THE SEGMENTAL SENSORY INNERVATION OF THE SKIN OF THE SHEEP

A thesis submitted in partial fulfilment of the requirements for the

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SUMMARY

The interest in the segmental basis of cutaneous sensory innervation evinced by the ancient Greeks was developed into a major contribution to experimental biology by the studies in man and animals by Sherrington, Head and Foerster. The present study is one of a number of more recent investigations of the dermatomes in animals from which a great deal of comparative information has been obtained. The particular significance of a study of the functional anatomy of the sheep in relation to veterinary medicine has been discussed.

The experimental work described in this thesis involved particular consideration of the following :

1. The features of the topographical anatomy of the vertebral column of the sheep which were found to be of importance in the experimental procedures.
2. The value of the "remaining sensibility" technique as a means of defining the dermatomes of the sheep.
3. The use of figurines and photographs in the schematic representation of the experimental results.
4. The justification for basing the definition of the dermatomes largely on the responses to pinch stimuli.
5. A discussion of the features of the dermatomes of the sheep in relation to embryological development and the observations which have been made in other species.
6. The changes in muscle tonus in the limbs which followed

section of the dorsal spinal nerve roots or damage to the spinal cord.

7. The aberrations in feeding, defecation, micturition and respiration produced by various dorsal root sections.

8. The major pathways in the spinal cord followed by the primary afferent fibres, as revealed by the Marchi technique.

9. A general consideration of the significance of studies such as the present, and their possible extension to include deeper somatic or visceral structures.

Details of the dorsal root sections undertaken have been provided in an appendix.

THE SEGMENTAL SENSORY INNERVATION OF THE SKIN OF THE SHEEP

CHAPTER I

INTRODUCTION

The first accounts of studies of the distribution of the cranial and spinal nerves appear in the Greek literature (Osler, 1921). In the fourth century B.C. Herophilus identified the fifth, seventh and tenth cranial nerves and postulated the separate existence of sensory and motor nerves (Osler, loc. cit.). The segmental distribution of the spinal nerves was not investigated until the second century A.D., when Galen studied the effects on respiration and posture of transection of the spinal cord at various levels (Singer, 1944). Galen also noted (Fulton, 1949) that ipsilateral paralysis and contralateral sensory loss followed lateral hemisection of the spinal cord: effects which were studied in greater detail by Brown-Séquard, 1600 years later.

Vesalius, in the sixteenth century, and Prochaska, in the eighteenth century, produced illustrations of the segmental arrangement of the spinal nerves (Brazier, 1959), but little new knowledge was gained until the nineteenth century. Magendie is generally credited (Fulton, 1949) with offering, in 1822, the first satisfactory evidence that sensory fibres are confined to the dorsal roots of the spinal nerves and that the ventral roots contain motor fibres. Charles Bell claimed prior discovery (Shaw,1839) of this primary division of function, now stated as the Bell-Magendie Law.

It was then realised that specific afflictions, notably tabes dorsalis (Duchenne, cited by Major, 1954) and herpes zoster (Head, 1893), could affect the nerve tracts in the spinal cord and/or cell bodies in the dorsal root ganglia, and produce trophic changes in the skin areas innervated by these. The pattern of distribution of spinal sensory fibres thus assumed importance in localising infections. Following Marshall Hall's discovery (Singer, 1944) of the difference between volitional action and unconscious reflex, sensory impulses from specific areas of the skin also came to be used, especially by Sherrington (1906) in the study of segmental reflex arcs.

Details of the segmental sensory distribution of the spinal nerves are now used (Fulton, 1955) in distinguishing peripheral nerve injuries from injuries to spinal roots, in localising spinal cord injuries, in identifying the origins of visceral pain, and in studying lamination of spinal tracts and topographical representations in the cortex. The area of skin which receives sensory fibres from a particular spinal nerve has become known as a "dermatome". Originally denoting a machine for cutting thin slices of skin (Greek derma - skin, temnos - to cut), the word first appears in the titles of papers by German authors, e.g. Winkler (1903).

The Early Studies of the Segmental Sensory Areas.

The following account of the work of Eckhard, Peyer, Türck, Krause, Voigt and Koschewnikoff is based on details given in Sherrington's (1893) review. Eckhard (1849) concluded, from a study of the sensory roots of the four most caudal spinal nerves in the frog, that the skin-fields do not correspond with the muscle-fields supplied by the same nerves. The skin-fields of the fifth cervical to first thoracic spinal nerves in the rabbit were found by Peyer (1853) to overlap. In his study of the brachial plexus and the lumbar nerves in the dog, Türck (1856,1869) severed only the spinal nerve which he wished to examine.

He deduced that some skin areas, especially in the neck and trunk, are exclusive to one nerve, while others are supplied by more than one nerve. After studying both reflex responses and nerve degenerations in the rabbit, Krause (1865) stated, as had Voigt (1864), that individual variations affect only the course of the fibres between the spinal cord and the periphery, and that a muscle is supplied by nerve fibres from the spinal nerve which innervates the overlying skin. These statements contradicted those of Eckhard: they are now considered erroneous, but are worth recalling because they emphasise the doubtful value of some of the early contributions. Koschewnikoff (1868) concluded that most skin-areas in the hindlimb of the frog are supplied by more than one nerve.

The cutaneous distribution of the spinal nerves has also been traced by anatomical dissection. Herringham (1887) dissected the brachial plexus in human cadavers and formulated several rules relating to nerve distribution. Two of these concerned sensory fibres. The first stated that, of two spots in the skin that nearer the pre-axial border tends to be supplied by the higher nerve. The second stated that, the lower of two spots in the pre-axial area tends to be supplied by the lower nerve, while in the post-axial area the lower spot tends to be supplied by the higher nerve. More extensive dissections were made by Bolk (1898). He could not define the dermatome boundaries precisely, but his definitions of the shape of the human dermatomes agreed closely with those defined for the monkey by Sherrington (1893,1898) with the technique of "remaining sensibility".

The interrelation between cutaneous and visceral pain was established when Head (1893) observed that in humans pain from visceral structures was often associated with tenderness in sharply-defined tracts of skin. These tracts corresponded exactly with the areas involved in cases of herpes zoster. Head used this "referred pain" in an extensive study of the dermatomes.

At this time, too, came the outstanding contributions of Sherrington. On the basis of his studies of the distribution of spinal nerve fibres in the cat, frog and monkey, Sherrington (1893) concluded that the skin areas supplied by each spinal nerve form one continuous field; that successive fields overlap, not only cranially and caudally but also, to a lesser extent, across the dorsal and ventral midlines; and that the coccygeal skin is segmentally posterior to that of the hindlimb. In his now classical studies of the dermatomes in the macaque monkey, Sherrington (1893,1898) used what Head (1893) called the "remaining aesthesia" method to overcome the difficulties produced by the overlapping of the dermatomes. He left the spinal nerve under study intact, and cut the dorsal roots of the adjacent spinal nerves to produce an insensitive zone on either side of the dermatome. Reactions were evoked by pinching the skin with fine-pointed forceps.

Dusser de Barrenne (1933) recalls that he demonstrated in 1910 that after strychnine sulphate solution is applied to a segment of the spinal cord a sharply circumscribed area of skin becomes hyperaesthetic, and that his pupil, De Boer, used this technique in humans to map the hyperaesthetic areas associated with each dorsal spinal root: De Boer (1916) found these area to be slightly smaller than those defined by Head.

In 1933 Foerster recorded the results of an extensive study of the human dermatomes. He used a combination of the "remaining sensibility" method and the antidromic vasodilatation resulting from the faradic stimulation of the distal portion of a divided dorsal root. Foerster found that individual variation may be considerable, and that the tactile dermatomes are greater than the pain and thermal dermatomes.

Kuhn (1953) cites studies in dogs by Cardazo (1937) and by van Rijnberk and Ten Cate (1937). Lower animals other than the frog have also been studied. Ariëns Kappers _et_ _al_ (1960) cite investigations in sharks (van Rijnberk, 1917), lizards (van Trigt, 1917) and birds (Sparvoli, 1907; Deelman, 1919; Miss Kaizer, 1924).

More Recent Studies.

In man changes in the sweating pattern associated with sympathetic disorders have been used in defining cutaneous sensory areas (Wright, 1952). Richter and Woodruff (1945) removed autonomic ganglia of the sympathetic trunk and then measured variations in skin resistance. Keegan and Garrett (1948) recorded, in man, the areas of diminished sensibility to light pin scratch which followed pressure on individual spinal nerves due to protruding intervertebral discs. Their maps of the dermatomes differ significantly from those of other workers in that they show the limb fields extending the length of the appendages as regular spirals from the dorsal midline.

The lumbosacral tactile dermatomes in the cat and monkey have been defined (Kuhn, 1953) by recording, with the aid of a cathode ray oscilloscope, the potentials evoked in individual spinal root filaments by the movement of hairs. Kuhn found that the skin-fields of the filaments were arranged in an orderly serial manner within each dermatome: however, the type, intensity and extent of the responses varied considerably.

Hekmatpanah (1961) used similar recordings in compounding the remaining dermatomes (first cervical to third lumbar) in the cat. More recently, the forelimb dermatomes in the raccoon, coatimundi and cat have been defined from microelectrode recordings (Pubols, Walker and Johnson 1965). Darien-Smith, Mutton & Proctor (1965) mapped the tactile cutaneous fields of the main divisions of the trigeminal nerve in the cat. They found, as had previous workers, that the extent of the overlap of sensory fields on the head is much less than that of the dermatomes.

In the ox, Schreiber (1955) has studied the cutaneous sensory areas of the head, limbs and trunk, and Schaller (1956) has defined the distribution of the cutaneous nerves of the trunk. Arnold and Kitchell (1957) used the "remaining sensibility" method in their study of the innervation of the abdominal wall of cattle. They refer to previous similar studies by Farquharson (1940), St. Clair (1940) and Emmerson (1940, 1941). In the course of his study of the innervation of the mammary gland in the sheep and the goat, Linzell (1959) defined some of the lumbar and sacral dermatomes in these two species by recording the action potentials initiated in dorsal root filaments by mechanical stimulation of the skin.

In all of these studies, the dermatomes have appeared on the neck and trunk as serial overlapping bands; this pattern being modified on the limbs. The limb dermatomes as defined by Pubols *et al.* (1965) are irregularly shaped.

The Present Study.

Apart from Linzell's investigation (*vide supra*), there does not appear to have been any previous study of the segmental sensory innervation of the skin of the sheep. Sheep are important to New Zealand's economy, and vigorous efforts are being made to increase sheep numbers and to improve growth and reproductive performances. Details of the sensory innervation of the skin could prove useful in experimental studies of some of the problems involved. Several diseases of sheep involving primarily the central nervous system and/or the skin are already causing concern. They include listeriosis, toxoplasmosis, focal symmetrical encephalomalacia, polioencephalomalacia, swayback, clostridial intoxications, contagious pustular dermatitis and photosensitivity reactions (N.Z. Veterinary Handbook, 1962). In this category there are also several important exotic diseases of sheep which could be introduced into New Zealand.

As already noted in a previous outbreak of the disease in this country (Brash, 1952), sheep with scrapie often show an intense irritation of the lumbar skin. Pseudorabies is typified by lesions in spinal ganglia accompanied by frenzied scratching, and the ovine encephalomyelitis virus can invade peripheral neurones and produce hyperaesthesia (Smith and Jones, 1966). It was felt that a more extensive knowledge of dermatomal innervation in the sheep might provide a better basis for the differential diagnosis of these diseases, especially those characterised by hyperaesthesia, as well as providing further information of value in comparative studies.

THE ANATOMICAL BACKGROUND

So far as the writer is aware there is not available a substantial standard source of reference on the anatomy of the spinal cord, the meninges and the spinal nerves in the sheep. Kühn and Oberröder (1960) give an account, in German, of the topographical anatomy of the lumbar and sacral regions of the sheep, and make special reference to the meninges in these regions. Summaries of the features

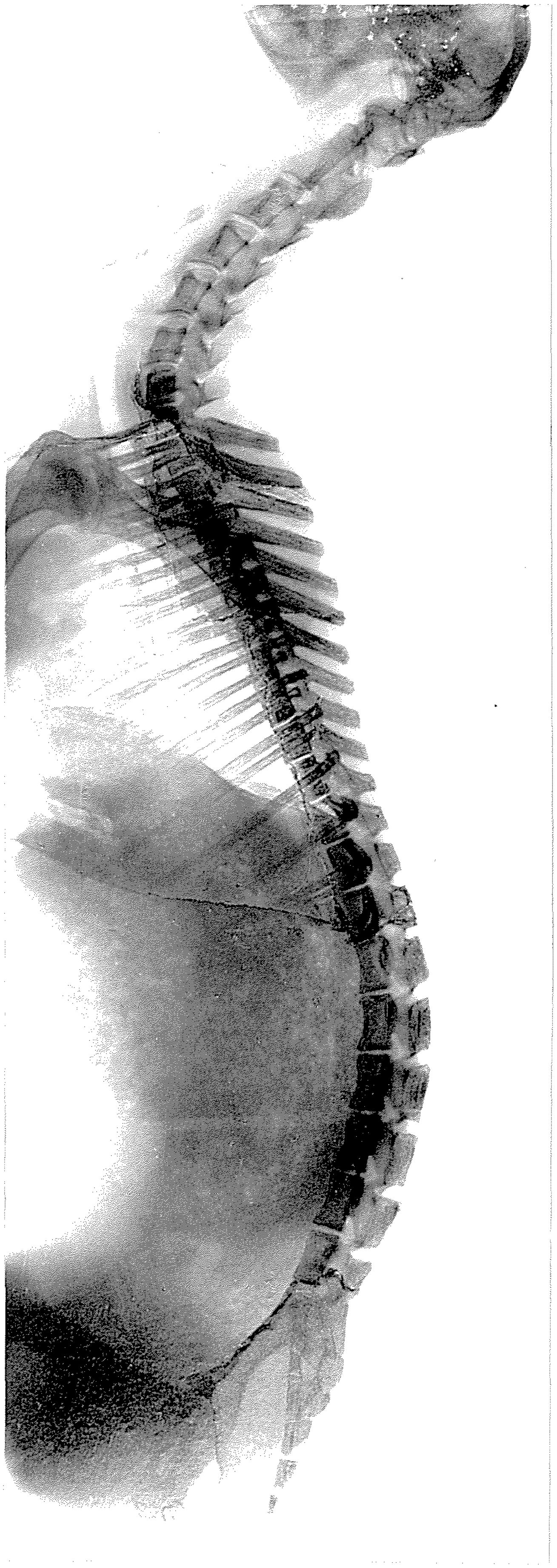

Fig. 1: Composite Radiograph of the Vertebral Column of the Sheep.

of the ovine skull and vertebrae, and of the associated ligaments and muscles are given by Sisson and Grossman (1955) and May (1964). The present account is based on observations made at autopsy in the sheep used in this study: it enumerates details which have proved important during surgery or the subsequent mapping of sensory areas.

The Vertebral Column.

In the vertebral column of the sheep there are seven cervical, twelve to fourteen thoracic, six or seven lumbar, and four sacral vertebrae. According to May (1964), there are also sixteen to eighteen coccygeal vertebrae. All of the sheep, used in this study had been docked, and had only three to five remaining coccygeal vertebrae . The thoracolumbar variation in these animals is summarised:

TABLE I

Numbers of Sheep with the tabulated combinations of thoracic and lumbar vertebrae

	Thoracic Vertebrae		
	T12	T13	T14
Lumbar Vertebrae			
L6	0	41	3
L7	1	7	0

The last ribs of several sheep, including those of two of the three with fourteen thoracic vertebrae, were rudimentary and asymmetrical.

The main features of the vertebrae are shown in the composite radiograph (Figure 1). The dorsal spines of the cervical vertebrae are short. That of the axis is broad. The dorsal spinous process of the first thoracic vertebra provided a useful landmark: it was much higher than that of the last cervical vertebra. In Romneys and Perendales (a Romney, Cheviot cross) its height was usually about half that of the

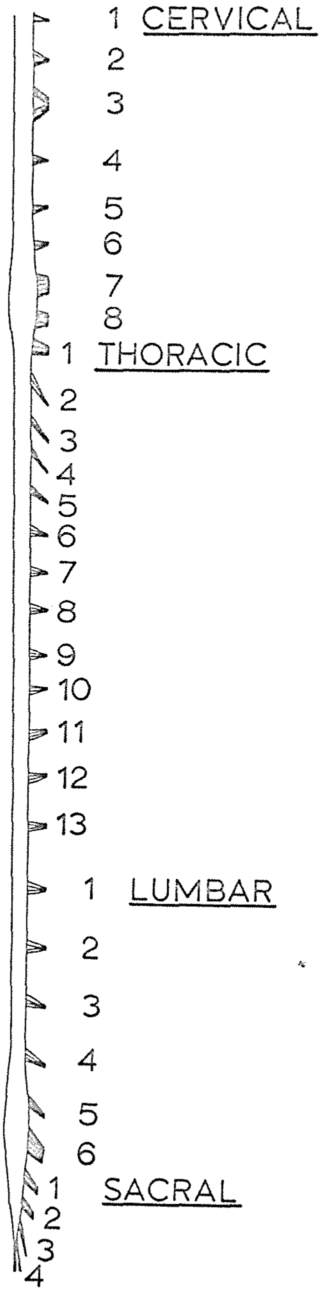

Fig. 2: Diagram of the Spinal Cord of the Sheep, showing the disposition of the dorsal rootlets of the spinal nerves.

second thoracic spine. In most Cheviots, however, it was almost as high as the second spine (Figure 1). This breed difference has been commented on previously by von Borstel (1952).

The heights of the thoracic dorsal spinous processes increase from the first to the fourth or fifth, and then decrease progressively to about the twelfth. The tips of the dorsal spines of the last two or three thoracic vertebrae are as broad as those of the lumbar vertebrae. The transverse processes of the lumbar vertebrae curve cranioventrally: they are of fairly uniform length, and the tips of all but the last were readily palpable, (except in the most obese of sheep.).

The dorsal arches of the sacral vertebrae were found to be incompletely fused. The heights of the sacral spinous processes, the extent of fusion, and the interval between the wings of the iliae were found to vary appreciably between individuals. The coccygeal vertebrae had small dorsal and lateral processes, and their dorsal arches were thin and much reduced. The first coccygeal vertebra is reported to fuse with the sacrum in adult sheep (May, 1964): fusion had not occurred in the animals used in the present study.

The Spinal Cord.

The spinal cord of the sheep is similar to that described in other domestic animals (Sisson and Grossman, 1955). As indicated in Figure 2, its diameter increases between the sixth cervical and the first thoracic segments to form the brachial enlargement. From the second thoracic to the fifth lumbar segments the diameter is smaller, and quite uniform. The lumbosacral intumescence involves the last two lumbar and the first sacral segments. Caudally, the diameter lessens abruptly, and in these sheep the terminal branches of the cauda equina arose within the coccygeal vertebra.

Figure 2 also indicates the disposition of the dorsal spinal nerve roots. The rootlets of the first cervical spinal nerve pass caudolaterally, those of the second and third nerves pass laterally, and those of the fourth, fifth and sixth extend somewhat cranially.

The rootlets of the seventh and eighth cervical nerves pass laterally: those of the first thoracic nerve extend very slightly caudally. The second thoracic nerve has the greatest backward inclination in this region. The degree of inclination then diminishes progressively, and the rootlets of the last three or four thoracic and the first two lumbar nerves pass laterally or even slightly cranially.

The rootlets of the first two lumbar nerves pass laterally: the backward inclination then increases. The third sacral and succeeding nerves have much-lengthened roots. May (1964) states that there are five pairs of coccygeal nerves, and that their branches form a dorsal and a ventral trunk on each side of the tail. The regular conus ascendens of man (Durward, 1964) and monkeys (Thomas and Combs, 1965) is thus not seen in the sheep: in this respect the spinal cord of the sheep resembles that of the ox and the horse (Habel, 1951).

Most of the dorsal root ganglia lie within the intervertebral foraminae: those of the third and fourth sacral nerves lie within the vertebral canal.

Some Features of Individual Spinal Nerves.

Some of the spinal nerves have features which permit ready identification. The third cervical spinal nerve arises over a relatively long length of the spinal cord, and its rootlets, both dorsal and ventral are in two distinct groups. In some sheep a similar but lesser separation of the rootlets of the fourth cervical nerve was observed. The sixth nerve is set somewhat apart from the succeeding trio of close-set nerves. The rootlets of the seventh cervical nerve are thicker than those of the more cranial nerves: they pass laterally and more or less horizontally. The rootlets of the next nerve are also thick, but they pass further ventrad. The pronounced backward inclination of the second thoracic nerve has already been noted.

