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Effect of body tilt on calf muscle performance and blood flow in humans

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Egaña, Mikel, and Simon Green. Effect of body tilt on calf muscle performance and blood flow in humans. *J Appl Physiol* 98: 2249–2258, 2005. First published January 20, 2005; doi:10.1152/japplphysiol.01235.2004.—To explore the effect of posture on muscle performance, we tested the effects of body tilt angle on the strength, endurance, and fatigue of, and blood flow into, the plantar flexors. Human subjects were fixed to a tilt table that could tilt them from the horizontal (0°) to upright (90°) position and enabled force to be applied to a footplate through isometric action of the right calf muscle. In *experiment 1*, six subjects performed a strength test and graded test (intermittent contractions) to the point of failure at three tilt angles (0, 47, and 90°). In *Experiment 2*, seven subjects performed a strength test and constant-force test [70% maximum force (F_{max}); intermittent contractions] to the point of failure in the horizontal and three inclined positions (32, 47, and 67°). In *experiment 3*, leg blood flow was assessed during constant-force exercise at two intensities (30 and 70% F_{max}) and two tilt angles (0 and 67°) in six subjects. Strength was not affected ($P > 0.05$) by tilt angle. Time to failure during the graded test was significantly higher at 47° (25.9 ± 2.0 min) and 90° (25.1 ± 3.0 min) than 0° (22.2 ± 2.6 min). Time to failure during the constant-force test was also significantly higher at 32° (7.1 ± 3.6 min), 47° (8.0 ± 5.2 min), and 67° (8.6 ± 5.6 min) compared with 0° (4.0 ± 2.6 min). When graded or constant-force exercise was performed with arterial flow to the leg eliminated, there were no differences in exercise time between the horizontal and an inclined position. During nonischemic exercise, leg blood flow was significantly higher during exercise in the inclined position. These results demonstrate that head-up tilt improves endurance of the plantar flexors, that this effect occurs in the absence of an effect on strength, and that it depends on an intact peripheral circulation. Moreover, the postural effect on muscle endurance appears to be due to a greater blood flow into the leg, an effect that is established during the initial contractions.

strength; endurance; fatigue

SMALL IMPROVEMENTS (~5–10%) in endurance occur when the body is tilted upright from a horizontal position. This effect occurs for men and women and, in all cases, has been shown for graded cycle exercise (5, 13, 23). Others have shown that fatigue during electrical stimulation of the abductor pollicis muscle is decreased or increased when the arm is lowered or raised from a horizontal position (6, 28). These findings suggest that the fatigue and endurance of working skeletal muscle are sensitive to the orientation of the limb or body to the gravitational vector.

It has been suggested that these postural effects on muscle fatigue and endurance are mediated by changes in the perfusion pressure acting across the active skeletal muscle (5, 6, 28). As the body is tilted up from the horizontal, the hydrostatic pressure of the blood in regions below the heart increases in proportion to the distance from the heart, and both arterial and venous pressures rise. During dynamic exercise, the pressure in the intramuscular veins is lowered toward zero after each contraction (12), and the perfusion pressure then depends on arterial pressure. Consequently, when the body is tilted up from a horizontal position, the arterial and perfusion pressure between muscle contractions increases (7). This helps explain the faster response of blood flow to the active limb during the first minute of submaximal exercise when the body is in a more inclined position (14, 15, 21). In turn, this effect appears to contribute to a faster O_2 uptake response during the early period of upright compared with supine exercise (9, 15) and, perhaps, contributes to a reduction in fatigue and improved endurance when the body is tilted up. This is speculative, however, because muscle fatigue and blood flow in response to a change in body tilt angle have not been assessed within the same study.

To further explore the postural effect on muscle performance, the aim of the present study was to test the effect of body tilt on calf muscle strength, fatigue, and endurance, and to see to what extent any postural effects observed depended upon an intact peripheral circulation. We then assessed the effect of body tilt angle on leg blood flow during exercise to further explore this role of the peripheral circulation.

METHODS

Overview. Three experiments were performed. *Experiment 1* tested the effect of body tilt on muscle strength and graded calf exercise performance, whereas *Experiment 2* tested the effect of body tilt on muscle strength and the performance of, and fatigue during, constant-force calf exercise. During additional tests in both experiments, ischemia was imposed during exercise to explore the role of the peripheral circulation in the postural effects observed. When we established that the postural effects depended upon an intact peripheral circulation, we then measured the effect of body tilt angle on leg blood flow during exercise in *Experiment 3*. The 12 subjects (11 men and 1 woman) who participated in these experiments were young (age: mean = 26.4 yr; range = 22–37 yr), nonsmokers, and free of any clinically significant disease that could affect their exercise performance. Informed consent was obtained from all subjects before their participation in this study. The procedures were conducted in accordance with the standards set by the Declaration of Helsinki (2000).

Calf exercise. Calf exercise was performed on an ergometer that could tilt subjects to several angles between the horizontal (0°) and upright positions (90°) (Fig. 1). This ergometer has two immobile footplates, each of which is connected to its own strain gauge and against which force can be applied through trying to plantar flex the foot about the ankle. The force was amplified and sampled at 40 Hz

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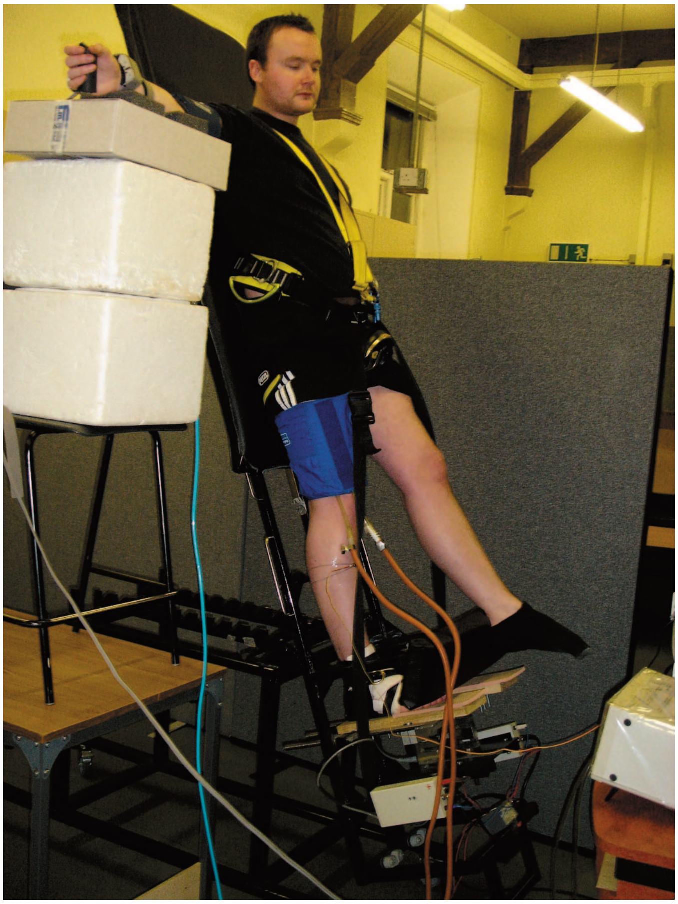

Fig. 1. A subject fixed to the calf exercise ergometer in a tilted position with *1*) a seat raised into the crotch to support the majority of the weight, *2*) the foot of the exercising limb strapped tightly into a leather boot attached to a footplate, *3*) the force-measuring assembly below the footplate, and *4*) a mercury-in-Silastic strain gauge (for blood flow measurements) fixed around the active calf and connected to a plethysmograph. Further details can be found in METHODS.

before being processed by a PowerLab analog-to-digital converter (ML 795, AD Instruments) and displayed on a screen for the subjects to see clearly (Chart v4.12, AD Instruments). Subjects used this visual display to regulate their own muscular effort and conform to specific instructions given by the investigator.

