Muscle blood flow is not reduced in humans during moderate exercise and heat stress

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SAVARD, G. K., B. NIELSEN, J. LASZCZYNSKA, B. E. LARSEN, AND B. SALTIN. *Muscle blood flow is not reduced in humans during moderate exercise and heat stress.* J. Appl. Physiol. 64(2): 649–657, 1988.—The effect of heat stress on circulation in an exercising leg was determined using one-legged knee extension and two-legged bicycle exercise, both seated and upright. Subjects exercised for three successive 25-min periods wearing a water-perfused suit: control [CT, mean skin temperature ($\bar{T}_{sk}$) = 35°C], hot (H, $\bar{T}_{sk}$ = 38°C), and cold (C, $\bar{T}_{sk}$ = 31°C). During the heating period, esophageal temperature increased to a maximum of 37.91 , 39.35, and 39.05°C in the three types of exercise, respectively. There were no significant changes in pulmonary O_2 uptake ($\dot{V}O_2$) throughout the entire exercise period with either one or two legs. Leg blood flow (LBF), measured in the femoral vein of one leg by thermodilution, remained unchanged between CT, H, and C periods. Venous plasma lactate concentration gradually declined over time, and no trend for an increased lactate release during the heating period was found. Similarly, femoral arteriovenous O_2 difference and leg $\dot{V}O_2$ remained unchanged between the three exercise periods. Although cardiac output (acetylene rebreathing) was not significantly higher during H, there was a tendency for an increase of 1 and 2 l/min in one- and two-legged exercise, respectively, which could account for part of the increase in total skin blood flow during heating (gauged by changes in forearm blood flow). Because LBF was not reduced during exercise and heat stress in these experiments, the additional increase in skin blood flow must have been met by redistribution of blood away from vascular beds other than active skeletal muscle.

circulation; temperature; skeletal muscle

OF CRITICAL IMPORTANCE for muscle function during exercise is the blood flow through active muscle. Recent reviews (20, 25, 26) have highlighted the competition between skeletal muscle and cutaneous vascular beds for the available cardiac output when a heat stress is imposed during exercise. Any large redirection of blood flow away from contracting skeletal muscle to the skin for thermoregulatory heat transport would ultimately result in a reduction in work output. On the other hand, adequate muscle perfusion at the expense of the cutaneous circulation could eventually lead to severe hyperthermia. A major increase in cardiac output does not occur (20, 26), but rather there is a marked redistribution of the cardiac output away from other organs and nonworking tissues. Both splanchnic and renal blood flows are reduced during exercise in the heat (23, 27) as a result of increased sympathetic vasoconstrictor outflow. The crucial question is then whether active skeletal muscle responds to this vasomotor outflow by reducing its flow. In humans, attempts have been made to assess blood flow changes in skeletal muscle during exercise with added heat stress, by measurements of changes in O_2 content (10, 36) and lactate (28, 30, 36) of blood coming from the active muscles, but no direct measurements have been made. The present study was thus undertaken to determine whether blood flow, determined directly by a thermodilution technique, is compromised during exercise in the heat under conditions where the thermoregulatory demands for heat loss are considerable but not extreme. The aim of the present study is therefore to determine first the effects of high mean skin temperature ($\bar{T}_{sk}$) and second the effects of combined increases in $\bar{T}_{sk}$ and core temperature on the working muscle blood flow. Three exercise models were chosen: one-legged knee extension (2) and two-legged bicycle exercise, both seated and upright. The advantage of the knee extension model is that the work is performed almost exclusively by one muscle group (quadriceps femoris), whereas with bicycle exercise it was possible to double the metabolic load imposed on the subjects during exercise over that during knee extension under similar conditions of heat stress. The effect of a further gravitational stress on leg blood flow was also determined using upright bicycling as an exercise model.

METHODS

Twelve healthy male subjects, 21–29 yr of age and 65–82 kg body wt, participated in the study. Each was fully informed of the immediate and long-term risks involved before giving his consent. Experiments were carried out at the same time of day and conducted in the winter and spring; presumably therefore none of the subjects was heat acclimatized.

Experimental models. In the first series of experiments (n = 6), a modified Krogh bicycle ergometer for knee extension was used (1). This model enables the study of local energy turnover and circulatory dynamics of one muscle group (i.e., the quadriceps femoris) under conditions where the whole-body O_2 uptake ($\dot{V}O_2$) remains fairly low. The dynamic work was performed with 60 contractions/min, with 1 contraction causing the lower part of the leg to move from ~90 to 150°. Subjects were seated in the exercise chair, adjusted for height and leg length, and support straps around hips and shoulders were used to secure the subjects. Each subject participated in two to three training sessions on the apparatus,

after which the maximal performance capacity of the leg was determined. This was considered to be the maximal work load the leg could sustain without recruiting extraneous muscles to stabilize the body during knee extension and was gauged by a steeper rate of increase of pulmonary $\dot{V}O_2$. All experiments were then performed at 80–85% of subjects' leg maximal performance capacity (range 30–42 W): the average pulmonary $\dot{V}O_2$ was ~1 l/min, which represented ~20–25% of the subjects' maximal $\dot{V}O_2$ as determined by a stepwise increase in work load to exhaustion within 4–6 min on a Monark bicycle ergometer. The metabolic stress (and hence whole-body $\dot{V}O_2$) imposed on the subjects was then increased in a series of experiments in which subjects performed two-legged bicycle exercise, at a work load sufficient to produce a pulmonary $\dot{V}O_2$ of ~2.2 l/min in the seated position, and 2.4 l/min in the upright position, representing ~50–60% $\dot{V}O_{2\,max}$. The same procedure was then followed for all three types of exercise.

