J. Physiol. (1952) 117, 391–400

ON THE BLOOD FLOW THROUGH RHYTHMICALLY CONTRACTING MUSCLE BEFORE AND DURING RELEASE OF SYMPATHETIC VASOCONSTRICTOR TONE

By H. BARCROFT, A. C. DORNHORST, H. M. McCLATCHEY AND J. M. TANNER

From the Department of Physiology, Queen's University Belfast, and the Medical School, St Thomas's Hospital, London

(*Received* 8 *February* 1952)

The blood flow through a muscle is characteristically increased during, and for some time after, its activity. In 1938 Grant showed that this increase did not depend on the integrity of the sympathetic nerves, and he attributed it to the local action of metabolites. Nevertheless, the sympathetic nerves do influence muscle blood flow, for Barcroft, Bonnar, Edholm & Effron (1943) have shown that when vasomotor activity is inhibited the blood flow through resting muscle is conspicuously increased. One might reasonably expect that a muscle entering exercise in this condition would be at an advantage in that the necessary level of blood flow would be more quickly reached, and thus a smaller metabolic debt incurred.

The experiments now to be described were done to study the effect of releasing sympathetic tone on the circulation in muscle during rhythmic exercise.

Principle of the method

It was assumed that the extent and duration of the hyperaemia following a standard exercise would be directly related to the concentration of metabolites in the muscles at the end of the exercise, and so would be inversely related to the total amount of metabolically available blood passing through the muscle during activity (Grant, 1938; Abramson, Katzenstein & Ferris, 1941). If this amount were increased by some procedure then, other things being equal, the post-exercise debt would be reduced. To see if release of vasoconstrictor tone had this effect, post-exercise blood flows were recorded under standard conditions before and after releasing vasomotor tone in the muscles by warming the body, and the results were compared.

EXPERIMENTAL

The subjects were healthy males aged 20–45 years. Experiments were done on the calf of the leg and the forearm.

Calf: series 1. Experiments were done on fourteen subjects. Room temperature was 20° C ± 1°. A water-filled plethysmograph was fitted to the calf of the leg, and the temperature of the water was maintained at 34° C (Barcroft & Edholm, 1943, 1945). The subject rested on a couch for 30 min while blood flows were recorded at 3 min intervals. He then performed five exercises lasting ¼, ½, ¾, 1 and 2 min respectively. To perform an exercise the subject pressed down a weighted pedal with the ball of his foot once per sec to the sound of a metronome. The apparatus has been described by Barcroft & Dornhorst (1949). After pressing down the pedal the subject relaxed the calf muscles as completely as possible and the weighted pedal restored the foot to its original position. The exercise was performed simultaneously with both feet on separate pedals to avoid movements of the pelvis. Records of the blood flow were made 0, 10, 20, 30, 45, 90 and 120 sec after each of the five exercises.

After doing the exercises and recording of the blood flows the subject was warmed to release vasoconstrictor tone in the calf muscles. The body was covered with blankets and one arm was immersed to above the elbow in water at 45° C. An initial period of about ¾ hr was allowed for the release of constrictor tone (Barcroft, Bonnar & Edholm, 1947); during this time the continued arrival of warm venous blood from the arm usually raised the body temperature to about 100° F. The five exercises were then repeated, the blood flows being recorded after each. Body heating continued during this procedure. Throughout the whole experiment the temperature of the water surrounding the calf in the plethysmograph was kept at the original temperature of 34° C.

To enable the reliability of the results to be tested, each subject returned on another day and his post-exercise blood flows were recorded once more. The second part of the experiment in which the body was heated was not done.

Calf: series 2. Experiments were done on nine subjects. Exercises of 1, 2, 4 and 8 min were performed before and during body heating. In the case of the longer exercises recording of the post-exercise blood flows continued for 5 min. In other respects the procedure was the same as in series 1.

