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CAROTID AND CARDIOPULMONARY BARORECEPTOR CONTROL OF SPLANCHNIC AND FOREARM VASCULAR RESISTANCE DURING VENOUS POOLING IN MAN

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SUMMARY

1. This study evaluated the contribution of carotid and cardiopulmonary baroreceptors to reflex splanchnic and forearm vascular adjustments during venous pooling in man. We compared (*a*) responses to lower body suction which produces venous pooling with (*b*) responses to lower body suction plus simultaneous application of neck suction. The rationale was that simultaneous application of neck suction, which stretches carotid baroreceptors, would minimize the contribution of carotid baroreceptors to circulatory adjustments produced by lower body suction.

2. Lower body suction at 40 mmHg decreased central venous pressure and arterial pulse pressure and increased forearm vascular resistance (plethysmography), splanchnic vascular resistance (indocyanine green dye clearance), and heart rate. Simultaneous application of neck suction prevented the tachycardia and most of the splanchnic vasoconstriction during lower body suction, but did not significantly attenuate the forearm vasoconstriction.

3. The major findings in this study are first, that the splanchnic vasoconstrictor response during venous pooling is mediated primarily through carotid baroreceptors, and secondly, that carotid and cardiopulmonary baroreceptors produce strikingly contrasting and non-uniform regional vascular responses during venous pooling. Cardiopulmonary baroreceptors exert the predominant influence on forearm vascular resistance, but appear to have only a minor influence on splanchnic vascular resistance. Carotid baroreceptors produce most of the splanchnic vasoconstriction during venous pooling, but have a minor role in the forearm vasoconstriction.

INTRODUCTION

When blood is pooled in leg veins during interventions such as upright tilting and lower body suction, arterial pressure is maintained by reflex tachycardia and vasoconstriction. Although the tachycardia and vasoconstriction usually have been attributed to reflexes arising in high pressure baroreceptors in the carotid sinus, two lines of evidence conflict with this concept. First, several studies (Johnson, Rowell,

Neiderberger & Eisman, 1974; Roddie, Shepherd & Whelan, 1957; Zoller, Mark, Abboud, Schmid & Heistad, 1972) suggest that cardiopulmonary baroreceptors contribute significantly to forearm vascular responses during changes in venous return in man. Secondly, Roddie & Shepherd (1957, 1958) reported that decreases in carotid sinus pressure in man do not produce forearm vasoconstriction. These investigators speculated that decreases in carotid sinus pressure might produce splanchnic vasoconstriction in man (Roddie & Shepherd, 1958), but did not measure splanchnic blood flow. Johnson *et al.* (1975) attributed splanchnic vasoconstriction during venous pooling to both cardiopulmonary and carotid baroreceptors. However, their study of responses to ramp lower body suction did not exclude the possibility that splanchnic vasoconstriction might originate primarily from cardiopulmonary as opposed to carotid baroreceptors.

The purpose of this study was to compare the relative contribution of carotid and cardiopulmonary baroreceptors in the control of splanchnic and forearm vascular resistance during venous pooling in man. We studied effects of (1) neck suction, (2) lower body suction at 40 mmHg, and (3) simultaneous application of neck suction and lower body suction.

Lower body suction produces tachycardia and vasoconstriction by decreasing central venous pressure and systemic arterial pulse pressure and thus activating reflexes arising in cardiopulmonary and carotid baroreceptors (Johnson *et al.* 1974; Zoller *et al.* 1972).

Neck suction decreases tissue pressure and increases transmural pressure and stretch on carotid baroreceptors (Eckberg, Cavanaugh, Mark & Abboud, 1975; Eckberg, Abboud & Mark, 1976; Eckberg, 1976; Kober & Arndt, 1970). This produces reflex bradycardia and hypertension. In contrast to pharmacologic methods for studying baroreceptor reflexes, neck suction permits study of reflex vasodilator as well as chronotropic responses. This feature of neck suction and the recent development by Eckberg *et al.* (1975) of an improved neck suction device provided the opportunity to determine the relative contribution of carotid baroreceptors in the control of splanchnic and forearm vascular resistance during venous pooling in man.

The rationale was that simultaneous application of neck suction during lower body suction would minimize the contribution of carotid baroreceptors to the circulatory adjustments during lower body suction. Thus, by comparing responses to lower body suction with responses to simultaneous neck and lower body suction, we might estimate the contribution of carotid and cardiopulmonary baroreceptors to the automatic adjustments.