Procedures and measurements. Subjects arrived in the morning, and catheters were advanced upstream into the femoral artery and vein. After catheterization, 10 skin thermocouples were placed as follows: 1 each on the chest, abdomen, and shoulder, 4 on the catheterized thigh, and 1 each on the opposite thigh, upper arm, and forearm. $\overline{T}_{sk}$ was calculated as the mean of all temperatures except those over the thigh of the catheterized leg, which was kept cool (thigh $\overline{T}_{sk}$ = 25–28°C) in all experiments (except in 3 of the one-legged experiments) by a water-perfused (0–3°C) cooling pad. Esophageal temperature (T_{es}) was measured at the level of the heart. Subjects were dressed in a water-perfused suit and water-impermeable coverall. Leg blood flow (LBF) was determined by a constant-infusion thermodilution technique, which has a high degree of reproducibility under a given set of conditions (2, 14) and is based, in part, on principles similar to those of Pávek et al. (22). The experimental setup for flow measurements consisted of an infusion pump (Harvard, model 2202A) with calibrated glass syringes cooled by ice bags, connected by a 60-cm polyethylene tube to a stainless steel coil (3.5-m tube, total volume = 46 ml). The coil was placed in a thermobox containing ice and water and connected to the venous catheter stopcock by a 20-cm insulated polyethylene tube. This experimental setup ensured that the temperature of the injectate was 0°C. The venous catheter (soft Teflon, 7-F, 12 cm long) was provided with four side holes (0.4 mm diam), placed on a helix over a distance of 1 cm, starting 1 cm from the tip. The thermistor catheter (Edslab TD probe 94-030-2.5-F) for measurement for LBF (2) was inserted through the venous catheter, and the tip was advanced 8–10 cm proximal to the infusion holes. The thermistor was connected to an Edslab computer, and the temperature signal was recorded continuously (Siemens, Elema Mingograph) for the whole infusion period (12–16 s). During exercise an infusion rate of 115 ml/min was selected to obtain a drop of ~0.6–0.8°C in femoral venous blood temperature. The total volume of the injectate was ~25–40 ml for each measurement. Blood flows were calculated as described by Andersen and Saltin (2). At rest, bolus injections of ice-cold saline were used (4 ml), and blood flows were immediately integrated and displayed on the Edslab computer. The femoral vein drains most of the hamstring and part of the gluteal and lower leg muscles, as well as superficial (subcutaneous and cutaneous) tissues via the vena saphena magna. The contribution of this "skin" blood flow to the measured femoral vein flow was evaluated in some additional experiments (n = 2) by the use of the ^{133}Xe clearance technique (31) during two-legged upright bicycle exercise with subjects wearing the water-perfused suit. ^{133}Xe dissolved in sterile saline was injected in the subcutis of the thigh (midportion of vastus lateralis) of both the control leg and under the water-perfused pad placed around the other thigh (circulating water temperature = 0–3°C). The subject rested for 15 min and then started to exercise until a T_{es} of 39°C and a heart rate (HR) of 180 beats/min were exceeded. During one-legged knee extension, no electromyogram (EMG) activity has been found in either hamstring or gluteal muscles (1), and flow to the lower leg could be disregarded because a cuff was inflated (>240 mmHg) just below the knee during sampling and blood flow measurements. Measured LBF was thus considered to be representative of the blood flow from the working muscle, quadriceps femoris. In the two-legged exercise experiments, no occlusion cuff was used, and thus the measured femoral venous blood flow was equated with whole-leg muscle blood flow because the femoral arterial and venous system serves all muscles predominantly involved in cycling (16).

Forearm blood flow (FBF) was measured by venous occlusion plethysmography with a Whitney mercury-in-Silastic strain-gauge (35). Movement artifacts during exercise were eliminated by suspending the arm at the level of the heart, in a sling from the ceiling, and by the shoulder strap. The arm was contained within the water-perfused suit, but a slit permitted the adjustment of the strain-gauge; the opening was then covered by a sheet of plastic draped over, but not in direct contact with, the forearm or strain-gauge. The forearm $\overline{T}_{sk}$ was therefore on the average ~0.5°C below and 1.0°C above that of $\overline{T}_{sk}$ during heating and cooling periods, respectively. Pulmonary $\dot{V}O_2$ was measured with the Douglas bag technique. A Tissot spirometer was used for volume measurement, and O_2 and CO_2 content of the exercise bags was determined with a paramagnetic (Servomex) and infrared (Beckman LB-2) system, respectively. Mean arterial blood pressure (MAP) and heart rate were monitored continuously via the femoral catheter; the blood pressure transducer was placed at the level of the leg. Cardiac output (CO) was estimated twice during each period, at 10 and 20 min, in one- and two-legged (seated) experiments by the acetylene-argon-O_2 rebreathing technique, using a mass spectrometer (7). The effect of the higher blood temperatures obtained during heating on the acetylene solubility coefficient was found to be negligible. No measurements of CO were taken during two-legged upright exercise. After all resting measurements were taken, subjects started to exercise. During the 1st 20–25 min of exercise (control, CT), no water was circulated through the suit; during the next 25-min period

(hot, H), hot water (45–47°C) was circulated; and in the final 25-min period (cold C), cold water (0–3°C) was used. LBF and $\dot{V}O_2$ were measured and blood was sampled at 3, 10, and 20 min of each period during one-legged exercise and at 3, 18, and 23 min of two-legged exercise. Three to four measurements of FBF were made every 5 min, and the mean of these values was calculated; $\bar{T}_{sk}$ and core temperatures were recorded every 2 min.

