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Studies on the nature of the peripheral sudomotor control mechanism

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INTRODUCTION

The sympathetic nervous system is involved in the control of heat-induced sweating in animals and man (Lovatt Evans & Smith, 1956; Kimura & Aoki, 1962; Waites & Voglmayr, 1963; Findlay & Robertshaw, 1965; Rains & Capper, 1965; Iwabuchi, 1967; Hayashi, 1968; Robertshaw & Taylor, 1969; Cotton & Van Hasselt, 1972; Jenkinson, 1973; Robertshaw, 1974). In most domestic and some wild animals, however, light microscopic techniques have failed to demonstrate a nerve supply to the sweat glands (Jenkinson, Sengupta & Blackburn, 1966; Jenkinson & Blackburn, 1967, 1968*b*; Jenkinson, 1973) and a recent electron microscopical study of the sweat glands in the haired skin of the dog led to the conclusion that they lack a direct innervation (Cotton, Van Hasselt & Bergers, 1975). It thus seems likely that, as postulated for the cow (Jenkinson *et al.* 1966), there is a peripheral non-neural component in the sudomotor control mechanism of most domestic animals.

This may be true of all mammals since, although the sweat gland acini of equines, primates (including man) and the footpads of the dog and cat have a closely associated nerve supply (Weddell, Palmer & Pallie, 1955; Weiner & Hellman, 1960; Jenkinson & Blackburn, 1968*a*; Bell & Montagna, 1972; Montagna, 1964, 1972; Aoki, 1973) and are believed to be innervated, there is little information on the nature or location of the nerve endings. It is possible, as suggested by Jenkinson (1973), that the closely associated nerve plexus is supplying the profuse capillary network around the glands. However, from a recent electron microscope study Uno & Montagna (1975) concluded that the sweat glands of the macaque monkey are innervated by both adrenergic and cholinergic nerves.

The objectives of the present study were (1) to test the validity of the conclusion, based solely on light microscopical observations, that the sweat glands of the cow, sheep, goat and cat are not innervated, (2) to locate the nerve terminals in species which have a plexus in close proximity to the sweat gland acini and, (3) to test the hypothesis that there is a peripheral non-neural link in the sudomotor control mechanism of mammals generally.

MATERIALS AND METHODS

Skin specimens were obtained from the backs of 4 castrated Ayrshire cattle, 3 female British Saanen goats, 4 castrated Finnish Landrace × Dorset Horn sheep, 4 castrated horses, 4 female cats, and from the footpads of these cats; all were adult. The samples from the cattle, sheep and goats were obtained by biopsy using the high-speed punch technique of Findlay & Jenkinson (1964). Those from the horses and cats were taken immediately after they had been killed. Skin samples were also obtained by biopsy from the backs of 5 adult male humans and from the finger of one; *post mortem* specimens were also obtained from the back, palm and axilla of an adult human female.

All pieces of tissue were immediately placed in 2% glutaraldehyde in 0·1 M-sodium cacodylate buffer at pH 7·3 (Sabatini, Bensch & Barrnett, 1963) and fixed for 3 hours. The tissues were then washed in 0·1 M-sodium cacodylate buffer pH 7·3, for a minimum of 4 hours. Post-fixation was carried out in 1% osmium tetroxide in 0·1 M-sodium cacodylate buffer for 1 hour. The tissues were then dehydrated either through graded alcohol or graded acetone solutions, cleared in propylene oxide and embedded in Epon–Araldite.

Cow, sheep, goat and cat

Four tissue blocks from the back of each of the 4 cattle, 3 goats and 4 sheep were sectioned at 1 μm on an LKB III ultratome using glass knives. One block from each species was cut serially and from the remainder, six sections 1 μm thick were cut sequentially every 10 μm through the block. The sections were examined under phase contrast either unstained or stained with 1% p-phenylene-diamine.

Ultrathin sections were also cut from additional blocks from each species and from the specimens of cat back, using an IVIC diamond knife. The sections, mounted on copper grids, were stained in alcoholic uranyl acetate followed by lead citrate (Reynolds, 1963) and examined with either a JEOL 100 C or an AEI EM6B electron microscope at an accelerating voltage of 80 kV.

Horse, cat footpad and man

Sections were cut at 0·5 μm on the ultratome, using a glass knife, from three blocks from each of the horses, cat footpads and from one of the human specimens. One block from each species was sectioned sequentially at 10 μm intervals and the remainder at 50 μm intervals. The sweat glands were thus studied at different levels within the skin and, because of their convolutions, at different angles. The 0·5 μm sections were examined with the electron microscope at 100 kV accelerating voltage.

Ultrathin sections, cut and processed as described above, were also taken from further blocks from each species.

Measurements

In all species the distance from the basement membrane of the sweat gland myoepithelium of the fibrocyte sheath surrounding the glands was measured at 3 places chosen at random on 100 gland sections. The distances of all nerves and blood vessels found within a 10 μm radius of the myoepithelial basement membrane were also recorded. The measurements were made from electron microscope photographs at calibrated magnifications between × 5000 and × 15000.

RESULTS

The fibrocyte sheath

In all the species studied a sheath of fibrocytes was observed surrounding the fundus of the sweat gland (Fig. 1). This sheath was sometimes seen as a single layer, but was more often composed of 2–4 closely associated processes from different fibrocytes, at least some of which were interconnected by desmosomes (Fig. 3). The fibrocytes, however, did not form an unbroken ring around the gland in every section, suggesting the presence of gaps in the sheath. Study of serial and sequential sections led to the conclusion that it was an integrated but loosely woven sheet of fibrocytes which surrounded the entire gland, including the duct.

Between this sheath and the basement membrane of the myoepithelium of the gland there was a layer of connective tissue, the fibres of which were noticeably finer than those of the collagen outside the sheath, and were interspersed with amorphous deposits and elaunin fibres (Figs. 2, 4, 8*a*). Analysis of variance showed that, although there was significant variation in the thickness of this region amongst animals within species, significant differences in the thickness of this layer were nevertheless found between species. It was much thicker in the goat than in the other species and considerably thinner in the glands of the cat back and cow ($P < 0{\cdot}01$) (Table 1).

