

## The Changes in Hematocrit, Hemoglobin, Plasma Volume and Proteins during and after Different Types of Exercise

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**Summary.** A group of 7 healthy males was studied after maximal exercise and during and after prolonged exercise of two types (approximately at 40 and 67% of their  $\dot{V}O_2$  max). Hematocrit, plasma proteins concentration, and hemoglobin were followed. Relative changes of plasma volume and total content of plasma protein were calculated from hematocrit changes. The mean corpuscular hemoglobin concentration was obtained by dividing hemoglobin by hematocrit. After maximal exercise, hemoconcentration with concomitant decrease of plasma volume (–13.0%) was found, with a corresponding increase in protein concentration (+12.9%) and without any protein content changes. Later normalisation at the 30th min of the recovery phase was shown. During prolonged submaximal exercise (67% of  $\dot{V}O_2$  max) the changes in hemoconcentration, plasma volume (–7.1%), and plasma protein concentration (+6.9%) reached the highest changes in the first 15 min of exercise, and no decrease in protein content was observed. After them the spontaneous tendency to the normalisation was found. No changes were registered in prolonged mild exercise (40% of  $\dot{V}O_2$  max). The ratio of hemoglobin to hematocrit remained unchanged during and after all types of exercise.

**Key words:** Maximal and prolonged exercise – Hematocrit – Hemoglobin – Plasma volume – Plasma protein.

Despite the hemodynamic, thermoregulatory and transport importance of maintaining an adequate blood volume during and after exercise, the nature of their changes remains unclear. Plasma volume measurement can be done by direct methods, or more recently, the plasma volume (PV) changes can be calculated from the values of some blood constituents such as hematocrit (Hct), hemoglobin (Hb), and plasma proteins (PP).

Beaumont et al. (1972) found in general a close agreement between the calculated (from venous hematocrit) and measured ( $^{131}\text{I}$ ) plasma volume after maximal and submaximal exercise. The slope of the regression between the calculated and measured values showed that they do not differ significantly. Costill and Saltin

(1974a) observed some discrepancy between measured plasma volume ( $^{125}\text{I}$  dilution) and changes in plasma volume calculated from venous hematocrit with the slight underestimation of calculated changes after intensive dehydration. Nevertheless the ratio of body hematocrit to venous hematocrit was not significantly altered during dehydration. Thus the use of venous hematocrit for estimating the percentage of changes in plasma volume provides valuable results.

Other investigations on plasma volume changes mention hemoconcentrations after maximal exercise (Poortmans, 1969; Beaumont et al., 1972, 1973). During prolonged submaximal exercise Ahlborg (1967) and Ekelund (1967) found hemoconcentration increases at the onset of work without any further changes till the end of exercise.

Saltin and Sternberg (1964) and Beaumont et al. (1972) found that in some of experimental subjects the plasma volume returned to its resting values already during prolonged exercise, but in most studies some quantities of liquids were ingested during exercise.

The object of the present study was to examine the effect of intensity and duration of exercise on hematocrit, plasma volume and plasma protein changes after maximal exercise and during and after mild and submaximal exercise without any replacement of fluid losses.

## Material and Methods

The studies were performed on seven healthy males aged 21–23 years. The characteristics of subjects are given in Table 1. In the first series of experiments the subjects performed the maximal exercise in the sitting position on bicycle. No further increase in oxygen consumption was used as criterion that maximal aerobic power was attained. Before examination an intravenous catheter was inserted into the cubital vein and blood samples were drawn without stasis before exercise and 5, 10, 15, 30 and 60 min after the termination of physical effort in supine position.

After one week the subjects performed prolonged exercise of 60 min duration at the relative workload  $67 \pm 7\%$  of their  $\dot{V}\text{O}_2$  max. On the 10th min of exercise the heart rate was  $148 \pm 6$  beats/min. Five consecutive blood samples were drawn after 5, 10, 15, 30 and 60 min of exercise, and five consecutive samples in the same intervals during recovery. After another week the workload  $40 \pm 2\%$  of their  $\dot{V}\text{O}_2$  max was performed with the same arrangement.

All examinations were done in the morning 2 h after a light breakfast. Before the experiments the subjects rested 30 min in supine position. No liquids were consumed before and during experiments.

The weight was measured before and immediately after the termination of each experimental series. The heart rate was monitored on ECG recorder. Gas exchange was estimated with the Douglas bag method. The expired air was analysed with a Zeiss Polarograph, and the volume with a dry spirometer. The room temperature was between 19–22° C, and the relative humidity about 40%.

