Running on land and in water: comparative exercise physiology

JAN SVEDENHAG and JAN SEGER

Department of Clinical Physiology,
Huddinge University Hospital,
and Department of Physiology III,
Karolinska Institute,
Stockholm, Sweden

ABSTRACT

SVEDENHAG, J. and J. SEGER. Running on land and in water: comparative exercise physiology. *Med. Sci. Sports Exerc.*, Vol. 24, No. 10, pp. 1155–1160, 1992. The effect of water immersion on cardiorespiratory and blood lactate responses during running was investigated. Wearing a buoyant vest, 10 trained runners (mean age 26 yr) ran in water at four different and specified submaximal loads (target heart rates 115, 130, 145, and 155–160 beats·min^{-1}) and at maximal exercise intensity. Oxygen uptakes ($\dot{V}O_2$), heart rates, perceived exertion, and blood lactate concentrations were measured. Values were compared with levels obtained during treadmill running. For a given $\dot{V}O_2$, heart rate was 8–11 beats·min^{-1} lower during water running than during treadmill running, irrespective of exercise intensity. Both the maximal oxygen uptake (4.03 vs 4.60 l·min^{-1}) and heart rate (172 vs 188 beats·min^{-1}) were lower during water running. Perceived exertion (legs and breathing) and the respiratory exchange ratio (RER) were higher during submaximal water running than during treadmill running, while ventilation (l·min^{-1}) was similar. The blood lactate concentrations were consistently higher in water than on the treadmill, both when related to $\dot{V}O_2$ and to $\%\dot{V}O_{2max}$. Partly in conformity with earlier cycle ergometer studies, these data suggest that immersion induces acute cardiac adjustments that extend up to the maximal exercise level. Furthermore, both the external hydrostatic load and an altered running technique may add to an increased anaerobic metabolism during supported water running.

BLOOD LACTATE, HEART RATE, OXYGEN PULSE, OXYGEN UPTAKE, PERCEIVED EXERTION, RESPIRATORY EXCHANGE RATIO, VENTILATION

In humans, head-out immersion in water (with an upward directed hydrostatic pressure gradient) leads to a central shift of blood volume (approximately 700 ml; 1). This results in several cardiorespiratory adjustments even *at rest*, including a 12–18 mm Hg increase in central venous pressure (1,9,17), a 180–250 ml increase in cardiac blood volume (roentgenometric measurements; 13,17), a 25% or more increase in stroke volume and cardiac output (1,11,14,20), no change or a small decrease in heart rate (1,11,14,20), no change or a very slight increase in blood pressures (systolic, diastolic, mean; 1,14,19,20), a 30% decrease in systemic vascular resistance (1), and a 6–8% decrease in vital capacity (5,17).

During immersion *exercise*, a higher stroke volume and unchanged or higher cardiac output (15,20), lower heart rates at intense but not moderate work loads (19,20), unchanged systolic blood pressure (19,20), and a higher breathing frequency but lower tidal volume (20) have been reported. Echocardiographic measurements also indicate greater left ventricular end-diastolic and end-systolic dimensions during exercise (19).

In recent years, supported running in water (with vest) has been employed more widely for rehabilitation exercise in patients with musculoskeletal ailments or in athletes with surgically, or otherwise, treated injuries. Most earlier immersion exercise studies have been performed with the cycle ergometer as the exercise tool. Recently, some aspects of supported (3) and unsupported (18,22,23) deep-water running have also been reported. The present study was performed to further evaluate the acute cardiorespiratory and peripheral adjustments encountered in this new mode of immersion and rehabilitation exercise.

MATERIAL AND METHODS

Subjects. Nine trained male middle- and long-distance runners and one male decathlete/short-distance runner participated in the study. They were all competing on a district to national level. Their mean age, stature, and body mass were 26.4 (range 17–35) yr, 1.82 (1.72–1.91) m, and 70.2 (63.2–92.6) kg, respectively. Their mean treadmill $\dot{V}O_{2max}$ ($N = 9$) was 4.69 (3.92–5.40) l·min^{-1}, 193 (164–214) ml·kg$^{-0.75}$·min^{-1}, and 66.6 (53.0–74.3) ml·kg^{-1}·min^{-1}. The study was approved by the Ethics Committee of the Karolinska Institute and informed consent was obtained from each subject.