Blood analyses. Blood samples were simultaneously drawn from the femoral artery and vein of the exercising leg. Blood O_2 saturations were measured on an OSM-2 hemoximeter (Radiometer, Copenhagen). The accuracy of the method was verified regularly by determination of O_2 content with a VanSlyke apparatus. Hemoglobin concentrations were also measured on the hemoximeter; the apparatus was calibrated with several fully oxygenated blood samples, analyzed spectrophotometrically by the cyanmethemoglobin method (11). Triplicate hematocrit determinations were made by centrifugation in microcapillary tubes. Plasma lactate was determined by deproteinizing whole blood in ice-cold 0.6 M perchloric acid, neutralized by KOH, frozen at −40°C, and analyzed by enzymatic fluorometry (18).

Statistics. Conventional statistical methods were used to calculate means ± SE. Nonparametric statistics were used for testing the significance of differences between related samples [Friedman test (32)]. Significance was set at the 0.05 level of confidence.

RESULTS

Systemic Responses

Temperature. From its resting level T_{es} increased gradually in CT (Fig. 1). In H, T_{es} rose steeply to maximal values measured at the end of H, of 37.91 ± 0.30, 39.35 ± 0.15, and 39.05 ± 0.23°C in one-legged, two-legged seated, and two-legged upright exercise, respectively (Fig. 1). The respective increases in T_{es} from CT to H were 0.65 ± 0.30 (NS), 1.40 ± 0.20 ($P < 0.05$), and 1.20 ± 0.23°C ($P < 0.05$). During cooling, T_{es} returned again to approximately the CT level in all three types of exercise.

From ~34 to 35°C in the CT, $\bar{T}_{sk}$ increased rapidly to 37.5–38.5°C during H of all types of exercise (Table 1). $\bar{T}_{sk}$ was highest ($P < 0.05$) during two-legged seated bicycling. In C, $\bar{T}_{sk}$ fell to ~30°C after 10–15 min of cooling.

Pulmonary O_2 uptake. There were no significant differences in pulmonary $\dot{V}O_2$ between CT, H, and C in the three exercise types (Table 1). $\dot{V}O_2$ was the highest during two-legged upright exercise at 2.4 l/min, although there was no significant difference between this value and the $\dot{V}O_2$ obtained during seated bicycling. During one-legged knee extension, $\dot{V}O_2$ was an average of 1 l/min.

Cardiac output. Absolute values of CO were high compared with those previously reported (21, 30) (Table 1). This is difficult to explain, but any relative changes between CT, H, and C periods of exercise could nevertheless be examined. No significant differences in CO were found between the 10- and 20-min measurements of CO or between CT, H, and C periods of either one- or two-legged (seated) exercise when mean values were compared. CO was significantly higher during two-legged than during one-legged exercise by 6–7 l/min.

Heart rate. During exercise, HR increased rapidly to a near steady-state value in the CT period (Table 1). HR then increased steadily in the H period to a maximal value of 184 beats/min measured at the end of the period in upright bicycling, compared with 144 and 169 beats/min during one- and two-legged (seated) exercise, respectively. In all experiments, HR decreased again to CT values within 10 min of exercise in C. HR was significantly higher during H than CT or C, and there were no differences between CT and C values in all three exercise types.

Stroke volume. No differences were found in stroke volume (SV) between the different exercise periods in either one-legged or two-legged seated exercise or between the two exercise types (Table 1).

Mean arterial blood pressure. MAP remained unchanged throughout the whole exercise period in all three exercise types (Table 1). MAP was significantly higher by ~30–40 mmHg during one-legged exercise than during two-legged exercise. The lowest MAP was observed in the upright position (96 mmHg), although this value was not significantly different from that obtained during seated two-legged bicycle exercise.

Local Responses

Temperature. Femoral vein temperature (T_{fv}) was significantly higher in H than in CT or C periods of one-legged and two-legged (upright) exercise (Table 2). There were no significant differences between T_{fv} and T_{es} in any of the exercise protocols, and T_{fv} changes closely paralleled those of T_{es}. In separate experiments ($n = 3$), muscle temperature was measured by a needle thermocouple at different depths in the quadriceps muscle, and large thermal gradients were found under the cooling pad (Table 3). Thus the slightly (NS) lower T_{fv} than T_{es} may have been due to a conductive cooling through relatively cooler surrounding tissues as a result of using the cooling pad around the exercising thigh. In addition, admixture of warm blood from the skin of the chest during heating, in combination with warm blood returning from the noncooled leg (2-legged bicycle exercise) may have contributed to the slightly higher T_{es} than T_{fv}.

Leg blood flow. LBF was not different between the three exercise periods in any of the exercise protocols (Fig. 2, Table 2). No evidence for a reduction in LBF during H was found in any of the experiments. The 1-l/min higher LBF in H and C than in CT (NS) in the two-legged (seated) exercise experiments was due to the very high LBF values found in one subject in these periods.

The possible contribution of the skin blood flow over the exercising leg to the measured leg (femoral vein) blood flow was evaluated in the following series of experiments. First, the effect of local skin temperature on femoral LBF was examined in three experiments in which the thigh T_{sk} was varied between 23 and 38°C during one-legged knee extension using a water-perfused pad placed around the thigh of the working leg. T_{es} in these experiments was in the same range as that recorded during the CT period of the one-legged exercise series