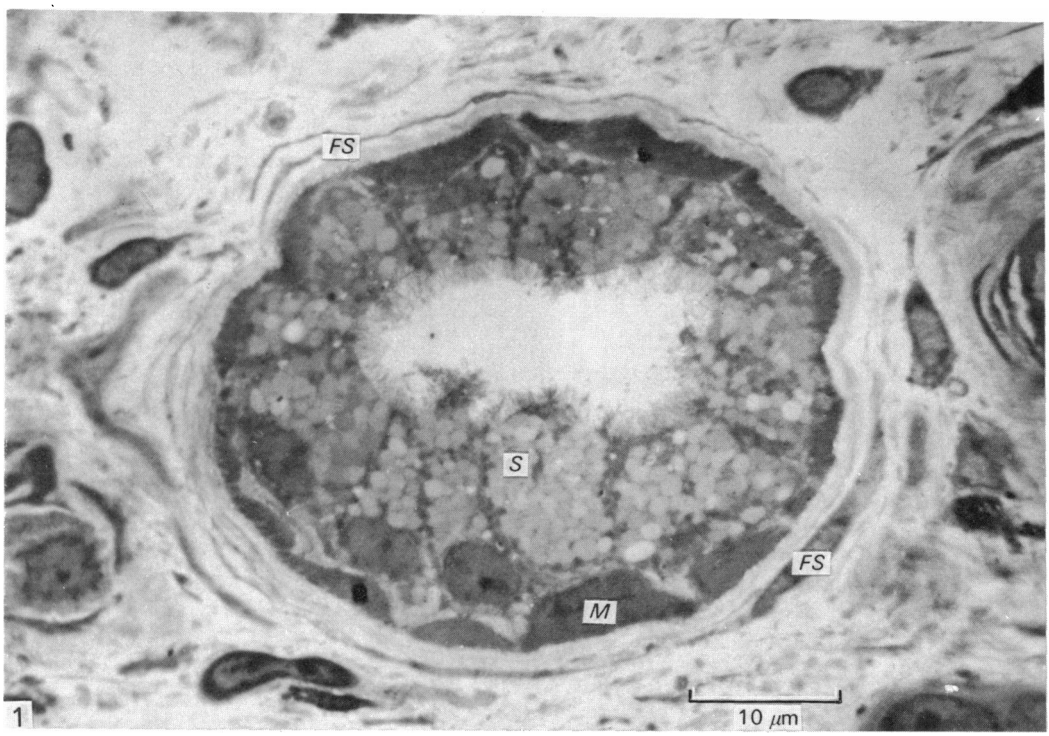
The nerves and blood vessels

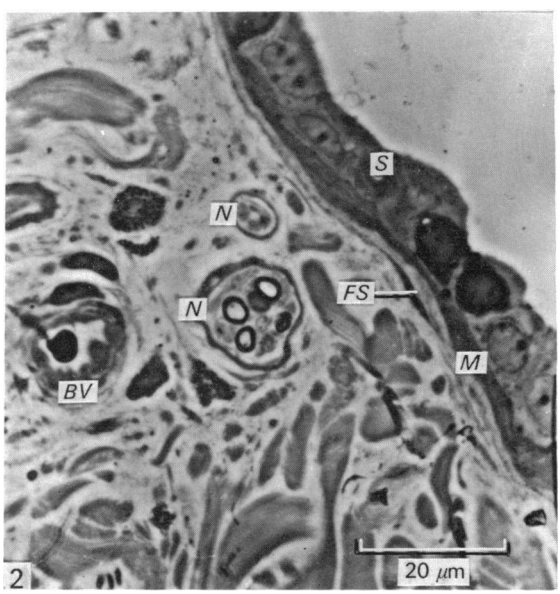
(*a*) *Cow sheep, goat and cat*

Nerves and blood vessels were rarely observed within 10 μm of the myoepithelium of the general body surface glands of these species; only small numbers were found even after study of sequential and serial sections (Table 2). Most of the nerves were myelinated bundles (Fig. 2). The unmyelinated nerves observed and traced were also small bundles, the fibres of which were still enveloped in a Schwann cell membrane (Figs. 4, 5). They were, like the myelinated nerves, closely associated with blood vessels. No varicosities were detected within 10 μm of the glands of any of these species. The mean distances of the unmyelinated nerves from the glands are given in Table 1. The nearest of these were 1·6, 1·7, 2·2 and 3·8 μm respectively from the myoepithelium of the cow, sheep, goat and cat, and situated as shown in Figure 5. No nerve bundle was closer than 0·3 μm to the fibrocyte sheath and none was seen to penetrate it. The mean distances of the blood vessels from the sweat gland myoepithelium are also shown in Table 1. Most of these were capillaries, although some post-capillary venules and larger vessels were detected and traced. The nearest capillaries were 1·7, 2·4, 2·2 and 2·8 μm respectively from the glands of the cow, sheep, goat and cat, and none was observed to penetrate the fibrocyte sheath.

(*b*) *Horse, cat footpad and man*

Nerves and blood vessels were more readily observed in close proximity to the more coiled sweat glands of these species, and they were present in almost every histological section. The nerves, which were mostly small unmyelinated bundles, and the blood vessels, the vast majority of which were capillaries, were not only more numerous but also closer to the glands than those of group (*a*) above (Table 1). Most of the nerves ran outside the fibrocyte sheath and between it and the blood vessels. The distance of the unmyelinated nerve bundles from the blood vessels could not be measured from the micrographs, which were taken primarily to show