Single-limb (i.e., right leg) exercise was performed in this study. The subject lay on the tilt table in the fully extended position. The right foot was tightly and comfortably strapped into a leather boot fixed to the footplate, whereas the left (nonexercising) foot was supported on a padded platform that lay ~30 cm anterior to the heel of the exercising foot. A pilot experiment established that this positioning of the nonexercising foot eliminated the additional force (100–200 N) created when it was placed in the boot; this effect occurred through dorsiflexion of the nonexercising foot and rotation about the pelvis that was then transmitted longitudinally through the exercising limb to its footplate. A padded seat was also raised up into the crotch to support the majority of the subject's weight (>80%) when inclined. Subjects were also harnessed to the ergometer to prevent the upward displacement of the body during each contraction, and, based on a pilot experiment, a "comfortably tight" harnessing of the subject was always applied. This was particularly important to do in the supine position as lighter or absent harnessing always resulted in lower maximum forces (F_{max}). Subjects were always positioned and harnessed in the horizontal position, and the force transmitted to the footplate by compression of the body was kept constant across all tests for a given individual.

F_{max}. On a separate day and before the graded and constant-force tests (see below), the highest force recorded during three to four maximal voluntary efforts (3-s contraction) at a given body tilt angle was taken as the F_{max} at that angle. At all inclined positions, maximum efforts were initiated within 5 s of being tilted from the horizontal; after each effort subjects were returned to the horizontal position and rested for 1 min before being tilted up again and asked to perform the next maximum effort.

Experiment 1 (strength and graded muscle endurance). In *experiment 1*, muscle strength and maximal, graded muscle performance were assessed at three tilt angles (0, 47, and 90°) in five men and one woman. After two familiarization sessions, F_{max} at the three tilt angles was determined on 1 day, and then, on 3 subsequent days, separated by at least 72 h, time to failure during a graded test was determined at the same tilt angles. The order of the angles at which strength and endurance tests were performed was randomized. During the graded test, isometric muscle actions were performed intermittently so that the calf contracted for 3 s and relaxed for 3 s. The force sustained during each contraction started at 100 N and was increased by 100 N every 3 min until the subject failed to reach the required force on two consecutive efforts, at which time the test was terminated. At inclined positions, the graded test was started within 10 s of tilting the subject from the horizontal.

Several weeks after these test sessions and when the postural effect on graded performance was known, four of the six subjects (three men and one woman) repeated the graded test at 0 and 47° on separate days, in a randomized order, and with the arterial flow into the leg stopped by inflating a thigh cuff to 250 mmHg. The F_{max} test was immediately preceded by rapid inflation of the cuff (within 0.5 s) while the subject was in the horizontal position and then rapid tilting to the predetermined angle (in the case of inclined positions). During the rest periods between maximum efforts, the cuff was deflated, and the ergometer returned to the horizontal position. Then immediately before the graded test, the cuff was rapidly inflated as the subject lay in the horizontal position, the subject was then shifted quickly to the predetermined tilt angle (in the case of inclined positions), and the test started.

Experiment 2 (strength and endurance during constant-force exercise). In *experiment 2*, muscle strength and performance during constant-force exercise were assessed at four tilt angles (0, 32, 47, and 67°) in seven male subjects. After at least two familiarization sessions, F_{max} at the four tilt angles was determined during a strength testing session. Then, on 4 subsequent days separated by at least 72 h, a constant-force test was performed. Before each constant-force test, F_{max} was determined as the highest of three maximum voluntary efforts, and then the rate of fatigue during, and time to failure on, the constant-force test were measured. During the constant-force test, isometric muscle actions were performed intermittently so that the calf contracted for 2 s and relaxed for 4 s. We selected this contraction-to-relaxation ratio (i.e., 1:2) because it is similar to the relative period of activation of the calf muscle during walking on flat and inclined terrain, something we had established through a pilot experiment conducted after *experiment 1*. The long-relaxation phase (4 s) was chosen to enable blood flow to be measured using plethysmography in *experiment 3*. The force of each contraction was 70% F_{max}, where F_{max} was the highest force achieved at any of the four tilt angles during the strength testing session. During each fifth contraction (i.e., *contraction 5*, *10*, *15*, etc.), a maximum effort was sustained for 2 s. The decline in force during these maximum efforts was described using a linear function ($y = a + b \cdot x$), where y is force, x is time, parameter a represents force at time $t = 0$ (i.e., F_{max}), and parameter b represents the rate of fatigue. Failure occurred when the force during submaximal contractions failed to reach the required force during two consecutive efforts, and at this point the test was terminated.

Several weeks after these test sessions and when the largest postural effect was known, four of the seven subjects repeated the constant-force test at 0 and 67° under ischemic conditions on separate days in a randomized order, as described for *experiment 1*.

Experiment 3 (leg blood flow during constant-load exercise). In *Experiment 3*, leg blood flow was assessed during constant-force tests at 0 and 67° in six subjects. Exercise was performed as described in *Experiment 2*, with the exception that maximal efforts during constant-force exercise were not performed. In addition to exercise at 70% F_{max}, exercise bouts were performed at a low intensity (30% F_{max}). This was done to provide insight into the validity of plethysmography to measure limb blood flow during exercise, as described below. Exercise was thus performed under four conditions, two intensities and two tilt angles, and on separate days. For each condition, three exercise trials, separated by 20–30 min of recovery, were completed. The duration of each exercise trial at 30% F_{max} was 6 min, whereas it ranged between 2 and 6 min at 70% F_{max}. Three subjects failed to complete 6 min of exercise at 70% F_{max} in the supine condition, and so only blood flow data collected over the same period (i.e., <6 min) during the supine and inclined positions were analyzed (see below).

