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INTRINSIC RHYTHMIC PROPULSION OF LYMPH IN THE UNANAESTHETIZED SHEEP

BY J. G. HALL, B. MORRIS AND G. WOOLLEY
From the Department of Experimental Pathology, John Curtin School of Medical Research, The Australian National University, Canberra, Australia

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Hewson (1774) remarked on the rhythmic contractility of the lacteals of birds, horses and dogs and he stated that the flow of lymph through lymphatics was due to peristaltic contractions occurring in these vessels. In 1833 Panizza discovered the existence of lymph hearts in reptiles and he described the rhythmic contractions of these organs and the part they played in returning lymph to the blood stream.

Although no such structures as lymph hearts exist in mammals, Ranvier (1889) drew an analogy between the enlarged contractile segments of lymph vessels near the attachment of the valves and the lymph hearts of frogs and noted the significance of lymphatic contractions in the propulsion of lymph. Since these early observations, the occurrence of rhythmic contractions has been described in lymphatics in the rat, guinea-pig, mouse, squirrel and man (Florey, 1927*a*, *b*; Carleton & Florey, 1927; Pullinger & Florey, 1935; Smith, 1949; Webb & Starzl, 1953; Kinmonth & Taylor, 1956).

It has been uncertain what part lymphatic contractions play in the propulsion of lymph from the peripheral tissues to the venous system. Lymph flow may in some circumstances be affected by several extrinsic factors such as muscle contractions, respiratory movements and tissue pressure, but the physiological significance of any one factor is difficult to assess. The general opinion, however, appears to be that lymph flow in mammals is dependent in the main on the presence of a pressure gradient along the valved lymphatics towards the venous system and more importantly on the continual massaging and aspirating effects of muscle and respiratory movements (Yoffey & Courtice, 1956; Rusznyak, Földi & Szabo, 1960; Mayerson, 1963).

There is, however, very little experimental evidence available from which an assessment of the relative importance of factors concerned in lymph flow can be made. This is mainly because very few investigations

have been made into the factors concerned in lymph flow in conscious unanaesthetized animals under physiological conditions.

This paper records the results of an investigation into the contractility of lymphatic vessels in the sheep and demonstrates the importance of rhythmic contractions in the propulsion of lymph.

METHODS

Merino ewes and wethers were used for all the experiments.

Chronic fistulae were established in a variety of lymphatic vessels according to methods which have been described previously (Lascelles & Morris, 1961*a*; Hall & Morris, 1962; Lindner, Sass & Morris, 1964). The lymphatics cannulated were the afferent and efferent vessels of the popliteal lymph node, the lumbar lymphatic trunk, the ovarian lymph duct, the mammary lymph duct, the deep cervical lymph duct, and the efferent lymphatic from the caudal superficial cervical (prescapular) lymph node. Two types of cannulation were done: in one, the lymphatic was cannulated against the direction of flow to collect the lymph draining from the vessel; in the other, the lymphatic was cannulated in two directions so that a loop of plastic tubing could be brought outside the animal thus enabling lymph to flow through the lymphatic and the plastic loop unimpeded. The ends of the exteriorized loop could be disconnected so that the lymph flow could be measured or a T-piece of tubing could be inserted so that pressure recordings could be made without interrupting the flow of lymph through the circuit. Preparations of this type in which lymph flowed through an exteriorized loop were made in the efferent lymphatic of the popliteal lymph node, the lumbar lymphatic trunk, the intestinal lymphatic trunk and the thoracic duct.

Measurements of pressure changes in lymphatics. All observations were made on sheep from 2 days to several weeks after operation.