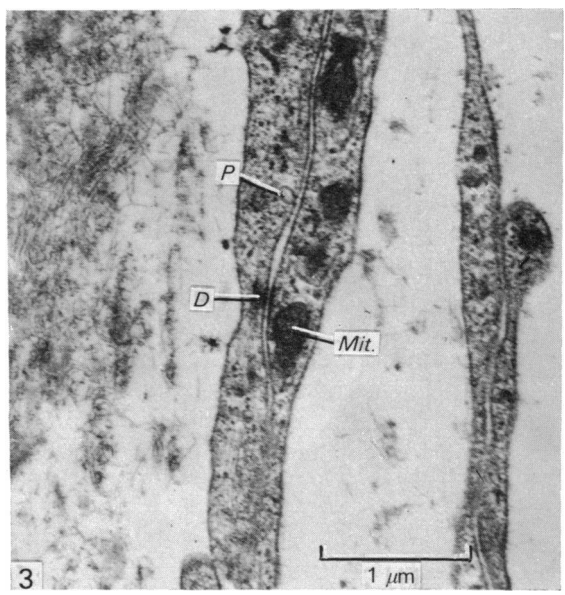
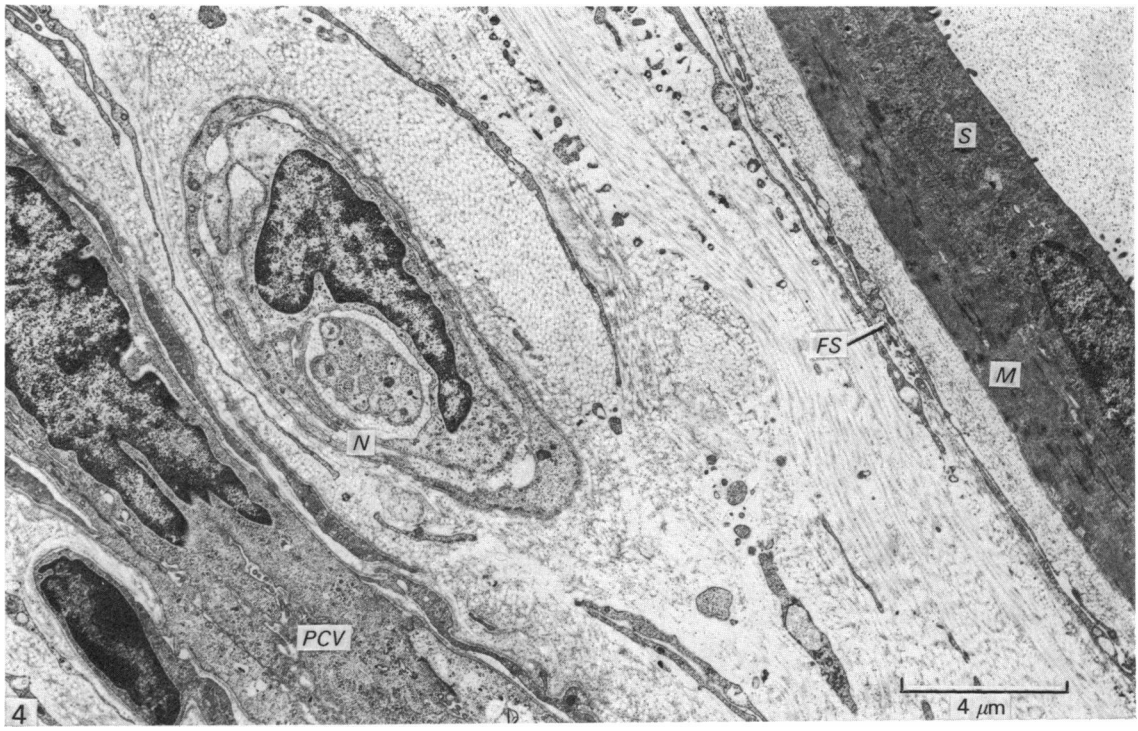


Fig. 1. Electron micrograph of a half micron thick section, using an accelerating voltage of 100 kV, from the sweat gland of the horse, illustrating the secretory epithelium (*S*), myoepithelium (*M*) and the fibrocyte sheath (*FS*), which surrounds the gland. 10 μm bar.

Fig. 2. Phase contrast micrograph of a 1 μm section from the sweat gland of the ox, illustrating the secretory epithelium (*S*), myoepithelium (*M*), fibrocyte sheath (*FS*), myelinated nerves (*N*) and a blood vessel (*BV*). The nearest nerve bundle is 6 μm from the myoepithelium of the gland. 20 μm bar.

Fig. 3. Electron micrograph from the fibrocyte processes which compose the sheath surrounding the gland. The processes have a few rough endoplasmic reticulum profiles, ribosomes, small mitochondria (*Mit*) microtubules and microfilaments. Pinocytotic vesicles (*P*) are occasionally found. Membranes of adjacent processes frequently maintain a close relationship with a gap of approximately 25 nm, and small demosomes (*D*) are found. A basement membrane is absent. 1 μm bar.