The results demonstrate that in man carotid baroreceptors result in most of the splanchnic vasoconstriction during venous pooling and that cardiopulmonary and carotid baroreceptors each produce strikingly non-uniform regional vasomotor responses.

METHODS

Methods. Fifteen healthy men, age 23–29 yr, were studied in the supine position in a warm room (26–27 °C). With superficial local anaesthesia, a polyethylene cannula (PE 90; o.d. 1·3 mm) was inserted percutaneously into a brachial artery for measurement of systemic arterial

pressure and sampling of arterial blood. Central venous pressure was measured with a cannula inserted into an antecubital vein and advanced into an intrathoracic vein. Arterial and venous pressures were measured with pressure transducers. Heart rate was calculated from the R-R interval of an electrocardiogram and expressed as beats/min.

Forearm blood flow. A mercury-in-silastic strain gauge plethysmograph was used to measure forearm blood flow (Zoller *et al.* 1972). This method of measuring limb blood flow has been discussed by Greenfield, Whitney & Mowbray (1963). The arm was elevated and supported so that the proximal part of the forearm was approximately 10 cm above the anterior chest wall. The strain gauge was applied 4–8 cm distal to the elbow to measure changes in forearm volume. A pneumatic cuff proximal to the elbow was inflated intermittently above venous pressure to produce venous occlusion. A cuff on the wrist was inflated to suprasystolic pressures during measurements to exclude the hand circulation from measurements. Forearm blood flow was calculated from the rate of increase of forearm volume during venous occlusion and expressed as ml./min. 100 ml. forearm volume. Forearm vascular resistance was calculated by dividing mean arterial pressure by forearm blood flow.

Splanchnic blood flow. Spanchnic blood flow was measured from the clearance of indocyanine green dye (ICG) using the constant infusion method as described and discussed by Rowell and colleagues (Johnson *et al.* 1974; Rowell, Detry, Profant & Wyss, 1971; Rowell, 1975, 1976).

After obtaining a blood sample for a blank, 12·5 mg ICG was injected I.V. followed by a sustained infusion at 0·5 mg/min. After a 20 min equilibration period, 3 ml. blood samples were obtained at 4 min intervals during control, experimental and recovery periods. Plasma concentrations of ICG were determined spectrophotometrically.

Measurements of splanchnic flow with the dye technique have compared closely with flowmeter measurements of combined hepatic arterial and portal venous flows in dogs over a range of flows produced by various interventions (Rowell, 1975).

The three major considerations with the constant infusion method for measuring splanchnic blood flow are: (1) the properties of the indicator, (2) the sites for blood sampling, and (3) corrections for differences between delivery of indicator to the organ and the actual removal rate of indicator if blood flow changes during the study.

ICG is a satisfactory indicator since it is cleared exclusively by the liver and has a high extraction efficiency (Fox & Wood, 1960).

Brachial arterial blood was obtained to measure the concentration of ICG flowing to the splanchnic region. Since Rowell *et al.* (1971, 1972) have demonstrated that hepatic extraction of ICG is approximately 85% and does not change significantly during changes in splanchnic flow with lower body suction, we did not catheterize the hepatic veins, but instead assumed a constant hepatic extraction of 85% ICG. This method of measuring splanchnic flow assuming a constant hepatic extraction of ICG of 85% has been employed previously by Johnson *et al.* (1974). The validity of this approach is supported by the observation that average control values in our study compare favourably to control values obtained by Rowell (1976) in studies where hepatic venous concentration was measured, not assumed. Furthermore, decreases in flow during lower body suction at -50 mmHg have been virtually identical when splanchnic flow was calculated using measured (Rowell *et al.* 1972) or assumed (Johnson *et al.* 1974) extraction of ICG. Accordingly, although measurement of hepatic venous concentration theoretically improves the accuracy of the measurement, previous studies have demonstrated that in normal subjects during activation of baroreceptor reflexes flow can be measured accurately from arterial concentrations and assumed hepatic extraction without the risk of catheterizing the hepatic veins.

