported here involved a variable period during which the subjects sat still (range 35–200 min), followed by pedalling for between 30 and 50 min on a sunken stationary bicycle. Core temperature was monitored using a rectal probe (Light Laboratories), skin temperature at six sites was measured using thermocouples, and an electrocardiogram record was continuously monitored on an oscilloscope. Expired air was collected at intervals by asking the subjects to breathe through a low-resistance flap valve and collecting expired gas in a Douglas Bag over a timed period (usually 5 min, range 2–5 min). Collections were made at least 5 min after initial immersion or the onset of exercise; the vast majority of the data was collected considerably later than this. The number of collections made during each experiment ranged from five to thirteen. The expired gas was mixed and the oxygen concentration of a sample measured using a paramagnetic analyser (Beckman E2). The volume expired over the timed period was measured by drawing the contents of the Douglas Bag through a gas meter (Gallenkamp GF 095) after drying by passage through a reservoir of copper sulphate crystals. One experiment was terminated because the core temperature had fallen to 35 °C and another because the core temperature had risen above 38·5 °C. On average the experiments lasted 120 min altogether (S.D. 39·09, range 65–220 min).

RESULTS

The relationship between $\dot{V}_E$ and $\dot{V}_{O_2}$ for the four subjects immersed in water is shown in Fig. 1. The relationship between $\dot{V}_E$ and $\dot{V}_{O_2}$ was linear both while the subjects were at rest: $\dot{V}_E = 17{\cdot}43\ \dot{V}_{O_2} + 3{\cdot}08$ ($r = 0{\cdot}881$, $n = 106$ and $P < 0{\cdot}001$), and during exercise: $\dot{V}_E = 17{\cdot}92\ \dot{V}_{O_2} + 5{\cdot}99$ ($r = 0{\cdot}734$, $n = 46$ and $P < 0{\cdot}001$).

The 95 % confidence interval for the slope of the best fit regression line for the data collected while the subjects were at rest is 15·61–19·25. Similarly the 95 % confidence interval for the slope of the best fit regression line for the data collected while the subjects were exercising is 12·87–22·98. In each case these figures, that indicate the

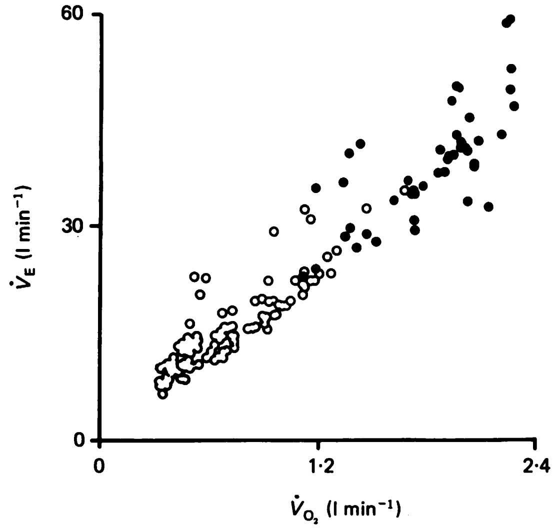

Fig. 1. The relationship between minute ventilation (l min^{-1}, standard temperature and pressure, dry (s.t.p.d.)) and minute volume (l min^{-1} s.t.p.d.). The open circles are when the subjects are at rest and the filled circles when the subjects are exercising.

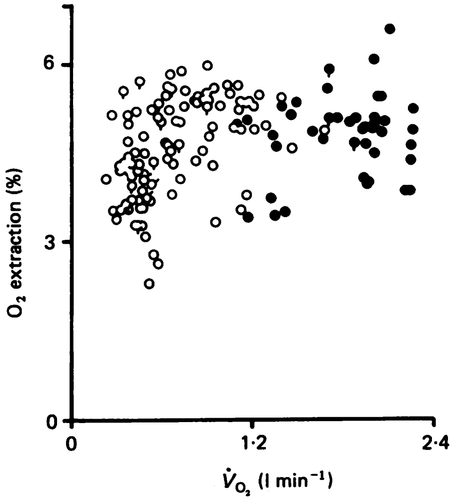

Fig. 2. The relationship between percentage oxygen extraction and minute volume (l min^{-1} s.t.p.d.). Open circles are when the subjects are at rest and the filled circles when the subjects are exercising. A tail is shown on the data that was collected first in each experiment.

limits between which there is 95 % certainty that the true value of the slope of the regression line lies, embrace the best fit value for the line calculated from the other group. Therefore, in this experiment no difference in the relationship between $\dot{V}_E$ and $\dot{V}_{O_2}$ was observed whether the increased $\dot{V}_{O_2}$ was caused by muscular thermogenesis alone or by a combination of exercise and shivering while immersed in water. Shivering alone was capable of producing a $\dot{V}_{O_2}$ greater than that produced by the lowest levels of exercise.