Leg blood flow was assessed using venous occlusion plethysmography. A thigh cuff was inflated before exercise and maintained throughout exercise at a pressure of 55 mmHg. Leg blood flow was assessed during the 4-s relaxation periods between contractions by measuring the change in leg volume using a mercury-in-Silastic strain gauge, placed around the widest girth of the calf, and a Hokanson EC-6 plethysmograph. The change in leg volume was only assessed when force had returned to within 10 N of a stable minimal value, the relaxed state, and only if this stable force value was maintained continuously for at least 3 s. Because blood flow was usually measured across two to three complete cardiac cycles (see Fig. 5*B*), each blood flow value during exercise represents an average blood flow during relaxation and not an average of the entire duty cycle. We chose to assess blood flow over as much of the relaxation period as possible, rather than just calculating a peak response over a single cardiac cycle, because it is this entire response that probably most affects O_2 availability and fatigue (see DISCUSSION), and such an averaging approach over a longer period would also tend to reduce measurement error. Although this increases the likelihood that venous outflow might occur, none of the strain gauge responses in the six subjects declined at any point during relaxation, which would have been a clear indication that venous outflow occurred. In a pilot experiment, we had observed that blood starts flowing into the leg only when the force fell below ~100–150 N (~10% F_{max}), even at high blood flows. Because the time spent between this force and zero as the muscle is relaxing is very short (<0.3 s), relatively little of the change in leg volume due to arterial inflow is likely to be missed.

A biexponential equation was fitted to each subject's blood flow response that was averaged from the three trials under each of the four conditions. This equation was chosen because, in >90% of the trials, it provided a goodness of fit, based on the adjusted R^2, that was better than a monoexponential or triexponential equation. The equation fitted was $y(t) = a + \mathrm{A1}\cdot[1 - e^{-(t-\mathrm{TD1}/\tau 1)}] + \mathrm{A2}\cdot[1 - e^{-(t-\mathrm{TD2}/\tau 2)}]$, where y is blood flow at time t, a is the y-intercept and approximates resting blood flow, parameters A1 and A2 are the amplitudes, TD1 and TD2 are the time delays, and τ1 and τ2 are the time constants of the fast and slow phases, respectively. The change in blood flow over the exercise period (i.e., total amplitude) was estimated using the biexponential equation, and the mean response time (MRT) of the entire response was calculated using the equation, $\mathrm{MRT} = [\mathrm{A1}/(\mathrm{A1} + \mathrm{A2})]\cdot(\mathrm{TD1} + \tau 1) + [\mathrm{A2}/(\mathrm{A1} + \mathrm{A2})]\cdot(\mathrm{TD2} + \tau 2)$, as described elsewhere (15). At 70% F_{max}, three subjects failed to complete 6 min of exercise in the supine position. In these cases, data beyond these exercise times to failure collected in the inclined position were eliminated from the curve fitting of the blood flow responses.

Mean arterial pressure and heart rate were measured continuously during exercise using a COLIN CBM7000 blood pressure monitor. Leg volume immediately after each contraction was calculated as a percentage of resting volume (100%) and was measured at the start of the pulsatile increase in leg volume during the relaxed state.

Statistical analyses. Effects of body tilt angle on F_{max}, time to failure, and rate of fatigue were identified using repeated-measures ANOVA, and differences were then located using Tukey's honestly significant difference test. Comparisons of performance variables under ischemic conditions (*experiments 1* and *2*) at two angles were made using a paired *t*-test. For *experiment 3* data, a two-way repeated-measures ANOVA was performed (main effects = intensity and body tilt angle), and differences were located using Tukey's honestly significant difference test or, for nonnormal data, a Wilcoxon's rank test. The level of significance was set at $P \leq 0.05$. All results are shown as means ± SD.

RESULTS

Experiment 1. F_{max} values determined during one testing session at 0, 47, and 90° are shown in Fig. 2*A*. There was no significant difference between these values. Times to failure on the graded test at these same three angles are shown in Fig. 2*B*. There was a significant difference between time to failure at 0° and the other two angles ($P < 0.05$), but no significant difference between 47 and 90°. The mean relative force achieved at the end of the graded test was 62, 70, and 70% F_{max} at 0, 47, and 90°, respectively.

F_{max} and time to failure under ischemic conditions at 0 and 47° are shown in Fig. 2, *A* and *B*, respectively. There was no effect of body tilt angle on F_{max} or time to failure under ischemia.

Experiment 2. F_{max} values determined during the strength testing session at 0, 32, 47, and 67° are shown in Fig. 3*A*. There was no significant difference between these values ($P > 0.05$). F_{max} values before each of the constant-force tests were also unaffected by tilt angle. These F_{max} values were also not different from those F_{max} values measured during the strength testing session. Times to failure on the constant-force test at these same four angles are shown in Fig. 3*B*. There was a significant difference between time to failure at 0° and the other three angles but no significant difference between 32, 47, and 67°. Fatigue during the four constant-force tests for the seven subjects are shown in Fig. 4. The *y*-intercepts and slopes of the fatigue responses at the four angles are shown in Table 1. Body tilt angle had no significant effect on parameter *a* (i.e., predicted F_{max}), but the rate of fatigue (parameter *b*) was significantly higher at 0° compared with the other angles.

F_{max} and time to failure under ischemic conditions at 0 and 67° are shown in Fig. 3, *A* and *B*, respectively. There was no effect of body tilt angle on F_{max}, rate of fatigue, or time to failure under ischemia. Fatigue during ischemic exercise was always significantly greater than during nonischemic exercise at a given intensity and tilt angle.

Experiment 3. F_{max} was assessed before the four conditions and, as in *experiments 1* and *2*, was not different between supine and inclined positions. Representative force and leg volume ("calf girth") recordings during single exercise trials at 70% F_{max} at 0 and 67° are shown in Fig. 5, *A* and *B*, respectively. Leg blood flow was calculated from the increase in leg volume and time over which it occurred during each relaxed state after a contraction. Under each condition, the average leg blood flow after each contraction for an individual

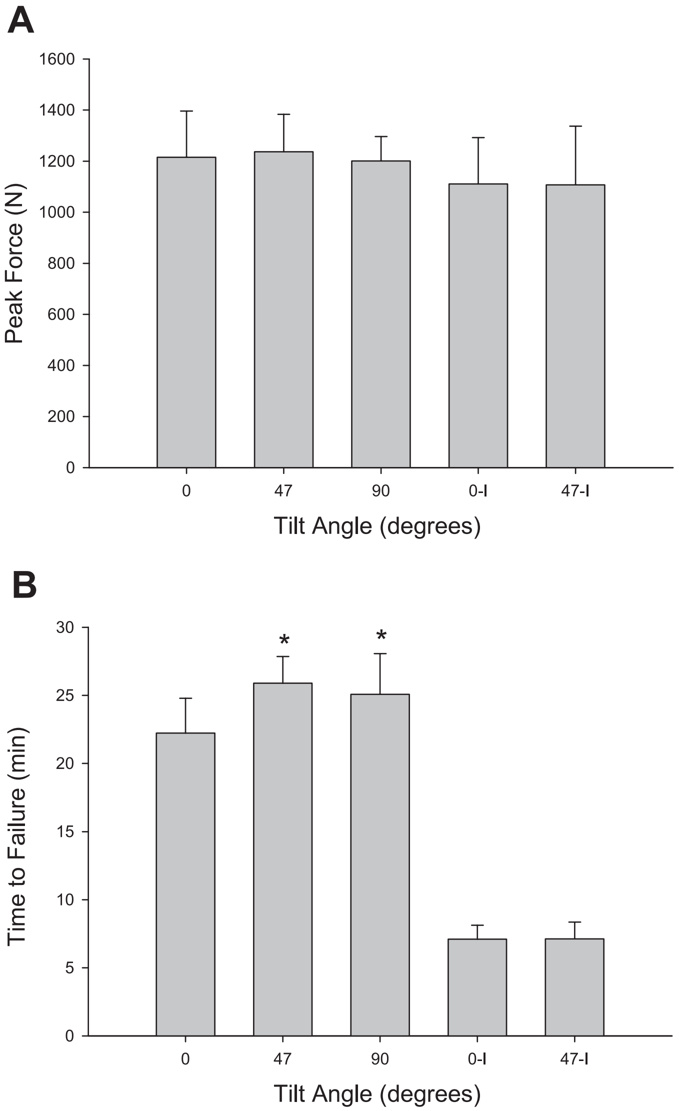

Fig. 2. *Experiment 1*. *A*: maximum force (F_{max}) (means ± SD) under nonischemic and ischemic conditions. *B*: time to failure (means ± SD) during graded exercise under nonischemic ($n = 6$) and ischemic (i.e., 0-I and 47-I) ($n = 4$) conditions.