The last thoracic nerve arises immediately caudal to the level of the last rib, and the last lumbar nerve arises at the level of the tubera coxarum. The third sacral nerve is much smaller than the second, and has a much greater caudal inclination. The fourth sacral nerve leaves the vertebral canal immediately caudal to the level of the hip joint.

The Meninges.

The spinal epidural space is large and contains much fat. In the cervical region the dura mater loosely surrounds the spinal cord: further caudad it is more closely applied. The subarachnoid space does not appear to extend to the dorsal root ganglia, for in most sheep the dorsal rootlets could be cut within 2-3 mm of the dura mater without release of cerebrospinal fluid. Fluid was released from the cervical and last lumbar roots in some sheep unless the severance was made further from the dura. Section of the terminal extension of the spinal cord at the level of the first coccygeal vertebra also released cerebrospinal fluid: in older animals the caudal limit of the subarachnoid space would be expected to lie further forward (Habel, 1964).

Blood Vessels.

Blood reaches the spinal cord through branches of the vertebral and sacral arteries and of the thoracic and lumbar branches of the aorta

(May, 1964). Small vessels, usually one to three in number, are interposed between dorsal rootlets. In many cases, especially in the posterior thoracic and in the lumbar regions a vessel comparable in size to a dorsal root filament traverses the epidural space up to 0.5 cm behind the root itself.

The main venous drainage is by means of the two longitudinal vertebral sinuses beneath the spinal cord. In two sheep of the Cheviot breed, however, the vertebral sinus was found to pass above the dorsal root of the first cervical spinal nerve. This change in position within the atlas is similar to that reported in the dog by Worthman (1956).

The Head.

The Skull.

In the sheep, the temporal wings of the sphenoid extend laterally to form the caudal border of the foramen ovale. The mandibular division of the trigeminal nerve, the middle meningeal artery, and the ventral cerebral vein pass through this foramen (May,1964). The concavity ventral to the foramen leads rostrally to the foramen orbitorotundum, from which emerge the ophthalmic and maxillary divisions of the trigeminal, together with the oculomotor and trochlear nerves. The pterygoid crest of the parietal bone forms a substantial prominence which overhangs the foramen orbitorotundum. The cornual processes of the frontal bones were rudimentary in the sheep used in this study.

The Cutaneous Sensory Nerves.

The trigeminal nerve provides the main sensory supply to the skin of the head, and has three main divisions (Westhues and Fritsch, 1964):

The ophthalmic division divides within the foramen orbitorotundum into the lachrimal, frontal and nasociliary nerves. The cornual braanch of the lachrimal nerve passes through the periorbita to the temporal skin. The several branches of the frontal nerve curve around the dorsal margin of the orbit. The cutaneous branch of the nasociliary nerve emerges at the medial canthus of the orbit and passes dorsal to the infraorbital recess.

The maxillary division lies immediately above the internal maxillary artery, and thus below the ophthalmic, oculomotor and trochlear nerves. It gives rise to the infraorbital nerve, which emerges from the homonymous foramen, and the zygomatic nerve, which supplies the skin below the eye.

The mandibular division gives off a deep temporal branch to the temporal skin. The superficial temporal nerve curves rostrally around the caudal border of the vertical part of the mandible to supply the skin below the eye, and sends a branch to join the dorsal buccal branch of the facial nerve.

The facial nerve emerges through the stylomastoid foramen; the glossopharyngeal, vagus and spinal accessory nerves emerge through the posterior foramen lacerum. The facial and vagus nerves send branches to the pinna of the ear; the auriculotemporal branch of the facial reaches the temporal skin.

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CHAPTER II

THE ISOLATION AND RECORDING OF THE CUTANEOUS SENSORY AREAS

The Animals Used:

Most of the sheep were young (6-8 months) ewes of the New Zealand Romney, Cheviot or Perendale breeds. Six 3-year-old rams of the Romney breed were also used. The majority of these animals came from the Massey University and Tuapaka flocks: the remainder were bought through the public saleyards.

The Isolation of the Cutaneous Sensory Areas.

The "remaining sensibility" method was used to isolate the various cutaneous sensory areas. The method was first used extensively by Sherrington (1893, 1898): its use overcomes the difficulties produced by the overlapping of the dermatomes. The definition of a trunk dermatome depended on the section of the dorsal roots of at least two spinal nerves cranial and caudal to the nerve under study. More extensive rhizotomy was required to define other dermatomes. The cutaneous distribution of the main branches of the fifth and seventh cranial nerves was defined similarly, by isolating, as far as possible, their sensory fields.

In an attempt to reduce the extent which the surgical interferences incapacitated the animals, isolations were often performed in two stages. This was considered particularly necessary in studies in the upper cervical and lumbosacral regions.

In many cases, the isolation of a particular dermatome provided an opportunity to define the cranial or caudal border of the next remaining intact dermatome. Again, such opportunities were not exploited fully because of a desire to limit the severity of the operations.

In the laminectomy operations most of the skin incisions were made in the dorsal midline. In some sheep, however, skin incisions were made 2-3 cm. to the opposite side to enable the extent of overlapping across the dorsal midline to be determined.

In sheep in which a sacral and a lumbar dermatome had been isolated dorsally but overlapped in the crutch, the local anaesthetic agent lignocaine hydrochloride B.P. ("Xylocaine", Astra) was injected epidurally at the sacrococcygeal joint. When the sheep no longer reacted to stimulation in the sacral field, the ventral extent of the lumbar dermatome was recorded. In sheep in which the maxillary division of the trigeminal nerve had been isolated on one side, its rostral extent in the vicinity of the dorsal midline was mapped after xylocaine had been infiltrated around the contralateral infraorbital foramen to abolish sensation in that area.

In the head region, the possibility that some cutaneous branches of the cranial nerves had been unintentionally left intact had to be considered. The extent of each upper cervical dermatome was therefore confirmed by severing the corresponding dorsal spinal nerve root by an approach through the initial incision line, and then checking that the outlined area was now insensitive. In all sheep, irrespective of the site of the laminectomy, the accuracy of the surgical sectioning was checked at autopsy.

Preparation.

The sheep were brought indoors several days before operation, shorn, placed in a portable crate and fed on chaffed hay supplemented with small quantities of fresh grass. Most animals appeared to accept their new environment within three or four days. The crates held the sheep approximately three feet above the floor: each animal was thus conveniently placed for nursing attentions and the mapping of sensory areas.

To reduce the risk of regurgitation of stomach contents during anaesthesia, food and water were withheld for 12-18 hours prior to operation. The operation site and the area in which mapping would be performed were closely clipped; the latter area was included at this stage to avoid the distress which clipping caused sheep with post-operative hyperaesthesia. An alcohol-iodine-alcohol sequence was used in skin preparation. All operative procedures were undertaken with appropriate precautions to maintain asepsis. Despite this infection of the vertebral canal was encountered in one sheep: it followed post-operative contamination of the wound. In several other sheep localised accumulations of pus 4-5 mm in diameter were found around some skin sutures, and in a group of three sheep a marked fibrous reaction was detected around chromic catgut sutures. It is probable these were all post-operative infections.

To reduce salivary and respiratory tract secretions 10-12 mgm of atropine sulphate ("Atropine Sulphate". B.D.H.) was injected subcutaneously 30-45 min before intubation. Pentobarbitone sodium B.P. ("Nembutal", Abbott) was used for induction in the first nine sheep. It was replaced by thialbarbitone sodium B.P. ("Kemithal", I.C.I.) which had the advantage of being shorter acting and of causing must less general depression.

With an endotracheal tube in place, anaesthesia was continued with a closed-circuit anaesthetic apparatus (British Oxygen Co.). This

THE OPERATING CRATE.

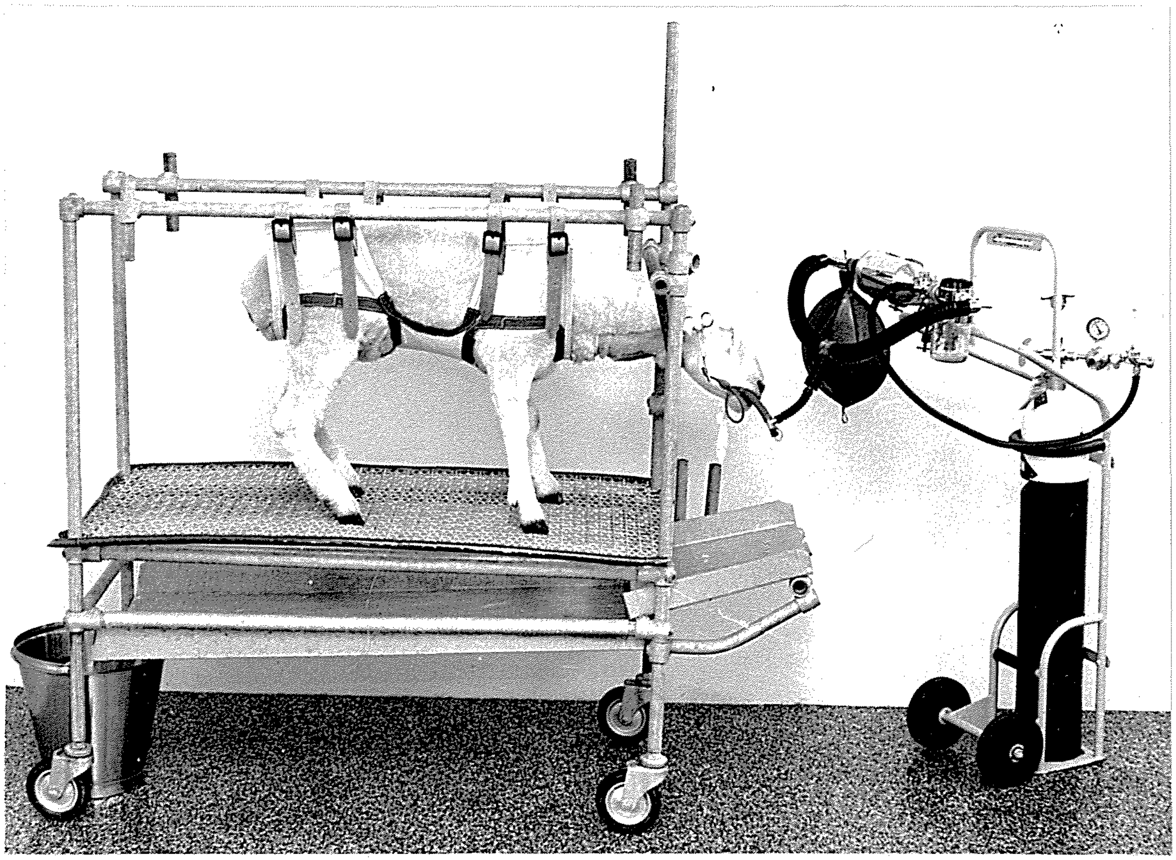


Fig. 3: The Operating Crate, showing an anaesthetised sheep prior to surgery.

equipment permitted good control of the depth of anaesthesia, using the volatile anaesthetic agent halothane B.P. ("Fluothane", I.C.I.). Halothane was shown to reduce the blood pressure considerably: this blood pressure depression reduced oozing from small vessels and assisted efforts to approach complete haemostasis.

In several sheep generalised trembling during anaesthesia created difficulties in surgery. Shivering is a feature of barbiturate anaesthesia and is believed to result from the effects of these drugs on the temperature regulating centres in the hypothalamus (Fulton, 1949). The trembling in these sheep was largely unaffected by changes in the ambient temperature; it was abolished by lowering the depth of halothane anaesthesia. The temperature in the operating theatre was maintained at 60°F to afford comfortable operating conditions and to avoid the increased surgical shock believed to be associated with higher temperatures during surgery (Mulcahy, 1964).

The sheep were held in the special portable operating crate shown in Figure 3. This crate offered several advantages. The sling held the animal upright, permitted convenient surgical access and resulted in minimal blood pressure levels dorsally. The anaesthetic apparatus (with a small gas cylinder) and the suction apparatus could be fitted to the crate, making it self-contained. Collapsible sides were fitted to confine the sheep during recovery. The drainage tray simplified cleaning.

The position of the sheep in the sling was adjusted (using wooden blocks and sandbags) to produce maximal dorsal flexion of the vertebral column at the operation site. As has been found in laminectomies in man (Pearce, 1957), careful positioning of the patient greatly increased the ease with which a laminectomy could be performed: this was especially apparent in the cervical region. In some upper cervical operations, and in operations on the head, the sheep was laid in ventral recumbency on an operating table which was tilted so that the head was higher than the caudal regions.

Surgical Procedure.

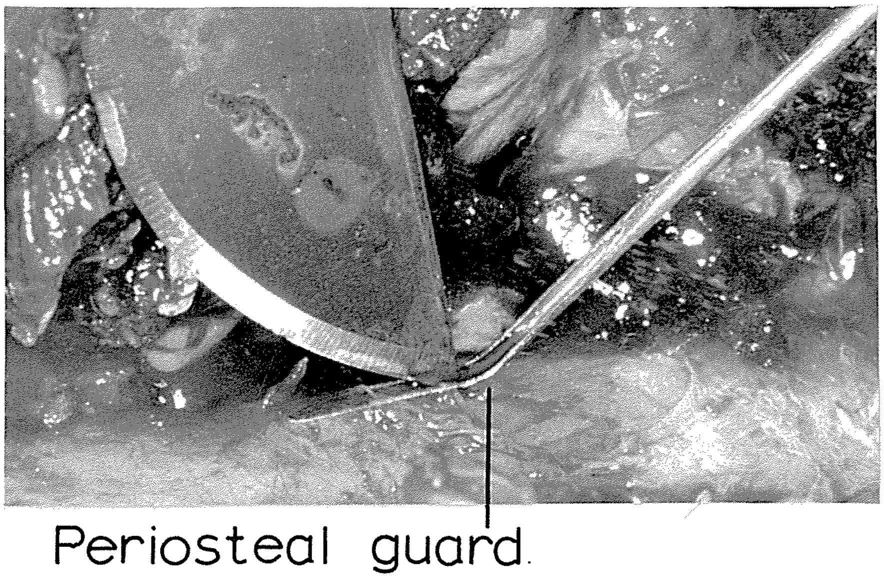
The first thoracic dorsal spinous process, the first lumbar vertebral transverse process, and the lumbosacral space served as primary landmarks; the remaining vertebral spinous processes afforded secondary landmarks. Each sheep was assumed initially to have thirteen thoracic vertebrae: the number of lumbar transverse processes could be counted - but for the difficulties involved all animals would have been screened radiologically. When this study was undertaken the restricted facilities available did not lend themselves to such procedures.

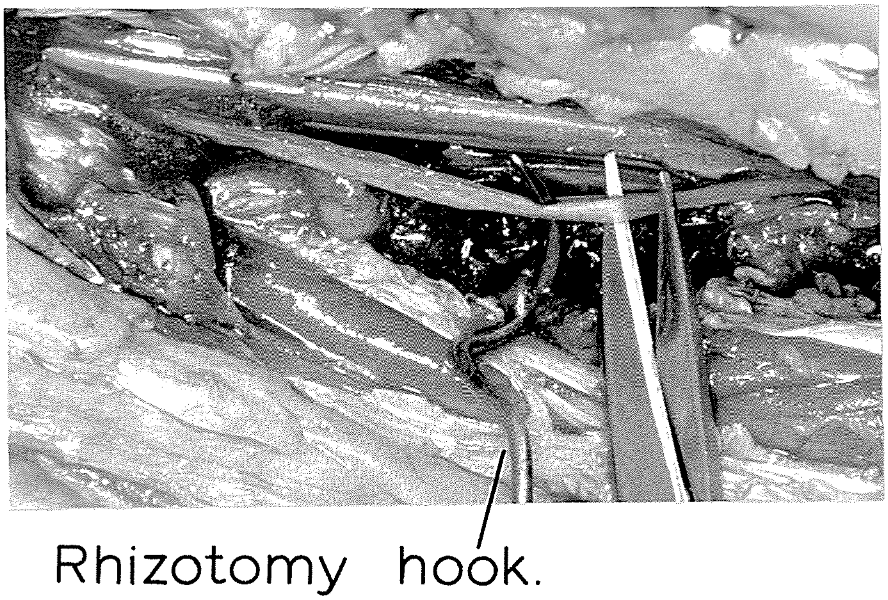
Shallow transverse cuts across the incision line were placed in the skin at regular intervals to assist accurate juxtaposition of the wound edges in the final suturing. The subcutaneous injection of 10-20 cc of warm (40°C) isotonic saline along the incision line greatly reduced haemorrhage.

A bold full-length incision exposed the connective tissue over the tips of the dorsal spinous processes. In the neck, the two parts of the funicular ligamentum nuchae were separated: its lamellar portion was split to expose the dorsal processes of the cervical vertebrae. Periosteal elevators were used to separate the attachments of ligaments and muscles from the dorsal spinous processes and the vertebral laminae.

Haemostats were applied on occasion to small vessels, but packing the wound with swabs soaked in warm saline or simply flooding the

SPECIAL INSTRUMENTS.





<u>Fig. 4</u>: The Special Surgical Instruments.

Upper - Periosteal Guard used to protect the spinal cord, which here is concealed by extra-dural fat.

Lower - Rhizotomy Hook used to elevate the dorsal root of the third sacral spinal nerve.

operative field with the saline usually served to control bleeding.

The use of retractors in the ends of the incision, combined with the dorsal flexion of the spine, produced sufficient lateral displacement of the longitudinal muscles. The major part of each dorsal spinous process was removed with straight-cutting bone forceps. Rongeurs were then used to remove the remainder of the spine and the dorsal section of the surrounding lamina. The periosteum lining the spinal canal was often ruptured during removal of the intervertebral connective tissue, with which it is intimately associated. To complete the laminectomy, the remaining periosteum was split longitudinally, using a special "periosteal guard" (made by splitting a 22G 1½ in. hypodermic needle lengthwise, Fig. 4) to protect the underlying spinal cord.

Suction was used to remove saline, blood and the extradural fat. In the first few operations the spinal dura mater was then opened longitudinally (again using the "guard"), and the dorsal roots of the spinal nerves cut within it. In all later operations the rootlets were severed outside the dura mater -- access was quite easy, loss of cerebrospinal fluid was avoided, and there was much less risk of trauma to the spinal cord.

A special "rhizotomy hook", made from a size 8 suture needle (Fig 4), was passed between the dorsal and ventral groups of rootlets of the appropriate spinal nerve. The dorsal rootlets were cut with a pair of small, angled, sharp-pointed scissors. The removal of a 1-2 mm length of each severed rootlet made subsequent confirmation of the severance much easier. Haemorrhage from small blood vessels within the dorsal root was controlled, again with warm saline, and the completeness of the rhizotomy checked. In many cases, the blood vessels traversing the epidural space behind each lumbar root was left intact. At the completion of the dorsal root sections, the longitudinal muscles were approximated with a single continuous suture. Additional sutures were used to eliminate dead space in the shoulder region, and the two parts of the funicular ligamentum nuchae were sutured together. The skin incision was closed with interrupted transverse mattress sutures, and sprayed with "plastic skin" ("Nobecutane",Evans). Most sheep were given a single intramuscular injection 500,000 U. benzylpenicillin ("Crystapen", Glaxo) at the conclusion of an operation.

The ophthalmic and maxillary divisions of the trigeminal nerve were cut as they emerged from the foramen orbitorotundum. Access was gained by removing the posterior part of the bony orbit and the contiguous rostral portion of the zygomatic arch. In most instances the mandibular division of the trigeminal nerve, and the other cranial nerves sectioned were approached through an incision immediately ventral to the external auditary meatus. Access to the mandibular nerve was also gained by cutting through the centre of the vertical part of the ramus of the mandible.

To facilitate the ready location of particular nerves in subsequent operations on the same animal, loops of size 0 multifilament stainless steel wire (or single strands thereof) were placed in the adjacent connective tissue or, in the case of the main divisions of the trigeminal nerve, placed loosely around the nerve itself. These "tagged" nerves could then be approached through an incision in the line of the initial operation.

Recovery.

In the 24-28 hours immediately after surgery particular care was directed to nursing each sheep. The animal was encouraged to eat and drink, and its position was adjusted frequently. When necessary, the sheep was assisted to micturate by supporting it in the appropriate stance and compressing its bladder through the ventral abdominal wall. When the ambient temperature was low, the sheep was kept in a controlled-temperature room (70°F) for the first day. Most were held in slings in the portable crates; the others were placed on a wooden platform on the floor. After section of the dorsal roots of nerves involving the forelimb, sheep tended to somersault backwards out of their slings while attempting to stand, unless they were restrained by straps looped loosely across their backs. Light plaster casts were placed on the fetlocks of partially or totally deafferentated limbs. These provided mechanical support and were thought to greatly assist the animal's readjustment. They also minimised abrasions to the skin of the foot.