When splanchnic flow changes during the course of serial measurements, as it did in this study, the dye infusion rate (I) no longer equals the dye removal rate (R). However, the constant infusion method can be utilized under these conditions if R can still be calculated (Rowell, 1976). This can be performed using the rate of change of dye concentration during the sampling interval. This calculation was utilized in our study. Splanchnic blood flow (s.b.f.) was calculated as $R/0{\cdot}85\ C_A$ (1-haematocrit). R was calculated from I minus the rate of change of dye concentration during the sampling interval $\{(C_{A2}-C_{A1})/\Delta t\}$ multiplied by the estimated plasma volume (0·045 L/kg body wt.). C_{A1} and C_{A2} indicate the dye concentration of systemic arterial blood at the beginning and end, respectively, of a sampling interval, and C_A indicates the average of C_{A1} and C_{A2}. Δt refers to the sampling interval of 4 min.

Lower body suction. Venous pooling was produced by application of lower body suction or subatmospheric pressure to subject's body below the iliac crests (Johnson *et al.* 1974; Zoller *et al.* 1972).

Neck suction. Stretch of carotid sinus baroreceptors was produced by neck suction (Eckberg *et al.* 1975, 1976; Eckberg, 1976) using a new device which permits rapid application of suction and is not uncomfortable. The subjects did not describe or display adverse physiological or emotional reactions to levels of neck suction employed in the study.

Design. In our initial experiments, we measured forearm blood flow, heart rate, arterial pressure and central venous pressure during (1) neck suction at 20 and 40 mmHg for 60–120 sec each, (2) lower body suction at 20 and 40 mmHg for 60 and 120 sec each, and (3) simultaneous application of neck suction at 40 mmHg and lower body suction at 20 and 40 mmHg for 60–120 sec in eight subjects.

Since results of these initial experiments indicated that carotid baroreceptors play a minor role in forearm vasoconstrictor responses during venous pooling and since other investigators (Roddie & Shepherd, 1958) had previously speculated that carotid baroreceptors might play a greater role in control of the splanchnic circulation, we measured splanchnic as well as forearm blood flow in the second series of experiments in seven other subjects. Splanchnic blood flow, forearm blood flow, and arterial pressure were measured during (1) neck suction at 40 mmHg for 6 min, (2) lower body suction at 40 mmHg for 6 min, and (3) simultaneous application of neck suction and lower body suction for 6 min. Each intervention was preceded by a control period and followed by a recovery period of 10 min each. The duration of interventions in this series was longer than in the first series because of requirements of the method for measuring splanchnic blood flow. The order of interventions in this and the initial series of experiments was randomized.

The studies were performed after obtaining the approval of the Human Subjects Review Committee and the informed, written consent of the subjects.

Statistical comparisons were performed with the *t* test for paired data (Steel & Torrie, 1960). Values of $P \leqslant 0{\cdot}05$ were taken as statistically significant.

RESULTS

Responses to neck suction. Arterial pressure and heart rate decreased during neck suction (Table 1). Forearm and splanchnic blood flow did not change significantly (Tables 1 and 2). Forearm and splanchnic vascular resistance tended to decrease during neck suction at 40 mmHg, but these changes were small and not statistically significant (Tables 1 and 2). Central venous pressure averaged $5{\cdot}9 \pm 0{\cdot}3$ (S.E.) mmHg before and $5{\cdot}9 \pm 0{\cdot}4$ mmHg during neck suction at 20 mmHg and $5{\cdot}8 \pm 0{\cdot}3$ mmHg before and $5{\cdot}7 \pm 0{\cdot}4$ mmHg during neck suction at 40 mmHg.

Responses to lower body suction. Lower body suction at 40 mmHg decreased forearm and splanchnic blood flow and increased forearm and splanchnic vascular resistance (Table 3 and Figs. 1 and 2). Central venous pressure decreased from $6{\cdot}0 \pm 0{\cdot}5$ to $1{\cdot}2 \pm 0{\cdot}5$ mmHg ($P < 0{\cdot}05$). Mean arterial pressure did not change significantly (Table 3), but pulse pressure decreased from $56{\cdot}4 \pm 3{\cdot}9$ mmHg to $50{\cdot}6 \pm 4{\cdot}6$ mmHg during lower body suction ($P < 0{\cdot}05$). Heart rate increased from 55 ± 3 to 63 ± 3 beats/min ($P < 0{\cdot}05$).