Forearm. A small series of experiments was done on four subjects. A water-filled plethysmograph was fitted to the upper part of the forearm; the temperature was kept at 34° C throughout the experiment. After an initial rest with recording of the forearm blood flows the subject performed three exercises each lasting 3 min. To do an exercise he gripped two vertical bars about 1½ in. apart and squeezed them together. The proximal one was rigidly fixed, the distal one raised a suitably weighted lever. The manoeuvre was repeated every second to the sound of the metronome. Between contractions the muscles were relaxed as completely as possible. The blood flows were recorded 0, ¼, ½, ¾, 1, 1½, 2, 3, 4 and 5 min after each exercise. After this the subject's body was heated by covering with blankets and immersing both feet to above the ankles in water at 45° C and after ¾ hr while the heating continued, the exercises were repeated and the blood flows recorded for the second time.

RESULTS

Calf: series 1. Table 1 shows the blood flow recorded on each of the fourteen subjects after one of the exercises, the ¾ min one. The averaged results are also shown. Considerations of space prevent the presentation of similarly complete data for the blood flows recorded on each of the subjects after the other exercises.

Fig. 1 shows the averaged results of the whole series. Comparison of the results obtained on the first (circles and continuous lines) and second (dots and broken lines) occasions shows that they were in very good agreement.

TABLE 1. Blood flow in the calf after exercising calf muscles for $\frac{3}{4}$ min

(Blood flow ml./100 ml. calf/min)

Subject no.	Time in sec from end of exercise: 0	10	20	30	45	60	90	120
	Before heating body							
1	12·9	9·6	5·7	3·9	3·4	2·7	2·5	3·0
2	15·0	15·6	12·0	7·5	4·5	4·2	3·3	3·3
3	12·9	10·8	6·6	4·2	3·3	2·1	2·4	2·1
4	13·5	9·9	8·7	5·1	3·9	3·6	3·0	3·3
5	7·0	10·6	5·0	3·6	2·6	2·2	2·2	2·0
6	21·3	10·8	7·2	5·1	3·9	3·1	2·5	2·2
7	40·5	18·0	11·0	6·7	4·6	4·5	4·2	4·7
8	15·3	9·4	7·4	3·1	3·3	3·4	3·0	2·8
9	16·0	13·2	8·8	6·4	5·2	5·6	5·1	5·0
10	22·5	16·5	14·4	7·8	6·0	5·4	4·5	4·3
11	13·8	8·1	4·9	4·7	3·7	3·4	2·9	3·1
12	13·3	8·5	4·3	4·1	3·3	3·7	3·1	3·5
13	16·4	13·0	10·8	8·6	6·8	5·6	6·1	6·3
14	11·0	8·8	6·6	6·7	3·3	1·9	2·3	2·4
Av.	**16·5**	**11·6**	**8·1**	**5·5**	**4·1**	**3·7**	**3·4**	**3·5**
	During body heating							
1	17·4	11·7	6·3	6·6	3·9	4·0	3·9	3·9
2	15·0	14·7	13·5	10·8	8·4	6·3	6·0	6·3
3	27·3	18·6	14·1	10·8	8·4	7·8	9·0	7·5
4	18·6	15·0	11·7	8·4	7·5	6·6	5·4	—
5	18·2	12·8	8·4	8·3	6·8	6·3	6·5	7·0
6	20·1	13·8	13·2	10·8	7·8	8·4	9·0	9·3
7	27·0	17·6	11·0	9·0	7·6	7·7	6·7	6·7
8	25·5	12·6	12·8	11·5	9·8	8·5	9·5	9·5
9	18·0	19·0	15·4	13·3	12·0	11·1	11·0	10·3
10	41·1	27·0	20·4	19·5	14·9	14·7	9·0	9·2
11	18·0	12·0	9·6	6·1	7·2	6·4	6·7	6·2
12	19·5	13·6	11·6	10·2	9·0	9·5	10·1	9·1
13	20·3	15·0	12·2	11·2	9·8	9·6	8·8	9·2
14	12·7	10·8	9·2	8·5	7·8	6·2	6·8	6·5
Av.	**21·4**	**15·3**	**12·1**	**10·4**	**8·6**	**8·1**	**7·7**	**7·7**
	Repeat without heating body							
1	20·4	15·6	11·7	7·8	6·0	4·2	4·0	3·9
2	22·5	12·0	10·8	5·1	4·2	3·0	3·0	3·0
3	24·0	18·3	12·3	7·5	4·6	4·8	4·0	4·2
4	24·0	21·0	16·5	8·1	6·0	5·4	3·7	3·9
5	11·7	10·5	7·2	3·0	2·4	2·1	1·8	1·5
6	18·0	12·6	6·0	5·8	5·0	2·4	2·4	2·6
7	24·4	13·4	7·4	4·8	3·8	3·2	3·2	3·2
8	7·8	7·8	5·4	4·8	4·8	4·3	2·6	1·8
9	18·0	15·6	11·4	9·0	5·4	5·4	5·7	5·4
10	12·9	9·0	9·9	6·0	5·4	4·2	4·2	3·9
11	15·6	12·6	8·1	6·0	3·9	3·6	3·6	3·3
12	11·1	7·6	5·4	4·3	3·0	3·3	2·4	3·0
13	26·0	19·2	13·4	11·8	9·6	9·2	7·8	8·8
14	10·6	9·0	6·3	3·5	3·1	2·0	2·0	2·0
Av.	**17·6**	**13·2**	**9·4**	**6·3**	**4·8**	**4·1**	**3·6**	**3·6**