was calculated, and an example of the leg blood flow responses in one subject, whose data are shown in Fig. 5, to the two tilt angles at 30 and 70% F_{max} are shown in Fig. 6. The parameter estimates, total amplitudes, and MRTs describing the blood flow responses under the four conditions are shown in Table 2. The total amplitude of leg blood flow was twofold higher ($P < 0.05$) at 70 vs. 30% F_{max} in both the horizontal and inclined positions, and these increases can be attributed to the significantly higher amplitudes of the fast (parameter A1) and slow (parameter A2) phases. Increasing the body tilt angle significantly increased the total amplitude at 30% F_{max} but not significantly at 70% F_{max} ($P = 0.19$). However, at both intensities, increasing body tilt resulted in a significantly higher amplitude of the fast phase (A1). As a proportion of the total amplitude, the amplitude of the fast phase (i.e., A1/total amplitude) was significantly greater in the inclined than the supine position at 30% F_{max} (69.5 ± 7.5 vs. 48.7 ± 10.9%) and 70% F_{max} (70.1 ± 17.3 vs. 52.7 ± 12.1%), and the amplitude of the slow phase (A2) as a proportion of the total amplitude was significantly lower in the inclined position at 30% F_{max} (31.2 ± 8.2 vs. 51.3 ± 10.9%) and 70% F_{max} (30.6 ± 17.2 vs. 55.0 ± 19.8%).

The responses of mean arterial pressure, heart rate, and leg volume to the first, middle, and last contraction during exercise under the four conditions are shown in Table 3. Mean arterial pressures at rest and during exercise at either intensity were not affected by tilt angle. Heart rate during rest was significantly greater in the inclined than supine position only at 30% F_{max}, but the change in heart rate (i.e., increase from this resting value) was not affected by tilt angle at either 30 or 70% F_{max}. On average, leg volume (percentage of resting value) was significantly lower ($P < 0.001$) during the first 2 min of exercise at 70% F_{max} in the inclined (99.2 ± 0.5%) than the supine position (99.8 ± 0.3%). This difference was established after the first contraction (Table 3: mean = 98.1 vs. 99.2%), although it was not quite significant ($P = 0.12$). At 30% F_{max}, leg volume was also, on average, lower ($P < 0.001$) throughout the 6 min of exercise in the inclined (99.0 ± 0.2%) vs. the

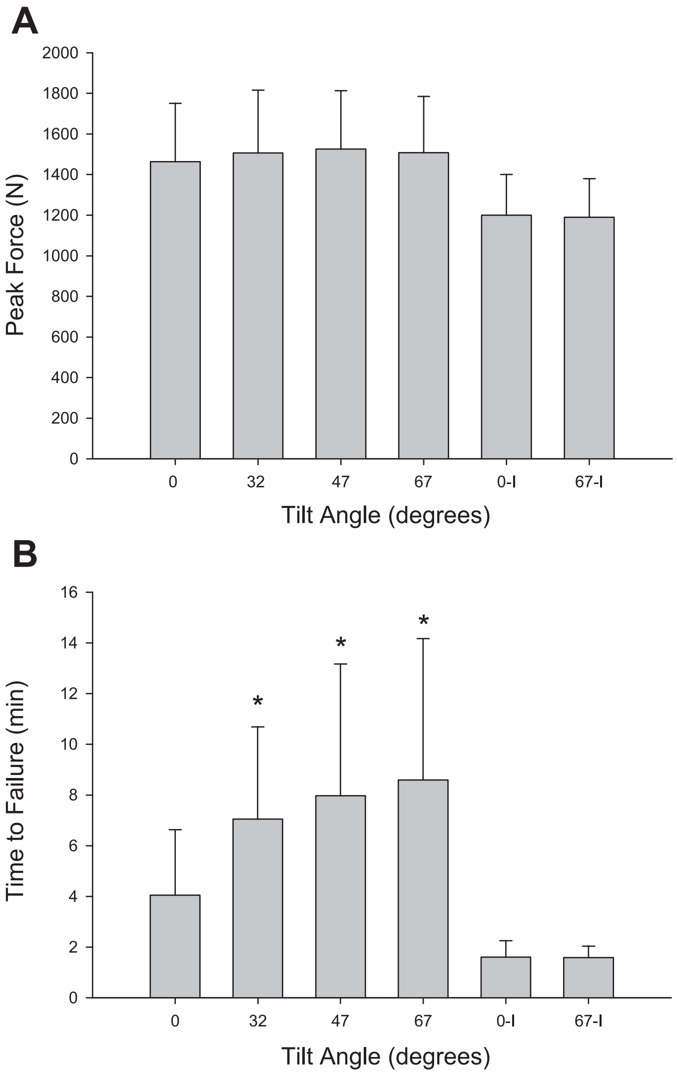

Fig. 3. *Experiment 2*. *A*: F_{max} (means ± SD) under nonischemic and ischemic conditions. *B*: time to failure (means ± SD) during constant-force exercise under nonischemic ($n = 7$) and ischemic (i.e., 0-I and 67-I) ($n = 4$) conditions.