Protocol. Submaximal and maximal water and treadmill tests were performed. For the water tests, an indoor swimming pool with a water temperature of about 25°C was used. The subjects, who were all able to swim, were equipped with a specially designed buoyancy jacket (Wet Vest, Bioenergetics Inc., Pelham, AL) of accurate size. Eight of the subject were experienced water runners (with vest), one of these had used the vest extensively due to a prior injury. The remaining two runners

0195-9131/92/2410-1155$3.00/0
MEDICINE AND SCIENCE IN SPORTS AND EXERCISE

Submitted for publication May 1991.
Accepted for publication February 1992.

had trained with the vest once before the test occasion. An experienced track coach had carefully instructed the subjects of the appropriate vest running technique (e.g., long strides, fists closed) and had also approved the running technique of all runners. On the test day, instructions of the exercise procedure were given. After a light warm-up lasting about 5 min, the subjects exercised 4 min each at four different exercise levels of progressive intensity (1-min pause in water in between, alongside the edge of the pool). The subjects were instructed to keep an even intensity (self-selected stride frequency) throughout each exercise level with target exercise heart rates of 115, 130, 145, and 155–160 beats$\cdot$min^{-1} at the four submaximal exercise intensities. As feedback for the proper intensity level, heart rates were registered continuously by radiotelemetry and shown on an analog pulse display (checked by ECG); values were then given to the subjects verbally and repeatedly. Expired air was collected through a mouthpiece designed for use during swimming and attached to a lightweight helmet (Fig. 1). The subjects ran alongside the swimming pool (deep-water part) and most of the equipment was loaded on a small wagon closely following the runner. At the ends of the swimming pool, the subject made a preinstructed outward turn. Heart rates were recorded on a Mingograph and expired air was collected in Douglas bags during the last 1–1.5 min of each exercise intensity level. Immediately after each exercise level, a blood sample for lactate determination was taken from a prewarmed earlobe (nicotine salve). At the same time, ratings of perceived exertion (breathing and legs separate) were given.

About 3–4 min after the completion of the fourth submaximal exercise level, the maximal water test was performed. The subject increased his water exercise intensity up to the maximal level within 1–2 min and maintained the intensity at this level. At subjectively slightly more than 1 min to exhaustion (after about 3–4 min), the runner gave a sign and heart rate and oxygen uptake measurements were commenced. During this last minute of exercise, the subject was verbally encouraged to give his maximal effort (with count-down). A blood lactate sample was obtained approximately 30 s after exhaustion.


Figure 1—Schematic drawing of the expired air collection procedure during supported running in water.

Approximately 2 wk after the water test the treadmill exercise test was performed. For the submaximal part, the same general protocol as in water was used (i.e., 5-min warm-up; 4 × 4 min, 1-min pause; earlobe blood samples). The treadmill velocities were chosen so as to obtain an oxygen uptake (l$\cdot$min^{-1}) similar to that in water for the corresponding load (nos. 1–4: mean 11.2, 13.0, 14.9, and 16.2 km$\cdot$h^{-1}). For some subjects at loads 1 and 2, however, it was not possible to quite attain the desired $\dot{V}O_2$ because of the low running velocities involved (lowest running speed used: 9.9 km$\cdot$h^{-1}). The maximal treadmill test was performed in a standardized way with an individualized set treadmill velocity (mean 15.9 km$\cdot$h^{-1}, range 13.5–17.0) and a 0.5° increase in slope every 30 s up to 4 min and every minute thereafter. During the latter part of the maximal test, expired air was collected continuously. Because of an injury that did not permit maximal (i.e., uphill) treadmill running and one failed water max test, comparisons of maximal exercise level were made for eight subjects (no change in submaximal values with or without these two subjects).

Methods. Oxygen uptake was determined from Douglas bags by volume measurements in a balanced wet spirometer and analysis of O_2 and CO_2 percentages in a mass spectrometer (Centronic 200 MGA, 20th Century Electronics, Ltd.). Douglas bag collection times were all longer than 30 s. Heart rates were determined from electrocardiograms; the mean of repeated measurements during the last min at each submaximal load was used. Blood lactate concentrations were determined according to a modified Barker and Summerson method (21). Perceived exertion was rated according to the 6–20 degree RPE Scale (4).