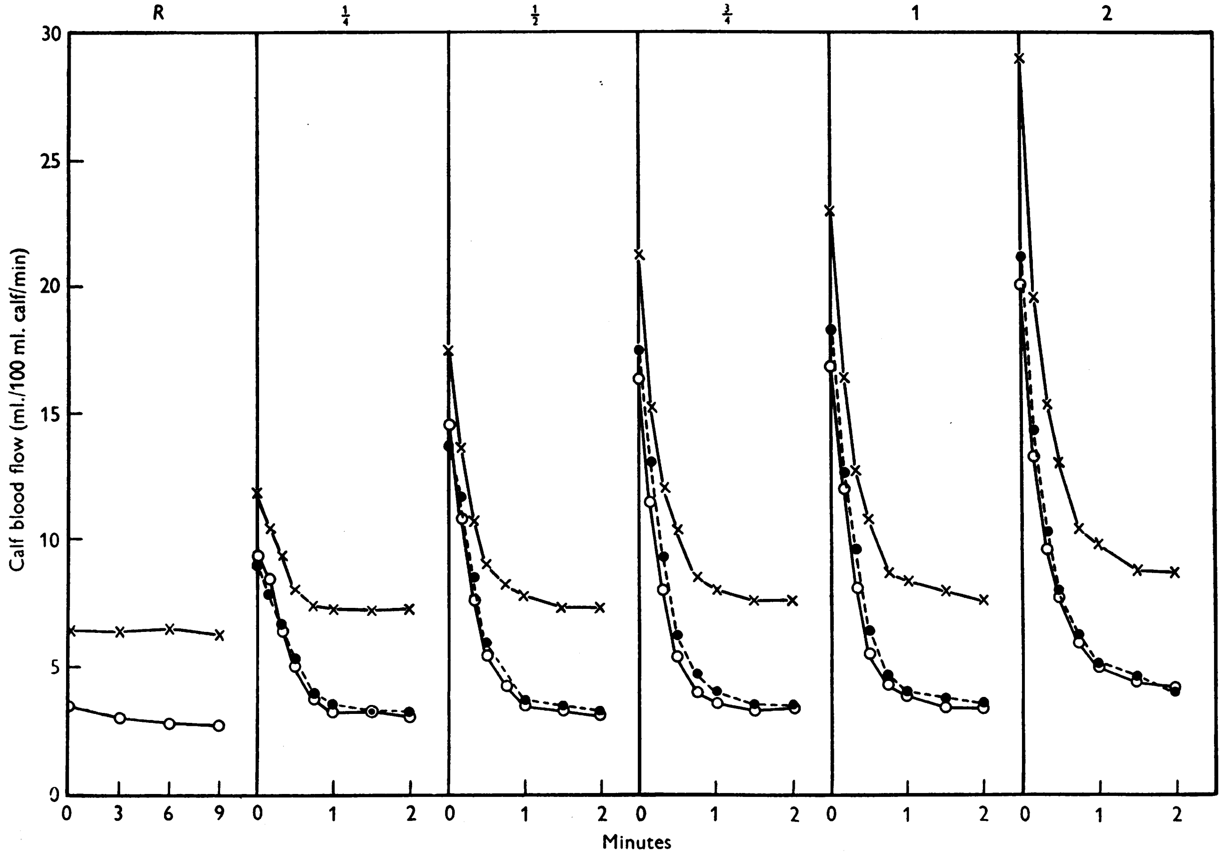

Fig. 1. Calf, series 1. Blood flow at rest, *R*, and following exercises lasting for $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$, 1 and 2 min, performed before (○——○) and during (×——×) heating the body; and repeated on another day without heating of the body (●- - -●). Averages of results obtained on fourteen subjects.