To measure the pressure pulses in a lymphatic cannulated against the direction of lymph flow, one limb of a stainless-steel T-piece was inserted into the end of the lymphatic cannula. Thirty centimetres of plastic tubing of the same internal diameter was attached to the other limb of the T-piece. This length of tubing provided a small arbitrary resistance which enabled pulse pressures generated in the lymphatic vessel to be recorded through the side arm of the T-piece. The open end of the outflow tube was adjusted to the horizontal plane through the head of the humerus of the standing sheep. The diameter of the plastic tubing used for cannulating the lymphatic vessels was governed by the size of the particular lymphatic. Tubing of 0·5 mm internal diameter (I.D.) was used for cannulating the afferent lymphatics of the popliteal node, while tubing of 0·8 mm I.D. was used for cannulating the efferent lymphatic of the popliteal node, the efferent lymphatic from the prescapular node, and mammary lymphatic and the hepatic lymph duct. The other larger ducts were cannulated with tubing of 1·35 mm I.D. The cannulae were 30 cm long; this length was sufficient to permit the sheep to move within the cage without pulling the T-piece out of position. In the case of re-entrant cannulations the re-entrant portion of the cannula was also 30 cm in length. Thus in both open-ended and re-entrant preparations there was a 30 cm length of cannular leading to and from the T-piece. Pressure recordings from both types of preparations could thus be compared directly in so far as the resistances of the cannulae were concerned.

The pressures from the side arm of the T-piece were transmitted to inductive transducers (New Electronic Products, England) and the amplified signals from the transducer were recorded by means of a direct-writing galvanometer recorder (New Electronic Products). The transducers were calibrated before, during and after each measurement by means of a single-limb mercury manometer.

The pressure recordings were photographed and traced, and the tracings photographed for reproduction.

Respiration rates were counted directly; lymph flow rates were measured by collecting the lymph in graduated vessels.

RESULTS

Visual observations

For a variety of experimental purposes, lymphatic fistulae were established in various lymphatics in over 100 sheep so that lymph could be collected from unanaesthetized animals under physiological conditions. In all these sheep lymph flowed spontaneously from the fistulae for several weeks.

Under basal conditions the mean rate of flow of lymph, as measured over periods of an hour or more, remained relatively constant in any given preparation, although there was considerable variation between individuals. Lymph flowed from cannulae in the afferent ducts of popliteal nodes at rates between 2 and 4 ml./hr, from the efferent ducts of the popliteal and prescapular nodes at 5–10 ml./hr, from the hepatic lymph duct and the lumbar trunk at 8–20 ml./hr, from the intestinal duct at 20–80 ml./hr, and from the thoracic duct at 50–200 ml./hr.

It was noted that in any individual preparation lymph did not flow from the cannula at a uniform rate. There were either periods in which no flow occurred alternating with periods of flow, or periods of slow flow alternating with periods of rapid flow. Often a few drops of lymph were expelled from the cannula in rapid succession and then flow would cease for a period before a further series of drops was expelled. In the popliteal, prescapular and ovarian lymphatic ducts, where the flow of lymph was less than 10 ml./hr, intervals of up to 30 sec often occurred when no lymph flowed from the cannula; in the thoracic duct and intestinal duct, where lymph flow rates were high, intervals of 2–5 sec occurred between periods of rapid flow. This intermittent formation of drops of lymph at the end of the cannulae was seen both in sheep standing in metabolism cages and in sheep grazing quietly in the paddock.

Occasionally, during the operations at which the cannulae were inserted, the lymphatic vessels were seen to be contracting rhythmically. These contractions seemed to occur as peristaltic waves; the contraction wave passed along the duct in the direction of lymph flow. Sometimes the contractions passed along the entire visible length of the exposed duct, while sometimes only one intervalvular segment was involved. On some occasions contractions were seen in the efferent lymphatic of the popliteal node, the lumbar lymphatic trunk, the mammary lymph duct and the cervical lymphatics of anaesthetized sheep. These contractions were most often

seen as soon as the lymphatic was exposed and they usually ceased after a few minutes.

After a lymphatic vessel had been cannulated it was possible sometimes to see that the contraction of the lymphatic coincided with the expression of drops of lymph from the end of the cannula. It could also be seen that the contractions were preceded by distension of the vessel, presumably due to a relaxation of the vessel wall before the contraction occurred.

During most operations rhythmic contractions of the lymphatic vessels were not seen even though the lymphatics proved to be irritable to mechanical stimulation and could be made to contract to thread-like proportions. It was thought that the absence of rhythmic contractions was probably due to the inhibitory effects of anaesthesia or surgical trauma and perhaps also to the slow formation of lymph in anaesthetized and recumbent sheep. None the less there was always a significant and characteristically intermittent flow of lymph from the limbs, head and neck and the mammary gland in the immediate post-operative period while the animal was still anaesthetized and when no muscular movements, other than those of respiration, were occurring. Similarly, in animals that were killed, lymph continued to flow in the same intermittent manner for a few minutes after death when all extrinsic propulsive forces presumably must have ceased.