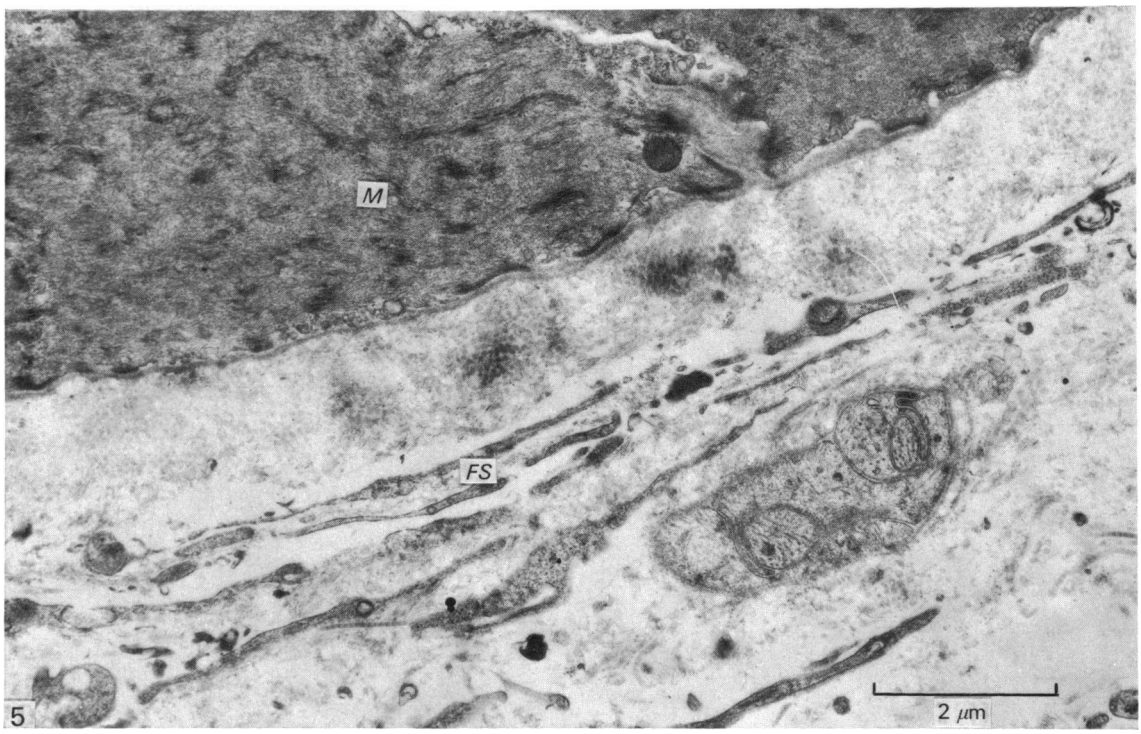
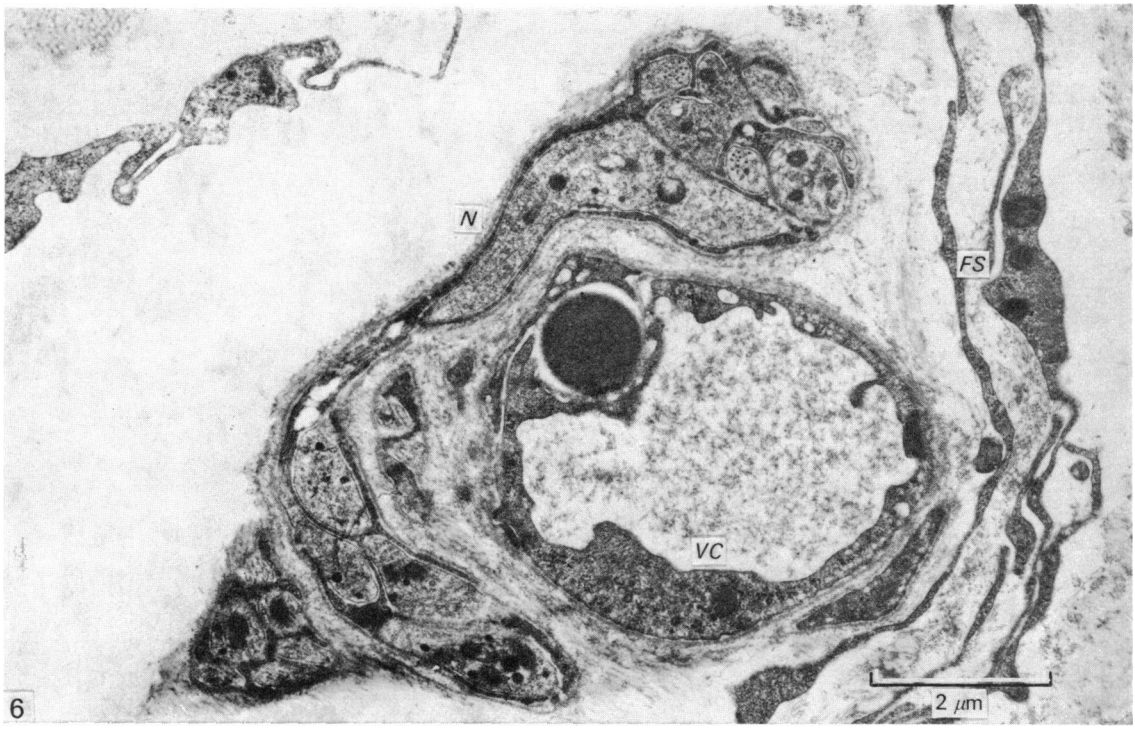


Fig. 4. Electron micrograph from the sweat gland of the ox. The lumen of the gland and secretory epithelium (*S*) are to the top right. The gland is surrounded by the fibrocyte sheath (*FS*). A small bundle of unmyelinated axons with surrounding sheath (*N*) and post-capillary venule (*PCV*) are respectively 11·4 μm and 12·3 μm from the myoepithelium (*M*) of the gland. 4 μm bar.

Fig. 5. Electron micrograph from the sweat gland of the sheep illustrating an unmyelinated nerve containing two small axons with Schwann cell wrappings lying outside the fibrocyte sheath (*FS*) and 2·5 μm from the gland myoepithelium (*M*). 2 μm bar.