Most of the sheep ate, drank and stood unaided the day after operation. They appeared alert and interested in their surroundings: this was taken to indicate that they were not grossly discomforted. Sheep thought to be distressed were injected with 100 mgm pethidine hydrochloride B.P. and 1.25 mgm levellorphan tartrate B.P. ("Pethilorfan 100", Roche), this had only a transient effect, and sheep which continued in distress were destroyed. Such destruction was performed primarily on humane grounds: it was also considered that records based on the reactions of a distressed sheep would be suspect. Similarly, sheep which appeared distressed at a later stage were destroyed, whether or not the mapping of the sensitive areas had been completed.

Recording.

The boundaries of the dermatomes were recorded by combining the results of a series of procedures :

1. Felt - pens were used to mark the boundaries of sensitive areas. The use of various coloured inks permitted pinch and touch areas to be mapped concurrently, and successive delineations to be compared. The first marks were placed on the wool; they were later clipped off and the skin itself marked. Marks on the skin persisted for several weeks, even if hidden beneath a regrowth of wool, unless subjected to rubbing through contact with the ground or the sling. In a few sheep, tattooing of "key points" was used to maintain a permanent record of the dermatome boundaries on a limb.

2. Standard figurines were prepared from photographs of a closely-clipped sheep on which prominent anatomical features (spine of scapula, costal arch, tuber coxae, etc) had been marked. The dermatomes as mapped on each sheep were copied onto these figurines.

3. Wherever possible, photographs of each sheep were taken with the animal in a normal standing position. Black-and-white prints were used in direct comparisons with the figurines. The images of projected colour slides were adjusted to give the "best fit" with a standard figurine, and the dermatome boundaries traced into this outline.

4. Sheep to be destroyed were anaesthetised with Nembutal, exsanguinated, and perfused with Kaiserling I solution, or buffered or neutral formalin (Gurr, 1962). Either of the latter two solutions was used when tissue was to be taken for Marchi stains. The dimensions of the sensitive areas were measured on the cadaver,

and their relations to bony landmarks noted. A description of the course of each boundary was also recorded. The lines of the dermatome boundaries were then cut into the underlying tissues; after the accuracy of the surgical sections and the numbers of thoracic and lumbar vertebrae had been checked, the positions of the dermatome boundaries in relation to the individual vertebrae were recorded.

5. Where applicable, embalmed limbs and heads were retained to allow direct comparisons between sheep to be made.

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CHAPTER III

THE EFFECTS OF DORSAL ROOT SECTION ON RESPONSES TO CUTANEOUS STIMULATION.

In the mapping of cutaneous sensory areas in humans, much use is made of the test-subject's description of the sensations which he experiences. In studies in animals, however, the definition of a change or loss in cutaneous sensitivity depends entirely on the observation of responses to definite adequate stimuli. The selection of a suitable stimulus has always been difficult. Sherrington (1893), in discussing the choice of a reflex to be used in the cat, stated :

> "It is evidently desirable for the purpose to choose as criterion of the existence of afferent nerve-fibres a reflex the quantitative amount of which is at least roughly estimable, a reflex not easily fatigued by repetition, not likely to be occasioned by extraneous occurrences during an experiment nor to be simulated by nervous actions arising intrinsically, and, above all, a reflex capable of being evoked to a clearly detectable extent by excitation even feeble in character."

It was found that the most definite and consistent responses obtained from these sheep followed pinching of the skin: responses to pinch stimuli were therefore used in mapping the cutaneous sensory areas. Reactions to prick and touch stimuli were also recorded when they were clearly apparent.

Pre-operative Responses to Stimulation.

The responses in the normal animal could be assessed after a training period of about half an hour. Repeated testing over this period was usually necessary before a sheep would neither struggle nor "sulk" after the pinch stimulus was applied. In the sheep used, the response to pinching of the normal skin was a slight transient twitching of the skin in an adjacent area. The intensity of the pinch applied was that which was just sufficient to evoke such a response.

The responses were modified when the sheep were restrained. An animal held sitting on its haunches would not always give definite responses to pinch stimuli applied to the skin of the trunk or limbs. The most obvious responses were obtained in sheep which were standing. Stimulation of the lower limbs or the head was then followed by a brisk flexion of the limb or a rapid withdrawal of the head. A response to pinching the outer aspect of the limb above the carpus or tarsus was a slight transient twitching of the skin over the lateral aspect of the thorax or abdomen. Pinching the skin of the perineal region evoked brisk twitching of the tail.

Reactions to pinch-stimuli delivered to the lateral aspect of the upper hind limb and to the ventral abdominal wall were quite variable. The position on the body surface also had considerable bearing on whether fatigue was manifest. Fatigue usually developed with repeated delivery of the stimulus, but was not apparent in responses to pinch stimuli applied below the carpus or tarsus or on the poll, lips, teats or perineum: indeed, most sheep became increasingly restless with repeated stimulation of these particular regions.

Responses to touching the skin with either the fingertips or the points of the forceps were inconsistent. When an animal was approached unexpectedly and touched even very lightly, it would start violently: yet the application of the same stimulus to the same spot at any stage during the remainder of the visit would often not produce any apparent response.

Post-operative Responses to Stimulation.

After section of the dorsal roots of all of the spinal nerves innervating an area of skin, no response could be evoked with pinch or touch stimuli delivered in that area. In no instance did section of the dorsal root of a single spinal nerve render any area of skin insensitive. Only a few of the dorsal spinal nerve roots were cut separately in this way, but those investigated included the seventh cervical and the second sacral, each of which innervates a large part of the skin of a limb.

(a) Hyperaesthesia.

As each animal recovered from anaesthesia it became apparent that the responses to stimuli delivered in the zone of operation were much augmented. Touching or pinching the skin innervated by intact nerves in this region produced a vigorous twitching of the skin, followed by frenzied biting and chewing movements and, at times, grinding of the teeth. The sheep would turn and bite or nibble vigorously at the skin near the point of stimulation or, if unable to turn in this manner, would bite on or nibble at the sides of the food and water vessels. Less extreme reactions were seen as rapid nibbling movements of the lips, commonly accompanied by an upward extension of the head and neck. These hyperaesthetic responses also appeared after "mock" operations, in which the dorsal roots were handled but not cut. No sharp demarcation between hyperaesthetic and normal areas was observed. The reactions tended to be most decisive in the dorsal parts of the body, and in the skin immediately cranial to the laminectomy zone.

This hyperaesthetic response was usually not seen after the second day: it persisted until the eighth day in a sheep in which the dorsal surface of the spinal cord had been rubbed with the suction tube.

In the three animals in which a second operation was performed in the thoracolumbar region a week after the initial interference, it was considered that the degree of hyperaesthesia was at least equal to that following the initial operation. In each of these sheep, however, an excessive reaction was no longer evident after the third day.

Touching the skin in an isolated dermatome, or in the adjacent part of the surrounding sensitive skin, with the moving blades of a pair of electric clippers produced a frenzied reaction which far exceeded the response to any other stimulus. The response could still be evoked one to two days after hyper-reaction to pinch stimuli was no longer apparent.

Sheep also reacted strongly to "slipping" of the skin between the points of the forceps, even when much less skin deformation appeared to be involved than when the skin was simply pinched and held. A reaction to "slipping" could often be obtained before any decisive responses to pinch or touch stimuli could be elicited from the skin in the ventral portion of a dermatome.

Within some parts of an isolated dermatome there was, in the first few days, often no definite twitch in response to a pinch stimulus. However, several pinches in an area later shown to be part of the sensitive field would result in the sheep making numerous small stepping movements, attempting to move away from the forceps, and then crouching and straining to micturate. This reaction could be obtained repeatedly, even when no urine was voided after the first response. Indeed, it was often the first indication, especially in the caudal half of the body, that a particular area under test would later prove to be part of an isolated dermatome. The reaction was particularly clear when the skin of the third and fourth sacral dermatomes was stimulated. The passage of faecal pellets often followed the first stimuli. Sheep whose hindquarter were supported in a sling did not, however, exhibit the contractions of the abdominal and perineal musculature which commonly accompanied defecation in these animals.

In the more ventral parts of the trunk dermatomes, maximal responses took up to five days to appear. The responses were then not only more decisive, they were much more easily elicited.

A sheep in which the sixth, tenth, and eleventh thoracic dermatomes were isolated made persistent attempts to shake itself on the second, third and fourth days. It was supposed that the animal associated some unpleasant stimulus with the skin of the trunk. No other evidence was found to suggest that a sheep might be experiencing unpleasant cutaneous sensations between tests. No scratching was seen.

b) Fatigue.

As in the normal animals before they were operated on fatigue occurred with repeated delivery of the stimulus. When defining the position of the boundary of a sensitive area, the onset of fatigue was delayed by moving from the insensitive zone toward the reactive zone, rather than in the opposite direction. Fatigue was not seen with the delivery of stimuli to the head, teats, perineum or the lower limbs. In other regions, the number of stimuli necessary to induce fatigue varied: on the trunk, and upper limbs, about half a dozen pinch stimuli within fifteen to twenty seconds was often sufficient. After repeated stimulation of the skin in these regions a sheep would cease to react to pinching which was severe enough to produce red spots in the skin.

(c) General Disturbances.

Sheep which were alarmed or distracted would often fail to give consistent reactions to stimuli, particularly to those applied near a dermatome boundary. The reactivity of the skin was reduced in the area immediately adjacent to a sling. In addition, sheep with urinary retention were generally less reactive than others. An animal with a partially deafferentated limb would often attempt to use the limb for support in standing, and while making such attempts often would not react to a stimulus delivered to the limb, even if this stimulus was adequate when the sheep was recumbent.

(d) Variation with Position on the Body Surface.

The most decisive reactions were obtained with pinch or touch stimuli delivered to the head, the dorso-lateral parts of the trunk, and the lower limbs. Responses from the base of the neck below the level of the shoulder joint, the ventral abdomen and crutch, and behind the stifle joint were consistently less vigorous then elsewhere. It was also often difficult to obtain decisive responses to pinch stimuli delivered to the medial aspect of the forelimb between the elbow and the carpus, or to the medial aspect of the hindlimb immediately above the tarsus. These differences were found in each of the dermatomes covering a particular area. In many cases it was noted that a sheep would respond to pinching of the ventral abdominal wall when it was standing, but not when recumbent.

(e) Variations between Responses to Pinch and Touch Stimuli.

Responses to touch-stimuli could often be obtained from an area slightly greater than that sensitive to pinch-stimuli. The greater extent (up to 1cm) of the touch field was particularly apparent on the trunk and upper limbs; however, the boundary of an area defined by touch

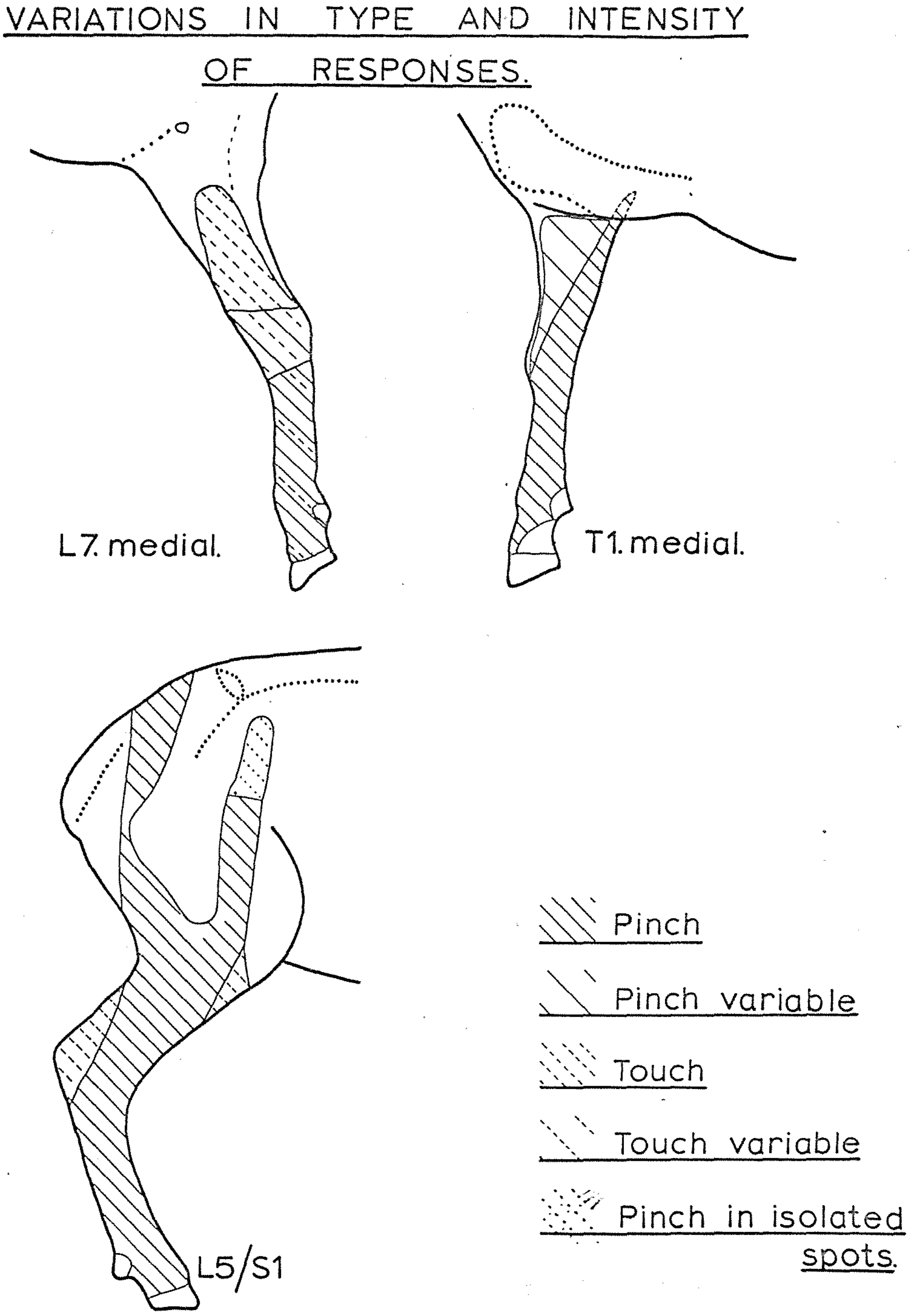


Fig. 5: Variation within individual dermatomes in the type and intensity of responses to pinch and touch stimuli.

was not as clear as that of a pinch field.

Variation in the intensity of response to either pinch or touch stimuli in the boundary zone was appreciable. It was usual for the dermatome boundary to be quite irregular when first mapped: with successive tests further spots were found to react decisively, and the boundary finally obtained usually followed a steady curve. Even after the gross position of a boundary had ceased to change, responses might not be obtained from a particular spot just within the boundary on one occasion, but would be apparent on the next. With one exception, discussed below, there did not appear to be any points within a dermatome which consistently failed to yield any response to pinch stimuli: however, investigation of this point was not exhaustive.

Apart from the variations noted above, three instances of specific variation between pinch and touch fields were discovered. These are illustrated in Figure 5, which is a diagrammatic representation of the following:

(i) In the T1 dermatome of one sheep, responses to pinch stimuli delivered to a triangular zone on the medial aspect of the forelimb were consistently more difficult to evoke than in the adjacent parts of the dermatome. Responses to touch stimuli delivered to any part of the medial aspect of the limb were indefinite and did not permit assessment of the relative intensity of stimulation needed to evoke a response.

(ii) In the L7 dermatome, the most distal skin on the medial aspect of the limb gave strong reactions to pinch and touch, that on the medial aspect of the tarsus yielded variable responses, and proximal to this, a zone sensitive only to touch appeared. In the three weeks for which the sheep was observed, the strongly reactive zone extended proximally over the medial aspect of the tarsus, and some indefinite responses to pinch stimuli were recorded above this joint.

(iii) In the third sheep the first sacral and several rootlets of the fifth lumbar dorsal spinal roots were left intact. In the fifteen days the animal was kept alive responses to touch but not pinch stimuli were obtained in areas behind the stifle and over the hamstring. Below the tuber coxae, the dorsal section of the reactive area yielded responses only to pinch stimuli: within this section responses were obtained only from clearly separated spots: the reactions were quite brisk. This was the only indication found that sensitivity to a particular sensory modality might be confined to specific points within a dermatome.

Sheep gave much more definite responses to touching closely clipped skin than they did even to extreme bending of locks of the fleece. They reacted even more strongly to traction on a wool fibre, or on a hair of the coronet.

Responses to pricking were found difficult to assess, but the prick-sensitive areas appeared to correspond with the pinch-sensitive zones.

Heat and cold stimuli were not applied.

(f) Variations with Time.

In some sheep reactions from the whole dermatome were apparent even before the animal had recovered from the anaesthetic sufficiently to take an interest in food. At this stage, recognition of the dermatome boundaries was possible, and was not complicated by the range of responses manifest by the fully conscious sheep. These reactions were noted particularly in respect of the areas of the upper cervical dermatomes, and on the head.

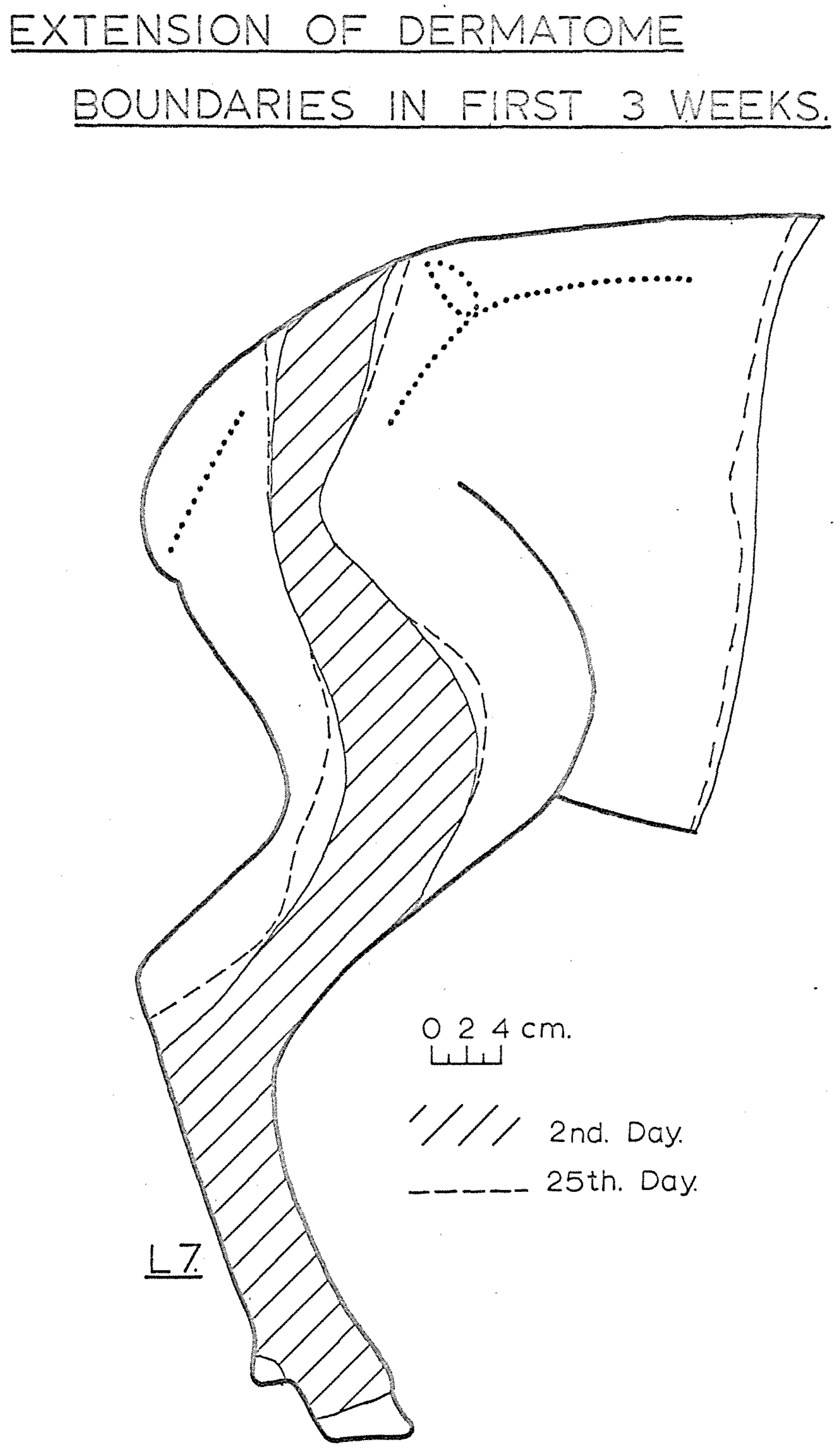


Fig. 6: The extension of the boundaries of the seventh lumbar dermatome between the second and the twenty-fifth days after operation.