Statistics. The relationship of $\dot{V}O_2$ (l$\cdot$min^{-1}) to the heart rate and oxygen pulse (submaximal exercise), and perceived exertion (all loads) of each subject for each of the runs on the treadmill and in water was analyzed by linear regression. Heart rate was also related to perceived exertion in an analogous manner. The individual slopes and intercepts and the calculated responses at $\dot{V}O_2$ values of 2.5 (heart rate), 3.0 (oxygen pulse), and 3.5 l$\cdot$min^{-1} (heart rate and perceived exertion) and at HR 150 beats$\cdot$min^{-1} (perceived exertion) were compared between exercise modes using a paired *t*-test. For the nonlinear relationships between $\dot{V}O_2$ and blood lactate, ventilation and RER, the interpolated responses at a $\dot{V}O_2$ of 3.0 l$\cdot$min^{-1} and 70% $\dot{V}O_{2max}$ (blood lactate) of each subject were compared between running in water and on the treadmill. Values are means ± SE.

RESULTS

$\dot{V}O_{2max}$. The maximal oxygen uptake was significantly lower during running in water (87.8 ± 2.4%) than during running on the treadmill (4.03 ± 0.13 vs 4.60 ± 0.14 $l \cdot min^{-1}$, $P < 0.01$).

Heart rate. The overall $\dot{V}O_2$-heart rate relationships for the four submaximal loads showed a tendency toward a lesser slope in water as compared with treadmill running (25.1 ± 2.1 vs 28.4 ± 2.3 $beats \cdot l^{-1}$, $0.05 < P < 0.1$). The calculated heart rate response at $\dot{V}O_2$ 3.5 $l \cdot min^{-1}$ was 10.9 ± 2.1 $beats \cdot min^{-1}$ lower in water than on land (155 ± 3 vs 165 ± 3 $beats \cdot min^{-1}$, $P < 0.01$; Fig. 2). The corresponding calculated heart rate difference at $\dot{V}O_2$ 2.5 $l \cdot min^{-1}$ was 7.6 ± 2.5 $beats \cdot min^{-1}$ (129 ± 3 vs 137 ± 2 $beats \cdot min^{-1}$; $P < 0.01$). There was a relatively large intersubject variability with one of the subjects showing a higher heart rate in water than on the treadmill. The Δheart rate (water − land) at $\dot{V}O_2$ 3.5 $l \cdot min^{-1}$ was significantly correlated with stature ($r = -0.74$, $P < 0.05$) but not with body mass ($r = -0.54$, NS) and $\dot{V}O_{2max}$ ($l \cdot min^{-1}$: $r = 0.05$, NS). The maximal heart rate was significantly lower in water than on the treadmill (172 ± 3 vs 188 ± 2 $beats \cdot min^{-1}$, $P < 0.01$).

Oxygen pulse. The oxygen pulse rose successively with increasing oxygen uptake both during running in water and on the treadmill; the only exception being at maximal exercise in water (Fig. 3). The slope of the $\dot{V}O_2$-oxygen pulse relationship tended to be steeper in water than on the treadmill ($0.05 < P < 0.1$). The calculated oxygen pulse at $\dot{V}O_2$ 3.0 $l \cdot min^{-1}$ was significantly higher in water than on land (21.1 ± 0.4 vs 19.8 ± 0.3 $mlO_2 \cdot beat^{-1}$, $p < 0.01$). The maximal oxygen pulse tended to be lower in water (23.4 vs 24.5 $mlO_2 \cdot beat^{-1}$, $0.05 < P < 0.1$).