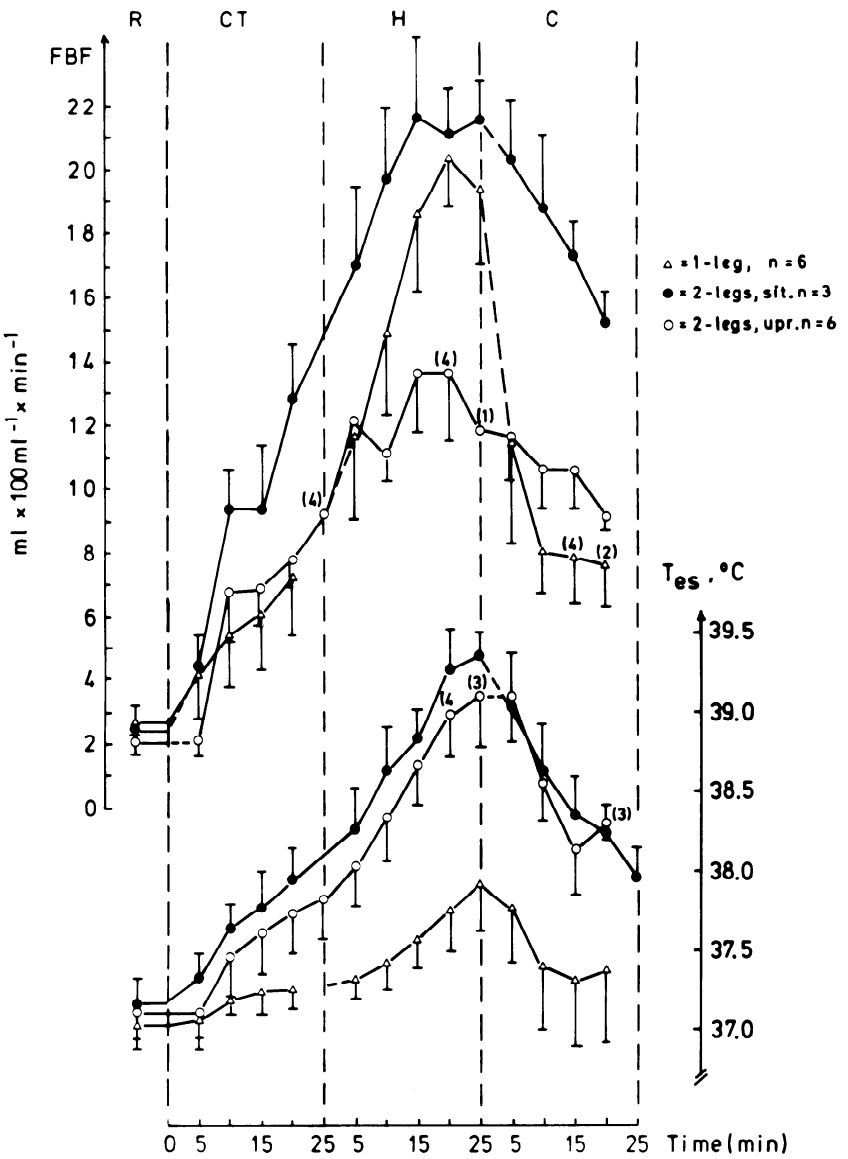

FIG. 1. Changes in esophageal temperature (T_{es}) and forearm blood flow (FBF) during 1-legged knee extension (1-leg; n = 6), 2-legged seated bicycle exercise (2-legs, sit; n = 3), and 2-legged upright bicycle exercise (2-legs, upr; n = 6). Resting values (R) and values obtained during 3 successive exercise periods (CT, control; H, hot; C, cold) are means ± SE.

(i.e., 37.3°C). No significant changes in measured LBF and in femoral arteriovenous (a-v) O_2 were observed.

In a second series of experiments the combined effects of local T_{sk} (thigh) and hyperthermia on skin blood flow in the thigh were evaluated from ^{133}Xe clearance measurements. Results indicate that there were no differences in the pattern of skin blood flow changes between the control thigh (T_{sk} = 36°C) and the cooled thigh (T_{sk} = 28°C) (Table 3). The measured perfusion increased gradually in step with T_{es} to a value ~10-fold above its resting value at 16 min of exercise (T_{es} = 37.8°C) and then gradually declined to a value ~6- to 7-fold above the resting flow after 50 min of exercise, whereas T_{es} continued to rise gradually toward its final value of 39.5°C. After cessation of the exercise a hyperemia was observed, which increased the perfusion to ~75 times its resting value. This estimated maximal perfusion was on the order of 500 ml·100 g^{-1}·min^{-1}. This represented a total thigh skin flow of ~3–4 l/min based on an estimated thigh skin and subcutaneous volume of 0.8 liter. According to the measured perfusion ratios, the thigh skin would then receive ~0.1 of this amount during exercise in the heat (i.e., 300–400 ml/min or <10% of the measured femoral vein flow). Thus, even if all this amount returned from the skin of the thigh via the femoral vein in the heating period, in combination with some blood from the skin of the lower leg, it would most likely not be detected, because the accuracy of the thermodilution method is only 10%. The effect of cooling the skin of the thigh on the measured LBF would also seem to be insignificant; nevertheless a cooling pad was used around the thigh to at least minimize the effect of a warm local T_{sk} on skin vasodilation and hence perhaps skin blood flow contribution to LBF. Data from the three one-legged experiments in which the cooling pad was not used were pooled with those in which the pad was used (n = 3), because no significant differences were found between the variables measured in these six experiments.