In other sheep, reaction to pinch stimuli appeared first in the dorsal part of the dermatome and in some instances, on the lower limb. The reactive area then extended progressively ventrad within the following 48 hours.

In all of these sheep, the dermatome mapped soon after the operation was slightly smaller than the final field. By the third week the sensitive field had further extended by up to one centimetre. Figure 6 shows a typical extension. The most decisive distinction between reactive and non-reactive skin was seen in the dorsal part of the dermatome.

Extensions rather greater than 1 cm were recorded behind the stifle and adjacent to the hamstring: they seemed to occur in those areas in which the responses to stimuli at both initial and later mappings were not as definite as elsewhere (compare with Fig. 5) Figure 6 shows that in the second mapping of the anterior limit of the insensitive zone, a small but distinct loop formed on the lateral abdominal wall. This was taken to indicate a greater local extension of reactivity. As will be discussed in Chapter IV, such flexures in the dermatome borders were not infrequent, even at the initial mapping. No further extension of the boundaries was noted within the maximum time that any sheep was kept after operation - namely two months.

Discussion.

After section of the dorsal roots of all of the spinal nerves supplying an area of skin there were no responses to stimuli delivered to this area. This finding that the cutaneous afferent fibres are confined to the dorsal roots is in accord with the Bell-Magendie Law. There was no evidence available to indicate whether efferent fibres are confined to the ventral roots.

The failure to detect a loss of sensitivity in any area of skin after section of a single dorsal root indicates that each of the areas examined was supplied by at least two spinal nerves. A more detailed study might show some reduction in sensitivity in part of the skin after section of a single dorsal root. Sherrington (1901) found, in monkeys, that section of one dorsal root abolished heat and pain sensitivity and reduced tactile sensitivity within a small area of skin in some individuals.

The possibility that some cutaneous afferent fibres pass through the paravertebral sympathetic chain must be considered. Visceral afferent fibres are found in this chain (Davis, Pollock & Stone,1932; Downman and Hazarika, 1962; Hazarika, Coote & Downman, 1964), and fibres carrying deep pain impulses have been recorded (de Jong and Cullen, 1963). Any cutaneous afferent fibres present in the chain could enter the spinal cord through the dorsal roots of spinal nerves above or below the operation zone. Van Harreveld and Smith (1952) isolated trunk dermatomes in the cat by cutting adjacent spinal nerves distal to the rami communicantes. They then performed a sympathectomy and found that pain sensitivity was lost from a small additional area on the anteroventral side of the dermatome. Downman and Hazarika (1962) demonstrated, however, that some of the thoracic white rami communicantes give off long branches which pass into the chest wall. They suggest that these branches reach the skin, and that they could have been cut in the sympathectomy procedure. If it were usual for the paravertebral sympathetic chain to contain cutaneous afferent fibres, total loss of sensitivity within regular bands of skin would not have appeared consistently in this study.

Hyperaesthesia was a striking feature of the immediate post-operative period. It resembled the secondary hyperaesthesia observed in humans (Fulton, 1955) in that it appeared when apparently normal skin was stimulated and disappeared by the third day. Fulton (*loc. cit.*) states that in such hyperaesthesia the threshold to stimulation is raised: this increase tends, however, to be masked by the increased intensity of the responses. An increase in receptor thresholds may explain why in some sheep no reactions were obtained at first from the more ventral parts of a dermatome.

The likelihood that hyperaesthesia is largely a result of surgical trauma is suggested by its appearance after "mock" operations in which the spinal nerve roots were handled, but not cut. Its persistence for eight days in a sheep with damage to (at least) the dorsal columns of the spinal cord, and its reappearance in other sheep after a second operation in the same zone would also seem to support this hypothesis. In their histological study of the effects of laminectomy, Peele and Windle (1946) found some damage to the dorsal columns of the spinal cord in all cases, even in those in which the dura mater had not been opened. The occurrence of some damage to the spinal cord itself during each laminectomy is also suggested by the transient posterior paresis which followed the mock operations.

The extensive lateral retraction of the longitudinal muscles from the surgical field is likely to have damaged branches of the dorsal rami of the spinal nerves: in one sheep a strip of skin adjacent to the dorsal midline was rendered insensitive, although the dorsal spinal nerve roots on that side had not been sectioned. In less extreme cases, this damage could have resulted in a lowering of the thresholds of the subcutaneous receptors in the area -- which might explain why the hyperaesthetic responses were particularly intense when stimuli were applied near the dorsal midline.

If, as seems probable, all parts of the skin are supplied by more than one spinal nerve, all points within an isolated dermatome or within the adjacent zones of reactive skin cranially and caudally will be partially deafferentated. That this partial deafferentation might influence the development of hyperaesthesia is suggested by the conclusion of Weddell, Sinclair & Feindel, (1948) that a reduction in the intensity of innervation will cause an alteration in the quality of pain.

The decisive reactions obtained from the dorsal and lateral aspects of the body could reflect a denser innervation of the skin of these parts and/or the presence of more specialised receptors. The areas producing variable responses to pinch or touch stimuli could have fewer receptors, or the receptors might respond to other stimuli, such as warmth or cold. The apparent absence of reaction to even severe pinching of the ventral abdominal wall in recumbent sheep, or in the limbs of sheep held sitting on their haunches is difficult to explain. Head (1893) has stated that the recumbency of a sick animal is a reflex response to pain and noxious stimuli: the change in posture is apparently accompanied by a change in the perception of cutaneous sensation.

The non-appearance of fatigue in the responses to stimuli delivered to the poll, lips and genitalia may be related to the presence of specialised receptors in these areas (Glees, 1961). The continuing sensitivity of the lower lip in particular, may be associated with its relatively wide cortical representation (Adrian, 1943). The absence of fatigue in responses to stimulation of the skin of the lower limbs could be a reflection of the importance of the flexion reflex in the avoidance of noxious stimuli (Sherrington, 1906); or, as discussed below, it could indicate that subcutaneous receptors have also been stimulated.

Only one sheep showed signs that it might be experiencing unpleasant cutaneous sensations between tests. There was no means of ascertaining whether any such sensations originated in the skin, in the peripheral nerves, or centrally. The lateral and ventral parts of the body of a sheep supported in a crate were in contact with the sling, yet this contact did not induce continuous hyperaesthetic reactions. This probably resulted from the rapid adaptation to a continuous stimulus which is characteristic of cutaneous receptors (Glees, 1961). Such an adaptation ventrally, might provide yet another explanation why the hyperaesthetic reactions were more intense dorsally.

The hyperaesthetic reactions seen in these sheep resembled closely the nibbling and biting reported as a feature of scrapie infections (Brash, 1953; Stamp, 1962). This suggests that the scrapie agent affects sensory pathways specifically. The change may be at both higher central and lower (spinal) levels, for although the major pathological changes in scrapie are confined to the brain, vacuolation of neurones may occur in any part of the neuraxis (Stamp, loc, cit). It seems significant that in spite of extensive rhizotomies in all regions of the spinal cord, accompanied in some cases by handling of the dorsal roots and the dorsal root ganglia of the spinal nerves left intact, no sheep was ever seen to scratch. This suggests that the scratching seen in sheep with scrapie is the result of a central abnormality.

Responses to pinch stimuli were used in mapping the cutaneous sensory areas because they were the most definite and consistent obtained. Pinch is not regarded, however, as a single sensory modality: it probably involves a combination of touch, pressure and pain (Kuhn, 1953). Appreciable mechanical deformation of the skin would also seem to be involved.

The brisk reactions to stimulation of the skin of the lower limbs may have arisen because the pinch stimuli also affected receptors in the subcutaneous tissues with which the skin of the lower limbs is closely attached. Lindblom (1965) discovered that in the distal glabrous skin of the monkey, tactile stimulation initiated discharges in two types of large-fibre sensory units. One group had intracutaneous receptors, circumscribed receptor fields, and responded only to touch. The other was supplied by subcutaneous receptors with extremely low thresholds, and responded to both touch and vibratory stimuli. In his study of the effects of the severence of a nerve in his own arm, Head noted immediately after the operation that the pressure of a blunt instrument was readily appreciated everywhere, but more careful examination showed a loss of awareness of light touch and a loss of two-point discrimination (Stopford, 1930).

The augmented responses to contact with moving clipper-blades suggest an increased sensitivity to vibratory stimuli. Since vibration impulses are transmitted through the dorsal columns of the spinal cord (Ranson & Clark 1959) they would be particularly likely to be modified by trauma to the spinal cord.

Brisk reactions were also obtained to "slipping" of the skin between the points of the forceps. Tapper (1964) has shown with touch receptors in the cat that the initial impulse frequency is related to the deformation velocity. Fulton (1955) states that vibratory sensibility is not a separate sense, but involves the perception of a temporal pattern of pressures. It would appear probable that in "slipping" it is the rate of change of deformation of receptors in the skin -- probably touch receptors -- which is important.

The touch fields were found to be greater than the pinch fields. This is in accord with the finding that in man (Foerster, 1933) and the monkey (Sherrington, 1893) the touch fields are more extensive than the pain fields. Several explanations of this difference have been offered. Trotter and Davis (1909, 1913) showed that in a zone of partial sensory loss, there was a quantitative reduction in sensitivity, rather than a separate system of nerve fibres as had been postulated by Head (Stopford, 1930). Weddell, Taylor & Williams (1955) have proposed that the differences between touch and pinch spots are probably based on a spatio-temporal coding of impulses; and Weddell, Palmer and Pallie (1955) have stated in their review that there is no evidence to support the idea that each of the primary cutaneous sensory modalities is subserved by a histologically distinct receptor. The demonstration that Meissner's Corpuscles and Pacinian Corpuscles have a constant and intricate structure (Cauna & Mannan, 1959) makes it likely, however, that the skin contains some specific receptors. And as Le Gros Clark (1958) has commented, a receptor could be modality-specific without this being apparent histologically.

In one sheep, particular spots in the area supplied by rootlets of the fifth lumbar spinal nerve were found to be sensitive to pinch stimuli, while adjacent spots were insensitive to either pinch or touch.

Spots in the skin sensitive to the particular modalities, pain, touch, cold or warmth have been mapped in man (Glees, 1961). This offers some further support for the idea of punctate sensibility. It is also in accord with Kuhn's (1953) report that there is some separation of the fibres subserving each sensory modality between the individual rootlets of a dorsal spinal nerve root.

Brushing of individual hairs has been used to induce dorsal root potentials in several studies (Weddel, Taylor & Williams, 1955; Kuhn, 1953; Hekmatpanah, 1961), and similar stimuli in the intact sheep might be expected to evoke some response from the animal. In this study gross bending of wool fibres failed to produce any apparent responses, yet light traction on a wool fibre evoked a brisk reaction. There may be some major differences between the innervation of hair and wool fibres: In a preliminary investigation of this possibility, sections of the skin of several sheep were stained supervitally with methylene blue, after the method of Miller, Ralston & Kasahara, (1958); some were counterstained with eosin. Figure 7 shows a dichotomy of fibres in the dermis, an aggregation of branches around wool follicles, and a plexus extending to the epidermis; these features suggest a close resemblance to the innervation of human skin, as illustrated by Le Gras Clark (1958). No attempt was made to use other techniques to confirm that the stained structures did represent nerve fibres. A more detailed study could also incorporate comparisons between different parts of the body surface.

Little extension of the dermatome boundaries was recorded within a two month period. The slight extension of the boundaries within the first few mappings has been noted previously by Sherrington (1893) to accompany the disappearance of the depression induced by spinal shock. Kuhn (1953) reported a steady dimunition in the amplitude of responses

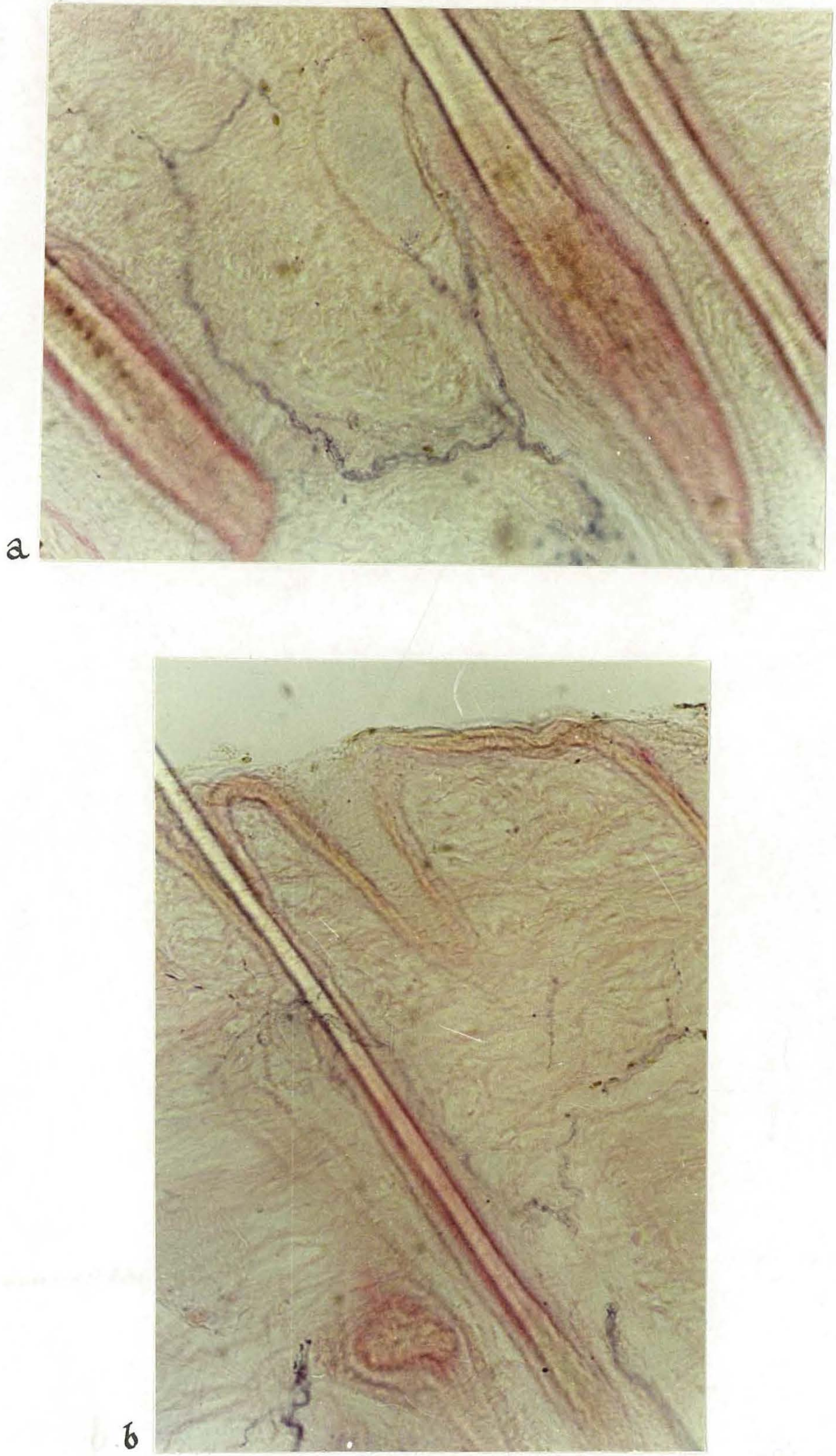


Fig. 7: Photomicrographs of the skin of sheep, stained supravitally with methylene blue and counterstained with eosin.

(a) Dichotomy of a nerve between two wool fibres (100x)

(b) Nerve fibres which surrounded a wool fibre and an associated sebaceous gland (100x).

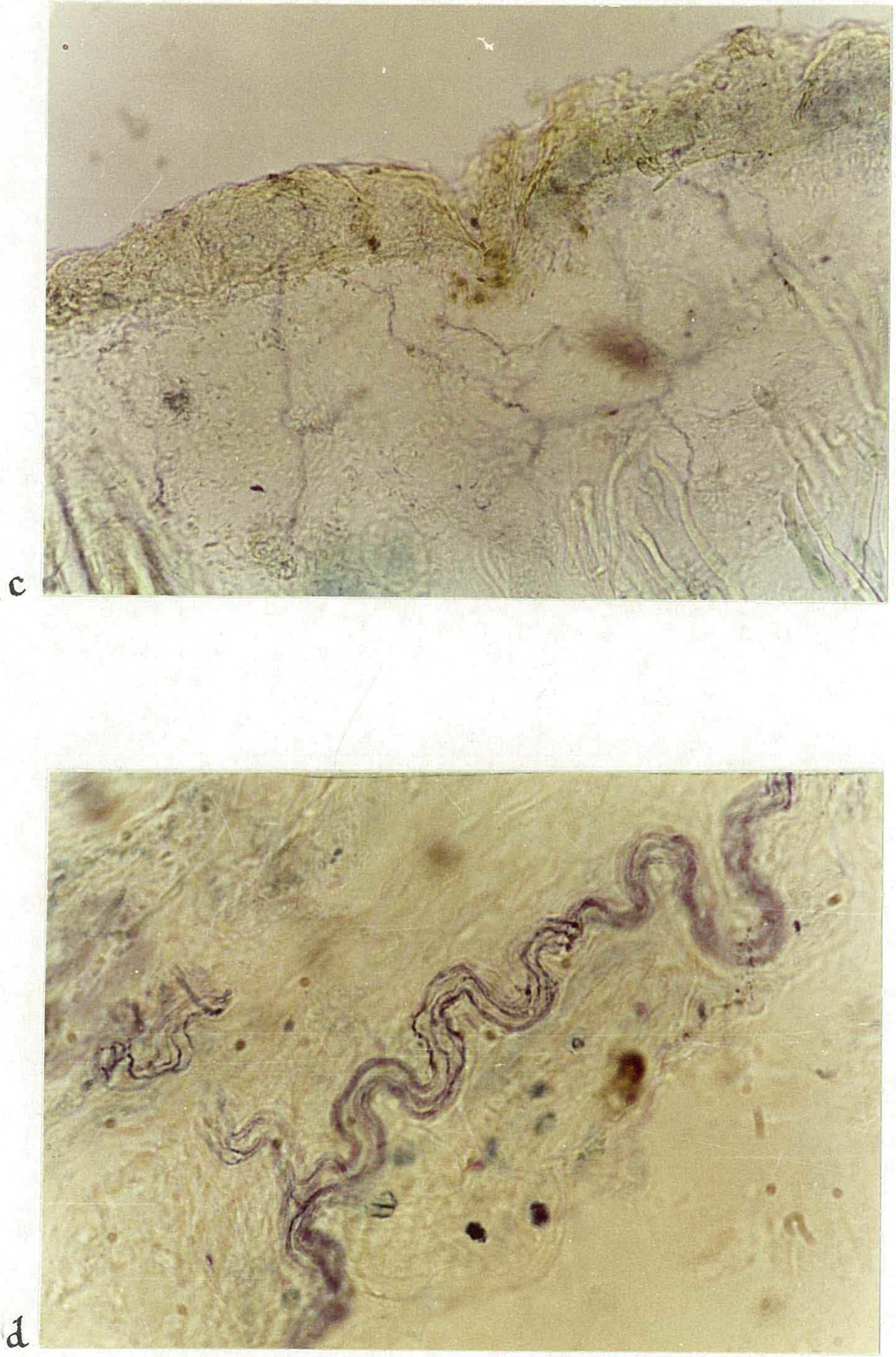


Fig. 7: Photomicrographs of the skin of sheep, stained supravitally with methylene blue.

(c) Plexus of nerve fibres extending to the epidermis (100x)

(d) Bundle of nerve fibres showing typical tortuous appearance.