Fig. 2 shows the relationship between oxygen extraction and $\dot{V}_{O_2}$ for the four subjects. The over-all relationship between percentage oxygen extraction and $\dot{V}_{O_2}$ is linear both at rest (percentage oxygen extraction $= 1{\cdot}10\ \dot{V}_{O_2} + 3{\cdot}87$, $r = 0{\cdot}427$, $n = 106$ and $P < 0{\cdot}001$) and during exercise (percentage oxygen extraction $= 0{\cdot}45\ \dot{V}_{O_2} + 3{\cdot}96$, $r = 0{\cdot}199$, $n = 46$ and $P < 0{\cdot}05$). However, the slope of the regression line is very shallow and the spread of the data is wide. Again the 95% confidence interval for the slope for both regression lines embraces the slope of the other line. This indicates that no significant difference in the relationship between percentage oxygen extraction and $\dot{V}_{O_2}$ was seen comparing data collected while shivering to that collected while both shivering and exercising

During collection of expired gas the average skin temperature was 26 °C, with a minimum recorded of 20 °C.

DISCUSSION

Head-out water immersion inevitably demands negative pressure breathing. This alters respiratory mechanics and increases the work of breathing (Hong, Cerretelli, Cruz & Rahn, 1969). Venous blood is redistributed to intrathoracic capacitance vessels and this presumably contributes to the diminished expiratory reserve volume (Hong *et al.* 1969) and the observed changes in ventilation–perfusion matching (Cohen, Bell, Saltzman & Kylstra, 1971). In the experiments reported here, a linear relationship between steady-state $\dot{V}_E$ and $\dot{V}_{O_2}$ during exercise while immersed has been observed. This result implies that the system controlling breathing in man is capable of adjusting $\dot{V}_E$ to match $\dot{V}_{O_2}$ in spite of an increase in the work of breathing or any ventilation–perfusion mismatching as a consequence of head-out water immersion.

Hyperventilation immediately follows immersion of naked subjects in water cooler than 25 °C; the response is absent if the water temperature is above 30 °C (Keatinge & Nadel, 1965). A rapid fall in $\dot{V}_E$ is seen after the hyperventilation of the first minute, and $\dot{V}_E$ returns to resting values within 5 min after immersion (Keatinge & Evans, 1961). The oxygen extraction measured soonest after immersion in the experiments reported here (in all cases more than 5 min after immersion) do not demonstrate hyperventilation at that time as a consequence of recent immersion in water cooler than 25 °C (see Fig. 2).

As emphasized in the Introduction, several experiments in man have shown that $\dot{V}_E$ is directly proportional to $\dot{V}_{O_2}$ up to a $\dot{V}_{O_2}$ of approximately two-thirds of an individual's maximum $\dot{V}_{O_2}$ when the increase in oxygen consumption is caused by various patterns of active or passive exercise. The experiments reported here demonstrate that the control system for respiration in man is capable of adjusting $\dot{V}_E$ to $\dot{V}_{O_2}$ when the increased oxygen consumption is caused by muscular thermogenesis. A similar result was observed in anaesthetized hypothermic dogs (Lim, 1960). In addition, in the experiments reported here the relationship between $\dot{V}_E$ and $\dot{V}_{O_2}$ has been shown not to be significantly different when the increased oxygen consumption is caused by either shivering or both exercise and shivering. It is likely that the degree of proprioceptor and mechanoreceptor activity in even severe shivering is different to that present during cycling. The results reported here reinforce the observation that in conscious man, $\dot{V}_E$ can be closely matched to $\dot{V}_{O_2}$ below the anaerobic threshold, despite large variations in the type and intensity of limb movements, in particular, when $\dot{V}_{O_2}$ is increased during thermal muscular tone, $\dot{V}_E$ is increased in direct proportion in a situation when the limbs are not perceptibly moving at all.

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