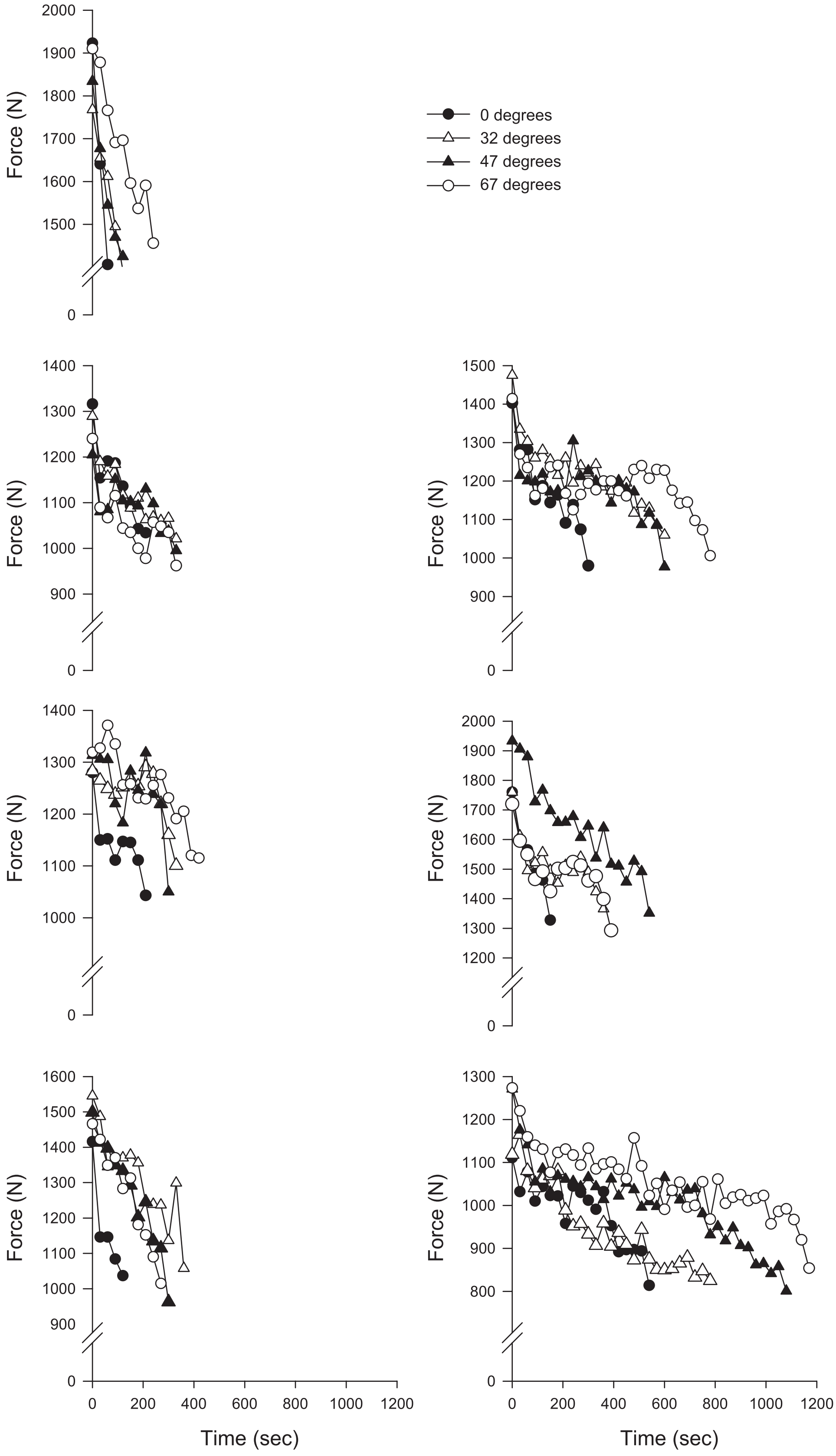

Fig. 4. *Experiment 2*. The decline in peak force during constant-force exercise in 7 subjects (*subjects 1–7*).

Table 1. *Experiment 2*

	Nonischemia (n = 7)				Ischemia (n = 4)	
Tilt angle, °	0	32	47	67	0	67
Parameter						
a, N	1,410±296	1,407±236	1,449±286	1,415±269	1,294±167	1,315±166
b, N/s	−2.46±2.86	−0.92±0.96*	−1.04±1.14*	−0.76±0.66*	−2.50±1.22	−2.38±0.79

Mean ± SD values for parameters *a* [predicted maximum force (F_{max}) at time $t = 0$ s] and *b* (rate of fatigue) obtained from fitting a linear equation ($y = a + bx$, where y is force and x is time) to the decline in maximum force during the constant-force test. *n*, No. of subjects. See Fig. 4 for individual responses. *Significantly different from 0° ($P \leq 0.05$).

supine position (99.3 ± 0.4%), although this difference was not established after the first contraction (Table 3).

DISCUSSION

The main findings of the present study were that the performance of graded exercise was prolonged significantly when the body was inclined from the horizontal position and that fatigue during constant-force submaximal exercise was diminished and time to failure prolonged at tilt angles above zero. In addition, these effects occurred in the absence of a postural effect on muscle strength and were abolished by leg ischemia. This latter finding was consistent with the greater increase in