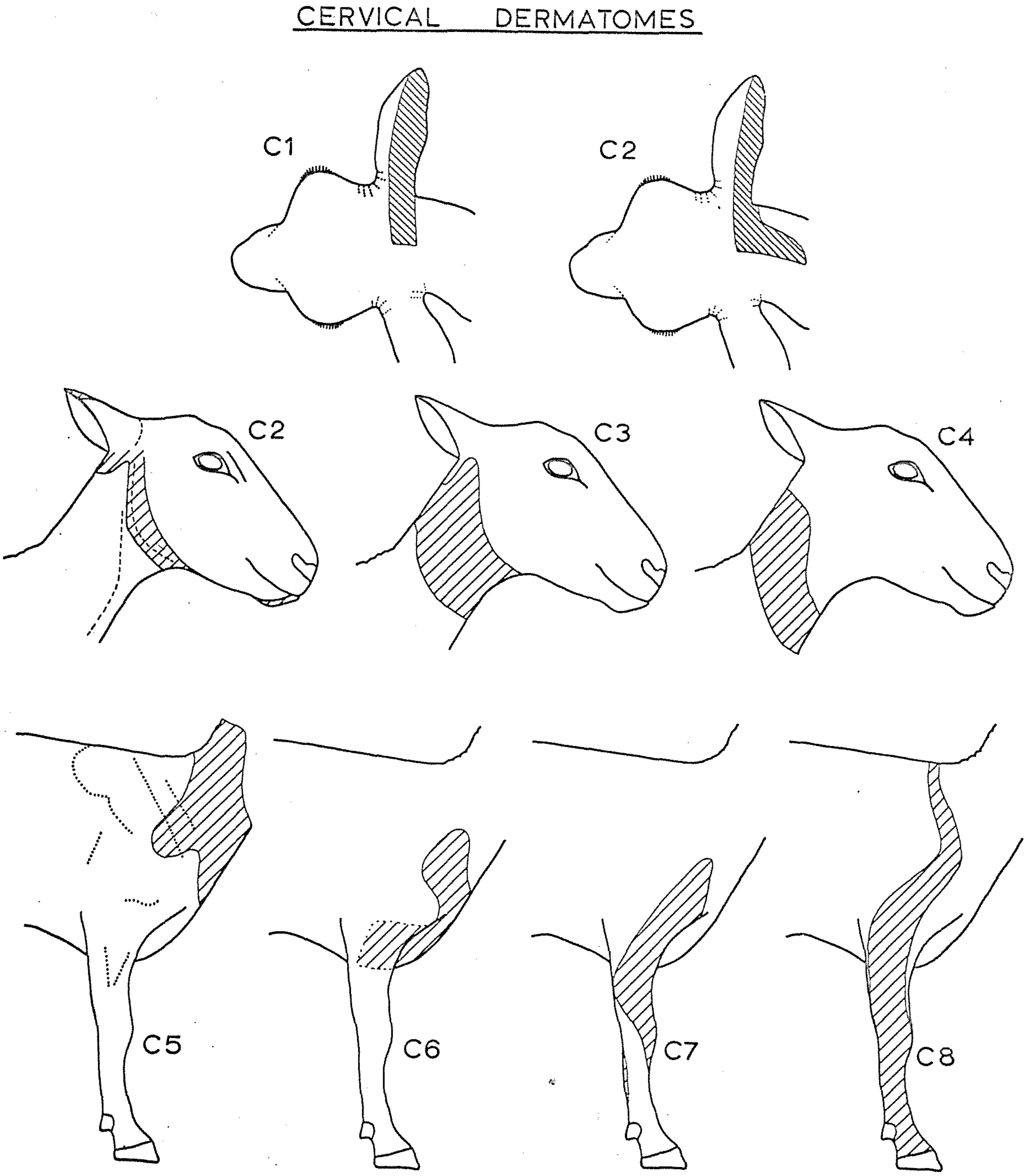
between the centre and the periphery of a skin zone. The extension of the boundaries by about a centimetre within three weeks could be due to changes within the remaining functional receptors in the vicinity. The extension occurred within the zone in which changes in the position of the boundary had been found between successive tests within the first week. Some outgrowth of fibres into the insensitive zone is also likely. Fitzgerald (1963) reports a 10 mm extension in six months in the pig.

CONCLUSIONS

1. Cutaneous afferent fibres were confined to the dorsal roots of the spinal nerves.
2. Section of single dorsal spinal nerve root was not followed by an obvious loss of sensitivity in any area of the skin.
3. Hyperaesthetic reactions appeared after laminectomy operations but did not persist for longer than three days.
4. Once hyperaesthesia had disappeared, the intensity and type of responses obtained after delivering stimuli to an isolated dermatome were similar to the reactions obtained from the sheep pre-operatively.
5. Reactions to pinch stimuli were more definite than the responses to touch stimuli.
6. The touch dermatome was more extensive than the pinch dermatome.
7. Fatigue was not seen on repeated delivery of a stimulus to the head, teats, lower limbs or perineum.
8. Fatigue developed readily on the trunk and upper parts of the limbs.
9. The intensity of the responses was modified considerably by general disturbances to the animal, and by altering its posture.

10. Responses to stimuli delivered in the boundary zone between sensitive and insensitive areas varied considerably between successive tests: the responses to stimulation of the central region of an isolated area were much more uniform.

11. Little extension of the dermatome boundaries occurred within two months: the greatest extension occurred dorsally and in those regions in which reactions were always variable.



<u>Fig. 8:</u> The Cervical Dermatomes. The levels of the boundaries in the dorsal midline are shown in Table 2, and details of the dorsal spinal nerve roots sectioned in each instance are provided in Table 12.

CHAPTER IV

THE SEGMENTAL CUTANEOUS SENSORY AREAS.

The Dermatomes.

Each dermatome, from the first cervical to the second coccygeal, was isolated in at least one animal. In many cases, the cranial and caudal borders were defined separately in other sheep.

The relations of the dermatome boundaries to the levels of the individual vertebrae are recorded in Tables 2 - 5, and details of the dorsal spinal nerve roots sectioned in each case are given in the Appendix (Tables 12-16). Some partial definitions are recorded in the Tables: the only records cited are those in which a large part of the boundary had been defined.

The various sensory areas are illustrated in Figures 8 -12. All of these areas are shown on the right side of the animal: where a dermatome had been isolated on the left side, a mirror image of the final record is presented.

TABLE 2

CERVICAL DERMATOMES

LEVELS OF DERMATOME BOUNDARIES IN THE DORSAL MIDLINE

Dermatome	No. of sheep	Anterior Border Level	Anterior Border No. of other sheep used	Posterior Border Level	Posterior Border No. of other sheep used	Extent
C1	1	On head	-	Atlanto-occipital joint	-	Band onto dorsal surface of ear
C2	1	On head	-	C1-C2	-	Overlies Mandible
C3	1	C1	1	C2-C3	3	Upper neck
C4	1	C1-C2	-	C5-C6	1	Central neck
C5	1	C1-C2	-	C6-C7	-	Lower neck
C6	1	-	-	-	-	Front of shoulder
C7	1	-	-	-	-	Spirals over dorsal aspect of forelimb
C8	2	C7-C8	-	C8-T1	-	Major part of forelimb

Annotations:

C1 - The sensitive area extended onto the dorsal surface of the pinna, but it was not possible to determine whether it included the inner surface of the pinna and the skin below the ear.

C2 - This relatively narrow dermatome overlay the caudal border of the vertical part of the ramus of the mandible, and then extended ventrally in the same curve to at least the level of the corner incisor tooth. The rostral limit could not be determined because contralateral afferent fibres were later found to extend into the lower lip in this animal.

C3 - A relatively wide dermatome, this lay immediately caudal to the ear. There was a distinct rostral flexure in the dorsal part of its anterior border.

C4 - The caudal border of this field curved evenly between the dorsal and ventral midlines. The anterior border was the more flexuous.

C5 - The caudal portion of the sensory area formed a loop which extended onto the front of the shoulder.

C6 - This skin field covered the base of the neck and the ventral part of the anterior thorax. It did not reach the dorsal midline.

C7 - The dermatome did not reach the dorsal or ventral midlines of the body. From the shoulder it spiralled over the dorsal forearm to include most of the medial surface of the limb, the whole of the medial chief digit dorsally and the dorsal adaxial surface of the lateral chief digit.

C8 - Above the carpus, this dermatome did not extend over the dorsal or the volar surfaces of the limb. It reached the dorsal midline, but not the ventral midline of the body, and it included the whole of the limb below the carpus.

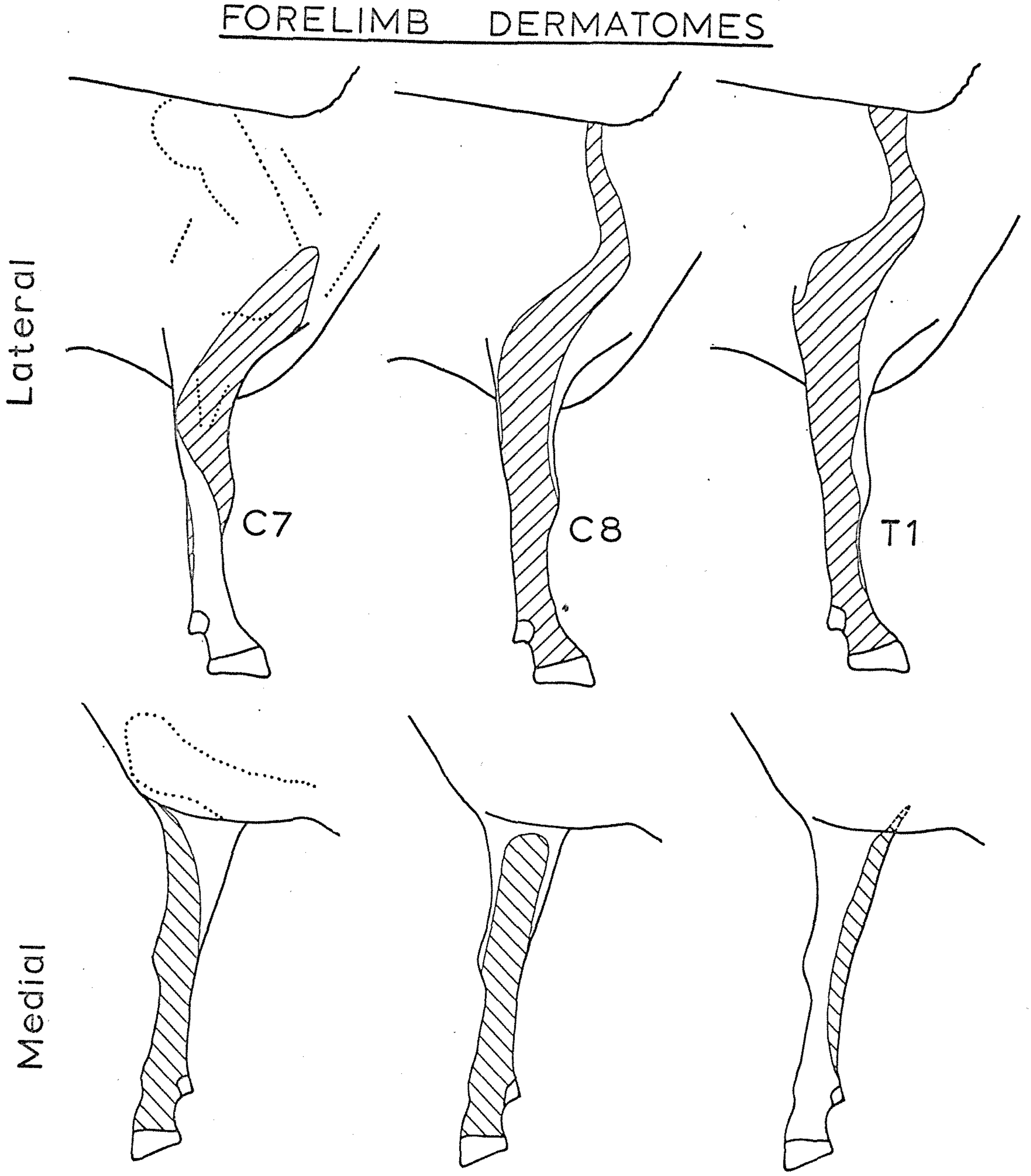


Fig. 9: The dermatomes extending over the forelimb. The result of a second isolation of the first thoracic dermatome is shown in Figure

When the eighth cervical and first thoracic dermatomes were first isolated, sensitive skin at the withers and in the lower limb was separated by an intermediate unreactive zone (Figure 13-1). It was thought that the nerve branches supplying this intermediate zone may have been damaged during surgery: each dermatome was therefore isolated in a second sheep, with as little lateral retraction of tissues as possible. In both cases an intermediate insensitive zone again appeared, but this time it regressed progressively until, on the fifth day, the extending sensitive areas merged. No repeat isolation of the sixth or seventh cervical dermatomes was attempted.

TABLE 3

THORACIC DERMATOMES

LEVEL OF DERMATOME BOUNDARIES IN THE DORSAL MIDLINE

Dermatome	No. of sheep	Level of Anterior Border	No. of other sheep	Level of Posterior Border	No. of other sheep	Extent
T1	2	T1	-	T3	(1)	Volar aspect of forelimb
T2	1	T2	-	T4	(1)	Behind shoulder
T3	1*	T3	-	T5-T6	1	Behind shoulder
T4	1*	T4	1	T6-T7	-	Immediately caudal to elbow
T5	2	T5	3	T7-T8	-	Regular band
T6	1	T6	2	T8-T9	1	Regular band
T7	1	T7-T8	-	T9	1	Regular band
T8	1	T8-T9	2	T10	-	Regular band
T9	1†	T9-T10	-	T11-T12	2	Regular band
T10	1	T10-T11	1	T13	1	Regular band
T11	1**	T11-T12	1	L1	1+(3)	Regular band
T12	1†	T12-T13	-	L2-L3	3	Regular band
T13	1	T13-L1	1	L3	1	Regular band
T14	-	-		-		-

* - Dermatome as isolated in another sheep, did not reach dorsal midline.

** - In another sheep, bilateral section of dorsal roots of two nerves on either side failed to isolate the dermatome.

† - The dermatome was isolated bilaterally in this sheep.

The figures in brackets, thus (1) refer to the number of cases in which partial isolation of the dermatome was performed.

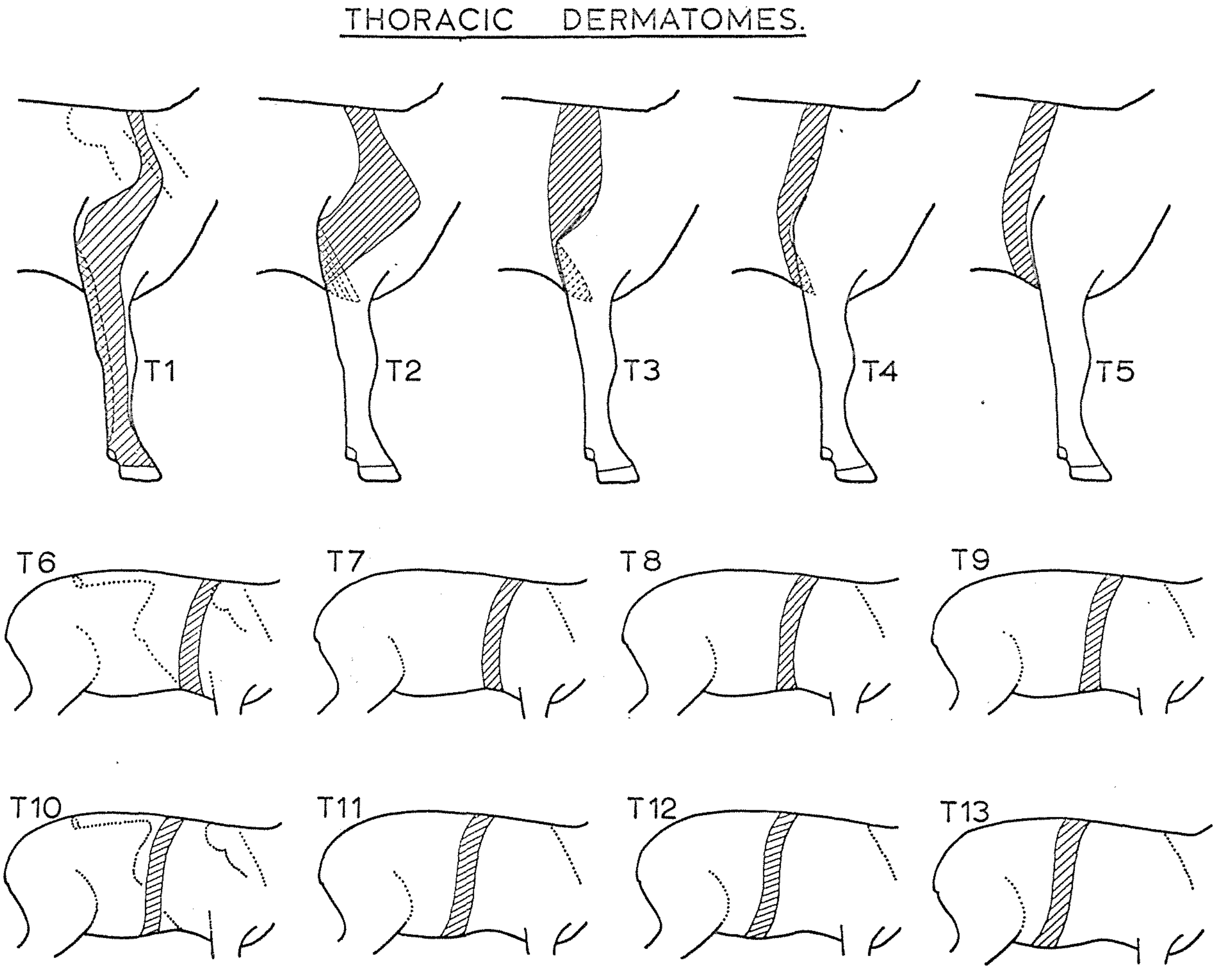


Fig. 10: The Thoracic Dermatomes. The levels of the boundaries in the dorsal midline are shown in Table 3, and details of the dorsal spinal nerve roots sectioned in each instance are provided in Table 13.

The Thoracolumbar Dermatomes.

Annotations:

All of the thoracic dermatomes extended as continuous bands between the dorsal and ventral midlines of the body.

T1 - The full skin field extended over most of the limb, apart from its dorsal surface as far as the fetlock. Only the caudal portion of the dermatome reached the ventral midline.

T2 - This dermatome expanded over the dorsal part of the limb behind the shoulder, and extended around the caudal border of the limb below the elbow and into the axilla.

T3 - The anterior border curved behind the scapula to a point just above the elbow, and then extended obliquely forward on the ventral thoracic wall. The regular curve of the posterior border lay just behind the elbow.

T4 - This was a fairly even band, except where it narrowed just behind the elbow.

The fifth thoracic to second lumbar dermatomes were found to be regular bands of similar width. Both borders of the fifth to eighth thoracic dermatomes and the cranial border of the ninth thoracic dermatome had the concavity of their curve directed forward. The curvatures of the caudal border of the ninth thoracic dermatome and of both borders of the succeeding dermatomes were sigmoid: the flexures increased progressively to bring the ventral portion of each successive dermatome further behind the level of the dorsal portion.

The position of the caudal border of each of the trunk dermatomes approximated closely to that of the cranial border of the next-but-one dermatome. Thus, the caudal border of the eleventh thoracic dermatome and the cranial border of the thirteenth thoracic dermatome both extended to the umbilicus.

The fourteenth thoracic dermatome was not isolated in any of the three sheep found to have fourteen thoracic vertebrae.