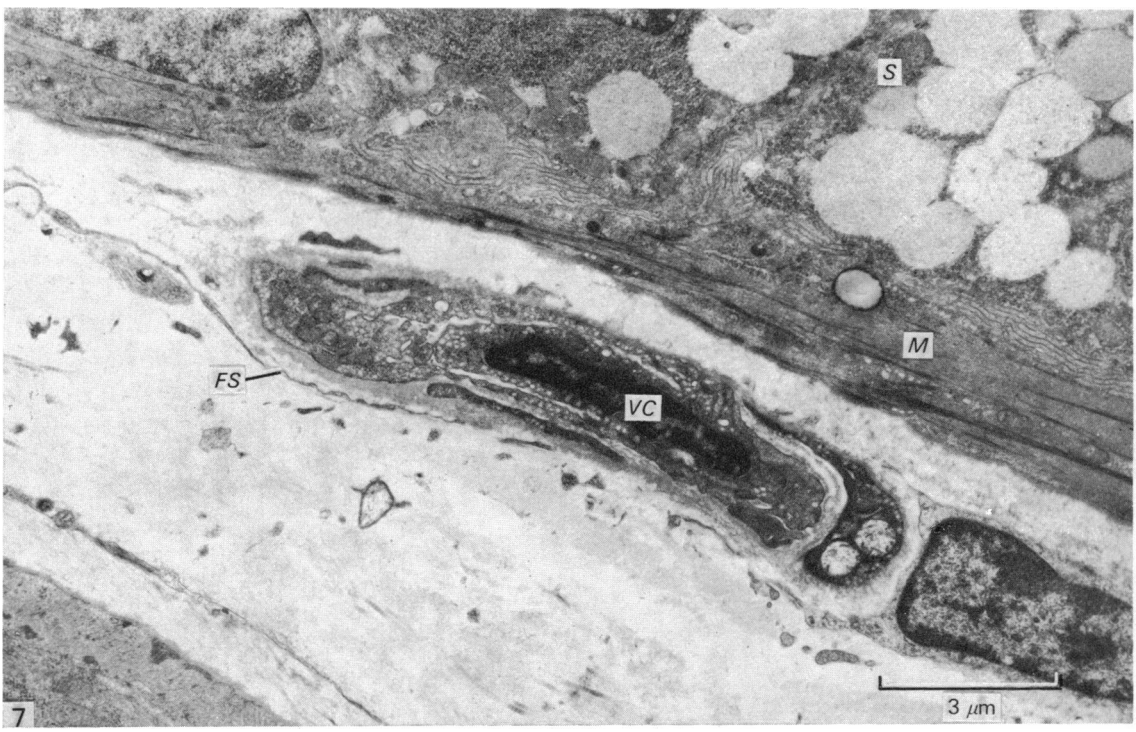
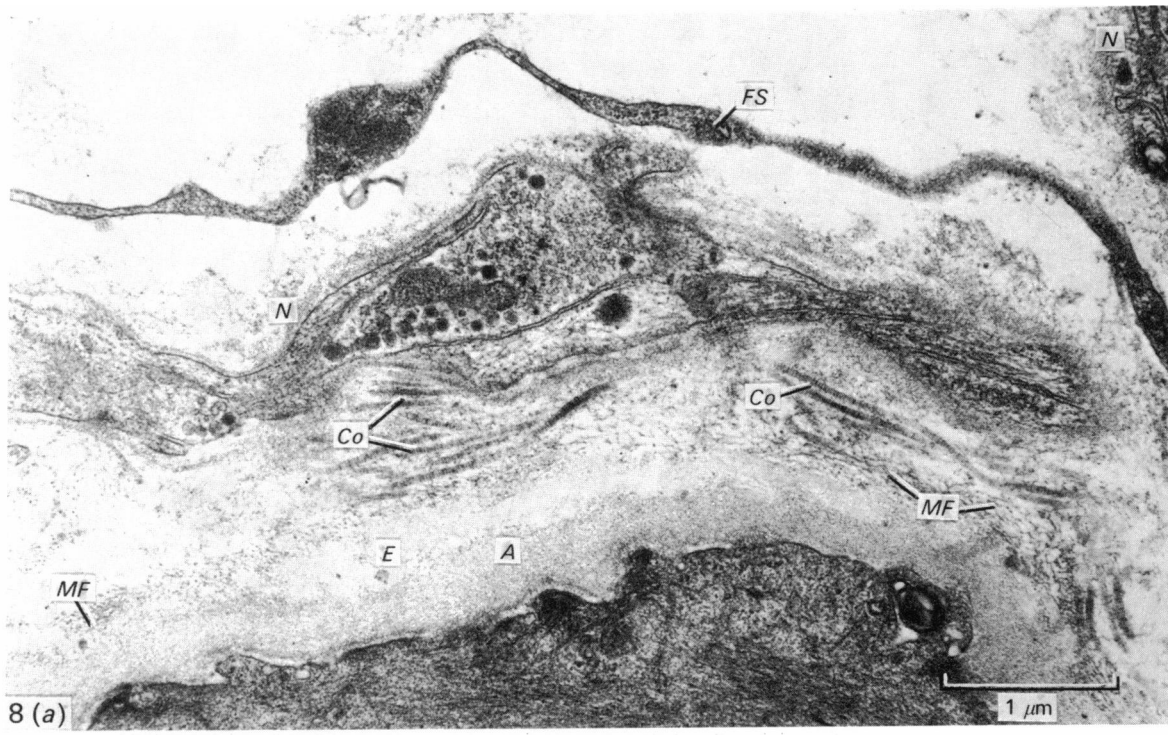


Fig. 6. Electron micrograph from the sweat gland of the horse showing a venous capillary (*VC*) just outside the fibrocyte sheath (*FS*), and with an associated nerve (*N*). 2 μm bar.

Fig. 7. Electron micrograph of the sweat gland from the footpad of the cat illustrating the occasional finding of a blood vessel, in this instance a venous capillary (*VC*), within the fibrocyte sheath (*FS*), and running approximately parallel to the gland myoepithelium (*M*). Secretory epithelium (*S*) is seen top right. 3 μm bar.