**Table 1.** Physical characteristics of studied subjects

|           | Age<br>(years) | Height<br>(cm) | Weight<br>(kg) | $\dot{V}\text{O}_2$ max<br>(ml · min <sup>-1</sup> · kg <sup>-1</sup> ) |
|-----------|----------------|----------------|----------------|---|
| $\bar{x}$ | 21.9           | 178            | 75.2           | 45.8  |
| $\pm$ SD  | 0.85           | 4.24           | 4.05           | 3.6   |

The values of hematocrit were obtained by the microhematocrit method in quadruplicate determinations. The raw hematocrit readings were multiplied by the factor ( $0.96 \times 0.91$ ) to correct for trapped plasma and to convert the venous hematocrit to whole body hematocrit. Plasma protein was estimated by biuret method, blood lactates by enzymatic method using Boehringer tests. Hemoglobin was measured by the spectrophotometric cyanhemoglobin method.

The equations of Beaumont et al. (1973) were used to calculate the proportional changes of plasma volume and protein content. Concentration of hemoglobin in red cells was obtained by dividing hemoglobin by hematocrit.

Current statistical methods were used. The paired sets of data were analysed by the *t*-test. The following symbols for probability levels of significance were used to reject the null hypothesis:  $P < 0.05$ .

## Results

### *Maximal Exercise*

The mean values of hematocrit increased by 7.7% immediately after termination of the maximal exercise (Table 2). Afterwards, a decline of hematocrit values was found, the resting values were attained in the 30th min of the recovery period.

The calculated plasma volume changes showed a decrease by -13% immediately after the termination with further increase to the resting values attained after 30 min of recovery.

The plasma protein concentration increased significantly after the termination of exercise by 12.9%, the following decrease in concentration attained the initial resting values in the 30th min. No change was found in plasma protein content as corrected for plasma volume changes during the whole recovery period.

The blood lactates increased at the 5th min after the termination to the peak values  $8.8 \text{ mmol} \cdot \text{l}^{-1}$  on the average, and did not reach the resting values till the 60th min of recovery.

### *Prolonged Exercise*

In the first type of prolonged mild exercise ( $40 \pm 2\%$  of  $\dot{V}O_2 \text{ max}$ ) the heart rate increased from 108 beats/min at the 10th min to 113 at the 60th min of exercise. The oxygen consumption rose from 1360–1373 ml  $\dot{V}O_2$ . The respiratory exchange ratio decreased from 0.91–0.86. The blood lactates reached  $1.70 \text{ mmol} \cdot \text{l}^{-1}$  at the 10th min of exercise. After a continuous decline, the resting values were reached at the 60th min of exercise.

No significant changes were observed in the mean values of hematocrit from +1.2 to -1.0% during exercise and in the recovery amounting about -2.5%.

Accordingly the calculated plasma volume showed only slight changes during exercise and recovery. Plasma protein concentration and plasma protein content remained constant during the experiment (Table 3).

In the second type of prolonged submaximal exercise ( $67 \pm 7\%$  of  $\dot{V}O_2 \text{ max}$ ) the heart rate increased from 148 beats/min at the 10th min to 169 at the 60th min of exercise. The oxygen consumption rose from 2037–2191 ml  $\cdot \text{min}^{-1}$ . The respira-

**Table 2.** Mean values for hematocrit, hemoglobin, plasma volume and plasma protein before (pre) and after maximal exercise ( $n = 7$ )