Pressure changes in lymphatics

The visual observations strongly suggested that lymph flow was due largely to intrinsic contraction waves occurring in the lymphatic vessels themselves. It remained, however, to demonstrate that these contractions did in fact generate the pressures necessary to propel lymph along the lymphatic vessels. Pressure recordings were obtained from the following lymphatics with open-ended cannulations: the afferent and efferent lymphatics of the popliteal node, the intestinal lymphatic trunk, the hepatic lymph duct and the lumbar lymphatic trunk. Pressure recordings were also made from exteriorized loops in the efferent lymphatic of the popliteal node and the lumbar lymphatic trunk.

In all cases pulsatile pressures were recorded. There was considerable variation between animals and between lymphatics in the frequency and amplitude of these pulsations. The frequency of contraction varied from less than 1/min to 30/min. In all cases contractions were completely asynchronous with respiratory movements. The pulse pressures varied from 1 to 25 mm Hg in different lymphatics and in different animals. For any individual lymphatic, however, the variation in the pattern of the contractions was considerably less. There appeared to be a relation between the rate of lymph flow and the pattern of the lymphatic contractions. Lymphatic pulses were more discrete with few double or distorted pulses

when lymph flow was slow. When lymph flow was fast there were often many double, overlapping and distorted pulses. The popliteal ducts characteristically showed discrete pulsations, whereas the intestinal duct often showed a more complex pattern of pulsation. The pressure patterns recorded from various lymphatics are shown in Figs. 1 to 4.

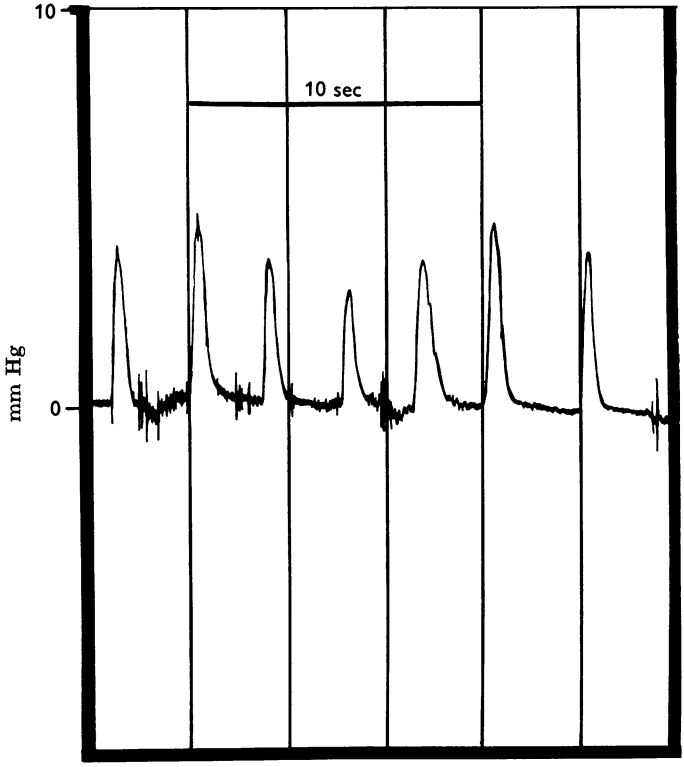

Fig. 1. The pressure pattern recorded from an efferent lymph duct of the popliteal node of a sheep with an open outflow cannulation of the duct. The rate of lymph flow was 6 ml./hr and the frequency of pulsations was 22/min. The small rapid fluctuations in the pattern which occur between the large pulse spikes were due to movements of the animal.