Femoral arteriovenous O_2 difference. There were no significant differences found in femoral (a-v) O_2 between the different exercise periods in any of the exercise types (Table 2). The highest values were observed during upright bicycle exercise, at ~16 ml/100 ml compared with 13 and 15 ml/100 ml during one- and two-legged (seated)

TABLE 1. *Systemic data: summary of circulatory and temperature changes*

Variable	*n*	Exercise	R	CT	H	C	Statistics
$\bar{T}_{sk}$, °C	6	1-leg	34.8±0.1	35.4±0.1	37.4±0.1	29.7±0.7	H > CT, C*
	3	2-legs, sit	35.1±0.1	35.6±0.3	38.5±0.5	31.3±0.6	H > C*
		2-legs, upr	34.0±0.7	34.3±0.4	37.7±0.6	28.8±1.0	H > CT, C*
$\dot{V}O_2$, l/min	6	1-leg	0.28±0.01	0.93±0.06	1.03±0.07	1.07±0.09	NS
	3	2-legs, sit	0.29±0.03	2.06±0.07	2.20±0.03	2.08±0.02	NS
	6	2-legs, upr	0.37±0.02(5)	2.27±0.01	2.39±0.04	2.40±0.02	NS
CO, l/min	3	1-leg	6.4±0.5	13.4±1.8	14.2±2.2	13.3±2.2	NS
	3	2-legs, sit	8.3±0.4	19.5±0.9(2)	21.3±0.8	19.7±1.1	NS
		2-legs, upr					
HR, beats/min	6	1-leg	72±2	109±3	144±7	109±2	H > CT, C*
	3	2-legs, sit	62±5	137±5	169±1	142±4	H > CT, C*
	6	2-legs, upr	70±6	157±3	184±3	164±4	H > CT, C*
SV, ml	3	1-leg	91±9	134±14	119±13	136±16	NS
	3	2-legs, sit	136±15	140±12(2)	130±6	132±8	NS
		2-legs, upr					
MAP, mmHg	5	1-leg	115±4	133±8	136±7	144±9	CT < C*
	3	2-legs, sit	112±4	112±9	113±9	107±8	NS
	6	2-legs, upr	106(1)	103±7	96±6	96±6(5)	NS

Values are means ± SE, measured at the end of each period (CT, control; H, heating; C, cooling) at rest (R), and during 1-legged knee extension (1-leg) and while bicycling seated (2-legs, sit) and upright (2-legs, upr). No. in parentheses represents no. of subjs if different from *n* column. $\bar{T}_{sk}$, mean skin temperature; $\dot{V}O_2$, O_2 uptake; CO, cardiac output; HR, heart rate; SV, stroke volume; MAP, mean arterial pressure; NS, no significant differences between 3 periods of exercise. * $P < 0.05$.

TABLE 2. *Local data: summary of circulatory and temperature changes in femoral vein*

Variable	*n*	Exercise	R	CT	H	C	Statistics
T_{fv}, °C	5	1-leg	36.61±0.11	37.27±0.12	37.58±0.11	37.18±0.17	H > CT*
	3	2-legs, sit	36.14±0.24	37.74±0.25	39.06±0.26	37.86±0.15	NS
	6	2-legs, upr		37.67±0.16	38.78±0.25	38.09±0.29	H > CT, C*
LBF, l/min	6	1-leg	0.37±0.07	5.21±0.71	5.53±0.62	5.92±0.72	
	3	2-legs, sit	0.18±0.02	5.93±0.92	6.95±1.23	6.79±0.77	NS
	6	2-legs, upr		5.83±0.50	5.90±0.58	5.45±0.60(5)	NS
LVC, $l \cdot min^{-1} \cdot mmHg^{-1} \cdot 10^{-2}$	5	1-leg	0.3±0.1	3.9±0.5	4.1±0.5	4.1±0.5	NS
	2	2-legs, sit	0.14±0.01	4.6±0.6	5.9±1.3	7.0±0.1	NS
	6	2-legs, upr		5.9±0.7	6.4±0.9	5.7±0.8	NS
Leg $\dot{V}O_2$, ml/min	6	1-leg	24±4	753±100	762±86	768±99	NS
	3	2-legs, sit	11±1	822±105	1,074±324(2)	1,121±81(2)	(NS)
	6	2-legs, upr		954±60	906±64	893±86(4)	NS
(a-v) O_2, ml/100 ml	5	1-leg	5.9±0.5	13.8±0.4	13.2±0.4	12.8±0.6	NS
	2	2-legs, sit	7.8±0.6	15.1±0.4	14.9±0.2	15.0±0.1	NS
	6	2-legs, upr		16.5±0.5	15.6±0.6	16.5±0.9(4)	NS

Values are means ± SE, measured in femoral vein of leg. Conventions as in Table 1. T_{fv}, femoral venous temperature; LBF, leg blood flow; LVC, leg vascular conductance; $\dot{V}O_2$, O_2 uptake; (a-v) O_2, arteriovenous O_2 difference. * $P < 0.05$.

TABLE 3. *Temperature gradients during 40-min bicycle exercise*

	Rest		Exercise				Recovery	
			16 min		40 min		2 min	
	−	+	−	+	−	+	−	+
T_{sk}, °C	32.5	26.8	36.1	27.8	35.8	27.6	36.0	28.5
T_{es}, °C	36.9		37.8		39.3		39.4	
T_m, °C								
2 cm			39.2	33.1	40.5	34.1		
3 cm			39.8	38.6	40.6	39.3		
4 cm			39.5	40.1	40.0	39.7		
Skin blood flow, $ml \cdot 100\ g^{-1} \cdot min^{-1}$	7	9	89	90	54	38	575	539

Temperature gradients were measured through quadriceps femoris muscle of 1 subject during 2-legged (bicycle) exercise in water-perfused suit (circulating water temperature = 48°C). Cooling pad was placed around thigh of 1 leg, and muscle temperature (T_m) was measured at 3 depths (2, 3, and 4 cm from surface) in both control (−) and cooled (+) legs. Thigh skin temperature (T_{sk}) is mean of measurements from 4 different sites over each of 2 thighs. Skin blood flow was estimated from ^{133}Xe clearance measurements in both legs at rest, during exercise, and at recovery. Cooling pad had no detectable effects on skin blood flow during exercise; steep increases in skin blood flow occurred at recovery in both legs. T_{es}, esophageal temperature.