| Time<br>in min | Hematocrit <sup>a</sup> |                   | PV<br>Δ%           | Hemoglobin        |                   | MCHC<br>% | Protein           |                    | LA<br>mmol · l <sup>-1</sup> |
|----------------|-------------------------|-------------------|--------------------|-------------------|-------------------|-----------|-------------------|--------------------|------------------------------|
|                | %                       | Δ%                |                    | g/100 ml          | Δ%                |           | g/100 ml          | ΔCn%               |                              |
| $\bar{x}$ pre  | 40.8                    |                   |                    | 14.4              |                   | 32.14     | 7.50              |                    | 1.15                         |
| ± SD           | 2.6                     |                   |                    | 0.3               |                   |           | 0.51              |                    | 0.26                         |
| After          |                         |                   |                    |                   |                   |           |                   |                    |                              |
| $\bar{x}$ 1st  | 44.3 <sup>b</sup>       | +7.7 <sup>b</sup> | -13.0 <sup>b</sup> | 15.8 <sup>b</sup> | +8.9 <sup>b</sup> | 32.44     | 8.56 <sup>b</sup> | +12.9 <sup>b</sup> | 8.18 <sup>b</sup>            |
| ± SD           | 2.4                     |                   |                    | 0.4               |                   |           | 0.59              |                    | 0.88                         |
| $\bar{x}$ 5th  | 43.8 <sup>b</sup>       | +6.9 <sup>b</sup> | -11.7 <sup>b</sup> | 15.6 <sup>b</sup> | +7.6 <sup>b</sup> | 32.43     | 8.40 <sup>b</sup> | +11.3 <sup>b</sup> | 8.81 <sup>b</sup>            |
| ± SD           | 2.1                     |                   |                    | 0.4               |                   |           | 0.56              |                    | 0.65                         |
| $\bar{x}$ 10th | 43.3 <sup>b</sup>       | +5.8 <sup>b</sup> | -9.8 <sup>b</sup>  | 15.2 <sup>b</sup> | +5.3 <sup>b</sup> | 32.00     | 8.18 <sup>b</sup> | +8.8 <sup>b</sup>  | 8.03 <sup>b</sup>            |
| ± SD           | 2.5                     |                   |                    | 0.2               |                   |           | 0.57              |                    | 0.72                         |
| $\bar{x}$ 15th | 42.5 <sup>b</sup>       | +4.0 <sup>b</sup> | -6.8 <sup>b</sup>  | 15.0 <sup>b</sup> | +3.9 <sup>b</sup> | 32.19     | 7.92 <sup>b</sup> | +5.8 <sup>b</sup>  | 5.65 <sup>b</sup>            |
| ± SD           | 2.4                     |                   |                    | 0.2               |                   |           | 0.63              |                    | 0.62                         |
| $\bar{x}$ 30th | 40.8                    | 0.0               | 0.0                | 14.7              | +2.0              | 32.73     | 7.54              | +0.9               | 2.83 <sup>b</sup>            |
| ± SD           | 2.1                     |                   |                    | 0.3               |                   |           | 0.62              |                    | 0.43                         |
| $\bar{x}$ 60th | 40.8                    | 0.0               | 0.0                | 14.7              | +2.0              | 32.73     | 7.48              | -0.1               | 1.93 <sup>b</sup>            |
| ± SD           | 2.1                     |                   |                    | 0.3               |                   |           | 0.61              |                    | 0.29                         |

Abbreviations to Tables 2, 3 and 4:

<sup>a</sup> Calculated from raw hematocrit readings  $\times (0.96 \times 0.91)$

<sup>b</sup> Significantly different from preexercise value ( $P < 0.05$ )

MCHC = mean corpuscular hemoglobin concentration =  $100 \times \text{Hb}/\text{Htc} \times 0.98$

Cn = concentration; Co = total content in plasma

tory exchange ratio decreased from 0.96–0.89. The blood lactates reached 3.87 mmol · l<sup>-1</sup> at the 10th min of exercise. After a slight continuous decline the resting value was reached at the 60th min after termination of exercise (Table 4).

The mean values of hematocrit reached the highest significant increase at the 10th min (+3.8%) and at the 15th min (+3.6%) of exercise. The values at the 30th and at the 60th min were no more significantly different from the resting values. During recovery, the mean hematocrit values fell below the initial resting values. The difference is significant at the 30th and the 60th min after termination of work.

**Table 3.** Mean values for hematocrit, hemoglobin, plasma volume and plasma protein before (pre), during and after submaximal exercise (40%  $\dot{V}O_2$  max) ( $n = 7$ )