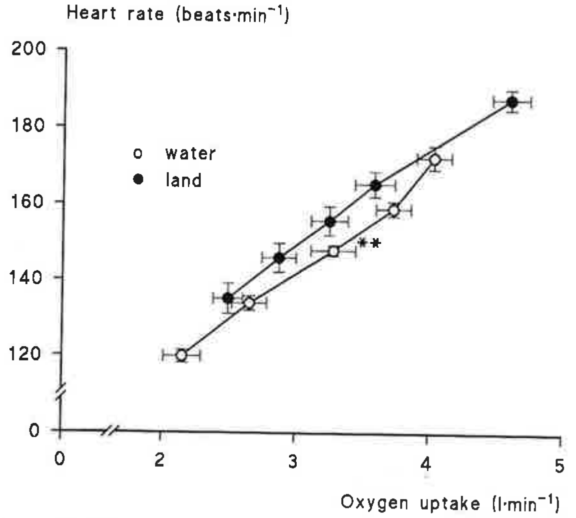

Figure 2—Heart rate in relation to oxygen uptake ($\dot{V}O_2$) during submaximal and maximal running in water and on the treadmill ($N = 10$). The calculated heart rates at $\dot{V}O_2$ 2.5 and 3.5 $l \cdot min^{-1}$ were lower (, $P < 0.01$) in water. Also the maximal oxygen uptake ($\dot{V}O_{2max}$) and maximal heart rate were lower ($P < 0.01$) for running in water. Values are means ± SE.**

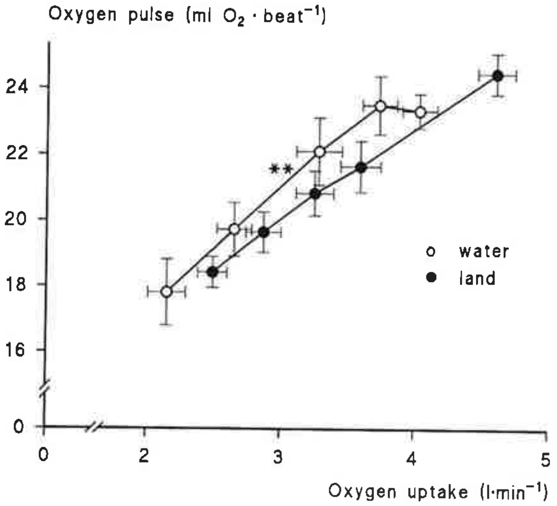

Figure 3—Oxygen pulse in relation to oxygen uptake ($\dot{V}O_2$) during submaximal and maximal running in water and on the treadmill ($N = 10$). The calculated oxygen pulse at $\dot{V}O_2$ 3.0 $l \cdot min^{-1}$ was higher (, $P < 0.01$) in water.**

Perceived exertion. Perceived exertion according to Borg was rated for breathing and legs separately. However, since the absolute values for breathing and legs throughout exercise were very similar in both the water and treadmill settings, only the leg results are presented. The calculated ratings at $\dot{V}O_2$ 3.5 $l \cdot min^{-1}$ (14.6 ± 0.6 vs 12.6 ± 0.7, $P < 0.01$; Fig. 4) and HR 150 $beats \cdot min^{-1}$ (14.2 ± 0.6 vs 10.4 ± 0.7, $P < 0.01$) were significantly higher during running in water than during treadmill running.

Blood lactate. The blood lactate curves in all subjects were shifted to the left in water compared to the treadmill, both when expressed relative to $\dot{V}O_2$ (Fig. 5) and to %$\dot{V}O_{2max}$ (Fig. 6). The interpolated blood lactate concentrations at $\dot{V}O_2$ 3.0 $l \cdot min^{-1}$ were 5.02 ± 0.30 and 1.33 ± 0.22 ($P < 0.01$), and at 70% $\dot{V}O_{2max}$ 4.57 ±

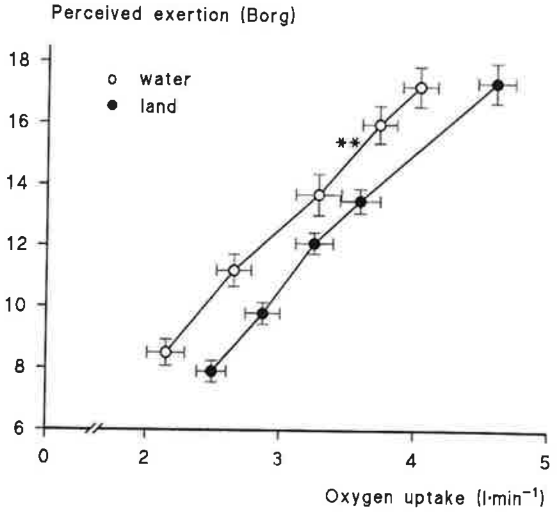

Figure 4—Perceived exertion in relation to oxygen uptake ($\dot{V}O_2$) during submaximal and maximal running in water and on the treadmill ($N = 10$). The calculated perceived exertion at $\dot{V}O_2$ 3.5 $l \cdot min^{-1}$ was higher (, $P < 0.01$) in water.**