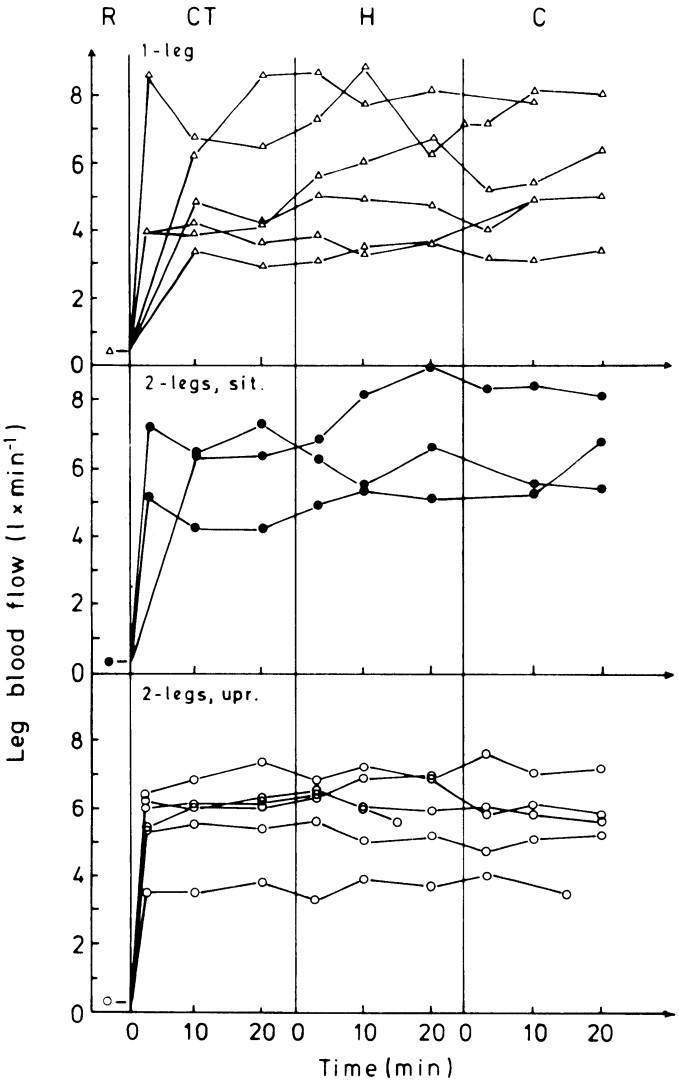

FIG. 2. Changes in leg blood flow with time during 1-legged knee extension (1-leg; $n = 6$), 2-legged seated bicycle exercise (2-legs, sit; $n = 3$), and 2-legged upright bicycle exercise (2-legs, upr; $n = 6$). Resting values (R) and values obtained during 3 successive exercise periods (CT, control; H, hot; C, cold) are presented for each subject.

exercise, respectively.

Leg O_2 uptake. The leg $\dot{V}O_2$, calculated from the femoral venous blood flow measurements and (a-v) O_2 differences, did not change significantly throughout the exercise period in all three types of exercise (Table 2). This was also suggested by the similar force tracings between exercise periods, which followed in all experiments except seated bicycling. As indicated above, in the two-legged seated bicycle exercise, one of the three subjects had very high LBF values, and thus calculated leg $\dot{V}O_2$ was also elevated; i.e., a doubling of this value to account for exercise of the other leg, added to the basal value, exceeded the pulmonary $\dot{V}O_2$. It may be that this subject performed more work with the catheterized leg. Mean values presented in Table 2 are therefore relatively high.

Leg vascular conductance. There were no significant differences in leg vascular conductance (LVC) between the three different exercise periods of one- and two-legged (upright) exercise (Table 2). During two-legged (seated) exercise, LVC showed a continuous increase from CT to C so that the final (C) value was significantly higher than the control LVC.

Lactate. Changes in arterial and venous plasma lactate with time are depicted in Fig. 3. There were no significant changes in venoarterial lactate differences or in lactate release, calculated from venoarterial differences and femoral venous flows, between CT, H, and C periods of exercise of all three exercise types. Venous plasma lactate increased to a maximum of 3.23 ± 0.85, 3.08 ± 0.05, and 1.63 ± 0.20 mM in the 1st 10 min of one-legged, two-legged (seated), and two-legged (upright) exercise, respectively, and then declined throughout the exercise period to minimal values of 1.05 ± 0.51, 1.40 ± 0.10, and 1.14 ± 0.32 mM, respectively.

Forearm blood flow. In all experiments, FBF was significantly higher during H than during CT or C periods of exercise (Fig. 1). Values of FBF were highest during two-legged seated exercise and lowest during upright exercise throughout the whole exercise period. FBF was significantly higher during two-legged exercise in the seated position than in the upright position during CT, H, and C. CT and C values of FBF were also significantly higher during two-legged (seated) exercise than during one-legged exercise, whereas similar maximal values were attained in the H period even though T_{es} was 1.4°C higher, at 39.4°C, during seated bicycling. In all experiments FBF decreased in the C period to control values.

DISCUSSION

The major finding of this study was that muscle blood flow in the working leg was not reduced over control values when a heat stress was imposed during moderate exercise. This was the case during one-legged knee extension and during both seated and upright two-legged bicycle exercise. Subsequent whole-body cooling also did not significantly change measured leg flows, which were, under all conditions, in the same range as those found in other studies (1, 2, 16). Previous studies have focused on changes in O_2 content of blood coming from active muscles (10, 36) or lactate (28, 30, 36) as indicative of changes in active muscle blood flow (MBF); i.e., any decrease in flow to the active muscles could be reflected in a lower $\dot{V}O_2$ and a higher blood lactate concentration occurring as a result of higher anaerobic energy production. During exercise in a hot environment, pulmonary $\dot{V}O_2$ has been shown to be the same (27), slightly lower (28, 36), or higher (13, 19) than control values. Arterial lactate concentration has been shown to be higher (13, 19, 28, 29, 36) or unchanged (30).