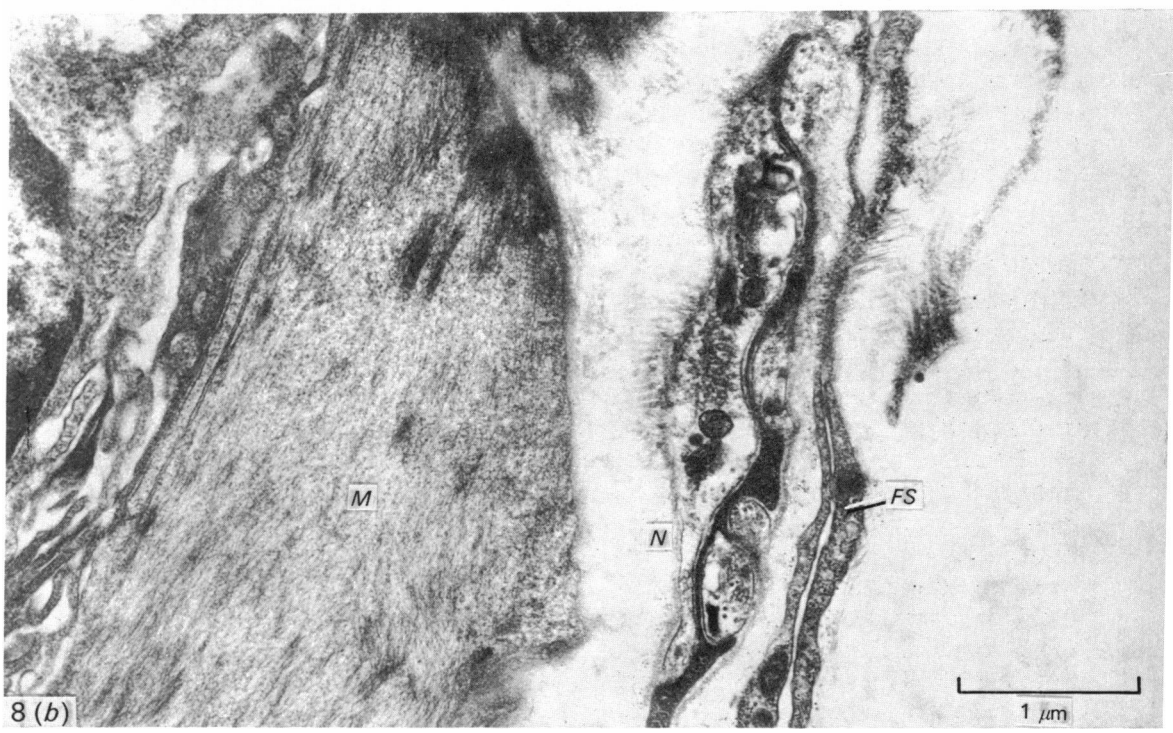


Fig. 8 (*a*). Electron micrograph showing unmyelinated nerves (*N*) associated with a human sweat gland. Most axons lie outside the fibrocyte sheath (*FS*): however, small groups of axons may be found, as shown, within it. The Schwann cell processes do not completely surround the axons, which contain numerous vesicles, both clear and dense cored. The nerve inside the sheath is 1·3 μm from the myoepithelium. Elaunin fibres (*E*), and associated microfibrils (*MF*), collagen (*Co*), and amorphous material (*A*) are seen between the sheath and the gland myoepithelium. 1 μm bar. (*b*). Electron micrograph from the sweat gland of cat footpad, again illustrating a small bundle of unmyelinated fibres (*N*) within the fibrocyte sheath (*FS*) and 0·6 μm from the myoepithelium (*M*). 1 μm bar.

Table 1. *Mean distances (μm), with their standard errors, of the fibrocyte sheath, blood vessels and nerves from the basal lamina of the sweat gland myoepithelium*

Species	Fibrocyte sheath		Capillaries		Unmyelinated nerves	
Cow	0·7±0·01	N = 300	5·3±0·5	N = 14	6·2±1·5	N = 5
Sheep	1·7±0·04	N = 300	5·4±0·8	N = 9	4·6±0·7	N = 10
Goat	2·5±0·04	N = 300	5·1±0·6	N = 12	4·2±0·4	N = 14
Cat	0·7±0·01	N = 300	6·3±0·5	N = 19	7·3±0·8	N = 4
Horse	1·3±0·02	N = 300	4·4±0·3	N = 45	2·8±0·3	N = 44
Cat footpad	1·3±0·03	N = 300	3·7±0·4	N = 44	3·3±0·3	N = 56
Man	1·4±0·03	N = 300	3·7±0·3	N = 37	1·5±0·1	N = 72

Blood vessels and nerves further than 10 μm from the basal lamina were not included.

Table 2. *Number of nerves and blood vessels found within 10 μm of the sweat glands of the cow, sheep, goat and cat back*

	Cow	Sheep	Goat	Cat
Myelinated nerve bundles	13	24	14	5
Unmyelinated nerve bundles	5	10	14	4
Capillaries	14	9	12	19

the distances of all nerves and blood vessels within 10 μm of the glands. There seemed, however, to be a close association between the unmyelinated nerve bundles and capillaries (e.g. Figure 6) in all three species, and the mean distances shown in Table 1 indicate that in the horse and cat footpad the nerves could well be closer to blood vessels than to the glands. The results for man, on the other hand, do not fit this pattern, a finding worthy of further investigation.

Some of the unmyelinated bundles (approximately 10–15 % in the horse and cat footpad and 25 % in man) were found within the fibrocyte sheath, and a few of the nerves both outside and within the fibrocyte sheath were fibres which exhibited possible sites of transmitter release. The nearest of these (Fig. 8) were within the sheath and 0·6, 0·4 and 0·5 μm respectively from the myoepithelium of the horse, cat footpad and human glands. Some capillaries, however, were also situated in this position within the fibrocyte sheath (Fig. 7). It was not possible to obtain, from the small number of varicosities observed, reliable estimates of their relative distances from the capillaries and glands, but the impression was gained that they were at least as near the capillaries as the glands. Both the capillaries and nerves ran parallel to the fibrocyte sheath, and there was no evidence of either crossing the region between the sheath and basal lamina of the myoepithelium to the myoepithelium itself, or of receptor sites on the myoepithelial membrane. The few nerves outside the fibrocyte sheath which exhibited possible sites of transmitter release were closer to blood vessels than to the gland surface.

DISCUSSION

The results substantiate earlier observations that there are few blood vessels or nerves in the vicinity of the sweat glands of the cow, sheep, goat and cat (Goodall & Yang, 1954; Jenkinson *et al.* 1966; Jenkinson & Blackburn, 1967, 1968*b*) and illustrate that the nerves are largely myelinated bundles situated in close association with blood vessels outside a fibrocyte sheath which surrounds the glands. This evidence, coupled with the findings that the small number of unmyelinated nerves found were bundles over 1·5 μm from the glandular myoepithelium, and that no varicosities were observed within 10 μm of the glands, indicates the absence of a nerve supply to the sweat glands. Some other organs, e.g. veins, which are believed to be innervated, can have endings up to 10 μm from the muscular media (Rhodin, 1968). Nerve endings are more than 10 μm from the sweat glands of the cow, sheep, goat and cat, unlike those of the cat footpad, horse and man which are within 0·5 μm of the glandular myoepithelium. These results, and those of Cotton *et al.* (1975) in the dog, therefore, establish the validity of the conclusion, based on light microscopy, that the sweat glands of the cow, sheep, goat, cat and dog are not innervated (Jenkinson, 1973). The results also support the view that there is a peripheral component between the sympathetic nervous system and the glands, in the sudomotor control mechanism of these species (Jenkinson, 1973).

The nature of this local control system is unknown, but in the absence of a direct glandular innervation it is likely that it is dependent on the action of the sympathetic nervous system on the local cutaneous blood supply. Sweating is closely associated with vascular activity, and in particular with increased blood flow (Lovatt Evans & Smith, 1956; Ingram, McLean & Whittow, 1963; Robertshaw & Taylor, 1969; Berne & Levy, 1972). However, *in vivo* and *in vitro* evidence indicates that sweat discharges are unlikely to be due solely to haemodynamic changes following vasomotor responses (Findlay & Robertshaw, 1965; Johnson, 1975), and that chemical transmission is also involved.