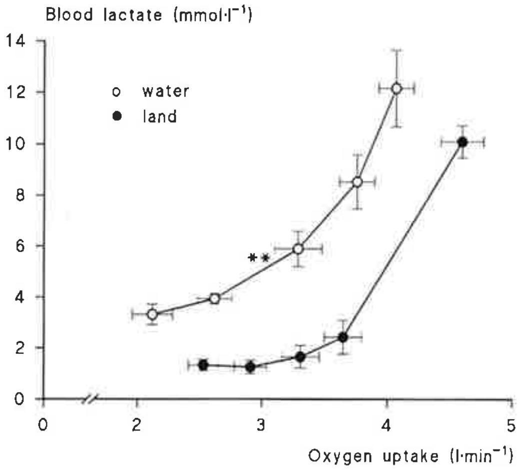

Figure 5—Blood lactate in relation to oxygen uptake ($\dot{V}O_2$) during submaximal and maximal running in water and on the treadmill ($N = 10$). In water the blood lactate curve was shifted to the left in all subjects with higher (**, $P < 0.01$) interpolated lactate concentration at $\dot{V}O_2$ 3.0 l·min^{-1}.

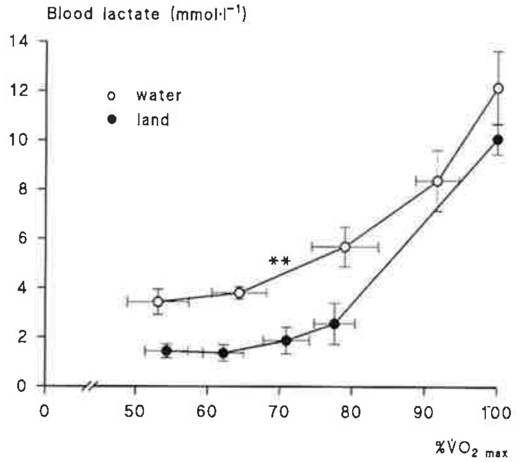

Figure 6—Blood lactate in relation to percentage of maximal oxygen uptake (%$\dot{V}O_{2max}$) during submaximal and maximal running in water and on the treadmill ($N = 10$). In water the blood lactate curve was shifted to the left in all subjects with higher (**, $P < 0.01$) interpolated lactate concentration at 70% $\dot{V}O_{2max}$.

0.20 and 1.47 ± 0.30 mmol·l^{-1} ($P < 0.01$) in water and on the treadmill, respectively. The blood lactate level 30 s after exhaustion tended to be higher during running in water (12.4 ± 1.3 vs 10.0 ± 0.6, $0.05 < P < 0.1$).

Ventilation. The submaximal and maximal ventilatory responses (l·min^{-1}, STPD) were similar in the two exercise modes (in relation to $\dot{V}O_2$, Fig. 7).

RER. The respiratory exchange ratio showed a somewhat varying response in different subjects. The interpolated RER at $\dot{V}O_2$ 3.0 l·min^{-1} was significantly higher in water than on the treadmill (0.982 ± 0.015 vs 0.946 ± 0.010, $P < 0.05$) (Fig. 8). The RER at maximal exercise tended to be lower in water (1.10 ± 0.04 vs 1.20 ± 0.03, $0.05 < P < 0.1$).

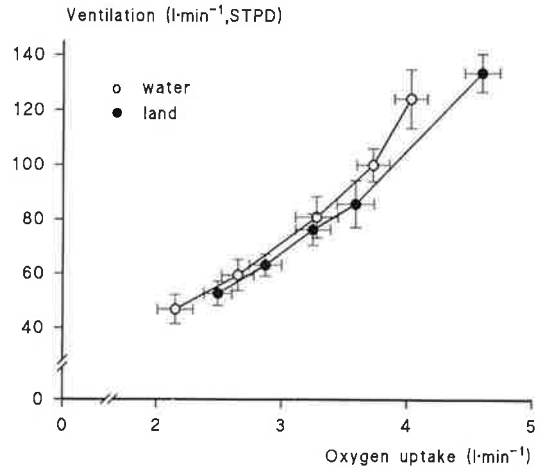

Figure 7—Total ventilation in relation to oxygen uptake ($\dot{V}O_2$) during submaximal and maximal running in water and on the treadmill ($N = 10$).