In the present study there were no significant changes in (a-v) O_2 differences, and thus leg $\dot{V}O_2$, or in pulmonary $\dot{V}O_2$ when subjects were heated during exercise, suggesting that no significant changes occurred in O_2 utilization of the working muscles during the entire period of exercise with one or two legs. In addition, after an initial increase, the venous lactate concentration gradually fell to its minimal value at the end of the final cooling period and no changes in femoral venoarterial lactate differences were found between CT, H, and C periods of exercise (Fig. 3). These results further support our find-

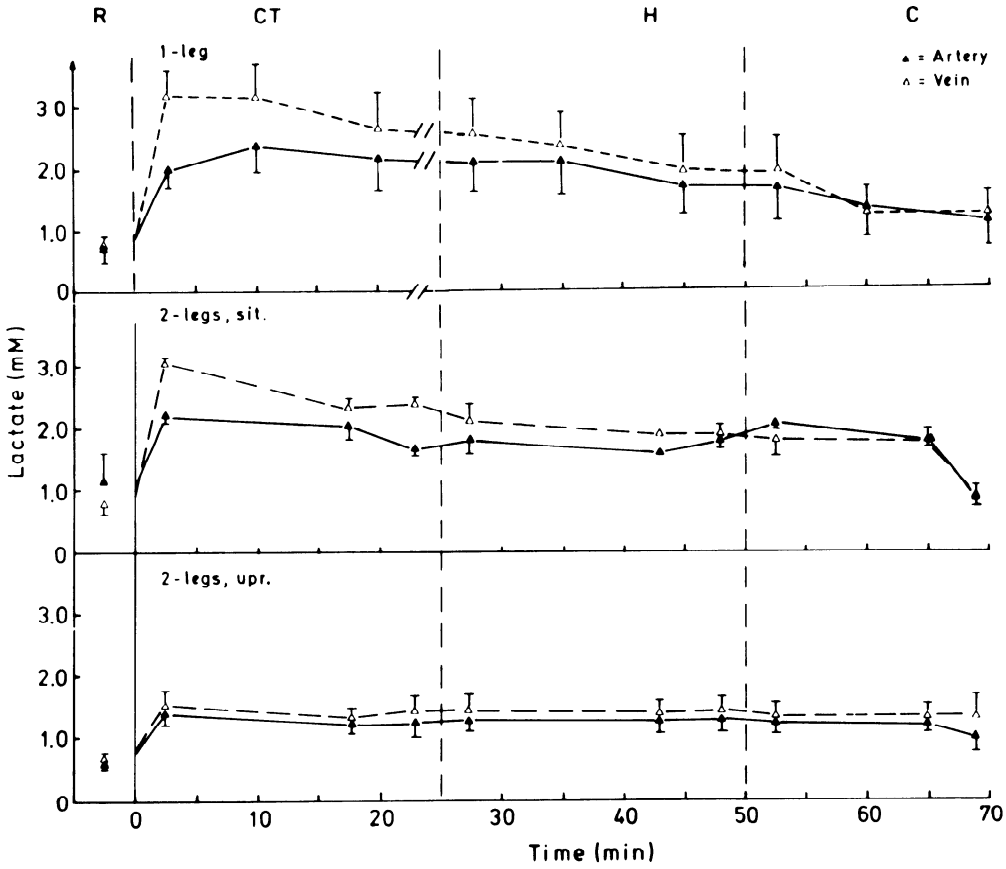

FIG. 3. Changes in arterial (—) and venous (-----) lactate concentration at rest (R) and during 1-legged knee extension (1-leg; $n = 6$), 2-legged seated bicycling (2-legs, sit; $n = 3$), and 2-legged upright bicycling (2-legs, upr; $n = 6$). Resting values and values obtained during 3 exercise periods (CT, control; H, hot; C, cold) are means ± SE.

ings of no effect of heat stress on directly measured femoral venous flow during light-to-moderate exercise. Of note is that our venous lactate and venoarterial lactate differences during heating are lower than those previously reported (13, 36). Part of the explanation may be that the relative work load used during our two-legged exercise experiments (50–60% $\dot{V}O_{2\,max}$) was lower than that in the study of Fink et al. (70–85% $\dot{V}O_{2\,max}$) (13) and second that our subjects were quite fit so that the venous lactate for a given absolute $\dot{V}O_2$ was lower than that in subjects in Williams' study (36). In our one-legged experiments, with subjects working at 80–85% of the leg peak performance capacity, lactate concentration may have been low due to the high performance of this small muscle group during exercise (2). Nevertheless the overall picture of plasma lactate changes over time observed in our experiments is typical for endurance exercise.

There was a tendency (NS) for CO to increase by ~1 l/min during one-legged exercise and by ~2 l/min during two-legged exercise. This latter increase is slightly lower than that found in previous studies in which similar whole-body heating experiments during exercise were performed (21, 30). This may have been due, in part, to the higher initial values of CO in the CT period in which $\overline{T}_{sk}$ and T_{es} were also higher. It would seem therefore that, in agreement with other studies (21, 25, 26, 30), CO was able to respond to the heat challenge by increasing, and, according to Rowell et al. (30), this additional flow would have been directed to the skin. No quantitative measurements of total skin blood flow during work are available. However, previous studies have shown that the changes observed in FBF during leg exercise (15) or body heating (9, 24) are confined to the skin, and thus these changes have been assumed to be representative of changes in skin blood flow over most of the body, as long as the local T_{sk} is not artificially clamped. A rough estimate of the total body skin blood flow increase during heating was made based on the method by Taylor et al. (34). The increase in total skin blood flow on heating calculated in this way was ~3 l/min. This is in agreement with our results on ^{133}Xe clearance in the skin and subcutaneous tissue of the thigh during exercise in the heat, which indicated that total skin blood flow was ~4 l/min, reflecting an increase of ~3 l/min in skin blood flow above resting values. This increase could be accounted for by both an increase in CO and a possible redistribution of blood away from splanchnic (28) and renal (23) vascular beds. Rowell (25) calculated that the additional vasoconstriction of these two regions during heat stress could redistribute 600–800 ml/min of blood to skin at moderate exercise intensities. Thus the increase in skin blood flow during exercise in a hot environment may represent the sum of the increment in CO and the redistribution away from visceral organs. Nevertheless the fact that the FBF measured in the three different types of experiments was increasingly reduced