TABLE 4

LUMBAR DERMATOMES

LEVEL OF BOUNDARIES IN THE DORSAL MIDLINE

Dermatome	No. of sheep	Ant. Border		Post. Border		Extent
		Level	No. other sheep	Level	No. other sheep	
L1	1*	L1-L2	1	L3	1	Regular band
L2	2	L2-L3	2	L4	3	Regular band
L3	5	L2-L4	-	L4-L5	1	Regular band
L4	2	L4-L5	-	L6	-	Regular band to below stifle
L5	3	L5-L6	1	S1-S2	-	
L6	1	L6-S1	2	S2	-	Major part of hindlimb
L7	1	L7-S1	-	S2	-	

* - Dermatome isolated bilaterally in this sheep

** - Partial isolations.

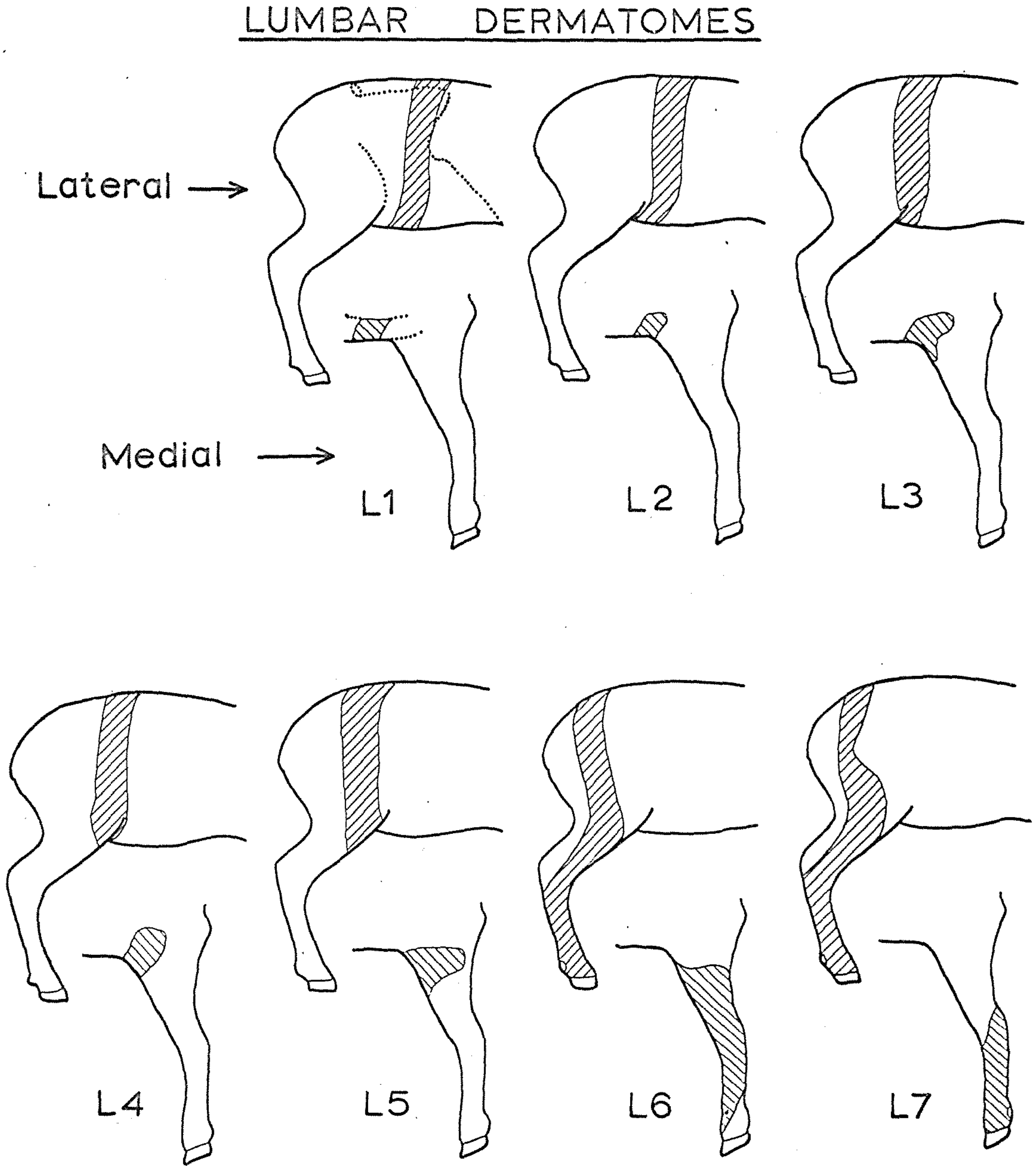


Fig. 11: The Lumbar Dermatomes. The levels of the boundaries in the dorsal midline are shown in Table 4, and details of the dorsal spinal nerve roots sectioned in each instance are provided in Table 14.

L2 - This skin field lay in front of the stifle, and extended to the most cranial part of the base of the teat.

L3 - Above the stifle, the dermatome overlay the cranial border of the hindlimb. It included the inguinal pouch, the mammary gland and the medial aspect of the stifle. In one animal the teat was insensitive.

L4 - The dermatome lay immediately in front of the tuber coxae, and covered the stifle joint. It included the whole of the mammary gland and teat ipsilaterally, and overlapped with the fourth sacral dermatome on the caudal part of this gland.

L5 - In two sheep with six lumbar vertebrae, the sensitive area overlay the tuber coxae and passed behind the stifle joint. In the standing animal the caudal border was practically vertical; it crossed the dorsal surface of the limb midway between the stifle and the hock. Medially, the dermatome extended almost to the caudal border of the limb. It lay caudal to the inguinal pouch and distal to the mammary gland, and thus failed to reach the ventral midline. In a sheep with seven lumbar vertebrae, the dermatome lay in front of the tuber coxae and extended onto the posterior abdominal wall above the stifle.

L6 - In a sheep with six lumbar vertebrae this dermatome extended from the dorsal midline of the body to include most of the limb distal to the level of the middle of the tibia, apart from the medial chief digit and the dorsal adaxial surface of the lateral chief digit. It did not approach the ventral midline. In the one ram studied there was no reaction from either the scrotum or the prepuce on that side.

L7 - The sensitive area extended over the lateral aspect of the limb to include the whole of the appendage below the tarsus. There was a distinct constriction in the field at the level of the hip joint. Medially, the area extended some distance proximal to the tarsus, but in the animal studied the responses to stimuli applied in this area were very variable.

TABLE 5

SACRAL AND COCCYGEAL DERMATOMES

LEVEL OF BOUNDARIES IN THE DORSAL MIDLINE

Dermatome	No. of sheep	Ant. Border		Post. Border		Extent
		Level	No. of other sheep	Level	No. of other sheep	
S1	1	S1-S2	2	S3-S4	-	Lateral aspect of hindlimb;medial metatarsus.
S2	1	-	2*	-	-	Caudal and lateral hindlimb
S3	4	S3-S4	1*	On tail	-	Caudal thigh
S4	3	S4-Cc1	1*	On tail	-	Base of tail,perineum
Cc1	-	S4-Cc1	6	On tail	-	Whole of docked tail, ipsilaterally.
Cc2	-	Cc2	2	On tail	-	

* - Partial isolations

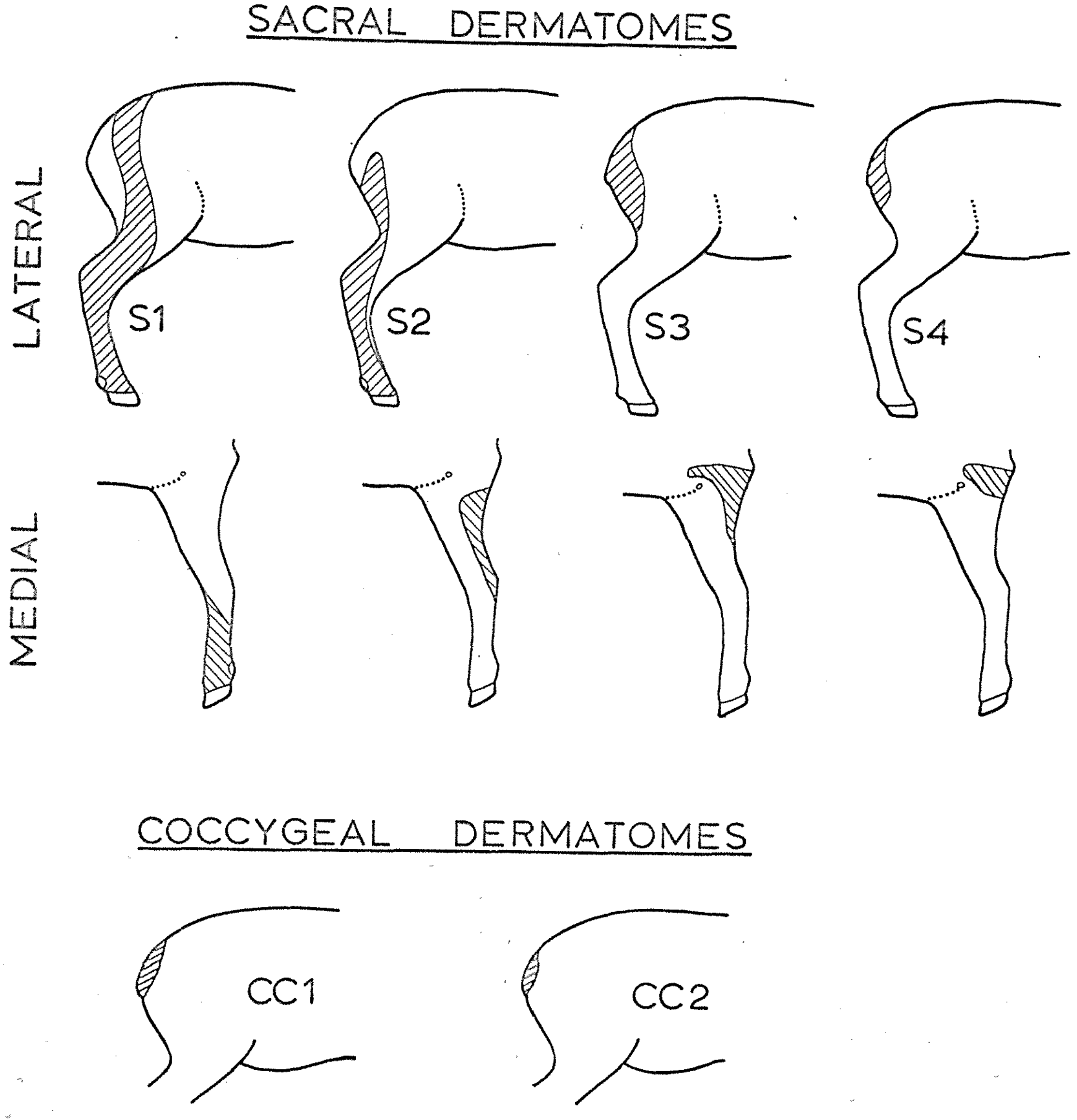


Fig. 12: The Sacral and Coccygeal Dermatomes. The levels of the boundaries in the dorsal midline are shown in Table 5, and details of the dorsal spinal nerve roots sectioned in each instance are provided in Table 15.

The Sacral and Coccygeal Dermatomes.

Annotations:

S1 - This dermatome extended over the lateral aspect of the hindlimb to include the whole of the limb distal to the middle of the metatarsus except for the dorsal surface of the medial chief digit. The caudal border overlay the hamstring. On the plantar surface of the limb it merged with the distal extension of the cranial border at the level of the tarso-metatarsal articulation. The dermatome reached the midline dorsally but not ventrally. In the one ram studied there was no reaction when pinch-stimuli were applied ipsilaterally to either the scrotum or the prepuce.

S2 - The dermatome did not reach either the dorsal or the ventral midlines. It extended over the caudal portion of the thigh and the caudal and lateral parts of the limb to include the lateral chief digit. Below the tuber calcis, the boundary lay in the centre of the plantar surface of the limb. In the ram in which this dermatome was isolated, there was no reaction from either the scrotum or the prepuce on that side.

S3 - This covered the caudal thigh and reached the dorsal midline. It extended onto the mammary gland but did not include the teat. In one ewe it was found to overlap with L3. In the one ram studied, the whole of the scrotal wall, both cranially and caudally, remained sensitive, as did the whole of the length of the prepuce.

S4 - The dermatome was restricted to a small area around and including the perineum. In a ewe it overlapped with L4. In the one ram studied there was no response to stimulation of the ipsilateral half of the scrotum. There was no distinct response, either, from

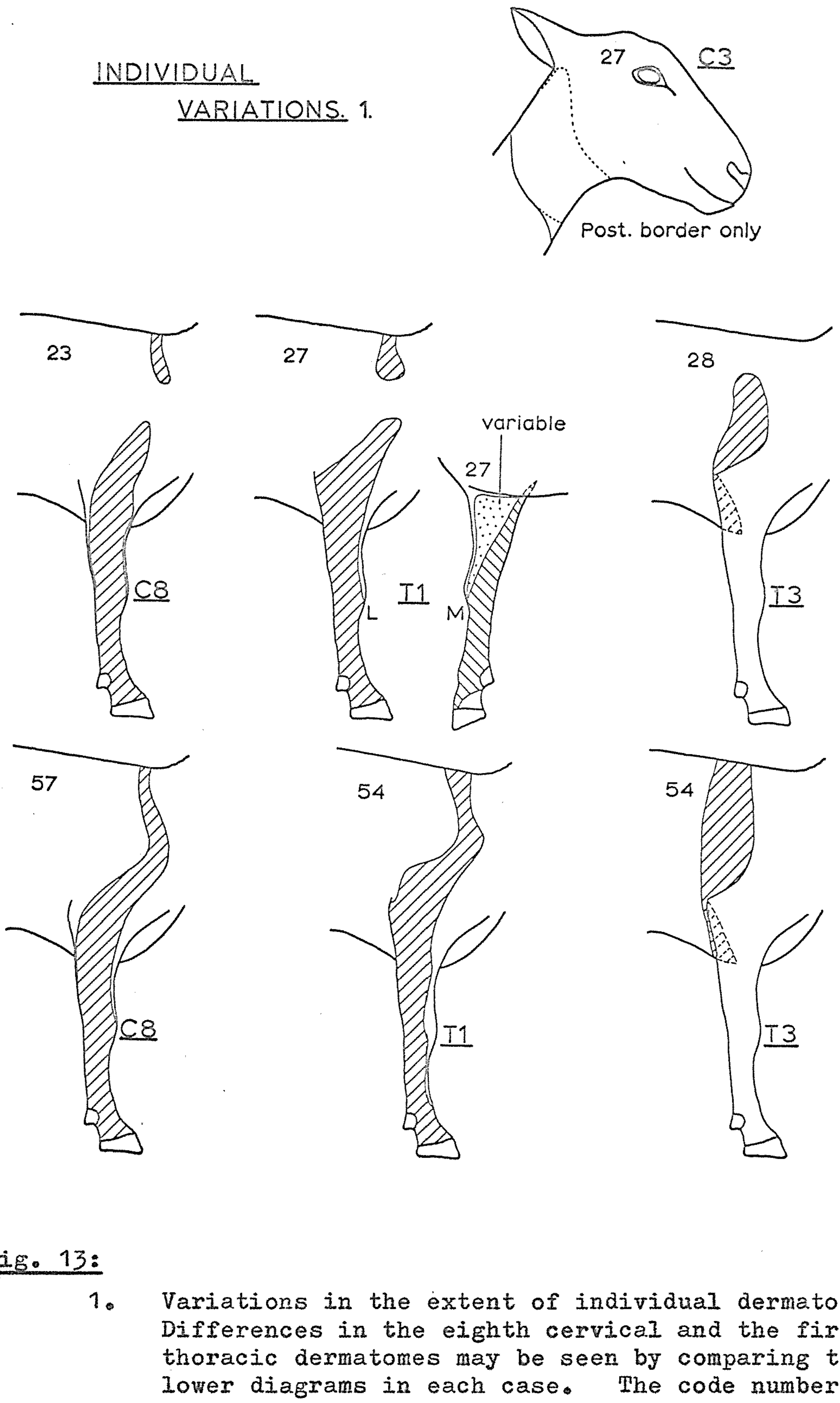


Fig. 13:

1. Variations in the extent of individual dermatomes. Differences in the eighth cervical and the first and third thoracic dermatomes may be seen by comparing the upper and lower diagrams in each case. The code number of each animal is quoted, and details of the dorsal spinal nerve roots sectioned are provided in Table 7.

the prepuce, but here the contralateral responses were also indefinite.

Cc1 and Cc2 - Only the first two coccygeal dermatomes were isolated. In one sheep, the anterior border of Cc1 coincided in the dorsal midline with the posterior border of S2. Because all of the sheep had been docked, neither dermatome could be delineated completely: each extended the full length of the tail stump, ipsilaterally.

Variation in Dermatome Boundaries.

Many of the dermatomes were isolated in only one sheep; few were isolated in more than two. The available evidence relating to the variations between the sheep in this study is summarised in Tables 6 and 7, and the more significant differences are shown in Figure 13.

TABLE 6

DERMATOMES SHOWING CLOSE AGREEMENT BETWEEN INDIVIDUALS

Dermatome	No. of sheep in which dermatome isolated
L3	5*
L4	2
S4	3

All of these sheep had 13 thoracic and 6 lumbar vertebrae

Details of the dorsal root sections are given in the Appendix

* - The level of each boundary in the dorsal midline varied within the width of a lumbar vertebra.

TABLE 7

DERMATOMES SHOWING APPRECIABLE DIFFERENCES BETWEEN INDIVIDUALS

Dermatomes	Code no. of sheep	Dorsal Roots Sectioned	Comment
C8	23 57	C4-C7, T1-T5 C4-C7, T1-T4	Intermediate insensitive zone in No. 23
T1	27	C4-C8, T2-T5	Intermediate insensitive zone in No. 27
T3	28	C4-T2, T4-T6 C5-T2, T4-T5	Field in No. 28 did not reach dorsal midline, and extended further forward than in No. 54.
T4	16 28	T2-T3, T5-T6 T1-T3, T5-T7	In No. 16, field did not reach the dorsal midline (on RHS)
T5	9 16	T3-T4, T6-T7 T3-T4, T6-T7	In No. 16, T2 and T5 merged below the elbow (on LHS)
T11	48 51	T9-T10,T12-T13 T9-T10,T12-L1	No insensitive areas in No. 48 width of eleventh thoracic dermatome in No. 51 comparable with that of adjacent dermatome in other sheep.
L2	15 41 51	T13-L1,L3-L4 T13-L1,L3-L5 T12-L1,L3-L5	In No. 41, L2 extended caudally to merge with L6 over the stifl the exact boundaries were not recorded.
L5	20(13/7)* 49 53(14/6)*	L3-L4, L6-S4 T13-L4,L6-S2 T13-L4,L6-Cc2	Includes post. abdominal wall in No. 20. Curved band between dorsal midline and stifle in No. 49.
S3	18	L4-S2, S4-Ccl,cord	
	29	L1-S2, S4-Ccl,cord	
	47	L5-S2, S4-Cc2,cord	In No. 47, dermatome extende laterally to depression in front of hamstring.
	56	L4-S2, S4 Ccl,cord	

\- -

* - numbers of thoracic and lumbar vertebrae; all other sheep listed in this Table had 13 thoracic and 6 lumbar vertebrae.

Variations were also seen in three of the dermatome boundaries defined separately:

C 3 - Below the jugular groove, the caudal border in one sheep (No. 27) extended further caudally than in other animals.

T 5 - In another sheep, (No. 54), the cranial border looped caudally at the level of the elbow.

T7/T8- In a third sheep, (No. 28), the cranial border of the seventh thoracic dermatome on the right side was at the same level in the ventral midline as the cranial border of the eight thoracic dermatome on the left side.

Variation Associated with Six/Seven Lumbar Vertebrae.

The position of the fifth lumbar dermatome in a sheep with seven lumbar vertebrae (No. 20) Figure 13 - 2 was similar to that of the fourth lumbar dermatome in the two sheep with six lumbar vertebrae. The last lumbar dermatome in the sheep with six lumbar vertebrae resembled the seventh lumbar dermatome in the animal in which this field was mapped. However, the cranial border of the seventh lumbar field was more flexuous dorsally, the reactions on the medial aspect of the limb were more variable, and the medial chief digit was not excluded from the field (Figure 11).

Bilateral Symmetry.