When the pressure in a lymphatic was increased by raising the outflow end of the cannula from the reference plane, the mean lymphatic pressure rose and at the same time the frequency of the pressure pulse increased, while usually the amplitude decreased. A pressure could be found at which lymph flow ceased but pulses were maintained (Fig. 5). When the cannula was clamped to prevent the outflow of lymph the contractions of the lymphatic vessel continued. The mean lymph pressure rose steadily to a maximum over a period of 5–10 min and at the same time the frequency of the lymphatic pulse increased. When the clamp was released and lymph

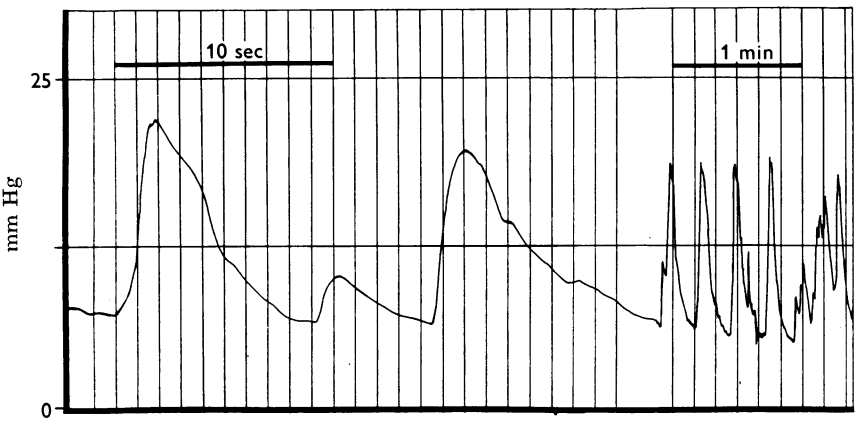

Fig. 2. The pressure pattern recorded from the efferent lymphatic of the hepatic lymph node of a sheep with an open outflow cannulation of the duct. The rate of lymph flow was 8 ml./hr and the frequency of pulsations was 6/min. Some of the irregularities in the pulses are due to respiration.

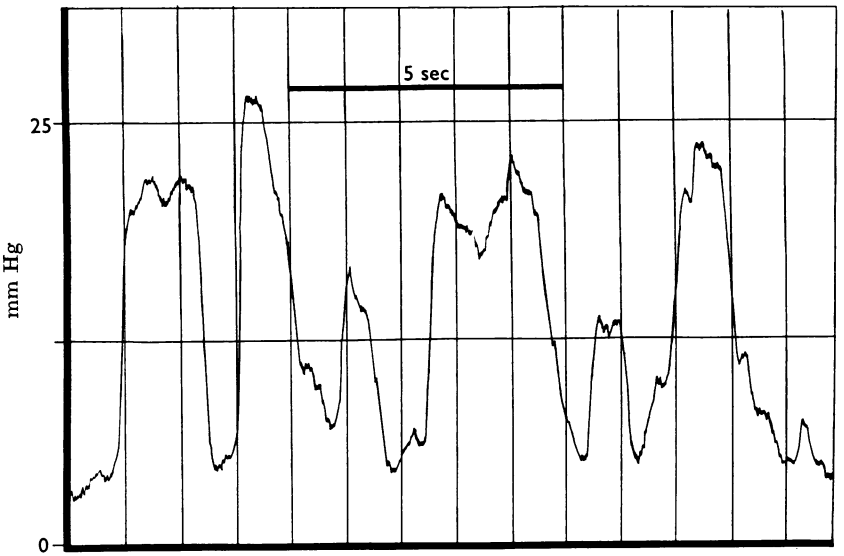

Fig. 3. The pressure pattern recorded from the efferent lymphatic of the hepatic lymph node of a sheep with an open outflow cannulation of the duct. The rate of lymph flow was 20 ml./hr and the frequency of the pulsations was 36/min. Some of the irregularities in the pulses are due to respiration.

flow began again, the pressure in the lymphatic fell rapidly and the basal pulse pattern was quickly restored (Fig. 6). The maximum mean pressures recorded in such an experiment have been about 55 mm Hg.

The pressure in an exteriorized shunt in an efferent lymphatic of the popliteal node was measured when the lymph was recirculating and when the shunt was disconnected. The pressure pulses when the lymph was recirculating were significantly greater than in the open-ended cannulation (Fig. 7).