| Time in min    | Hematocrit <sup>a</sup> |            | PV $\Delta\%$ | Hemoglobin |            | MCHC % | Protein  |                     | LA mMol.l <sup>-1</sup> |
|----------------|-------------------------|------------|---------------|------------|------------|--------|----------|---------------------|-------------------------|
|                | %                       | $\Delta\%$ |               | g/100 ml   | $\Delta\%$ |        | g/100 ml | $\Delta\text{Cn}\%$ |                         |
| $\bar{x}$ pre  | 41.1                    |            |               | 14.5       |            | 32.15  | 8.13     |                     | 1.03                    |
| $\pm$ SD       | 1.8                     |            |               | 0.5        |            |        | 0.68     |                     | 0.18                    |
| During         |                         |            |               |            |            |        |          |                     |                         |
| $\bar{x}$ 5th  | 41.6                    | +1.2       | -2.0          | 14.7       | +1.4       | 32.16  | 8.14     | +0.1                | -0.7                    |
| $\pm$ SD       | 2.7                     |            |               | 0.7        |            |        | 0.46     |                     | 0.37                    |
| $\bar{x}$ 10th | 41.2                    | +0.2       | -0.3          | 14.4       | -0.7       | 31.78  | 8.06     | -0.9                | -0.4                    |
| $\pm$ SD       | 2.3                     |            |               | 0.5        |            |        | 0.37     |                     | 0.29                    |
| $\bar{x}$ 15th | 40.9                    | -0.5       | +0.9          | 14.5       | 0.0        | 32.29  | 8.05     | -1.0                | +0.9                    |
| $\pm$ SD       | 2.0                     |            |               | 0.5        |            |        | 0.52     |                     | 0.38                    |
| $\bar{x}$ 30th | 40.7                    | -1.0       | +1.7          | 14.6       | +0.7       | 32.73  | 8.06     | -0.9                | +2.0                    |
| $\pm$ SD       | 2.1                     |            |               | 0.7        |            |        | 0.56     |                     | 0.26                    |
| $\bar{x}$ 60th | 40.8                    | -0.7       | +1.2          | 14.4       | -0.7       | 32.07  | 8.15     | +0.2                | +2.3                    |
| $\pm$ SD       | 1.7                     |            |               | 0.1        |            |        | 0.41     |                     | 0.16                    |
| After          |                         |            |               |            |            |        |          |                     |                         |
| $\bar{x}$ 5th  | 40.8                    | -0.7       | +1.2          | 14.5       | 0.0        | 32.36  | 8.03     | -1.2                | 0.0                     |
| $\pm$ SD       | 1.7                     |            |               | 0.3        |            |        | 0.54     |                     | 0.12                    |
| $\bar{x}$ 10th | 40.3                    | -2.0       | +3.4          | 14.5       | 0.0        | 32.80  | 8.11     | -0.2                | +3.2                    |
| $\pm$ SD       | 2.1                     |            |               | 0.5        |            |        | 0.65     |                     | 0.18                    |
| $\bar{x}$ 15th | 40.1                    | -2.5       | +4.3          | 14.1       | -2.8       | 31.75  | 8.05     | -1.0                | +1.6                    |
| $\pm$ SD       | 2.1                     |            |               | 0.6        |            |        | 0.52     |                     | 0.09                    |
| $\bar{x}$ 30th | 40.1                    | -2.5       | +4.3          | 14.4       | -0.7       | 32.72  | 7.98     | -1.9                | +2.3                    |
| $\pm$ SD       | 2.1                     |            |               | 0.3        |            |        | 0.41     |                     | 0.14                    |
| $\bar{x}$ 60th | 40.2                    | -2.2       | +3.7          | 14.3       | -1.4       | 32.35  | 8.00     | -1.6                | +2.0                    |
| $\pm$ SD       | 2.1                     |            |               | 0.4        |            |        | 0.57     |                     | 0.08                    |

Accordingly the calculated plasma volume showed a significant decrease in the first 15 min of exercise, but in subsequent time intervals the difference as compared to the resting value was no more significant. After the termination of work the plasma volume returned rapidly to the resting value, exceeding them significantly by 7.6% at the 30th min of recovery.

The plasma protein concentration is significantly higher between the 10th and the 30th min of exercise (+6.9%). Further decrease during and after exercise makes the difference as compared to the resting values (+4.3%) insignificant. The calcu-

**Table 4.** Mean values for hematocrit, plasma volume and plasma protein before (pre) during and after submaximal exercise (67%  $\dot{V}O_2$  max) ( $n = 7$ )