Effects of simultaneous neck and lower body suction. Simultaneous application of neck suction did not significantly attenuate forearm vasoconstriction during lower body suction (Table 3 and Figs. 2 and 3) but it prevented most of the splanchnic vasoconstriction during lower body suction (Table 3 and Fig. 2). Simultaneous application of neck suction also prevented the tachycardia during lower body suction; heart rate averaged 57 ± 2 in control and 56 ± 2 beats/min during combined neck and

TABLE 1. Responses to neck suction

	Neck suction (20 mmHg)			Neck suction (40 mmHg)		
	Control	Neck suction (early)	Neck suction (late)	Control	Neck suction (early)	Neck suction (late)
Heart rate (beats/min)	52·5 ± 3·0	43·1* ± 2·9	47·0* ± 2·4	51·5 ± 2·7	37·6* ± 2·4	46·4* ± 2·1
Mean arterial pressure (mmHg)	90·8 ± 3·1	81·9* ± 2·8	85·5* ± 3·0	90·4 ± 2·7	77·2* ± 2·9	80·6* ± 3·8
Forearm blood flow (ml./min.100 ml.)	4·6 ± 0·6	3·9 ± 0·5	3·8 ± 0·3	4·4 ± 0·7	4·0 ± 0·5	3·8 ± 0·4
Forearm vascular resistance (mmHg.ml./min.100 ml.)	23·3 ± 3·3	23·4 ± 2·7	23·8 ± 2·6	25·3 ± 4·4	21·3 ± 2·0	22·5 ± 2·8

Entries are mean ± S.E. for eight subjects in the first series of experiments. Splanchnic blood flow was not measured in these experiments.

* Values significantly different from control ($P < 0·05$).

Early response for heart rate refers to maximal prolongation of *R-R* interval expressed as beats/min; this usually occurred in the 1st or 2nd interval after application of neck suction. Early response for arterial pressure and forearm blood flow refers to values obtained during the 1st 15 sec. Late response indicates values obtained during the last 45 sec.

TABLE 2. Comparison of splanchnic and forearm vascular responses to neck suction

	Neck suction (40 mmHg)		
	Control	Neck suction	Recovery
Splanchnic blood flow (l./min)	1·81 ± 0·23	1·78 ± 0·25	1·90 ± 0·21
Splanchnic vascular resistance (mmHg.l./min)	56·8 ± 8·1	50·1 ± 7·5	56·3 ± 7·7
Forearm blood flow (ml./min.100 ml.)	3·41 ± 0·46	3·56 ± 0·51	3·42 ± 0·51
Forearm vascular resistance (mmHg.ml./min.100 ml.)	29·5 ± 4·2	25·1 ± 3·8	27·8 ± 3·1
Mean arterial pressure	90·6 ± 3·4	78·2 ± 2·5*	88·6 ± 3·5

Entries are mean ± S.E. for seven subjects in the second series of experiments.

* Value significantly different from control ($P < 0·05$).

Control values for splanchnic blood flow in this series of experiments are average of two consecutive measurements before intervention (3rd and 7th min before). Values during neck suction are the average of two measurements during the intervention (1st and 5th min). Recovery values are average of two consecutive measurements after intervention (3rd and 7th min after). There were no significant differences between the two consecutive measurements which were averaged in any period.

Control values for forearm blood flow are average of four consecutive measurements during the 3rd min before intervention. Values during neck suction are average of measurements during 1st and 5th min. Recovery values are measurements during 3rd min after intervention.

lower body suction. Central venous pressure decreased from 5·7 ± 0·2 to 0·7 ± 0·6 mmHg during combined neck and lower body suction ($P < 0·05$); this decrease was not significantly different from that during lower body suction alone.

DISCUSSION

Lower body suction and neck suction. The finding that neck suction prevented most of the splanchnic vasoconstriction during lower body suction suggests that

TABLE 3. Comparison of splanchnic and forearm vascular responses to venous pooling (lower body suction) and combined neck suction and venous pooling