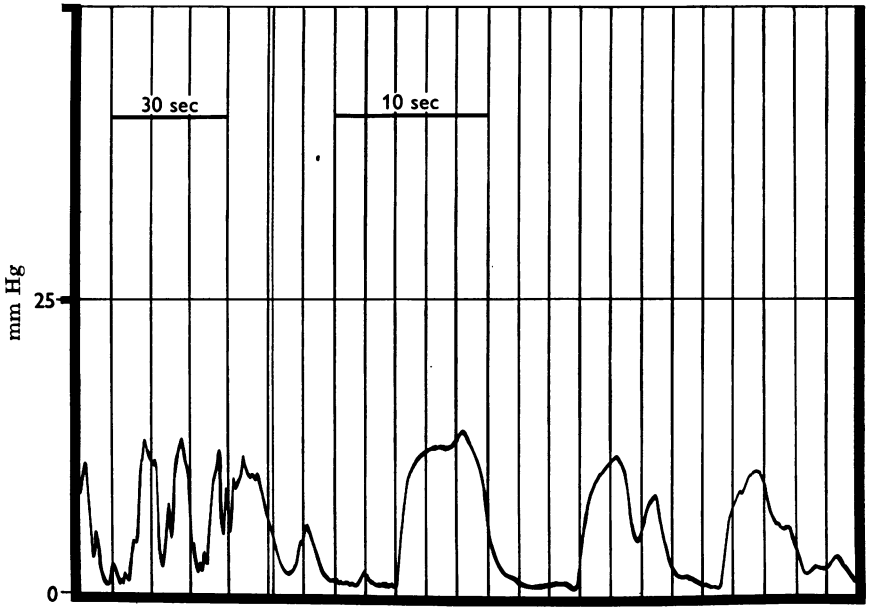

Fig. 4. The pressure pattern recorded from an intestinal lymph duct of a sheep with an open outflow cannulation of the duct. The rate of lymph flow was 35 ml./hr and the frequency of the pulsations was 26/min.

If extrinsic pressures are important in promoting lymph flow, it should be possible to detect their transmission to lymphatics and to measure and identify these pressures in the preparations used. In the case of leg lymphatics pressures were transmitted to lymphatics during muscle contractions and small pressure changes were recorded when the animal flexed the corresponding hind leg. These can be seen in Figs. 1 and 7 as the smaller fluctuations in the basal pressure. The slightly larger occasional spikes in the basal pressure were due to movements of the connecting tube. In these experiments the pressures transmitted from muscle movements were less than 0·2 mm Hg in amplitude or less than 5 % of the pulse amplitude produced by the intrinsic contractions of the lymphatics. Since these small fluctuations occurred infrequently and at random they are unlikely to

affect lymph propulsion very much. In the case of lymphatics in the abdominal cavity extrinsic pressures due to respiratory variations of intra-abdominal pressure and gut movement could be transmitted in the lymphatics. Again in some cases small pressure variations were superimposed on the intrinsic pulses. For example, respiratory effects can be seen in Figs. 2 and 3. These do not exceed 0·5 mm Hg and they are superimposed on pulses varying from 9 to 22 mm Hg. Because of the small amplitude of these minor fluctuations it was impossible to observe whether

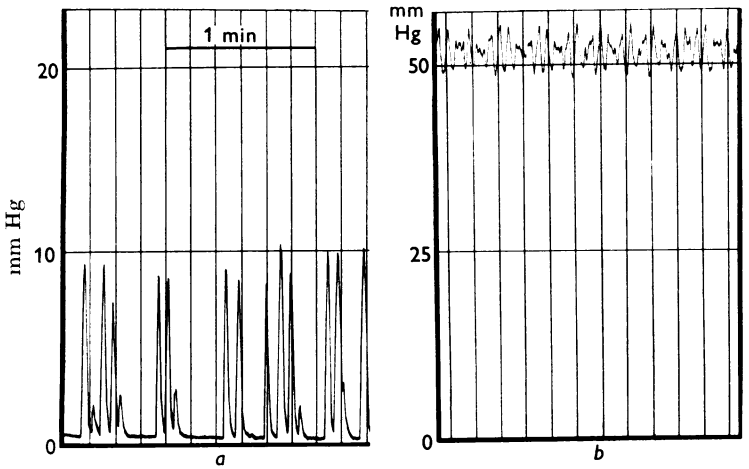

Fig. 5. The pressure pattern recorded from a lumbar lymph trunk of a standing sheep with an open outflow cannulation of the duct. (*a*) Basal pressure pattern recorded with the outflow at the level of the head of the humerus. Rate of flow 12 ml./hr, frequency of pulsations 8/min. (*b*) Pressure pattern recorded with the outflow 68 cm above the head of the humerus. No lymph was flowing. Frequency of pulsations 22/min.