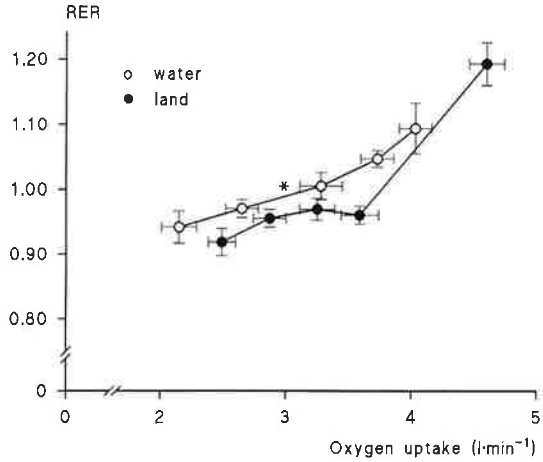

Figure 8—Respiratory exchange ratio (RER) in relation to oxygen uptake ($\dot{V}O_2$) during submaximal and maximal running in water and on the treadmill ($N = 10$). The interpolated RER at $\dot{V}O_2$ 3.0 l·min^{-1} was higher (*, $P < 0.05$) in water.

DISCUSSION

During running in water (wearing a vest) the movement pattern is clearly different, and the muscle mass engaged is probably larger than in cycle ergometer exercise. Therefore, running in water offers a new possibility of studying circulatory and metabolic adjustments in connection with exercise during immersion.

In the present study, heart rate at a given submaximal $\dot{V}O_2$ was lower during running in water than during treadmill running. At high exercise intensities this is in conformity with earlier cycle ergometer studies (2,19,20). Unsupported long-term deep-water running has also been reported to lower submaximal heart rate relative to $\dot{V}O_2$ (18). This effect is thought to be due to an increased stroke volume (15,20) secondarily to increases in central blood volume, central venous pressure, and therefore preload. A preload-mediated higher stroke volume may also explain the higher oxygen pulse in submaximal water running in the present subjects.

Sheldahl et al. (19,20) observed that cycle ergometer heart rates during immersion were lowered only at higher work loads, with $\dot{V}O_2$ at or above 2.0 – 2.4 $l \cdot min^{-1}$ or 75 – 80% $\dot{V}O_{2max}$. Differences in sympathetic neural outflow and cardiac output were suggested as possible explanations. No such clear intensity-dependent effect on the heart rate difference between water and land exercise was seen in the present study. Thus, the calculated HR difference at $\dot{V}O_2$ 2.5 $l \cdot min^{-1}$ (62% of water $\dot{V}O_{2max}$) was only slightly lower (−7.6 $beats \cdot min^{-1}$) than at $\dot{V}O_2$ 3.5 $l \cdot min^{-1}$ (87% $w\dot{V}O_{2max}$; −10.9 $beats \cdot min^{-1}$). The reason for the discrepancy is not known, but the higher aerobic capacity of the present subjects and/or the different exercise mode (with probably larger muscle groups involved) could account for the difference.

In earlier studies a large intraindividual variation in the exercise heart rate or cardiac output responses to immersion have been commented upon (20,23). This includes the HR response to running in water without supportive flotation as recently reported (23). Also in the present study a relatively large intraindividual variation was found, with one subject having higher submaximal heart rates (at a given $\dot{V}O_2$) in water than on the treadmill. We also found a significant correlation between ΔHR (water – land) and height. This may indicate that taller subjects (with the legs at a greater depth during water running and with a larger hydrostatic pressure component in the distal leg in treadmill running) get a relatively better venous return and thus a greater preload and stroke volume during running in water than do subjects of shorter stature. Still, if present, other stature-related differences (e.g., in heat exchange) could also add to such an effect.

It has been shown that the cardiovascular adjustments to water exercise are dependent on water temperature (2,7,14,15). For instance, in arm-leg cycle ergometer exercise at a water temp of 33°C no difference compared with the $\dot{V}O_2$-HR relationship in air was seen, while at 25 and 18°C the mean heart rates in water were, respectively, 10 and 15 $beats \cdot min^{-1}$ lower (15). Apart from the water hydrostatic pressure gradient effect, temperature-mediated vasoconstriction/dilatation may therefore also be important for the central hemodynamics during water exercise (16). In the present study we found a heart rate reduction at 25°C similar to that found by McArdle et al. (15). On the other hand, they reported that at this temperature (25°C) the three leanest subjects complained of cold discomfort and were noticeably shivering at submaximal work (with a resultant increase in $\dot{V}O_2$); no such discomfort was indicated by the present subjects after the warm-up.