The first lumbar dermatome was isolated bilaterally in one sheep, and the ninth and twelfth thoracic dermatomes were similarly isolated in a second animal. The dermatomes in these sheep appeared symmetrical, and the positions of the corresponding boundaries coincided in the dorsal and ventral midlines. In the animal in which an attempt to isolate the eleventh thoracic dermatome was unsuccessful, the failure was bilateral. In the dorsal and ventral midlines of other sheep, the levels of the

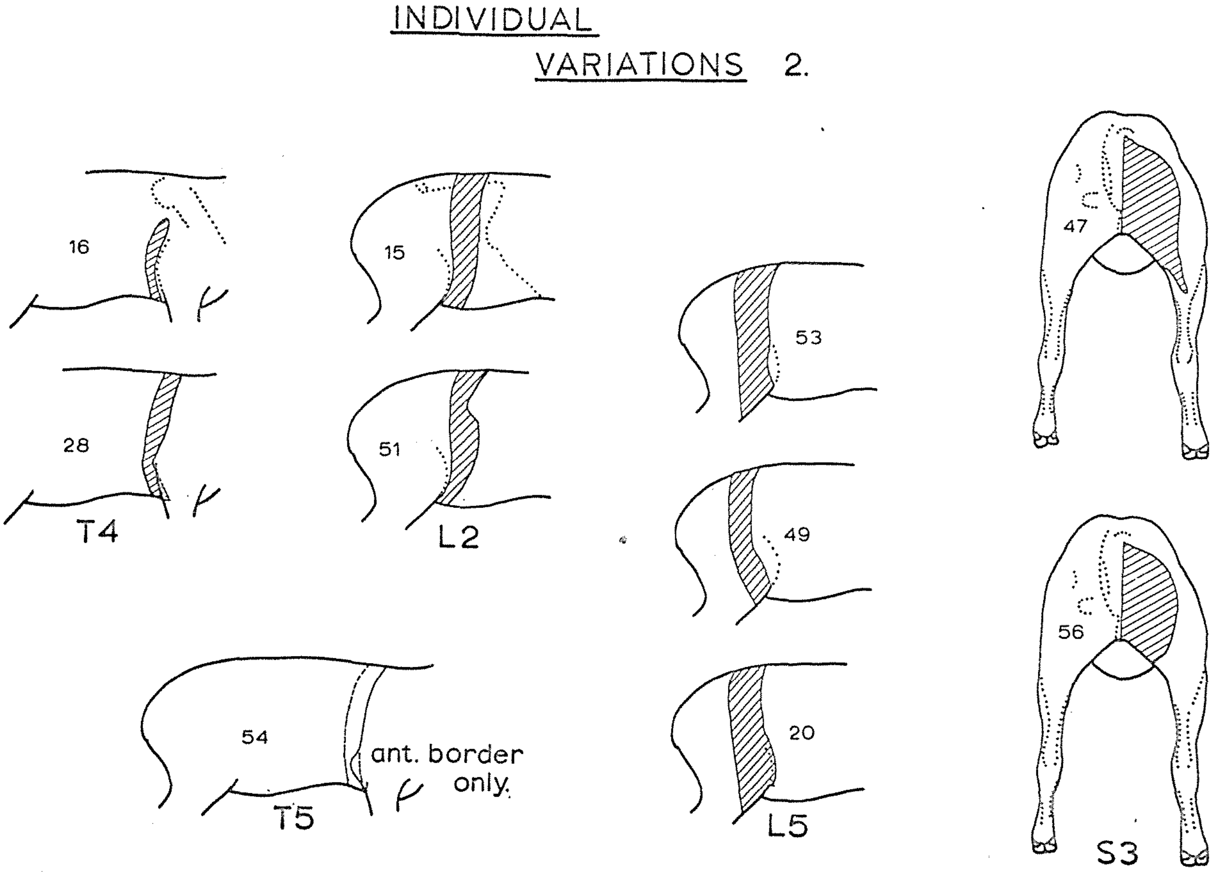


Fig. 13:

2. Variations in the extent of individual dermatomes. Differences in the fourth thoracic, the second and fifth lumbar, and the third sacral dermatomes may be seen by comparing upper and lower diagrams in each case. The code number of each animal is quoted, and details of the dorsal spinal nerve roots sectioned are provided in Table 7.

boundaries of successive dermatomes on either side showed a regular serial disposition. This was taken to indicate that corresponding boundaries on either side would have been found at the same levels.

Overlapping.

In the animals in which multiple isolations were made, the levels of successive dermatome boundaries in the dorsal and ventral midlines indicated that in most, if not all, cases each of these dermatomes overlapped appreciably with the adjacent dermatome cranially and caudally. In the neck and trunk, the extent of this cranio-caudal overlap between successive dermatomes was considered to amount to approximately one-half of the width of each dermatome. This deduction was based on the following additional observations:

(i) The position of the cranial border of one dermatome appeared to correspond closely with that of the caudal border of the next-but-one dermatome as defined in other sheep, or as seen on the opposite side of the same animal.

(ii) When every third thoracolumbar spinal nerve was left intact, the alternate bands of sensitive skin were usually wider than the intermediate bands of insensitive skin.

(iii) In the few cases (C3, C7, L1, L2, S2) in which a single dorsal spinal nerve root was sectioned, no areas of insensitive skin were found. (If the cranio-caudal overlap was less than one-half, the central part of each dermatome would be supplied by only one spinal nerve).

Overlapping on the shoulder was not studied in detail, but the seventh cervical dermatome was found to overlap with the second thoracic and the sixth cervical dermatome to overlap with the first thoracic dermatome. No attempt was made to demonstrate an overlap in the axilla between the sixth cervical and the third or fourth thoracic dermatomes.

In the crutch the third lumbar dermatome was shown to overlap with the third sacral, and the fourth lumbar to overlap with the fourth sacral dermatome . Most of the skin of the lower limbs, both fore and hind, was included within three dermatomes, seventh and eighth cervical and the first thoracic dermatome ; the last lumbar and the first two sacral.

The maximum extension of the dermatomes across the dorsal and ventral midlines was, with the two exceptions noted below, less than 0.5 cm. This very limited crosslap was also noted on the scrotum and prepuce of the rams studied. Appreciable overlap across the midline of the lower lip was recorded, and in one animal in which virtually the whole of one side of the head and neck had been deafferentated, the ventral border of the insensitive zone lay 1.0 - 1.5 cm. to the ipsilateral side of the ventral midline for almost the whole extent of the zone.

The Sensory Fields of Individual Dorsal Rootlets.

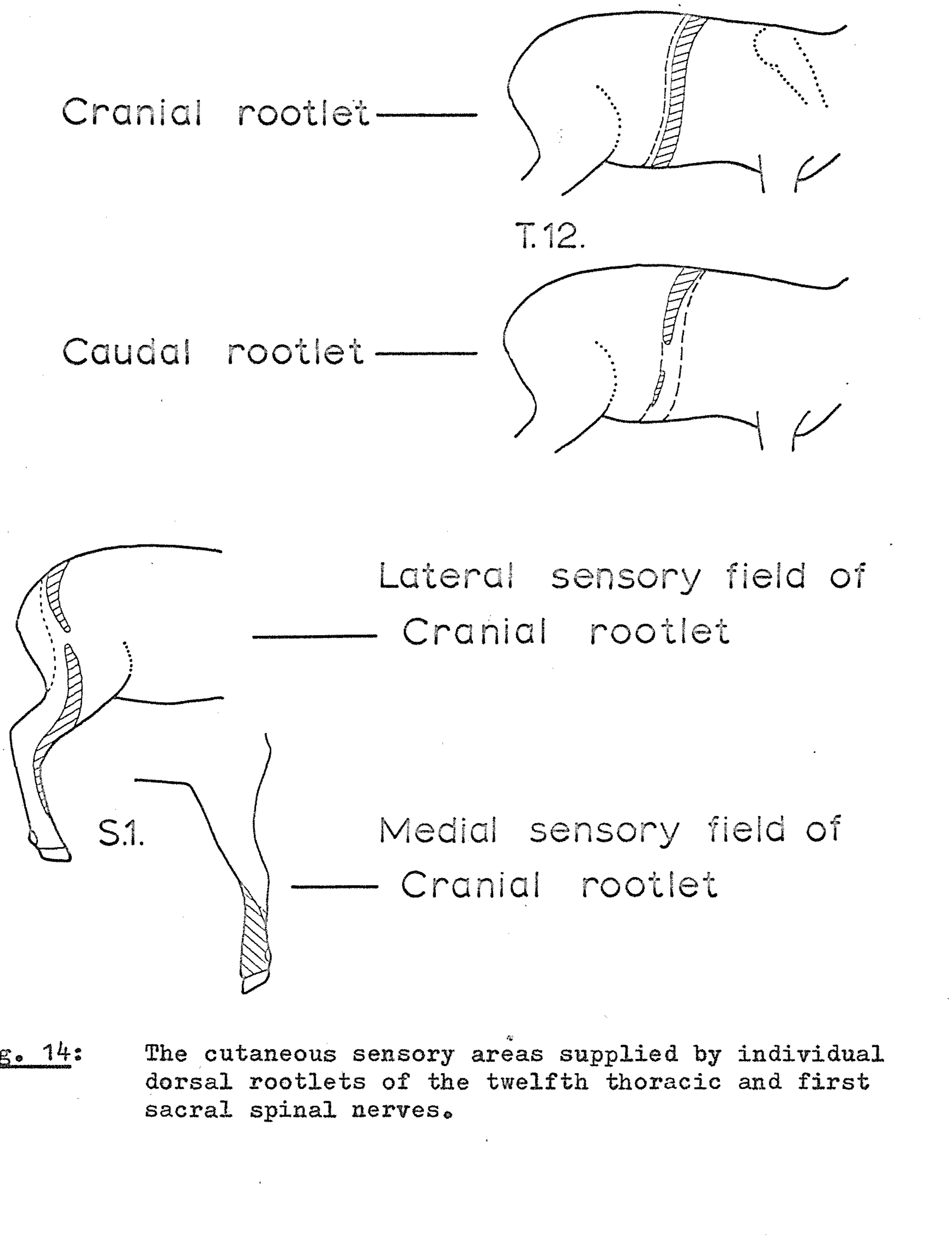
Many workers, including Sherrington (1893), have presented evidence that the fibres in each filament of a dorsal spinal nerve root are distributed throughout the dermatome. However, Kuhn (1953) demonstrated, in the cat and the monkey, that each dorsal rootlet innervates only a limited portion of a dermatome, and that there is a serial overlap between the fields of successive filaments. He has also found that while most dorsal rootlets contain afferent fibres from both skin and muscle, others contain fibres from only one of these sources. Limited fields for each dorsal rootlet have also been recorded by Hekmatpanah (1961), Pubols et al (1965) and Darien-Smith et al (1965).

In view of these findings, a limited investigation of the sensory fields of some individual dorsal rootlets in the sheep was undertaken. The following details were recorded:

(i) The dorsal rootlets of the third cervical spinal nerve were

CUTANEOUS SENSORY AREAS

Supplied by individual Dorsal Spinal Rootlets



<u>Fig. 14:</u> The cutaneous sensory areas supplied by individual dorsal rootlets of the twelfth thoracic and first sacral spinal nerves.

found invariably to be in two distinct groups. When the caudal group was severed in one sheep, the position of the caudal border of the skin area supplied by the cranial group of rootlets coincided with the position of the caudal border of the whole dermatome as defined in other sheep.

(ii) The skin field of the most cranial rootlet of the twelfth thoracic spinal nerve extended as a continuous even band between the dorsal and ventral midlines. The field of the most caudal rootlet of this nerve was discontinuous: an insensitive area was interposed immediately below the costal arch. Below this, the field was quite narrow, and the reactions to stimuli applied to the skin became increasingly indefinite: the field did not reach the ventral midline. The field of the second rootlet lay caudal to that of the first (Figure 14).

(iii) The skin field of the most cranial rootlet of the first sacral spinal nerve was found to be in two parts: the upper section extended from the dorsal midline to just below the hip joint; the lower section extended from behind the stifle over the dorsolateral surface of the limb as far as the fetlock, and over the medial aspect of the limb below the tarsus. (Figure 14). The most caudal rootlet of the same nerve was isolated in another sheep. A rectangular area 2 x 3 cm in the gluteal region was found to be sensitive intermittently to pinch-stimuli: the responses were, however, very variable.

The Sensory Innervation of the Skin of the Head.

Five sheep were used in a partial definition of the distribution of the cutaneous sensory branches of the cranial nerves. The surgical incisions below the ear and behind the eye restricted the extent to which the sensory innervation of the auriculotemporal region could be defined.

The Trigeminal Nerve Field.

The skin field of each division of the trigeminal nerve was determined by severing the other two trigeminal divisions, the facial nerve, and

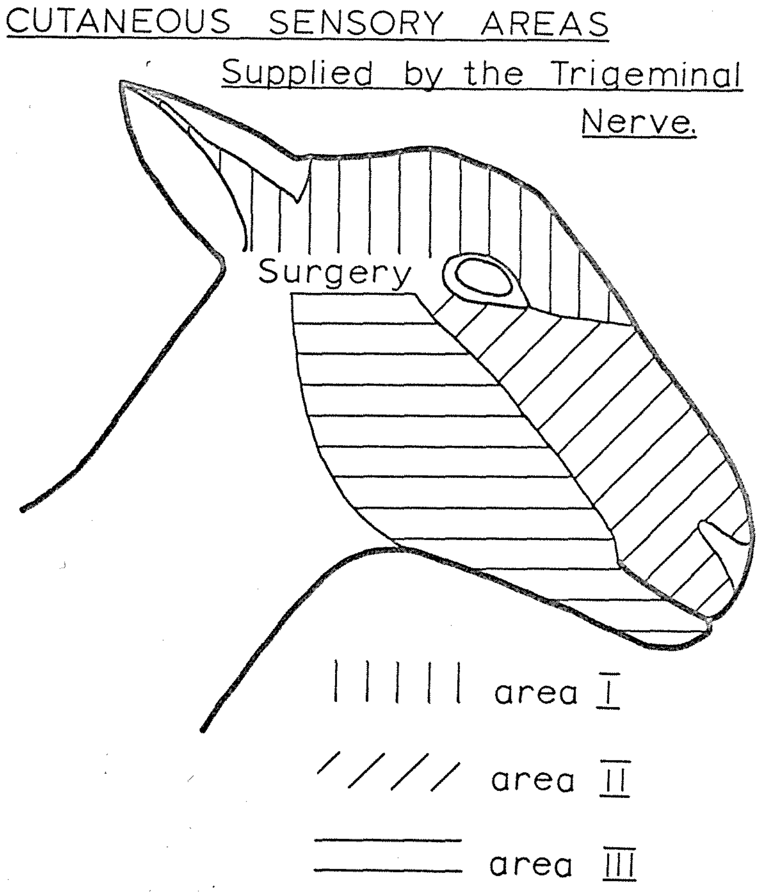


Fig. 15: The cutaneous sensory areas supplied by the main divisions of the trigeminal (fifth cranial) nerve.

Area I - Ophthalmic division
Area II - Maxillary division
Area III - Mandibular division

A limited extension of the maxillary innervation inside the nares is not shown.

the dorsal roots of the upper cervical nerves. The areas are shown in Figure 15.

(i) Ophthalmic division - (Area I): This covered the temporal and frontal regions. The rostral limit extended obliquely from the medial canthus of the eye to the dorsal midline of the face. The most caudal limit was mapped in two sheep: in both it extended along the anterior aspect of the pinna, and then lay perpendicular to the dorsal midline.

(ii) Maxillary division - (Area II): The skin field covered the face below and in front of the eye, and included all of the upper lip and nostril ipsilaterally. The zygomatic branch supplied a semicircular area of skin immediately below the eye.

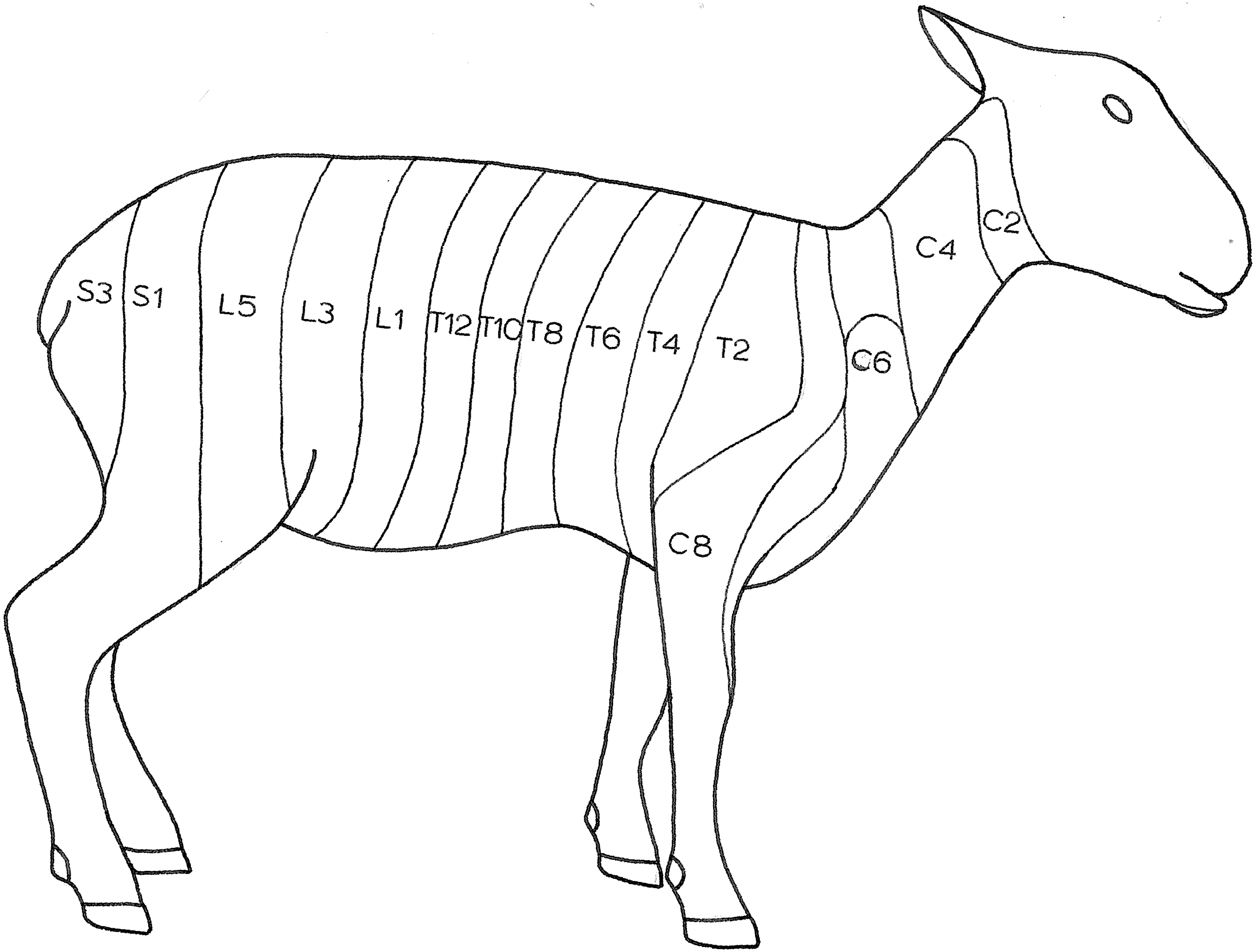
(iii) Mandibular division - (Area III): This area extended over the ramus of the mandible and included the lower lip. In one sheep an appreciable overlap across the midline of the lower lip was found.

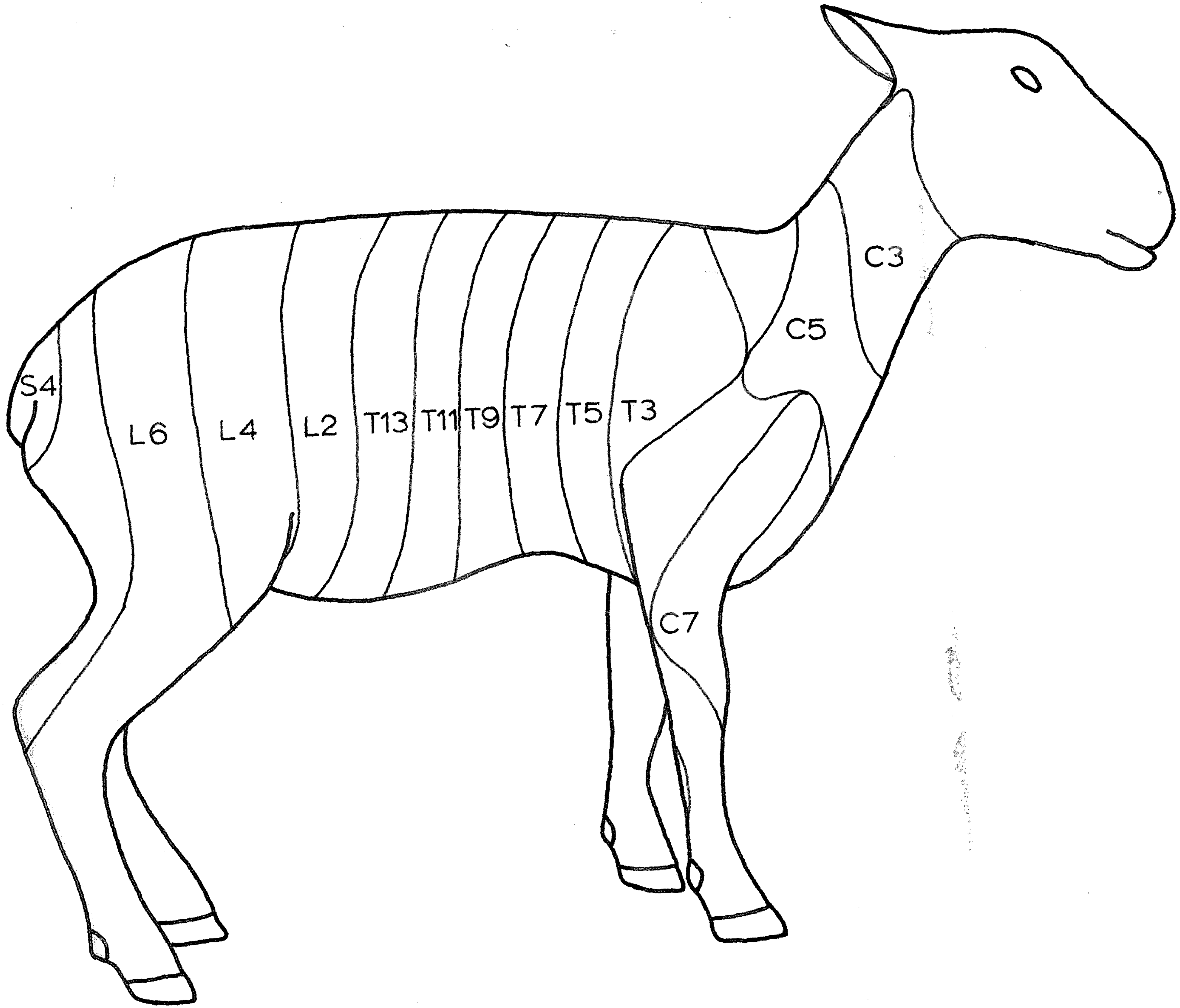
The Facial and Vagus Nerve Fields.