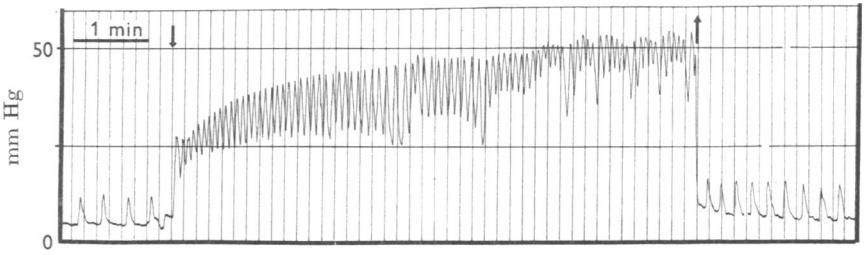

Fig. 6. Pressure pattern recorded from an efferent lymphatic of the popliteal lymph node of a sheep with a re-entrant cannulation of the duct. At the point marked by the first arrow the cannula was clamped to stop the flow of lymph. At the second arrow the clamp was released and lymph flow began again. Lymph flow from the disconnected shunt was 5 ml./hr and the frequency of contractions was 5/min. After clamping the frequency of contractions was 15/min.

or not they coincided precisely with respiratory movements and they may possibly be artifacts due to unavoidable slight movements of the connecting tube to the transducer during respiration. Similar minor variations in pressure were recorded from the intestinal and lumbar lymph ducts.

Since there appeared to be a relation between the rate of lymph flow and the rate and amplitude of the lymphatic pulse the effect of the rate of flow of lymph on lymphatic contractions was studied. A sheep with a cannulated lumbar lymphatic trunk was given an intravenous infusion

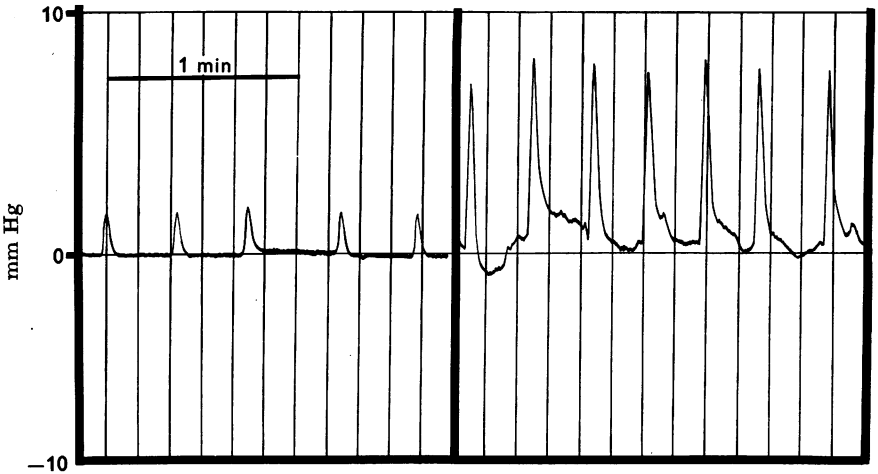

Fig. 7. The pressure pattern recorded from an efferent lymphatic of the popliteal lymph node of a sheep with a re-entrant cannulation of the duct. (*a*) Open outflow with shunt disconnected. Rate of lymph flow 6 ml./hr, frequency of contractions 3–4/min. (*b*) Re-entrant flow with the shunt closed. Frequency of contractions 3–4/min.

of Ringer–Locke's solution at the rate of 625 ml./hr for 4 hr. As the rate of lymph flow rose the frequency and amplitude of the lymphatic contractions also increased. The lymph flow rose from a pre-infusion rate of 8 ml./hr to a maximum of 42·4 ml./hr after $3\frac{1}{2}$ hr. At the height of the lymph flow response the rate of contractions had increased from a mean of 6/min to 12/min and the pulse amplitude had increased from a mean of 7·2 mm Hg to a mean of 10·6 mm Hg.

Pressure changes in the thoracic duct

The pattern of the pressure pulses in the thoracic duct differed from those in other lymphatics. There were larger pressure fluctuations due to respiratory movements superimposed on the slower intrinsic pulses. The intrinsic pulses were of lesser amplitude than those mostly found in other lymphatics.