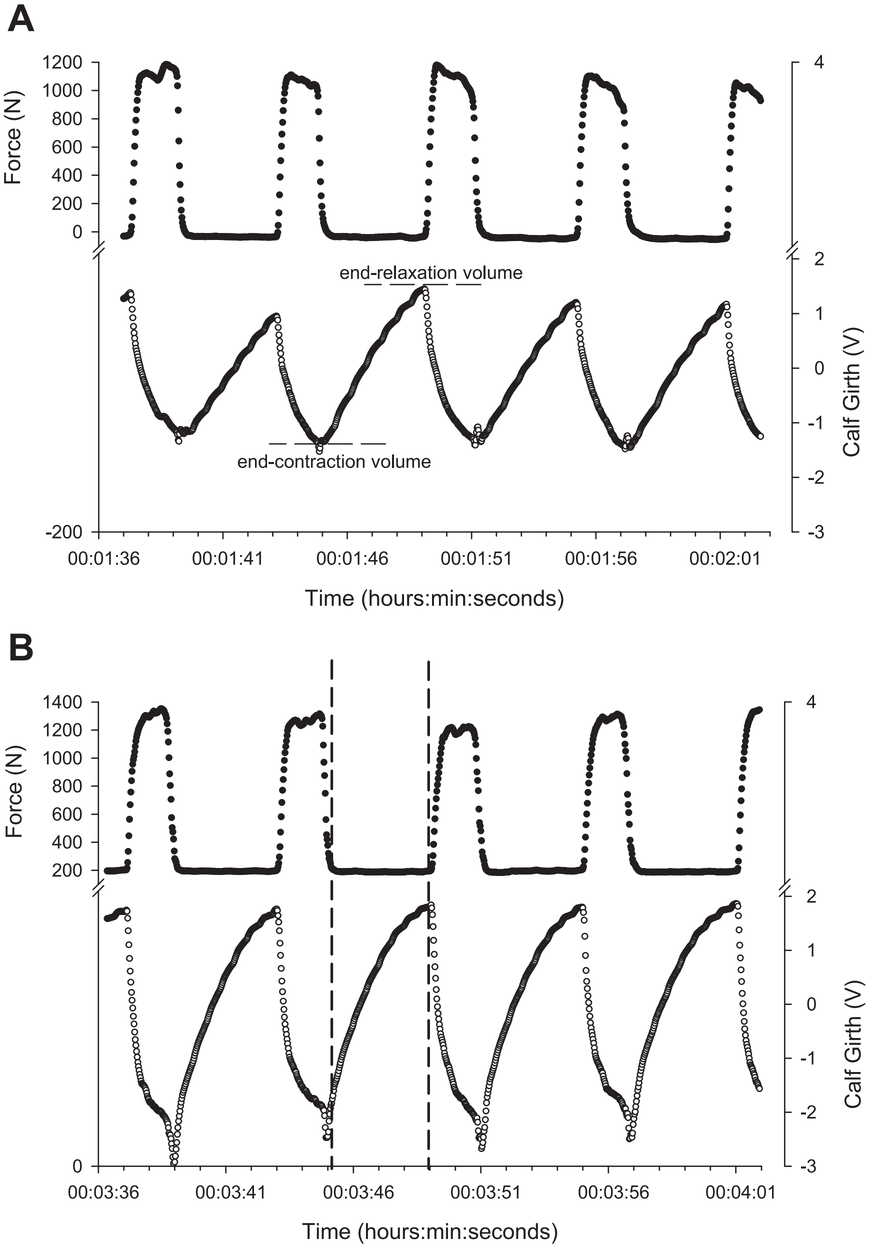

Fig. 5. *Experiment 3*. Force and calf girth traces during the last 30 s of exercise at 70% F_{max} at body tilt angles of 0° (*A*) and 67° (*B*) in 1 subject. *A*: the 2 dashed horizontal lines indicate the volumes at the end of the second contraction (end-contraction volume), shown in this series of force and plethysmography traces, and the end of the period of relaxation after this contraction (end-relaxation volume). It is the change in leg volume between each pair of end-contraction and end-relaxation volumes that is used to calculate blood flow in response to each successive contraction. *B*: the 2 vertical dashed lines indicate where the force trace has returned to a stable baseline and a relaxed state occurs. The relaxed state begins at the *left* line and ends at the *right* line. The change in calf girth during this relaxed state is used to calculate blood flow. Please refer to METHODS for further details and the criteria used to determine the period of the relaxed state.

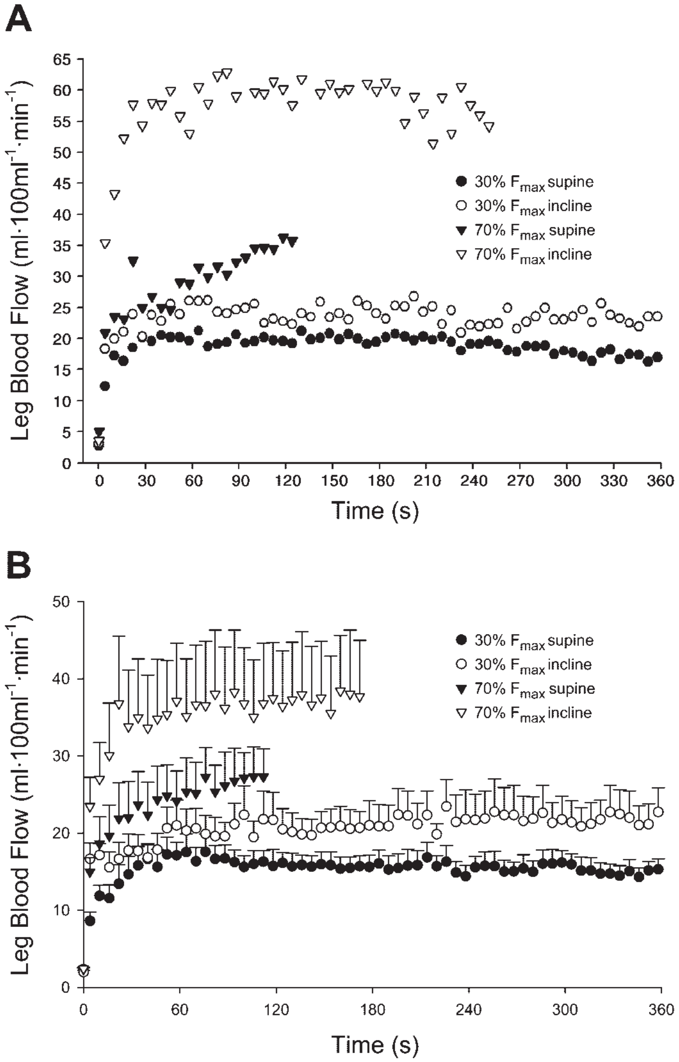

Fig. 6. *Experiment 3*. *A*: leg blood flows during exercise at 2 tilt angles (0 and 67°) at 2 intensities (30 and 70% F_{max}) in 1 subject. *B*: leg blood flows during exercise at 2 tilt angles (0 and 67°) at 2 intensities (30 and 70% F_{max}) in all subjects (means and SE). The times over which the leg blood flows are shown for exercise at 70% F_{max} are limited to the shortest exercise times sustained by the poorest-performing subject.

leg blood flow, particularly during the early period of exercise, when in an inclined position.

Experiment 1: tilt and graded muscle performance. Studies of endurance on maximal graded cycle tests consistently show a modest, yet significant, improvement of 5–10% when the body is tilted upright from a supine position (5, 13, 23). In the present study, subjects completed a similar graded test in the sense that it began at a low effort, the effort was increased in a stepwise manner each few minutes, and the total duration was of the order of 15–30 min. A key difference was that exercise was restricted to a relatively small muscle group. Despite this difference, similar improvements were observed in the two inclined positions (47 and 90°) compared with the horizontal position (i.e., 17% increase; Fig. 2*B*). These findings extend those made previously for cycle ergometry and demonstrate that the postural effects on performance of graded exercise are similar for exercise involving relatively small or large masses of muscle.

Experiment 2: tilt, muscle fatigue, and endurance during constant-force exercise. Before this study, there were no data on the effect of postural change on muscle fatigue or endurance during voluntary, constant-load exercise involving lower limb muscles. The intensity of the constant-force test in the present study was relatively high (70% F_{max}) and closely approximated the highest achieved during the graded test (i.e., 62–70% F_{max}). Time to failure on this test was increased by up to 100% when the tilt angle was increased from the horizontal (Fig. 3*B*), and the rate of fatigue was decreased by >50% (Fig. 4, Table 1). These effects were much larger than those observed for graded exercise (Fig. 2*B*).

The intensity of constant-load exercise used in the present study would have been close to that which maximizes O_2 uptake and leg blood flow, given that this intensity is above that which subjects failed at during progressive incremental exercise in the supine position and equal to the maximal intensity achieved during the same test in the inclined positions. At such an intensity, the ability to resist fatigue and increase time to failure would probably be more dependent upon blood flow than might be observed at much lower intensities, such as those during the earlier phases of the graded test. Given that the postural effect on performance is likely to be mediated, at least in part, by its effects on leg blood flow (see later discussion), the relatively larger postural effect observed for high-intensity, constant-load exercise (than graded exercise) might be attributed to the relatively stronger influence of blood flow on performance of this type of exercise.