| Time<br>in min | Hematocrit <sup>a</sup> |                   | PV<br>$\Delta\%$  | Protein           |                     |                     | LA<br>$\text{mMol} \cdot \text{l}^{-1}$ |
|----------------|-------------------------|-------------------|-------------------|-------------------|---------------------|---------------------|---|
|                | %                       | $\Delta\%$        |                   | g/100 ml          | $\Delta\text{Cn}\%$ | $\Delta\text{Co}\%$ |   |
| $\bar{x}$ pre  | 41.2                    |                   |                   | 7.71              |                     |                     | 1.13                                    |
| $\pm$ SD       | 2.5                     |                   |                   | 0.38              |                     |                     | 0.35                                    |
| During         |                         |                   |                   |                   |                     |                     |   |
| $\bar{x}$ 5th  | 42.2                    | +2.4              | -5.8              | 8.11              | +4.9                | -1.1                | 3.15 <sup>b</sup>                       |
| $\pm$ SD       | 2.3                     |                   |                   | 0.65              |                     |                     | 1.62                                    |
| $\bar{x}$ 10th | 42.9 <sup>b</sup>       | +3.8 <sup>b</sup> | -7.1 <sup>b</sup> | 8.18 <sup>b</sup> | +5.7 <sup>b</sup>   | -1.5                | 3.87 <sup>b</sup>                       |
| $\pm$ SD       | 2.1                     |                   |                   | 0.65              |                     |                     | 1.26                                    |
| $\bar{x}$ 15th | 42.7 <sup>b</sup>       | +3.6 <sup>b</sup> | -6.8 <sup>b</sup> | 8.28 <sup>b</sup> | +6.9 <sup>b</sup>   | 0.0                 | 3.76 <sup>b</sup>                       |
| $\pm$ SD       | 2.1                     |                   |                   | 0.68              |                     |                     | 1.27                                    |
| $\bar{x}$ 30th | 42.3                    | +2.7              | -5.2              | 8.28 <sup>b</sup> | +6.9 <sup>b</sup>   | +1.8                | 3.53 <sup>b</sup>                       |
| $\pm$ SD       | 2.8                     |                   |                   | 0.48              |                     |                     | 1.64                                    |
| $\bar{x}$ 60th | 42.5                    | +3.1              | -5.9              | 8.06              | +4.3                | -1.6                | 2.55 <sup>b</sup>                       |
| $\pm$ SD       | 2.5                     |                   |                   | 0.72              |                     |                     | 0.73                                    |
| After          |                         |                   |                   |                   |                     |                     |   |
| $\bar{x}$ 5th  | 41.7                    | +1.2              | -2.2              | 7.74              | +0.4                | -1.9                | 2.44 <sup>b</sup>                       |
| $\pm$ SD       | 2.6                     |                   |                   | 0.86              |                     |                     | 1.01                                    |
| $\bar{x}$ 10th | 41.3                    | +0.8              | -0.6              | 7.70              | -0.1                | -0.8                | 1.91                                    |
| $\pm$ SD       | 2.9                     |                   |                   | 0.79              |                     |                     | 0.96                                    |
| $\bar{x}$ 15th | 40.4                    | -1.9              | +3.7              | 7.44              | -3.6                | 0.0                 | 1.65                                    |
| $\pm$ SD       | 2.7                     |                   |                   | 0.52              |                     |                     | 0.71                                    |
| $\bar{x}$ 30th | 39.6 <sup>b</sup>       | -4.0 <sup>b</sup> | +7.6 <sup>b</sup> | 7.40              | -4.2                | +3.2                | 1.39                                    |
| $\pm$ SD       | 2.6                     |                   |                   | 0.37              |                     |                     | 0.65                                    |
| $\bar{x}$ 60th | 40.0 <sup>b</sup>       | -2.9 <sup>b</sup> | +5.4 <sup>b</sup> | 7.50              | -2.8                | +2.5                | 1.02                                    |
| $\pm$ SD       | 1.8                     |                   |                   | 0.27              |                     |                     | 0.25                                    |

lated plasma protein content values showed insignificant changes during exercise and recovery.

No changes were found in the hemoglobin/hematocrit ratio at both the maximal and the prolonged mild exercise. Thus the mean corpuscular hemoglobin concentration was constant (Table 2, 3).

The weight loss was 0.16 kg (-0.21% of the total body weight) in the maximal exercise, 0.45 kg (-0.56%) after the mild, and 0.83 kg (-1.07%) after the submaximal prolonged exercise.

## Discussion

The results obtained after maximal exercise are partly in agreement with the observation of Beaumont et al. (1973), who found in the 25th min of recovery a decrease in the plasma volume by about 5%. In our study the normalisation of plasma volume

was observed between the 15th and the 30th min of the recovery phase after maximal exercise and the increase of plasma protein concentration is generally in agreement with the decrease of plasma volume. Therefore our results show a lower decline of plasma protein content. This findings is not in line with the conclusions of Keys and Taylor (1935) who believed that small amounts of protein leak out the vascular compartment during intensive effort. Our results could be interpreted as the tendency to the normalisation of osmotic relation in the blood.