The magnitude of the pressure fluctuations due to respiration depended upon the rate and depth of the respiration. In two preparations with exteriorized shunts pressures were recorded from the caudal and cranial cannulae. The cranial cannula was clamped during recording. Recordings made from the cannula inserted caudally in the duct near the diaphragm were not affected to any extent by respiratory movements. When recordings were made from the cranial end of the cannula with no lymph flowing, the pressure in the duct showed pronounced fluctuations with respiration. In this case pressure changes due to respiration were for the most part below atmospheric pressure and they had clearly an aspiratory effect. If the end of the cannula was open, air was rapidly drawn into the duct. Bleating, coughing and cudding also had large transitory effects upon the pressures recorded from the thoracic duct. In a preparation in which side pressures in the thoracic duct were measured at intervals on consecutive days mean pressures were characteristically between 3 and 5 mm Hg.

Previous investigators have described effects of various drugs including L-adrenaline on lymphatic motility (Florey, 1927*a*; Smith, 1949). In a sheep in which there was an exteriorized shunt of the efferent lymph duct of the popliteal node and a single outflow cannulation of the thoracic duct the following observations were made. Single intravenous injections of L-adrenaline (100 μg) had an equivocal effect on the pressures recorded from the thoracic duct, while the intravenous infusion of adrenaline (50 μg/min) for period of 15 min had no effect on the lymph pressure or the flow rate of lymph. However, the direct injection of adrenaline (5 μg) into the popliteal lymph duct was followed promptly by a response in the thoracic duct. There was an increase in the mean pressure from 3·4 to 8 mm Hg and a rapid two-fold increase in lymph flow rate. A rise in pressure and increased flow rate occupied 20 sec and was followed by a slow fall to the original mean pressure during the subsequent four minutes. During the time that the pressure and flow rate were raised the frequency of the lymphatic pulses increased twofold.

Histology of lymphatic vessels in sheep

The histological structure of the various lymphatics of the sheep was examined to identify the presence of contractile elements in the walls of these vessels. In all the lymphatic vessels from which recordings were made smooth muscle fibres were present. There appeared to be more muscle fibres in relation to the diameter of the vessel in the walls of small lymphatics such as the afferent vessels of the leg and the ovarian lymphatics than there were in the thoracic duct. When lengths of small lymphatics were isolated from tissues after fixing *in situ* it was often found that the diameter of the intervalvular segments differed widely. Some segments

between valves appeared contracted while others were widely dilated. This appearance confirmed that the segments of lymphatic vessels between the valves could contract independently of one another.

DISCUSSION

The experimental results presented do not permit any detailed analysis of the nature of the lymphatic pulse but they do show that, in the sheep, lymph flow from peripheral lymphatics to the thoracic duct is predominantly due to the intrinsic rhythmic contractions of the lymphatics. Any factor which is concerned in the propulsion of lymph along lymphatic vessels can only operate in so far as interstitial fluid is being formed at a sufficient rate in the tissues to keep the lymphatic terminals continually filled. In this regard lymph flow will be discussed in terms of those factors which affect the formation of tissue fluid and those factors which affect the movement of tissue fluid from the interstitial spaces into and along the lymphatics to the blood stream.

The massaging effects of muscle movement on lymphatics have been considered previously to play probably the most important role in propelling lymph along lymphatic vessels (cf. Mayerson, 1963). There is no doubt that in anaesthetized animals such as the dog, cat and rabbit there is very little lymph flow from the limbs and head and neck unless these parts are moved passively and massaged (Morris, 1956). In the lactating ewe when the udder is massaged by hand or sucked by the lamb, the lymph flow increases greatly for a short period of time (Lascelles & Morris, 1961*b*). However, in none of these instances can an increased lymph flow be sustained for any length of time once the preformed lymph has been removed from the tissue spaces. In these situations then the rate of formation of lymph is very slow and the filling of the lymphatic terminals is also slow. Smith (1949) has shown that the stimulus to lymphatic contractions is the filling and distension of the vessels. A similar mechanism is seen to operate in sheep and, in any situation where the rate of lymph formation is low, the contractile mechanism of the lymphatics will remain unstimulated. Furthermore, in the present observations of leg lymphatics it has been seen that muscular movement is minimally transmitted to the lymphatics.