In conformity with earlier studies (8;19 although NS;22), the maximal heart rate was lower in the present subjects during supported running in water. This may be due to an increase in heart volumes, preferentially at the atrial level (13). In contrast with cycle ergometer findings (8,19), but in accordance with unsupported deep-water running (22), we also found a decrease in the maximal oxygen uptake with immersion. Again, the exercise mode and/or higher aerobic capacity of subjects may be the most likely explanation of the difference. Regarding the former, a longer muscular contraction duration could limit muscle blood flow resulting in a lower cardiac output and thereby $\dot{V}O_2$ (as has been shown for swimming; 12). Still, an influence of the somewhat different max test procedures between water and treadmill in the present study (e.g., water max: one Douglas bag with a slightly longer collection time) cannot be excluded.

The perceived exertion for breathing (data not shown) and legs during submaximal exercise was higher during running in water, both when related to $\dot{V}O_2$ and to HR. Furthermore, the blood lactate concentrations were consistently higher in water exercise, related to both $\dot{V}O_2$ and $\%\dot{V}O_{2max}$. This is also compatible with the higher RER during submaximal running in water than on the treadmill. This higher anaerobic (i.e., non-oxidative) metabolism during immersion is probably partly due to a lowered perfusion pressure in the legs during running in water with a resultant decrease in total muscle blood flow and/or maldistribution. Supine cycle exercise with leg positive pressure (LPP) has earlier been reported to raise blood lactate and local leg muscle fatigue in a similar manner (10), whereas cycle ergometer lactate levels during immersion has been found to be unaltered during submaximal exercise (6). Although the subjects were well familiarized water runners, they were less conditioned in water than on land. The altered running technique in water with an altered muscle activation pattern (due to the absence of a support phase) as well as longer absolute muscular contraction times (see above) may also have added to the higher anaerobic metabolism. On the other hand, the pendulant arm work (fists closed) during water running is probably not of major significance for the determined blood lactate levels in the present study because of the relatively small muscle mass and shallow water depths involved.

With immersion or supine leg positive pressure, plasma, or blood lactate concentrations may be reduced at peak cycle load (6,10). For the latter study, peak load (in watts) was also lower. This may be related to an increased muscle-to-blood lactate gradient due to restriction of blood flow in working muscles (as earlier hypothesized, 10). With unsupported deep water running, Town and Bradley (22) noted a lower post-maximal blood lactate level in water than on land. In contrast, we found no significant difference in this respect; rather, blood lactate tended to be higher after the water max. The reason for this discrepancy between studies is not known but could be related to a greater maximal ability to recrute additional muscle groups with supported water running or to differences in water temperature.

In summary, immersion-induced central redistribution of the blood volume leads to acute cardiac adjustments that extend to running exercises of both low and high intensity. Thus, submaximal and maximal heart rates and the maximal oxygen uptake are all lowered. Furthermore, both the external hydrostatic pressure and an altered running technique may add to an increased anaerobic metabolism during supported submaximal water running, with resultant changes in the respiratory exchange ratio and perceived exertion but not in total ventilation.

We thank Ann-Marie Widebäck and Liv Rydén for expert laboratory assistance.

The study was supported by grants from the Karolinska Institute.

Address for correspondence: Dr. Jan Svedenhag, M.D. Ph.D., Department of Clinical Physiology, Huddinge University Hospital, S-141 86 Huddinge, Sweden.