	Lower body suction (40 mmHg)		Neck suction (40 mmHg) Lower body suction (40 mmHg)	
Splanchnic blood flow (l./min)				
Control	1·68 ± 0·18		1·68 ± 0·21	
Response		−0·42 ± 0·04*		−0·31 ± 0·09*
Recovery	1·57 ± 0·15		1·59 ± 0·19	
Splanchnic vascular resistance (mmHg/l. per min)				
Control	58·7 ± 7·0		60·0 ± 80·5	
Response		+24·1 ± 4·3*		+5·1 ± 4·4
Recovery	64·8 ± 8·4		64·2 ± 8·1	
Forearm blood flow (ml./min.100 ml.)				
Control	3·36 ± 0·48		3·57 ± 0·39	
Response		−0·92 ± 0·16*		−1·32 ± 0·19*
Recovery	3·53 ± 0·72		3·50 ± 0·48	
Forearm vascular resistance (mmHg.ml./min.100 ml.)				
Control	30·7 ± 4·7		28·2 ± 4·0	
Response		+12·5 ± 1·9*		+10·5 ± 2·3*
Recovery	32·2 ± 5·8		30·4 ± 4·4	
Mean arterial pressure (mmHg)				
Control	90·6 ± 3·5		90·4 ± 4·7	
Response		+2·3 ± 1·1		−12·0 ± 2·4*
Recovery	92·9 ± 4·6		93·4 ± 4·5	

Entries are mean ± S.E. for seven subjects in the second series of experiments. Response indicates value during intervention minus control value. See legend to Table 2.

* Significant ($P < 0·05$) responses.

carotid baroreceptors produce most of the splanchnic vasoconstriction during venous pooling in man. Since neck suction did not significantly attenuate the forearm vasoconstriction during lower body suction, we concluded that the forearm vasoconstriction resulted mainly from reflexes originating in cardiopulmonary baroreceptors.

We should consider the possibility that the forearm vasoconstriction resulted from reflexes originating in aortic baroreceptors in response to the fall in arterial pressure. Experiments in dogs suggest that aortic baroreceptors do not contribute appreciably to reflex adjustments during decreases in arterial pressure (Dampney, Taylor & McLachan, 1971; Donald & Edis, 1971; Edis, 1971; Hainsworth, Ledsome

& Carswell 1970). In particular, aortic baroreceptors do not appear to be very responsive to decreases in pulse pressure (Angell James & Daly, 1970). In addition, the finding that neck suction prevented tachycardia during lower body suction suggests that aortic baroreceptors did not contribute appreciably to the reflex responses during venous pooling.

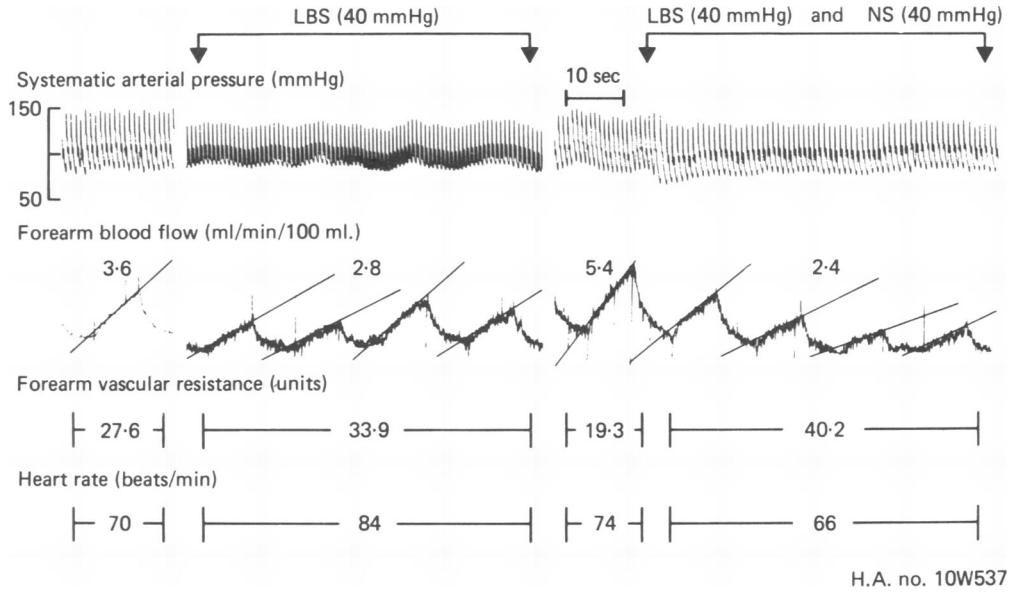

Fig. 1. Comparison of responses to lower body suction (LBS) and to combined lower body suction and neck suction (NS) in one subject. Simultaneous application of neck suction prevented tachycardia, but did not inhibit the forearm vasoconstriction which occurred during lower body suction alone. Values for forearm blood flow during interventions are average of the four determinations during the intervention.