For both graded and constant-force exercise, a plateau in the postural effect on endurance or fatigue was observed at a body tilt angle of ~32–47°. For graded exercise, the mean values for time to failure at 47 and 90° were almost identical. However, it should be noted that some subjects complained of discomfort (i.e., testicular compression) during parts of the test at 90° that could have limited performance. For this reason, during the

Table 2. *Experiment 3*

Condition: Force Tilt Angle	*a*, ml·100 ml^{-1}·min^{-1}	A1, ml·100 ml^{-1}·min^{-1}	A2, ml·100 ml^{-1}·min^{-1}	Total Amplitude, ml·100 ml^{-1}·min^{-1}	τ1, s	τ2, s	MRT, s
30% F_{max} 0°	3.16±0.21	6.17±2.58*†	6.47±2.46*	12.65±4.02*†	2.3±1.5	24.0±10.6	17.1±7.2
30% F_{max} 67°	3.20±0.13	12.72±4.25	5.84±3.26	18.43±6.75*	2.9±3.7	67.2±41.5	27.4±19.6
70% F_{max} 0°	3.39±0.60	13.59±5.21†	14.24±6.28	25.95±8.71	1.8±2.0	82.2±98.0	57.9±81.8
70% F_{max} 67°	3.06±0.38	23.63±13.68	10.67±8.81	34.16±18.55	1.8±1.9	52.9±38.4	19.1±18.6

Parameter estimates, total amplitudes, and mean response times (MRT) of the blood flow responses under the four exercise conditions. A1 and A2, amplitudes for fast and slow phases, respectively; τ1 and τ2, time constants of fast and slow phases, respectively. *Significantly different from higher intensity at same tilt angle ($P \leq 0.05$). †Significantly different from inclined position (67°) at same intensity ($P \leq 0.05$).

Table 3. *Experiment 3*

	Tilt Angle, °	30% F_{max}				70% F_{max}			
		Rest	First	Middle	End	Rest	First	Middle	End
MAP, mmHg	0	92±7	92±8	93±7	96±8	89±5	87±7	90±3	94±4
	67	87±4	89±8	88±7	91±7	88±8	89±9	91±9	92±5
HR, beats/min	0	66±8*	69±8*	72±7*	73±5*	71±9	77±10	85±10	88±11
	67	80±8	81±10	83±10	86±5	76±12	83±13	87±11	94±15
Leg volume, %	0	100	98.7±1.1	98.9±2.0	100.0±1.2	100	99.2±0.5	100.1±1.5	100.2±1.9
	67	100	98.7±0.7	99.0±1.0	99.0±1.3	100	98.1±1.2	99.2±2.0	99.6±2.8

Mean arterial pressure (MAP), heart rate (HR), and leg volume (percentage of rest) before and during exercise at two intensities and two tilt angles. First, middle, and end: first, middle, and last contractions, respectively, across the exercise period. See RESULTS for further analysis of leg volume data. *Significantly different ($P \leq 0.05$) from 67° at the same time and intensity.

subsequent constant-force test, we limited the highest tilt angle to 67° during which subjects did not complain of discomfort, other than that felt local to the exercising muscle group. Despite this, no significant difference in exercise time or rate of fatigue was observed between the three inclined positions. These data on graded and constant-force exercise suggest that the postural effect on muscle fatigue and endurance is probably limited to a range of ~30–50° beyond the horizontal, at least for the plantar flexors.

However, it is worth noting that the average time to failure during constant-force exercise at 67° was higher than that observed at 32°, and the relative difference (i.e., 21%) was similar to the significant postural effect observed for graded exercise (i.e., 0° vs. 47 or 90°). Figure 4 illustrates the considerable variation in postural effect on muscle fatigue and time to failure among the seven subjects, with some subjects almost doubling their exercise times at 67° compared with 32°. Although the present study cannot shed light on the causes of this individual variation, these data suggest that the range of tilt angles across which muscle performance is affected might vary widely among subjects, and this deserves further attention.

Because the ability to resist fatigue and endure exercise depends, to some extent, on the strength of muscle relative to the force generated, it was possible that postural effects on exercise performance in this and other studies were mediated partly by effects on muscle strength. In the present study, we tested the effect of body tilt angle on calf muscle strength before the performance of both the graded and constant-force tests and observed no effect (Figs. 2*A* and 3*A*). In addition, the *y*-intercept of the linear function that describes the fatigue response during constant-force exercise (i.e., parameter *a*, Table 1), which is a predicted value of muscle strength, was also unaffected by body tilt. Consequently, the postural effects on muscle fatigue and endurance observed in the present study cannot be attributed to concomitant effects on muscle strength.

Although the physiological explanation of the postural effect on muscle fatigue and endurance is far from clear, the literature suggests that both blood flow (6, 28) and perhaps O_2 supply (8, 9, 15) to working muscle are involved. As a first step to exploring this in the human calf, we reasoned that, if blood flow plays an important role, then preventing arterial blood flow into the leg should reduce the postural effect that we and others observed. In the present study, endurance in the horizontal and inclined positions was not different for either graded (Fig. 2*B*) or constant-force exercise (Fig. 3*B*) when performed under ischemia. This demonstrates that the postural effects observed under conditions of normal blood flow were completely abolished under ischemic conditions, suggesting that arterial blood flow into the leg mediates the postural effect on calf muscle fatigue and endurance.

Experiment 3: leg blood flow, intensity, and tilt angle. The main aim of *Experiment 3* was to test the effect of body tilt on leg blood flow during high-intensity exercise, so as to provide insight into the tilt-induced reduction in muscle fatigue and improvement in endurance observed in *Experiment 2*. As expected on the basis of other findings (14, 15, 21, 25), the fast phase was significantly higher in the inclined than the supine position (70% F_{max}: Table 2), whereas the slow phase tended to be lower, although not significantly ($P = 0.17$). As a proportion of the total amplitude of the response, the fast phase contributed a significantly higher fraction in the inclined vs. supine position (70 vs. 53%), despite the total amplitude being 30% higher ($P = 0.19$) in the inclined position. These data demonstrate that leg blood flow is increased over the first few minutes of calf exercise in the inclined position and that this increase is entirely due to the greater amplitude of the fast phase that is essentially complete after the first contraction.

The relatively greater muscle blood flow in response to the first contraction (i.e., fast phase) in the inclined position at 70% F_{max} can be explained by either a greater increase in vascular conductance and/or perfusion pressure. An increase in vascular conductance is effected through vasodilation, and more recent evidence suggests that vasodilation can occur within 1–2 s after the cessation of a brief (1 s) muscle contraction (17, 25, 27). Given that the duration of each muscle contraction during exercise in *experiment 3* was 2 s and the following relaxation period during which an average flow was calculated was 4 s, vasodilation can contribute to the blood flow response to the first contraction. During supine exercise, for example, the 400% increase in blood flow in response to the first contraction (parameter A1) relative to resting levels must be primarily explained by an increase in vascular conductance, assuming that perfusion pressure only rises by ~25% from 70 to 88 mmHg, where venous pressures at rest and after the first contraction are taken to be 15 and 0 mmHg, respectively (see below for further discussion). Importantly, however, it is thought that the degree of vasodilation and rise in vascular conductance are not altered by limb position (25). Consequently, it is unlikely that the amplifying effect of body tilt on the fast response of blood flow in *experiment 3* is explained by a greater increase in vascular conductance per se. Rather, as described below, the difference in the magnitude of the initial hyperemic response (A1, Table 2) can be explained by a gravity-induced difference in arterial pressure acting at the level of the working muscle, perhaps in concert with vasodilation (25).