Again when a sheep with a lymphatic fistula of the hind leg is exercised, the lymph flow increases many fold (Morris, B., Searle, G. & Heath, T. J., unpublished). In this case the increased flow can be maintained for as long as the sheep is being exercised. Whilst exercise and muscle movements bring about a great increase in lymph flow, it is clear that it must do this by effecting an increase in the rate of formation of tissue fluid and this in itself will stimulate lymphatic contraction quite apart from any effects muscle move-

ments may have on massaging lymph along lymphatics. It has been seen that lymph flow through lymphatics of the legs and through several other lymphatics occurs unrelated to muscle movement and, in the case of the liver, ovaries and uterus, it is difficult to imagine how muscle movements could greatly influence the propulsion of lymph along the lymphatics of these organs.

The situation in the thoracic duct is different, however, for once lymph enters the thorax pressure changes due to respiration can aspirate the lymph into the thoracic duct. Here again, however, the supply of lymph to the thoracic duct is probably dependent on the propulsion of lymph from the peripheral tissues by the rhythmic contractions of the lymphatic vessels.

The system responsible for the propulsion of lymph in the sheep would seem to function in many respects in a way analogous to the lymph hearts of lower animal forms. As interstitial fluid forms, the increase in tension in the tissue spaces and muscle movements would force lymph into the absorbing terminals of the lymphatic system. Once in the lymphatics the rhythmic contractions of these valved vessels propel the lymph rapidly into the main lymph ducts. In the thorax the additional factor of respiratory pressure fluctuations helps to carry the lymph into the venous system. As the rate and amplitude of contraction of the lymphatic vessels is influenced by the amount of fluid entering the lymphatics, an important intrinsic mechanism exists in the lymphatic vessels which regulates the removal of fluid from the tissue spaces of various parts of the body, at a rate proportional to its rate of formation.

Although these results directly concern only the sheep, as far as we know they are the first experiments of this kind to be done on conscious animals. There is no reason to suppose that the lymphatic system of the sheep is unique, especially in view of the considerable evidence for contractility of lymphatic vessels in other species. The fact that in anaesthetized animals of several species no evidence of rhythmic contractility has been found for lymphatic vessels does not eliminate the possibility that this mechanism may still be present but suppressed by experimental conditions. It should be remembered that in many instances the phenomenon was not observed in sheep under anaesthesia, whereas in all conscious animals lymphatic contractions were readily recorded. While anaesthesia and surgery may or may not affect lymphatic contractions *per se*, they undoubtedly do reduce the rate of formation of lymph, which will in turn reduce the frequency and extent of lymphatic contractions.

SUMMARY

1. Lymphatic fistulae were established in conscious sheep in the afferent and efferent vessels of the popliteal lymph node, the lumbar lymphatic trunk, the ovarian lymph duct, the mammary lymph duct, the intestinal lymphatic trunk, the hepatic lymph duct, the thoracic duct, the deep cervical lymph duct and the efferent lymphatic from the caudal superficial cervical lymph node.

2. The flow of lymph from all these lymphatic fistulae was intermittent with a characteristic rhythm that was unrelated to muscle movements and except in the case of the thoracic duct unrelated to respiration.

3. Pulsatile pressures were recorded from the various lymphatics: pulse pressures ranged from 1 to 25 mm Hg with pulse frequencies from 1 to 30/min. The magnitude of the pressure pulses and their rate increased as the rate of lymph flow increased.

4. When the various lymphatic cannulae were clamped to prevent lymph flow the pressures in the lymphatics rose and the frequency of contractions increased. Maximum pressures recorded were 60 mm Hg.

5. It was possible to detect effects of muscular, circulatory and respiratory movements on the pressure records from lymphatics other than the thoracic duct but these effects were small.

6. The pressure record from the thoracic duct showed intrinsic rhythmic pulsations on which were superimposed fluctuations in pressure which were due to respiration.

7. The conclusion was drawn that in the unanaesthetized sheep the intrinsic rhythmic contractions of the valved lymphatic vessels are primarily responsible for the propulsion of lymph from the periphery to the thoracic duct. As the strength and frequency of these contractions are related to the rate of lymph formation, this mechanism acts to control the removal of tissue fluid at a rate proportional to its rate of formation.

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