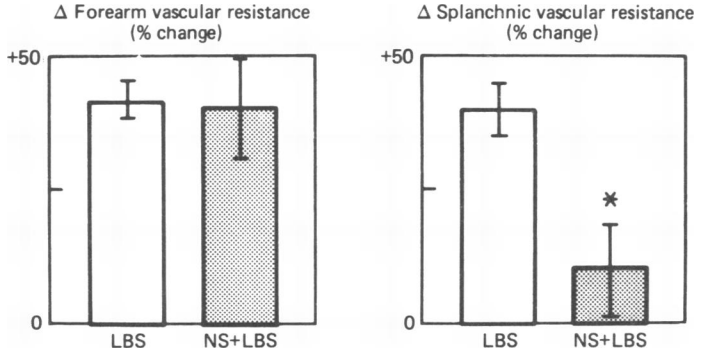

Fig. 2. Comparison of splanchnic and forearm vascular responses to lower body suction (LBS) and to combined lower body suction and neck suction (NS). Entries are mean ± S.E. for seven subjects in second series of experiments. Response (Δ) indicates value during intervention minus control value. As shown in Table 3, control values before LBS did not differ significantly from control values before combined NS and LBS. Asterisk indicates a significant ($P < 0{\cdot}05$) difference between response to LBS *vs.* response to combined NS and LBS.

We also considered the possibility that lower body suction might have triggered reflex forearm vasoconstriction by distending and stimulating sensory receptors in the kidney. However, this seems unlikely since stimulation of renal afferent fibres reportedly inhibits sympathetic activity (Ueda, Uchida & Kamisaka, 1967; Aars & Akre, 1970). Thus, although we cannot completely exclude a role for aortic or other visceral reflexes it seems most likely that the forearm vasoconstriction resulted mainly from cardiopulmonary baroreceptors.

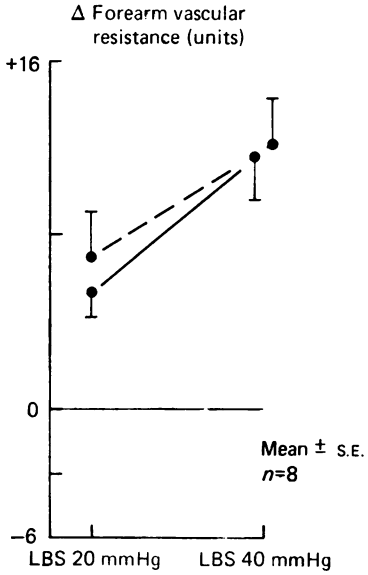

Fig. 3. Comparison of increases in forearm vascular resistance during lower body suction (LBS) at 20 and 40 mmHg alone (continuous line) and during combined lower body suction and neck suction (interrupted line). Responses (Δ) indicate values during intervention minus control value. Neck suction did not decrease the forearm vasoconstrictor response to either level of lower body suction.

Studies in animals have demonstrated baroreceptors in atria (Paintal, 1953), ventricles (Mark, Abboud, Schmid & Heistad, 1973; Öberg & Thorén, 1972; Sleight, 1964), and pulmonary vessels (Coleridge & Kidd, 1963; Ledsome & Kan, 1977). These receptors signal via medullated and non-medullated afferent fibres in vagal (Thorén, Donald & Shepherd, 1976) or sympathetic (Malliani, Lombardi, Pagani, Recordati & Schwartz, 1975) pathways. Receptors in atria, ventricles, and lung with non-medullated vagal afferent fibres have been shown to exert tonic inhibition of the vasomotor centres (Thorén *et al.* 1976). It is tempting to speculate that receptors with non-medullated afferents might be involved in the reflex forearm vascular responses in man, but it should be emphasized that the precise type and location of cardiopulmonary receptors which mediate the forearm vascular response in man cannot be determined from these experiments.

Neck suction. Forearm and splanchnic vascular resistance tended to decrease slightly during neck suction, but these decreases were not statistically significant (Tables 1 and 2). Thus, in the resting state neck suction did not exert significant effects of forearm and splanchnic vascular resistance.