Comparison of the resting blood flows on the unheated subjects in the first experiment (circles and continuous lines) with those obtained later in the same experiment during body heating (crosses and continuous lines) shows that the blood flow was about doubled by releasing vasoconstrictor tone, as found previously by Barcroft *et al.* (1947).

Apart from the difference in the general level of the flow the post-exercise blood flows obtained before and during heating of the body look very much alike. So as to compare them more closely they have been redrawn in Fig. 2 after subtraction of the respective post-exercise resting rates (which will be seen in each case under the letter *R* in Fig. 2). Warming the body did not cause any consistent alteration in the pattern of the post-exercise blood flows. The blood debts (areas under the curves) after each of the exercises will be seen under the letter *D* in Fig. 2. After the $\frac{1}{4}$ and $\frac{1}{2}$ min exercises the debt was slightly less during heating, after the $\frac{3}{4}$ min one it was the same, and after the 1 and 2 min ones it was slightly more.

The results of all the exercises done before heating have been averaged, as have the results of all those done during heating; the two resulting curves are shown in Fig. 4. The averaged resting blood flows have been subtracted in each case. The agreement between the two curves is remarkable; the difference in the debts is only 3%, the debt contracted during heating the body being slightly the greater.

Calf: series 2. Fig. 3 shows the averaged results of the post-exercise blood flows obtained on nine subjects, after subtraction of the respective average rates of flow. The blood debt recorded during heating was slightly increased after the 1, 2 and 4 min exercises and slightly reduced after the 8 min one. Fig. 4 shows the averages of all the post-exercise flows obtained before and during heating respectively after subtraction of the average resting rates in each case. As in series 1, the behaviour of the circulation after exercise was the same whether the body was being warmed or not. The difference in the blood debts was only 5%, the debt contracted during warming the body being slightly the greater.

Forearm. Experiments were done on four subjects only. Fig. 4 shows the averaged results of all the post-exercise blood flows recorded before and after heating respectively. The resting rates have been subtracted. In this case, too, warming the body had little effect on the blood debts. That recorded during heating was the smaller by 10%.

The results obtained on the calf and forearm may be summarized as follows. Warming the body did not produce any consistent change in the pattern of the post-exercise hyperaemia. During the warming the debt was slightly increased in the 1, 2 and 4 min calf exercises and in the forearm ones. It was slightly reduced in the $\frac{1}{4}$, $\frac{1}{2}$ and 8 min calf exercises and in the averaged results of all the calf exercises in series 1 and 2.