Ahlborg (1967), Ekelund (1967), Saltin and Stenberg (1964) found that during submaximal exercise ( $f_H$  140–160 beats/min) the hemoconcentration takes place in the first 10 min of work, this value remains constant till the termination of exercise, the plasma volume decreased by about 5–8%. However the experimental subjects were allowed to drink water as desired. Beaumont et al. (1972) registered the increase in plasma volume (+5.4%) when consumption of water was allowed. The discrepancies in the findings of quoted authors can be interpreted by the intake of some amounts of fluid. According to the recent study of Costill and Saltin (1974b) the rapidity of the gastric emptying is dependent on the volume, composition and temperature of ingested fluid, and the rehydration is influenced by these factors and so it remains uncertain.

In all types of our experiments no replacement of body fluid losses was attempted and a similar decrease in plasma volume by 5–7% was found in prolonged submaximal exercise (67% of  $\dot{V}O_2$  max) at the 10th min of exercise and the consecutive blood samples reveal a spontaneous tendency to the normalisation. This could imply that the ingestion of water is not decisive for plasma volume changes. At the lower level of workload (40% of  $\dot{V}O_2$  max) only insignificant changes of plasma volume were found in our study, whereas Ekelund (1967) found a decrease in plasma volume (10%) at a similar level of workload. The explanation of this difference is difficult and it could ensue from different experimental arrangement. Senay (1972) found that the vascular volume depends even on other factors such as environmental temperature. Vascular volume increased during mild exercise in low temperature. It decreased at the same work when carried out in higher temperature.

Bergström et al. (1971) demonstrated an increased water content in muscle cells after maximal exercise. The accumulation of lactate and other metabolites exerts an osmotic effect which may explain the draw of water into the muscle fibres. Thus the decreased plasma volume could be explained by the shift of plasma water into the working muscle cells. The muscle lactate was not examined in this study, but several studies proved that the blood lactate is related to the muscle lactate, however its concentration in blood is lower and the peak values are delayed. In our experiments the increase in blood lactate was parallel to the decreasing plasma volume, but a significant correlation was found in the first min after the maximal exercise only ( $r = 0.77$ ).

In our experiments at both the short maximal and prolonged submaximal exercises, the plasma protein content remains relatively constant despite of the plasma volume changes, which could be of some importance for maintaining an adequate blood volume during exercise. From the comparison of the values obtained in the recovery after short maximal exercise and during and after prolonged exercise of a both types it may be concluded that the maximal exercise intervenes more deeply in water balance.

**References**

1. Ahlberg, B.: Capacity for prolonged exercise in man. *Försvarsmedicin* **3**, Suppl. 1 (1967)
2. van Beaumont, W., Greenleaf, J. E., Juhos, L.: Disproportional changes in hematocrit, plasma volume changes and proteins during exercise and bed rest. *J. appl. Physiol.* **33**, 55–61 (1972)
3. van Beaumont, W., Strand, J. C., Petrofsky, J. S., Hipskind, S. G., Greenleaf, J. E.: Changes in total plasma content of electrolytes and proteins with maximal exercise. *J. appl. Physiol.* **34**, 102–106 (1973)
4. Bergström, J., Guarneri, G., Hultman, E.: Carbohydrate metabolism and electrolyte changes in human muscle tissue during heavy exercise. *J. appl. Physiol.* **30**, 122–125 (1971)
5. Costill, D. L., Saltin, B.: Changes in the ratio of venous to body hematocrit following dehydration. *J. appl. Physiol.* **36**, 608–610 (1974a)
6. Costill, D. L., Saltin, B.: Factors limiting gastric emptying during rest and exercise. *J. appl. Physiol.* **37**, 679–683 (1974b)
7. Ekelund, L. G.: Circulatory and respiratory adaptation during prolonged exercise of moderate intensity in the sitting position. *Acta physiol. scand.* **69**, 327–340 (1967)
8. Keys, A., Taylor, H.: The behaviour of the plasma colloids in recovery from brief severe work and the question as to the permeability of the capillaries to proteins. *J. biol. Chem.* **109**, 55–67 (1935)
9. Poortmans, J. R.: Influence of physical exercise on proteins in biological fluids. In: *Medicine and sport*, Vol. 3. (J. R. Poortmans, ed.), pp. 312–327. Basel-New York: Karger 1969
10. Saltin, B., Stenberg, J.: Circulatory response to prolonged severe exercise. *J. appl. Physiol.* **19**, 833–838 (1964)
11. Senay, L. C., Jr.: Changes in plasma volume and protein content during exposures of working men to various temperatures before and after acclimatization to heat: Separation to the roles of cutaneous and skeletal muscle circulation. *J. Physiol. (Lond.)* **224**, 61–81 (1972)

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