at comparable skin and core temperatures in relation to the metabolic and orthostatic demands (Fig. 1) suggests that a regulatory vasoconstriction took place in this vascular bed. The maximal level of skin blood flow attained during one- and two-legged (seated) exercise was thus the same, even though T_{es} was significantly higher with two legs; similarly, in the upright position, FBF was significantly lower than during seated bicycle exercise, even though the metabolic cost of the exercise was approximately the same. Such heat- and gravity-induced cutaneous vasoconstriction, as indicated by these reductions in FBF, have been reported previously (8, 20, 25); Rowell (26) has suggested that it occurs because of strong baroreceptor activation induced by changes in arterial and central venous pressures so that blood pressure homeostasis is maintained. This cutaneous vasoconstriction and the absence of any detectable change in working muscle blood flow in all three exercise protocols suggest that *1*) during one-legged knee extension, the central circulation was able to meet the blood flow demands of both skin and muscle for heat loss and metabolic requirements, respectively, and *2*) during two-legged bicycle exercise (seated and upright) CO was still able to meet the blood flow demands of the exercising skeletal muscles, although a threshold for skin blood flow was met at the expense of thermoregulation and heat loss from the body so that MAP was maintained in the heat in accordance with Rowell et al. (30). Williams et al. (36) have suggested that at high levels of work intensity during acute heat exposure, muscle metabolism takes precedence over heat regulation. However, this situation cannot be tolerated for long, because, in addition to the reduction in the cutaneous circulation, blood flow is also directed away from other vascular beds (23, 27, 28). Rowell et al. (29) also found that during treadmill exercise of short duration at a high work intensity in the heat, CO could no longer be maintained by increasing HR. Indeed, in these extreme conditions, maximal levels of HR had been reached so that compensation for the decreased SV, resulting from peripheral displacement of the vascular volume, was no longer possible, and CO was reduced below control values at a given $\dot{V}O_2$; MAP was also decreased by 4–8 mmHg in these experiments. It would thus be interesting to examine the working MBF under these conditions of lowered CO and MAP as well as during upright walking or running exercise in which the orthostatic stress is considerably increased. The effect of an environment that allowed for free sweating on the relationships between central and peripheral circulation, as opposed to the effect of the conditions in the present study with a water-perfused suit, may also be different. Blood pressure regulation superimposed on thermoregulation may in these cases lead to a reduction in blood flow in exercising skeletal muscle with a subsequent decrease in $\dot{V}O_2$ and rapid accumulation of lactate. Experiments are currently under way to examine the effects of heat stress on leg blood flow during upright walking at 60% $\dot{V}O_{2\,max}$ in the hot environment [(air temperature T_{air}) = 40°C].

In a recent study of sheep walking on a treadmill in the heat, Bell et al. (5) found a 35% reduction in active MBF, measured by the microsphere technique, which was accompanied by a marked increase in respiratory frequency and blood flow to upper respiratory tract tissues, because panting is a major avenue of heat loss in sheep. Thus, in this species, the blood flow to heat loss effector organs would seem to increase in spite of a falling MAP and active muscle MBF during exercise in the heat.

One interesting question that can be asked then is what sets the degree of vasoconstriction in the vascular tree of an exercising limb? It is known that both nonexercising (6) and exercising (33) skeletal muscles are recipients of increased sympathetic vasoconstrictor outflow during exercise, and there is ample evidence showing that working muscle can further respond to vasomotor stimuli (4, 33). Thus local vasodilator mechanisms may overcome, to a large extent, any constrictor drive during exercise. In addition, metabolic changes within active muscles might elicit reflexes from their chemosensitive nerve fibers, thus modulating the degree of vasodilation within the muscle vascular bed (25, 26). Also, thermoregulatory reflexes have been shown to influence markedly vasomotor outflow during heat stress and exercise (20, 21). A role for arterial baroreceptors in the regulation of the degree of vasodilation in active muscle has also been postulated (12, 25, 26). The combination of heat stress and upright exercise leads to arterial and central venous pressure changes that might elicit strong baroreflexes (26) and changes in sympathetic outflow to exercising skeletal muscle. However, the role of the baroreflex in regulation of blood flow to various vascular beds, including active skeletal muscle, remains controversial, and the effects of exercise and heat stress on the sensitivity of such a mechanism are unknown.

In conclusion, results from this series of experiments have demonstrated that the blood flow to active skeletal muscle is not reduced when an additional heat stress is imposed during both seated and upright exercise of moderate intensity. Redistribution of CO away from other vascular beds under these conditions and a possibly compromised skin blood flow may contribute to the maintenance of exercising MBF. In the competition for the available CO, it is thus skin blood flow that is reduced at the expense of additional thermoregulatory heat loss. Flow to active muscles may be regulated by arterial and/or cardiopulmonary baroreflexes, which ensure adequate perfusion and delivery of O_2 and nutrients to this vascular bed.

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