The most likely transmitters are catecholamines; adrenaline and noradrenaline both have a direct action on the sweat glands of the cow, sheep, goat and dog, although adrenaline is the more potent (Findlay & Robertshaw, 1965; Robertshaw, 1968; Johnson, 1975). Catecholamines can be transported from the blood stream to the sweat gland (Iwabuchi, 1967; Robertshaw & Taylor, 1969; Mabon & Jenkinson, 1971), and increased levels of circulating catecholamines induce sweating despite the fact that skin circulation may be reduced (Ingram *et al.* 1963; Iwabuchi, 1967; Hayashi, 1968).

Local injection of acetylcholine fails to stimulate sweating in the cow, sheep or goat (Kimura & Aoki, 1962; Findlay & Robertshaw, 1965; Hayashi, 1968), although it does elicit a response in the dog (Aoki, 1955); its sudomotor action is direct and is apparently independent of that of adrenaline (Iwabuchi, 1967; Cotton & Van Hasselt, 1972). The pharmacological action of acetylcholine in the dog, however, does not necessarily imply physiological function, since the sweat glands of this species, unlike those of the cow, sheep and goat, contain little or no cholinesterase (ChE) (Iwabuchi, 1967; Jenkinson & Blackburn, 1968*b*; Bell & Montagna, 1972), and have a lowered threshold to locally administered cholinergic agents.

The evidence thus strongly indicates that the peripheral link between the sympathetic nervous system and the glands involves the vascular supply, chemical transmission and catecholamines. At present one can only speculate on the source

of the peripheral catecholamines, although it seems likely that they are either derived from the circulation or produced locally near the capillaries during sympathetic action on them.

One possible mechanism is that, as postulated for the horse (Lovatt Evans & Smith, 1956), when a non-sweating animal is at rest the skin circulation is adjusted predominantly by sympathetic nerves to skin vessels, to admit only such an amount of blood as will bring (or release) in unit time a sub-threshold quantity of catecholamine. Monoamine oxidase (MAO) on the glands (Jenkinson *et al.* 1966; Jenkinson & Blackburn, 1967, 1968*b*) would prevent the initiation of sweating by low concentrations of catecholamine. Sweating would thus result from the action of factors, particularly sympathetic stimulation, which augment either blood flow or the catecholamine content of the blood, and hence increase the amount of catecholamine released to the gland. Circulating catecholamines play a part in the sweating response to heat in the sheep, and to asphyxiation stress in the dog (Waites & Voglmayr, 1963; Iwabuchi, 1967; Hayashi, 1968). Although Findlay & Robertshaw (1965) concluded that there was no adrenomedullary component in the sweating response of the ox to moderate heat stress, their results are not inconsistent with the concept of peripheral catecholamine transfer from the blood, since the technique of splanchnicotomy which they used does not appreciably reduce the plasma nor-adrenaline level (Robertshaw & Whittow, 1966).

An alternative mechanism would be the release of locally stored catecholamines in response to sympathetic activity, either directly or as a result of vascular changes. Mast cells containing dopamine have been demonstrated in close association with the cutaneous blood vessels of cattle (Jenkinson *et al.* 1970), and the possibility of their being a source of local transmitter cannot be discounted. Detailed study of the peripheral system is required before the sudomotor mechanism in the cow, sheep, goat, cat and dog can be fully elucidated. The possibilities discussed above and illustrated in Figure 9, however, provide working hypotheses for such investigations.

The sweat glands of man, the horse and cat footpad also respond, apparently directly (Johnson, 1975), to adrenaline and nor-adrenaline (Lloyd, 1959; Takahashi, 1964; Foster, 1968; Robertshaw & Taylor, 1969; Foster, Ginsburgh & Weiner, 1970) and contain MAO (Yasuda & Montagna, 1960; Jenkinson & Blackburn, 1968*a*, *b*). The action of adrenaline, although synergistic, is apparently independent of that of acetylcholine which also activates the sweat glands of these species (Chalmers & Keele, 1951; Lovatt Evans & Smith, 1956; Foster & Weiner, 1970; Foster, Haspineall & Mollel, 1971; Warndorff & Hamer, 1974). Adrenaline has been detected in horse sweat (Brunaud & Pitre, 1945), and circulating adrenaline is implicated in the control of exercise-induced sweating in both the horse and monkey (Robertshaw & Taylor, 1969; Robertshaw, Taylor & Mazzia, 1973). Chromaffin cells associated with capillaries are present in the skin of man and the cat (Nordesta & Adams-Ray, 1957). It thus seems probable that the peripheral mechanism involving catecholamine transfer, either from the blood or from local stores, on sympathetic activity, is also present in these species.

The more profuse blood supply, and the relatively short distance which transmitters require to travel to the glands, however, indicate not only a more sensitive system, but also additional control by direct action of transmitters released at the sympathetic nerve endings (Fig. 9). Although most of the nerves were, as also illustrated by Uno & Montagna (1975) for the macaque monkey, adjacent to, but