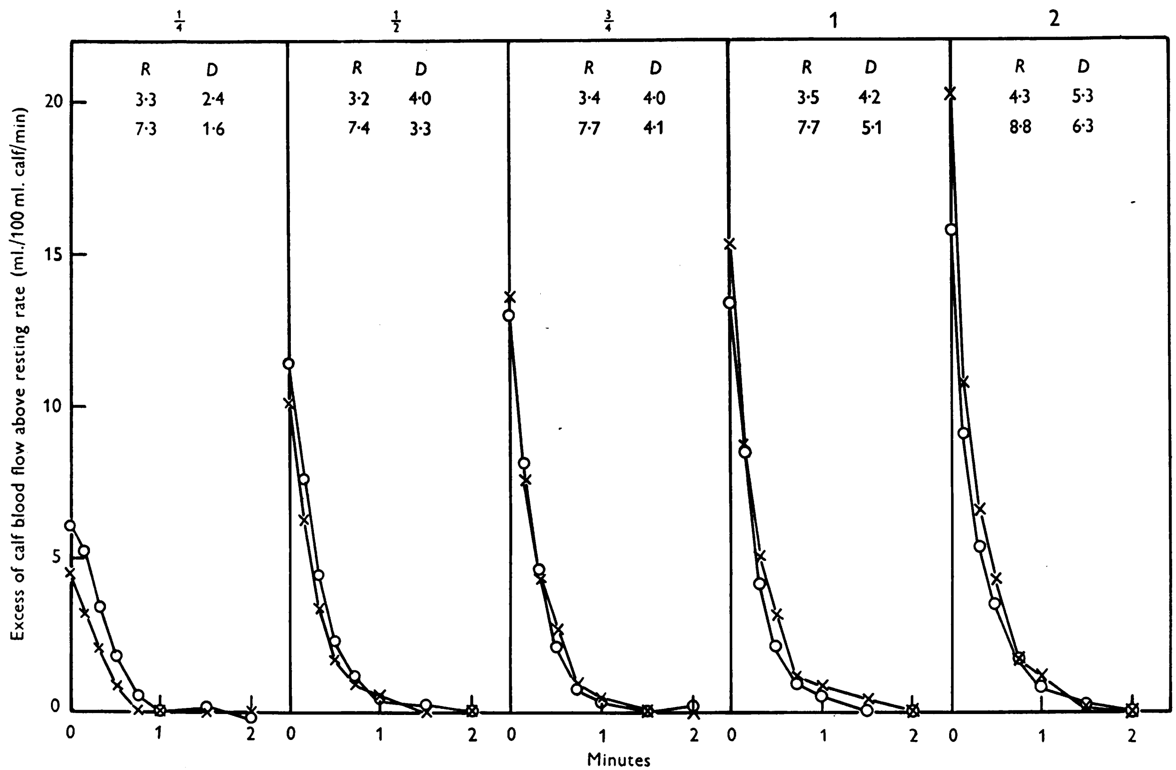

Fig. 2. Calf, series 1. Excess of blood flow over the resting rate recorded after exercises lasting ¼, ½, ¾, 1 and 2 min, performed before (○——○) and during (×——×) heating of the body. *R*, post-exercise resting rates before and during heating the body respectively. *D*, blood debts, in ml., before and during heating the body respectively. From the same data as Fig. 1.

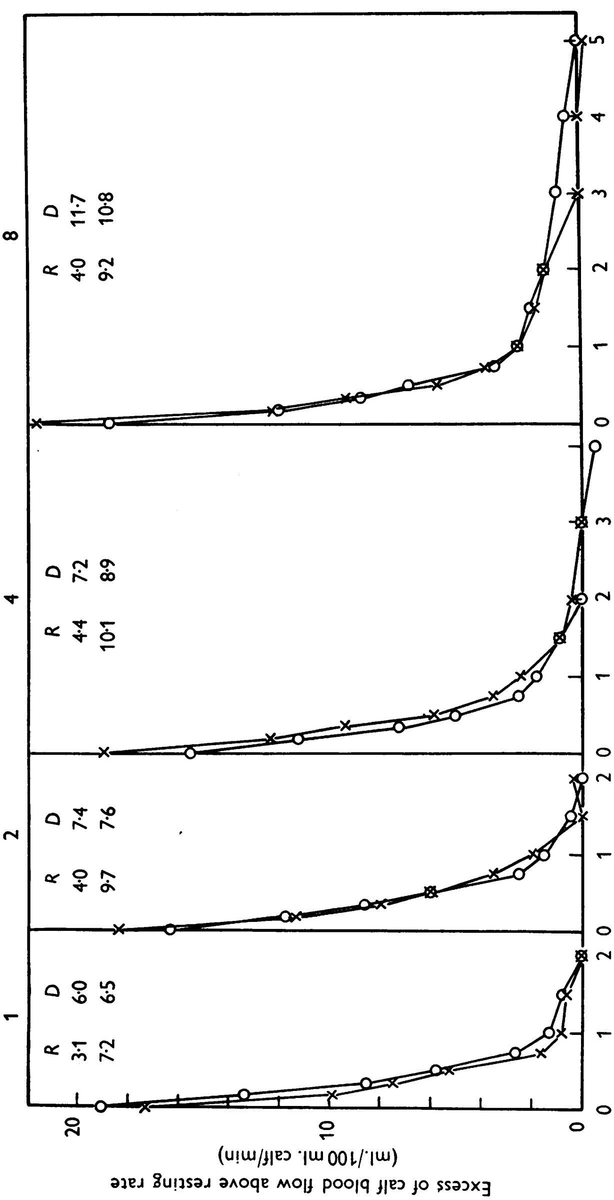

Fig. 3. Calf, series 2. Excess of blood flow over the resting rate recorded after exercises lasting for 1, 2, 4 and 8 min, performed before (○——○) and during (×——×) heating the body. *R*, post-exercise resting rates before and during heating the body respectively. Averages of results obtained on nine subjects.