REFERENCES

1. Arborelius, M., U. I. Balldin, B. Lilja, and C. E. G. Lundgren. Hemodynamic changes in man during immersion with the head above water. *Aerosp. Med.* 43:592–598, 1972.
2. Avellini, B. A., Y. Shapiro, and K. B. Pandolf. Cardio-respiratory physical training in water and on land. *Eur. J. Appl. Physiol.* 50:255–263, 1983.
3. Bishop, P. A., S. Frazier, J. Smith, and D. Jacobs. Physiologic responses to treadmill and water running. *Physician Sportsmed.* 17:87–94, 1989.
4. Borg, G. Perceived exertion as an indicator of somatic stress. *Scand. J. Rehabil. Med.* 2:92–98, 1970.
5. Buono, M. J. Effect of central vascular engorgement and immersion on various lung volumes. *J. Appl. Physiol.* 54:1094–1096, 1983.
6. Connelly, T. P., L. M. Sheldahl, F. E. Tristani, et al. Effect of increased central blood volume with water immersion on plasma catecholamines during exercise. *J. Appl. Physiol.* 69:651–656, 1990.
7. Craig Jr., A. B. and M. Dvorak. Comparison of exercise in air and in water of different temperatures. *Med. Sci. Sports* 1:124–130, 1969.
8. Dressendorfer, R. H., J. F. Morlock, D. G. Baker, and S. K. Hong. Effects of head-out water immersion on cardiorespiratory responses to maximal cycling exercise. *Undersea Biomed. Res.* 3:177–187, 1976.
9. Echt, M., L. Lange, and O. H. Gauer. Changes of peripheral venous tone and central transmural venous pressure during immersion in a thermo-neutral bath. *Pflügers Arch.* 352:211–217, 1974.
10. Eiken, O. and H. Bjurstedt. Dynamic exercise in man as influenced by experimental restriction of blood flow in the working muscles. *Acta Physiol. Scand.* 131:339–345, 1987.
11. Farhi, L. E. and D. Linnarsson. Cardiopulmonary readjustments during graded immersion in water at 35°C. *Respir. Physiol.* 30:35–50, 1977.
12. Holmér, I., E. S. Stein, B. Saltin, B. Ekblom, and P.-O. Åstrand. Hemodynamic and respiratory responses compared in swimming and running. *J. Appl. Physiol.* 37:49–54, 1974.
13. Lange, L., S. Lange, M. Echt, and O. H. Gauer. Heart volume in relation to body posture and immersion in a thermo-neutral bath. A roentgenometric study. *Pflügers Arch.* 352:219–226, 1974.
14. Lin, Y. C. Circulatory functions during immersion and breath-hold dives in humans. *Undersea Biomed. Res.* 11:123–138, 1984.
15. McArdle, W. D., J. R. Magel, G. R. Lesmes, and G. S. Pechar. Metabolic and cardiovascular adjustment to work in air and water at 18, 25, and 33°C. *J. Appl. Physiol.* 40:85–90, 1976.
16. Rennie, D. W., P. Di Prampero and P. Cerretelli. Effects of water immersion on cardiac output, heart rate, and stroke volume of man at rest and during exercise. *Med. dello Sport (Turin)* 24:223–228, 1971.
17. Risch, W. D., H.-J. Koubenec, U. Beckmann, S. Lange, and O. H. Gauer. The effect of graded immersion on heart volume, central venous pressure, pulmonary blood distribution, and heart rate in man. *Pflügers Arch.* 374:115–118, 1978.
18. Ritchie, S. E. and W. G. Hopkins. The intensity of exercise in deep-water running. *Int. J. Sports Med.* 12:27–29, 1991.
19. Sheldahl, L. M., L. S. Wann, P. S. Clifford, F. E. Tristani, L. G. Wolf, and J. H. Kalbfleisch. Effect of central hypervolemia on cardiac performance during exercise. *J. Appl. Physiol.* 57:1662–1667, 1984.
20. Sheldahl, L. M., F. E. Tristani, P. S. Clifford, C. V. Hughes, K. A. Sobocinski, and R. D. Morris. Effect of head-out water immersion on cardiorespiratory response to dynamic exercise. *J. Am. Coll. Cardiol.* 10:1254–1258, 1987.
21. Ström, G. The influence of anoxia on lactate utilization in man after prolonged muscular work. *Acta Physiol. Scand.* 17:440–451, 1949.
22. Town, G. P. and S. S. Bradley. Maximal metabolic responses of deep and shallow water running in trained runners. *Med. Sci. Sports Exerc.* 23:238–241, 1991.
23. Yamaji, K., M. Greenley, D. R. Northey, and R. L. Hughson. Oxygen uptake and heart rate responses to treadmill and water running. *Can. J. Sport Sci.* 15:96–98, 1990.