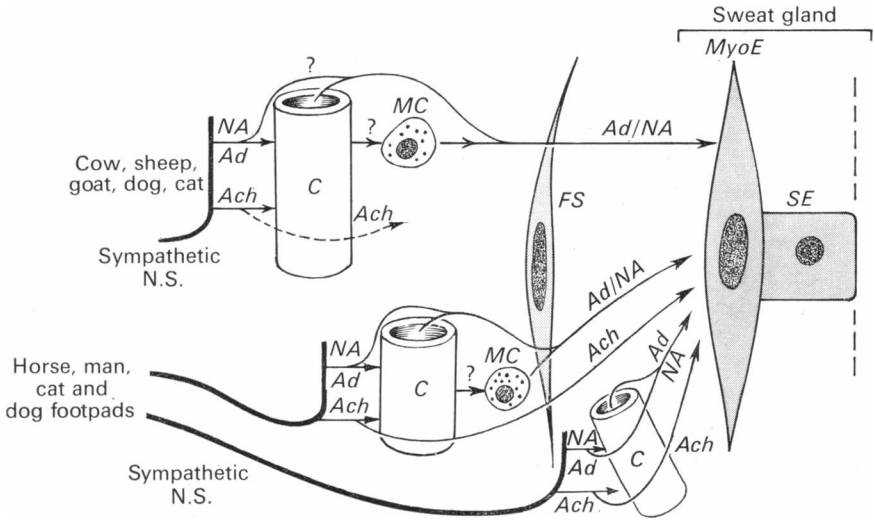


Fig. 9. A diagram illustrating the concept of a basic sudomotor mechanism in all species. It is envisaged that, as shown for the cow, sheep, goat, cat and dog, the action of sympathetic adrenergic and cholinergic nerves on cutaneous blood vessels (*C*) elicits a local transfer to the gland of threshold quantities of adrenaline (*Ad*) and nor-adrenaline (*NA*) either from the circulation or from cellular stores (*MC*) in close apposition to capillaries. It is postulated that the catecholamines penetrate the fibrocyte sheath (*FS*) around the glands, stimulate the myoepithelium (*MyoE*), and are destroyed by MAO in the glands. It is suggested that in the glands of some species such as the horse, man and the cat and dog footpads, direct control by transmitters [catecholamines and acetylcholine (*ACh*)] released at the sympathetic endings, especially from nerves located within the fibrocyte sheath, has become the predominant mechanism.

outside, the fibrocyte sheath, varicosities traced within the sheath were only 0·4–0·6 μm from the myoepithelium and could thus be expected to have a direct influence on the glands. It can therefore be considered, as concluded by Uno & Montagna (1975) for the macaque, that the sweat glands of man, the horse and cat footpad are innervated, although the nerves may well be as close to capillaries as to the glands. Both adrenergic and cholinergic sympathetic nerves have been found around the glands of the macaque monkey (Uno & Montagna, 1975). The variations in the pharmacological responses of the different species may be partly due to differences in the ratio of adrenergic to cholinergic sympathetic fibres in the vicinity of the glands, and perhaps also to the relative concentrations of MAO and ChE on them. In the horse, adrenaline appears to be the principal transmitter (Robertshaw & Taylor, 1969; Johnson, 1975). On the other hand, the classical demonstration of acetylcholine in the cat footpad on stimulation of the abdominal sympathetic chain (Dale & Feldberg, 1934), the reduction in glandular ChE during sweating and the presence of ChE in sweat (Aoki, 1966), and the effectiveness of atropine in inhibiting sweating (Collins, Sargent & Weiner, 1959; Foster & Weiner, 1970), pinpoint acetylcholine as the principal stimulatory agent in man, the horse and cat footpad.

The comparative evidence, therefore, favours the concept that the basic sudomotor mechanism in all species involves the action of sympathetic adrenergic and cholinergic nerves on the cutaneous blood vessels thereby eliciting a local catecholamine transfer to the gland. In blood vessels of other locations direct cholinergic and adrenergic vasomotor actions have been demonstrated (Furchgott, 1955; Somlyo &

Somlyo, 1970). In species such as man an additional, and probably more important, mechanism, involving the action of transmitters released at the nerve endings, has resulted from the close proximity of the blood supply and sympathetic nerves to the glands. However, the mechanism of sweating may involve other transmitters besides adrenaline, nor-adrenaline and acetylcholine. Sweating in response to direct radiant heat is not abolished in the goat by atropine or dihydroergotamine (Kimura & Aoki, 1962), or in man by atropine or procaine (Randall, 1947). Stretching the skin of the dog results in a sweat response which is not affected by atropine or dihydroergotamine, even in areas deprived of sympathetic innervation in animals whose adrenal glands have been medullectomized (Iwabuchi, 1967). Thus, in addition to the main transmitters, other locally produced substances, such as bradykinin (Berne & Levy, 1972; Johnson, 1975), would seem to be capable of reaching and activating the sweat glands.

The fibrocyte sheath around the glands has not been described previously, and its function is undefined. It forms a framework, comparable to the veil cell sheath surrounding the venous part of the micro-circulatory bed (Rhodin, 1968), which is presumably capable of physical change during glandular contraction. The region between it and the gland consists, as has been shown in man, mainly of bundles of elaunin fibres interspersed with an amorphous material (Cotta-Pereira, Guerra Rodrigo & Bittencourt-Sampio, 1975). In addition to the typical cytological features of fibrocytes, maculae adhaerentes were observed between adjacent processes of fibrocytes in the sheath. Fibrocytes do not usually exhibit specialised cell contacts, although they have been observed in pathological and fetal tissue (Greenlee & Ross, 1967; Gabbiani & Manjo, 1972; Gabbiani, Manjo & Ryan, 1973). While the fibrocyte sheath forms an extensive covering around the glands, gaps are not infrequent. However, in addition to the distinct morphological features, the layer of connective tissue and basal lamina within the sheath may have selective permeability properties (Chvapil, 1967; Gupta, Hall, Maddrell & Moreton, 1976). The myoepithelium is of known importance to glandular contraction (Murphy, 1960), and the ability of catecholamines to penetrate the sheath and enter the sweat suggests that the myoepithelium rather than the sheath is the target organ of local transmitters. Further studies of both the cellular and extracellular sheathing layers of the sweat glands are in progress.

SUMMARY

Electron microscopical studies of the sweat glands of the body surface of the cow, sheep, goat and cat demonstrated that there were few nerves or blood vessels near the glands. No varicosities were found within 10 μm of the glands, and the small number of unmyelinated nerve bundles traced were over 1·5 μm from the glandular myoepithelium, and situated outside a fibrocyte sheath surrounding the glands. It was concluded that the sweat glands of these species are not innervated.

Unmyelinated nerve fibres were more abundant around, and were closer to, the sweat glands of man, the horse and cat footpads, and varicosities were observed within the fibrocyte sheath close enough to have a direct influence on the glands.

It is postulated from the comparative evidence that the basic sudomotor mechanism is the same in all species, involving the action of adrenergic and cholinergic nerves on the cutaneous blood vessels and local catecholamine transfer to the gland; and that in species such as man where the blood supply and sympathetic nerves are

in close proximity to the glands, transmitters released at the sympathetic nerve endings, in particular acetylcholine, will, in addition, have a direct action on the glands.

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