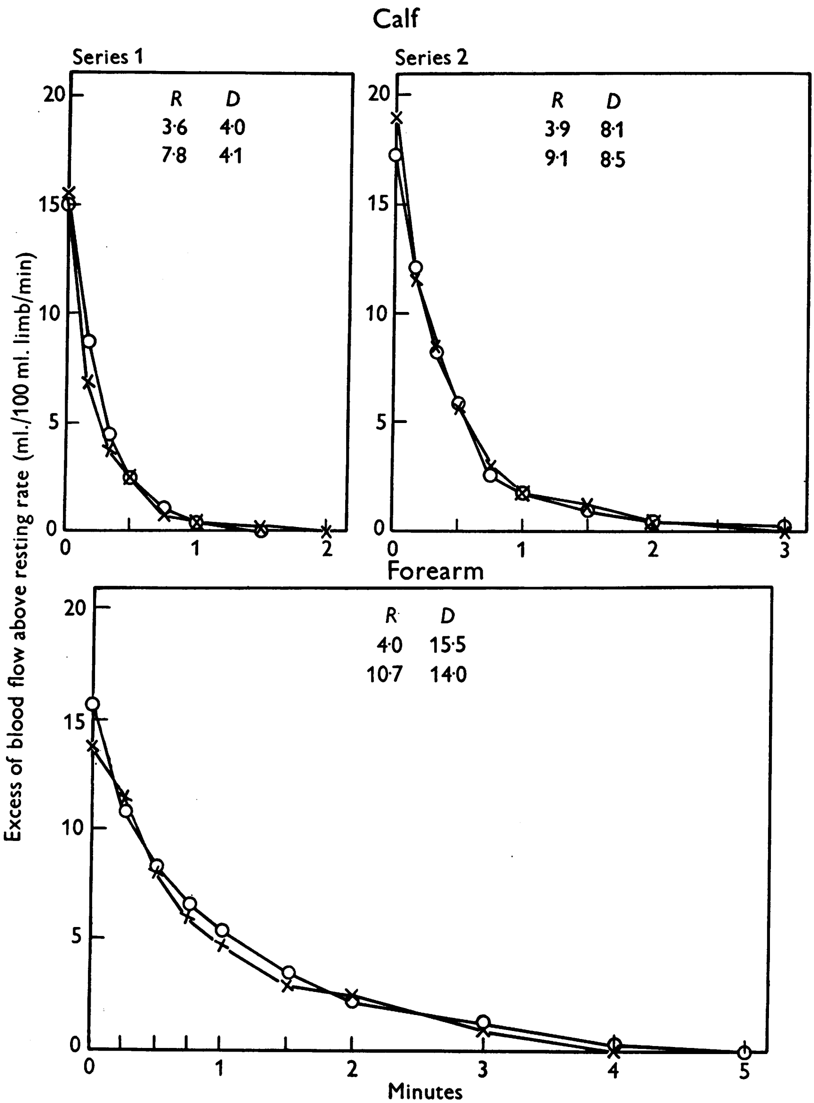

Fig. 4. Composite curves of excess blood flow over resting rates of flow recorded following exercises performed before (○——○) and during (×——×) warming the body. *R*, post-exercise resting rates before and during warming the body respectively. *D*, blood debts, in ml., before and during warming the body respectively.

DISCUSSION

On the assumption outlined in the introduction, we expected that the blood debts would be consistently less when the exercise took place during warming the body. Figs. 1–4 make it plain that this was not the case. Indeed, very little difference can be seen between the debts obtained before and during heating;

what difference there is appears to be of the same general order as that between the debts when the exercises are done without heating on different days (Fig. 1).

As warming the body and releasing tone did not affect the blood debt, it is unlikely that it can have affected the concentration of the metabolites in the muscles at the end of the exercises or the metabolically available blood flow through them during activity. Therefore it is unlikely that the vasomotor centre plays any useful part in the regulation of the changes that occur in muscle blood flow as a result of rhythmic activity.