When the body is tilted up, a hydrostatic pressure is applied to blood in vessels below the level of the heart and in proportion to the vertical distance between that volume of blood and the heart. The hydrostatic pressure acting at the midpoint of the calf in the inclined position in *experiment 3* can be estimated using the equation, ρgh, where ρ is density of blood at a hematocrit of 0.45 (1,056 kg/m^3, Ref. 3), g is gravitational acceleration (9.81 m/s^2), and h is the vertical distance between the heart and midpoint of the calf (0.92 m for a man 1.85 m tall tilted at 67°). Based on these values, the hydrostatic pressure acting at the midpoint of the calf in the inclined position is ~70 mmHg, adding to the mean arterial pressure (87 mmHg) prevailing at rest (Table 3) and possibly also raising venous pressure at the same level by a similar amount (7). There are two contrasting views on how this gravity-induced increase in arterial pressure results in an increase in perfusion pressure and muscle blood flow after a single muscle contraction, and the controversy revolves about the role of venous pressure and the muscle pump (11).

Folkow et al. (7) first showed that body tilting increased calf perfusion during calf exercise and attributed the effect to the "muscle pump." They proposed that, in an inclined position, the hydrostatic pressure that acts on the arterial and venous side at rest is removed from the venous side upon relaxation of the muscle, when the venous blood within the muscle has been expelled by the preceding contraction. This results in a greater increase in perfusion pressure than would be observed in the supine position where no hydrostatic component to blood pressure is present. If it is assumed that venous pressure is reduced to zero immediately after the first contraction, as others have done (24), tilting to 67° would increase the perfusion pressure acting across the calf muscle by 80%, a value very similar to the tilt effect on the amplitude of the fast phase of leg blood flow at 70% F_{max} (i.e., 74% increase). A central idea in this explanation is that any change in venous pressure affects perfusion pressure (10, 11). In contrast, others invoked the "vascular waterfall" model of the circulation, developed to explain blood flow in collapsible arteriolar vessels (18), to argue that the perfusion pressure cannot be influenced by changes in venous pressure and the muscle pump (16, 22). In this model, the downstream pressure that affects perfusion pressure is an arteriolar "critical closing pressure" that is influenced by vascular tone (4, 18). If this is true under the conditions of the present study, and given that vascular tone in the lower limbs is likely to increase with body tilt (15), then it is the gravity-induced rise in arterial pressure (80%) in the presence of vasodilation that results in the larger increase in blood flow in the inclined position, independent of any effect of venous emptying and lowering of venous pressure.

Muscle force production during repeated contractions is very sensitive to changes in perfusion pressure and blood flow, at least at moderately high to high intensities of effort. For example, during electrically induced submaximal contractions (40% maximal voluntary contraction) of the adductor pollicis muscle in humans, a sudden elevation in the perfusion pressure induced by rapidly lowering the arm below heart level significantly increased muscle force production within seconds after the change in limb position (6, 28). Similarly, in a canine hindlimb preparation, a sudden reduction in blood flow to contracting muscles (60–70% maximal oxygen uptake) significantly reduced force within just a few seconds (8). Under these latter conditions, the effect of blood flow on muscle force production was mediated entirely by the availability of O_2 and, possibly, its effect on known inhibitors of muscle force production (i.e., ADP and P_i) (8). These data demonstrate that muscle fatigue during moderately intense exercise is very sensitive to changes in muscle blood flow and that this effect is likely to be mediated by changes in O_2 delivery. In the present study (*experiment 2*), a significant lowering of F_{max} was already evident at 30 s of high-intensity exercise, and tilting to inclined positions blunted this effect. It is tempting to suggest that this early effect of body tilting on fatigue is due to its positive effect on the fast phase of leg blood flow. Beyond this early period of exercise, fatigue continued to occur in both positions but at a slower rate when in the inclined position. This might be due to the fact that blood flow remained relatively higher for several minutes after the fast phase was complete (Fig. 6).

To our knowledge, this is the first study to use venous occlusion plethysmography to measure limb blood flow, contraction by contraction, during exercise. Although we have yet to compare plethysmographic estimates of limb blood flow with those measured using Doppler ultrasound, several lines of evidence from the present study support the utility of plethysmography as a measure of limb blood flow during exercise. First, at the intensities of exercise used in the present study (i.e., 30 and 70% F_{max}), the exercise-induced rise in blood flow into the leg occurs during relaxation (2, 20), and because the limb is fixed and relaxed during relaxation, the change in limb volume, and thus blood flow, over this period can be accurately measured. Second, the amplitude of the blood flow response was increased twofold by a 2.3-fold increase in intensity (Table 2), and this is consistent with the linear relationship between exercise intensity and blood flow (1, 19). Third, that the tilt effect on the fast phase of the blood flow response, at both intensities, can be entirely explained by the calculated gain in perfusion pressure supports the accuracy of the flow estimates. Fourth, others have shown that inclining the upper torso increases the amplitude of the fast phase, and decreases the amplitude of the slow phase, of femoral arterial flow during knee extensor exercise performed at a moderate intensity (15). This is supported by the present findings at the moderate intensity (Table 2). Collectively, these findings support the validity of our blood flow estimates.

One limitation of venous occlusion plethysmography is that blood flow into the limb is reduced progressively as the venous volume rises across consecutive cardiac cycles (26). This results in a curvilinear blood flow response during the whole period of relaxation (Fig. 5) and may lower blood flow compared with nonoccluded conditions. This effect would be more pronounced at higher blood flows when venous volume and pressure rise more quickly during relaxation. This might help explain why the total amplitudes of the blood flow response to exercise in the supine and inclined position were not statistically different ($P = 0.19$) at 70% F_{max} and that the difference in total amplitude at this intensity (32%) was slightly less than that observed at the lower intensity (46%). In addition, because flow after each contraction was measured over several cardiac cycles (see Fig. 5), there is a possibility that this enabled the veins to fill completely and venous pressure to rise to a level that caused venous outflow, which is more likely to occur when arterial inflow is very high. Such an effect is more likely at 70% F_{max} in the inclined position, and, if it occurred, it would contribute to an underestimate of the true leg blood flow and the lack of significant difference in the total amplitude of blood flow between the inclined and supine positions at the high intensity. We tried to reduce this possibility by using a cuff pressure that prevented venous outflow and a decline in the strain gauge tracing during the relaxation periods, something we had established through a pilot study performed prior to *experiment 3*. Other factors, such as a higher measurement error at higher flows and a ceiling effect for leg blood flow, might also explain this lack of statistical difference. Methodological studies focused on the reproducibility and accuracy of plethysmographic estimates of blood flow measured across the maximum range possible are required to clarify these issues.

In conclusion, this study has demonstrated that the endurance of calf muscle is improved as the body (and leg) is tilted from the horizontal to an inclined, head-up position, that this effect occurs in the absence of an effect on strength, and that it depends on an intact peripheral circulation. We then showed that the fast phase of leg blood flow is increased considerably in a tilted position and that this effect contributed entirely to the positive effect of body tilting on leg blood flow observed during several minutes of exercise. This suggests that the tilt-induced increase in the fatigue resistance and endurance of calf muscle is mediated by a larger response of blood flow to the first contraction.

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