It might be noted that a tendency for vascular resistance to decrease in the presence of a fall in arterial pressure suggests slight withdrawal of vasomotor tone (Burton, 1965). A fall in arterial or distending pressure would be expected to produce a 'passive' decrease in vascular calibre and thus a 'passive' increase in vascular resistance if there were no change in vasomotor tone. Therefore, the finding of a tendency for vascular resistance to fall in the face of a decrease in arterial pressure suggests withdrawal of vasomotor tone, but the magnitude of decrease in vasomotor tone probably was slight.

The absence of substantial forearm vasodilatation during neck suction is consistent with two previous studies (Bevegård & Shepherd, 1967; Ernsting & Parry, 1957) but differs from a third study (Beiser, Zelis, Epstein, Mason & Braunwald, 1970). One explanation for the absence of significant vasodilatation during neck suction might be that carotid baroreceptors have negligible effects on vasomotor tone. An alternative explanation might be that carotid baroreceptors restrain adrenergic discharge, but that in the resting state neurogenic constrictor tone is at a low level and the capacity for reflex vasodilatation is minimal. If the former explanation were correct, then one would not have expected neck suction to prevent increases in neurogenic constrictor tone during lower body suction. If the latter were correct, one would have expected neck suction to prevent increases in tone. As discussed previously, neck suction prevented increases in splanchnic resistance during lower body suction, but did not prevent increases in forearm resistance (Table 3). These findings suggest that stretch of carotid baroreceptors can restrain adrenergic discharge to splanchnic vessels, but does not exert significant restraint on adrenergic discharge to forearm vessels in man.

An alternative explanation might be that carotid baroreceptors influence both circulations, but that effects on the forearm circulation are obscured by differences in stimulus–response relationships of forearm and splanchnic vessels. For example, one might argue that lower body suction at 40 mmHg produces supramaximal vasoconstrictor discharge to forearm vessels. If true, adrenergic discharge and vasoconstriction could remain at maximal levels during lower body suction despite an inhibitory effect of neck suction. This explanation seems excluded, however, because neck suction also failed to inhibit forearm vasoconstriction during lower body suction at 20 mmHg (Fig. 3). Lower body suction at 20 mmHg produced less increase in forearm vasoconstriction than did suction at 40 mmHg. Thus, neck suction failed to exert a significant influence on forearm circulation at three levels of vascular resistance (control, lower body suction 20 mmHg and lower body suction at 40 mmHg).

We considered the possibility that the responses during combined neck suction and lower body suction might have involved reflex interactions besides cardiopulmonary and carotid baroreceptors. Room temperature was between 26 and 27 °C during each study. The subjects did not exercise during the study and did not describe or display apprehension, coughing or increased swallowing during interventions. Eckberg *et al.* (1975) have demonstrated that chemoreceptors do not participate in the responses to neck suction, since the responses are not altered by breathing 100 % oxygen. Accordingly, we believe it is unlikely that the responses during neck suction and lower body suction involved major interactions with other reflexes such as thermal, somatic, tracheal or chemoreceptor reflexes.

We also considered the possibility that the changes in the splanchnic circulation

during lower body suction might have been related to a local mechanical effect and not to a reflex. However, the finding that neck suction, a reflex stimulus remote from the abdomen, inhibited most of the splanchnic vasoconstriction suggests that it was reflexly mediated.

We conclude that the inhibitory effects of neck suction on tachycardia and splanchnic vasoconstriction during lower body suction resulted from stretch of carotid baroreceptors.

Non-uniformity of baroreceptor control. Non-uniform vasomotor responses during activation of baroreceptor reflexes have previously been demonstrated in experimental animals (Abboud, 1972; Little, Wennergren & Öberg 1975; Mark *et al.* 1973; Öberg & Thorén, 1972). The studies in animals suggest that afferent impulses from baroreceptors are integrated and differentiated in the central nervous system so that sympathetic outflow to the regional circulations is non-uniform. The present study extends our knowledge of non-uniformity of baroreceptor control of regional circulations. It delineates important differences in the patterns of responses during activation of cardiopulmonary *vs.* carotid baroreceptor reflexes in man. Furthermore, when compared to studies in animals (Thorén *et al.* 1976) this study suggests differences in patterns of response to activation of baroreceptor reflexes in animals and man. In animals carotid baroreceptors have a greater influence on muscle circulation than do cardiopulmonary receptors (Thorén *et al.* 1976). This study suggests that in man cardiopulmonary baroreceptors have the greater influence on muscle circulation.

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