The only escape from this conclusion appears to be the following one. Warming the body as described raises the mouth temperature $\frac{1}{2}$–1° C. Conceivably this might bring into play two new factors, each of them tending to alter the blood debt.

(i) The release of tone by the vasomotor centre causing increase in muscle blood flow during exercise, tending to reduce the debt.

(ii) Increase in the temperature of the muscles causing increased metabolism during exercise, tending to increase the debt.

The equal and opposite action of these two factors might account for the fact that warming the body does not alter the blood debt. However, as warming the body by the method used in these experiments did not affect the resting blood flow in the sympathectomized forearm (Barcroft *et al.* 1947) it seems unlikely that it would have done either in the forearm or calf in the present investigation.

It is indeed curious that releasing sympathetic tone and increasing muscle blood flow (Barcroft *et al.* 1943, 1947) should have no effect whatsoever on the debt contracted during exercise. With sympathetic tone released, the muscle entered and emerged from exercise with a flow greater than that of the control, and it seems almost inevitable that the flow during exercise was higher too. Yet this surplus was apparently no advantage. The explanation of this is unknown. It is, however, possible that there are two separate circulations in muscle, one under sympathetic control and unrelated to muscle metabolism, the other subservient to metabolic needs. On this hypothesis the basal level of the circulation in skeletal muscle could be controlled by the vasomotor centre while the circulatory changes during activity proceeded quite independently. However, the anatomical evidence for two circulations is inconclusive. There is no suggestion of their existence in Spalteholtz's classical description of muscle blood vessels (1888). On the other hand, Zweifach (1949; personal communication, 1951) has recently seen minute arterio-venous anastomoses in muscle and found them to be controlled by sympathetic nerves. It is important to see if this can be confirmed.

While we have shown that a decrease of the normal degree of sympathetic tone does not facilitate the local circulatory adjustments in exercising muscle, it does not follow that an increase of sympathetic tone above the normal would not prove a hindrance, since in these circumstances larger vessels supplying both types of circulation might be constricted.

SUMMARY

1. The effect of releasing sympathetic vasoconstrictor tone on the circulation in the muscles of the calf and forearm during rhythmic exercise has been examined.

2. Sympathetic tone in the muscle vessels was released by slightly raising the body temperature.

3. This did not reduce the blood debt following standard exercises.

4. On the assumption that the blood debt is inversely related to the amount of metabolically available blood passing through the muscle during activity, it is concluded that this amount is not increased by release of sympathetic tone.

5. It is therefore unlikely that the local circulatory response to rhythmic contraction is facilitated by inhibition of nervous vasoconstrictor tone.

6. The basal level of the circulation in skeletal muscle is controlled by the vasomotor centre, but the changes taking place during activity appear to proceed quite independently. A possible explanation is suggested.

The authors wish to thank the subjects for their assistance, also Dr R. H. Sloane and Mr J. Wylie for the design and construction of the apparatus used for the calf exercises, and the Medical Research Council for financial aid.

The experiments performed at Queen's University, Belfast, were done in January 1948.

REFERENCES

Abramson, D. I., Katzenstein, K. H. & Ferris, E. B., Jr. (1941). *Amer. Heart J.* **22**, 329.

Barcroft, H., Bonnar, W. McK. & Edholm, O. G. (1947). *J. Physiol.* **106**, 271.

Barcroft, H., Bonnar, W. McK., Edholm, O. G. & Effron, A. S. (1943). *J. Physiol.* **102**, 21.

Barcroft, H. & Dornhorst, A. C. (1949). *J. Physiol.* **109**, 402.

Barcroft, H. & Edholm, O. G. (1943). *J. Physiol.* **102**, 5.

Barcroft, H. & Edholm, O. G. (1945). *J. Physiol.* **104**, 161.

Grant, R. T. (1938). *Clin. Sci.* **3**, 157.

Spalteholtz, W. (1888). *Abh. sächs. Ges. (Akad.) Wiss.* **14**, 509.

Zweifach, B. W. (1949). Factors regulating blood pressure. *Transactions, Third Conference, Josiah Macy Foundation.* New Jersey: Progress Associates.