In one sheep the whole of the skin of the head and neck on one side (apart from the ear) was rendered insensitive after section of the trigeminal nerve (the mandibular division was approached through the ramus of the mandible) and the first cervical to fourth thoracic dorsal spinal nerve roots. This was taken to indicate that the cranial nerves did not conduct impulses from the skin of the neck. The facial nerve was then severed: a complete loss of sensitivity of the inner surface of the pinna resulted. However, the possibility of damage to the auricular branches of the vagus nerve could not be excluded. In other sheep, cutting the ophthalmic divisions of the trigeminal nerve and the auriculotemporal branch of the facial nerve rendered the anterior dorsal surface of the pinna insensitive.

DISCUSSION

Most of the dermatomes appeared as regular, serial overlapping bands which extended between the dorsal and ventral midlines. Comparisons between the positions of successive fields indicate that, in general terms the cranial or caudal half of one trunk dermatome supplied the


S3
S1
L5
L3
L1
T12
T10
T8
T6
T4
T2
C2
C4
C6
C8


S4
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C7
C5
C3

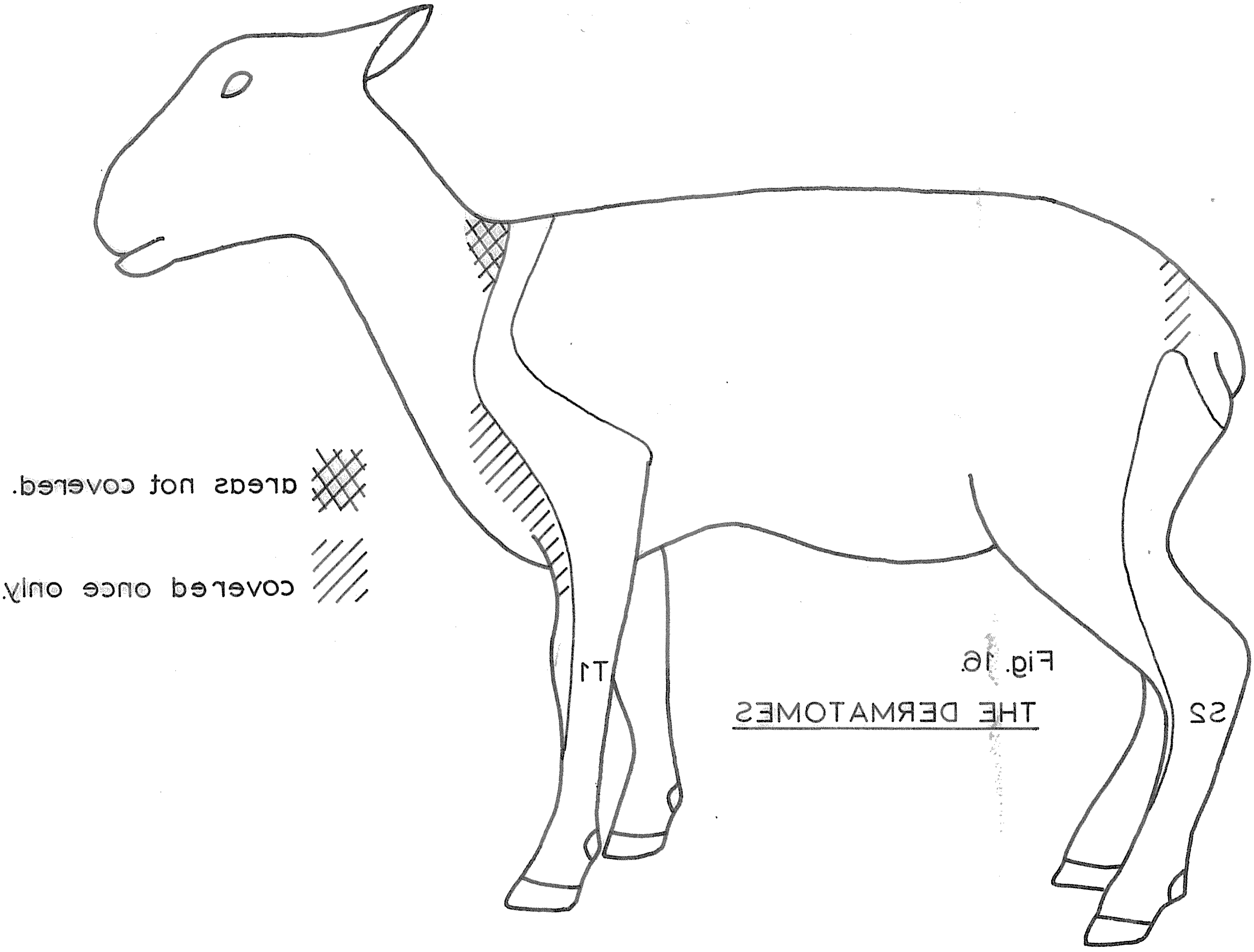

Fig. 16.

THE DERMATOMES

same skin area as the adjacent half of the next dermatome - that is, there was a cranio-caudal overlap of each dermatome over about one-half of the field of the next dermatome. (Figure 16). This may be compared with the same degree of overlap in man (Foerster, 1933) and the monkey (Sherrington, 1893), and with the one-third overlap found in the dog (Ariens Kappers _et al._, 1960) and the two-thirds overlap reported in the cat (De Boer, 1916; Helmatpanah, 1961).

The general statement that the cranio-caudal overlap is about one-half implies that this degree of overlap exists between most pairs of adjacent dermatomes: within any one animal slight variations might occur and this generalisation might not be correct. Estimates of the degree of overlap are complicated by variations in the widths of successive dermatomes, even where each dermatome is itself quite regular. A cranio-caudal overlap of less than one-half would mean that where the central portion of each dermatome was supplied by only one spinal nerve, it would be an "exclusive area". The statement that in the dog this overlap is only one-third offers support for the otherwise seemingly incongruous finding by Türck (1858) that section of a single spinal nerve in this species is regularly followed by the appearance of an area of insensitive skin. If this overlap was less than one-half in some individual sheep, "exclusive areas" would then exist in this species. No exhaustive study of this possibility was made, but "exclusive areas" have not been recorded in either man or monkeys - species in which this overlap is also one-half. In the present study, individual variations in the extent of the dermatomes were in the direction of a greater, not a lesser degree of overlap.

As discussed in the previous chapter, the touch fields were more extensive than the pinch fields, and the warmth and cold fields could be expected to be intermediate between these two. Since the fields of the other sensory modalities are more extensive than the pinch areas, they will show a greater degree of overlap: the figure of one-half obtained in this study is therefore likely to be a minimal estimate of the extent of the cranio-caudal overlap.

There is a restricted overlap of the cutaneous sensory areas across the dorsal and ventral midlines of the body. The formation of the segmental pattern in which the spinal nerves are found depends on a preceding metameric arrangement of the myotomes (Arey, 1954). It would seem that the influence of this metamerism maintains a division between the two sides of the body throughout development. Any such influence is likely to be strongest at the primary site of differentiation in the dorsal midline area: this would explain why variations were found in the extent of the ventral but not the dorsal cross-laps. The appreciable crosslap in the lower lip of sheep could be a secondary development due to the great use made of the lower lip in prehension. Sherrington (1898) found a similar crosslap in Macacus. The sheep also makes some use of its upper lip in prehension; if the foregoing argument holds, some greater degree of crosslap would also be expected here: it was not observed. Bilateral symmetry appeared to be maintained to a large degree: this also suggests the persistence of a strong metameric influence.

The pattern of the distribution of the cutaneous sensory areas thus appears to be very similar to that already found in other species. The features of each region will now be considered.

The Neck.

The third to the sixth cervical dermatomes are relatively broad. This appears to be the result of a comparatively great cranio-caudal elongation of the neck region during its development. Ariens Kappers et al (1960) point out that man has a longer neck than monkeys, and a lesser degree of overlap of the cervical dermatomes. They support Brouwer's (1914) claim that when an area enlarges the root areas are drawn apart. The sheep has a longer neck than man, yet in the present study the degree of overlap of the cervical dermatomes was similar to that observed between the trunk dermatomes. This increase in the length of the neck would also explain the failure of the third and fourth cervical dermatomes in the sheep to extend onto the shoulder as they do in primates and cats (Bolk 1898; Sherrington, 1898; Hekmatpanah, 1961).

The first three cervical dermatomes have special features. The apparent limitation of the first cervical dermatome to the occipital region is similar to that in those animals in which this dermatome has been found to be present; the dermatome is not present in man or monkeys (Sherrington 1893; Foerster, 1933). The rostral extension of the second cervical dermatome ventrally over the mandible is consistent with a rostral extension of the first branchial arch (Patten, 1956). An abrupt rostral flexure appeared in both the caudal border of the second cervical dermatome and the cranial border of the third cervical dermatome. This suggests a mutual cranial displacement of these borders on the lateral aspect of the neck. In all of the sheep examined the rootlets of the third cervical spinal nerve were found to be in two groups. This indicates that fusion of two metameric units has possibly occurred: such fusion would explain the relatively great width of the third cervical dermatome.

The Trunk.

The trunk dermatomes both in this study and in all previous reports in mammals have been shown to be quite regular. Modification in the positions of these dermatomes is seen in the forelimb region. The fifth cervical and the second and third thoracic dermatomes extend over the scapula, and the third and fourth thoracic dermatomes are reduced in width at the level of the elbow, but extend ventrally into the axilla. These modifications can be related to the outgrowth of the forelimb and the relative narrowness of the dorsal portion of the eighth cervical and first thoracic dermatomes.

The progressive displacement of the ventral portions of the lumbar dermatomes probably reflects the relatively late straightening of the dorsal flexure of the caudal region of the foetus (Straightening of the caudal part of the foetus from its initial flexure along its longitudinal axis). Expansion of the ventral abdominal wall would accompany such straightening, and could result in there being fewer sensory receptors per unit area of skin. If such attenuation of receptors does occur, it would explain the lesser intensity of the responses to stimulation of the skin in this area, compared to stimulation of other areas.

On the lateral aspect of the hindlimb the dermatomes have the same serial cranio-caudal disposition as on the abdomen, but on the medial aspect, the caudal lumbar dermatomes show a progressive distal displacement down the limb. This absence of an abrupt distinction between the dermatomes supplying the trunk and those extending over the hindlimb probably results from the comparatively late development of the hindlimbs (Arey, 1954).

The Tail.

The first two coccygeal dermatomes could not be mapped completely, but they and the third and fourth sacral dermatomes all extended over the remainder of the (docked) tail. In the species of lizards studied by van Trigt (1917) the spinal cord extended the full length of the tail and each tail segment was supplied by a separate spinal nerve: the tail dermatomes therefore resembled the trunk dermatomes in their disposition. In mammals, however, the spinal cord terminates in the lumbar or sacral regions, and in the case of the sheep only five pairs of coccygeal nerves remain to innervate the tail (May, 1964). It seems likely that all of the coccygeal dermatomes in the sheep extend over most of the tail, as they do in monkeys and cats (Sherrington, 1893, Kuhn, 1953).

The Genitalia.

The mammary glands develop as local modifications of the epidermis (Patten, 1956) and are therefore included in the fields of the dermatomes which supply the surrounding skin. Individual variations in the positions of the dermatomes are to be expected: Linzell's (1959) illustrations do not show the third lumbar dermatome to extend onto the teat, and this omission was also recorded in one sheep in the present study.

The second, third and fourth lumbar, and the third and fourth sacral dermatomes extended over the mammary glands of the ewes used in the present investigation. In their study of lumbar dermatomes in the cow, Arnold and Kitchell (1957) found that the second to the fifth lumbar fields extended onto the mammae. The extension of the fifth lumbar dermatome would be expected from the greater relative size of the udder in the cow. The ewes in the present study were young: the fifth lumbar dermatome may also extend onto the fully - developed mammary gland of a mature sheep.

There is a simple explanation for the further cranial extension of the caudal sacral dermatomes in the male: the prepuce and scrotum are derived from the caudal region of the foetus. (Patten, 1956). In the present study, the third sacral dermatome was the only field shown definitely to extend over the scrotum and prepuce. The ventral extent of the fourth sacral dermatome was uncertain, and the dermatomes cranial to the sixth lumbar were not studied in the rams. Arnold and Kitchell (1957) found that in the bull the second lumbar dermatome reached the cranial margin of the base of the scrotum and that the third lumbar dermatome included the whole of this organ: they did not investigate the fourth, fifth or sixth lumbar fields. Larson and Kitchell (1958) found that in both the bull and the ram, sensory fibres to the prepuce arose from the thirteenth thoracic to the fourth lumbar spinal nerves.

There is general agreement between the definitions of the lumbo-sacral dermatomes in the present study and those of Arnold and Kitchell (1957) and Linzell (1959). A more complete study of the innervation of the external genitalia in cattle and sheep is required, however, before more detailed comparisons between these species can be made.

The Limbs.

The disposition of each of the dermatomes which extend over the limbs can be related to the changes which occur during the development of the tetrapod limb. The developing limb first projects laterally,

DERMATOMES IN THE LOWER LIMBS.

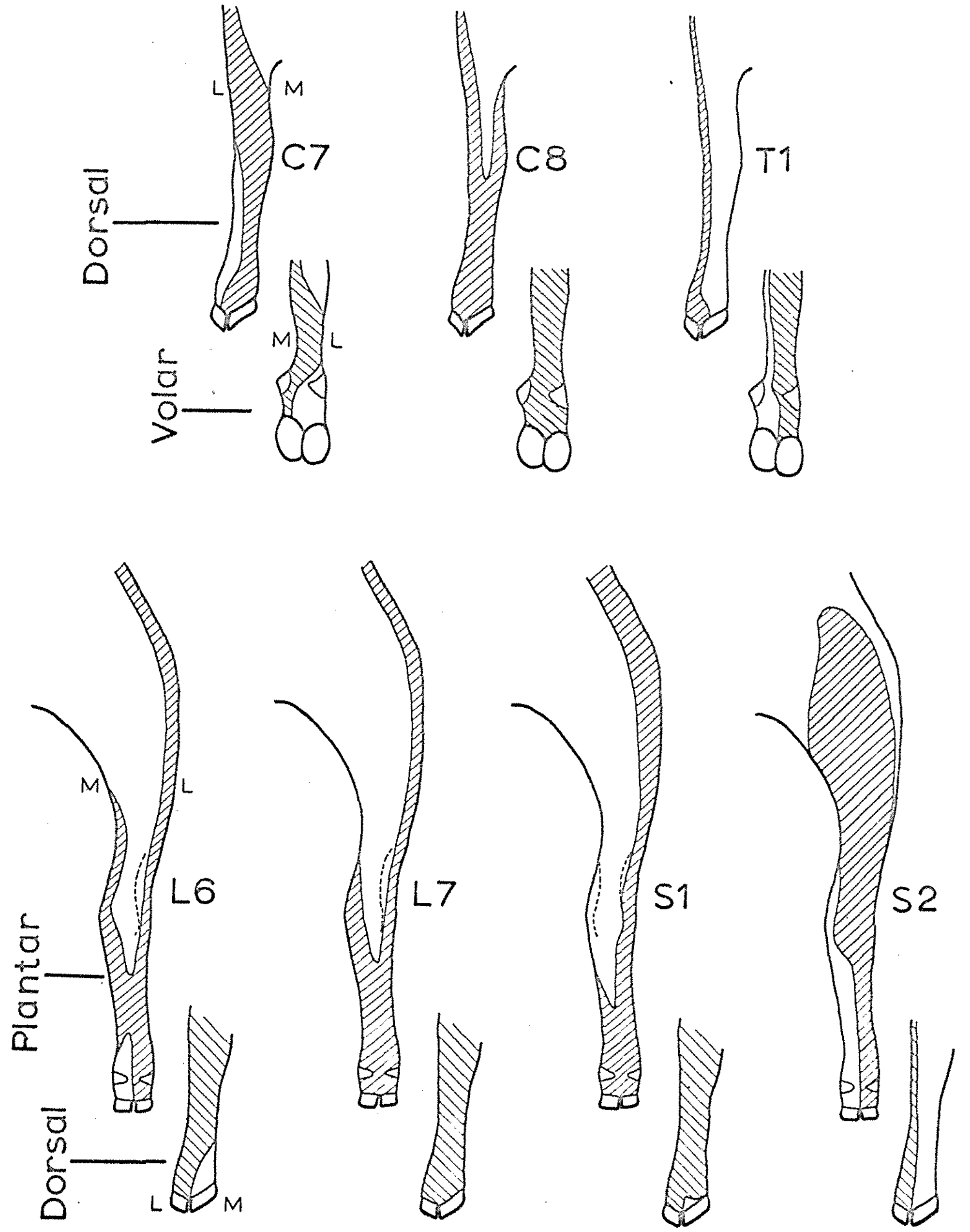

Fig. 17: The dermatomes in the lower parts of the fore and hind limbs. The seventh and eighth cervical and the first thoracic dermatomes are shown in the lower forelimb, and the sixth and seventh lumbar and the first and second sacral dermatomes are shown in the lower hindlimb.

(L – Lateral, M – Medial).

and then bends ventral at the elbow or stifle: later the elbow rotates backward, accompanied by pronation of the lower limb, and the stifle rotates forward (Gregory and Raven, 1941; Arey, 1954).

The spiralling of the seventh cervical dermatomes on the forelimb offers the most dramatic confirmation that such developmental changes have occurred. The caudoventral sweep of the seventh and eighth cervical and first thoracic dermatomes between the shoulder and the elbow regions would have been produced by a backward rotation of the elbow. The progressive shift in the positions of these fields from the medial toward the lateral aspect of the lower limb (Figure 17) is consistent with the lateral surface being initially the more caudal.

The hindlimb dermatomes also reflect developmental changes. The caudal lumbar and the first sacral dermatomes extend ventrocranially toward the stifle: this joint having rotated forward. The evidence in the lower hindlimb is more difficult to interpret. Little difference was found between the last lumbar dermatome (whether the sixth or the seventh lumbar) and the first sacral dermatome. Each of these fields, as well as the second sacral dermatome, was isolated in a single sheep, and the contributory evidence of dermatome boundaries available from other individuals did not include data relating to the digits. If a forward rotation of the limb had occurred during development, the medial aspect would have been initially the more cranial. The most cranial of the relevant limb nerves, i.e. the sixth/seventh lumbar spinal nerves, would therefore be expected to supply the more medial aspects of the lower hindlimb. The medial chief digit was not, however, included in the sixth lumbar dermatome. On the plantar surface, the second sacral dermatome is restricted to the lateral aspect of the limb (Fig. 17):

this is consistent with a rotation of the limb. Appreciable differences were found between the two isolations of the first thoracic dermatome in the forelimb, and it is likely that similar differences between individuals exist in the hindlimb. It seems that further isolations of these hindlimb dermatomes must be made before more definite conclusions can be drawn.

In the limbs of the sheep, the primitive pentadactyl limb (Napier, 1961) is reduced even further than it is in carnivores: only the (fused) third and fourth metacarpals/metatarsals are evident (May, 1964) A close correspondence between species is still evident, however. In the forelimb, the position of the seventh cervical dermatome boundary on the fourth digit is similar to that in Macacus, as shown in Sherrington's diagrams (1893). The eighth cervical dermatome included all of the limb below the carpus, as it does in the cat and the racoon (Publos et al., 1965). A strip of insensitive skin appeared on the dorsal surface of the limb over the carpus when the eighth cervical dermatome was isolated in one sheep, and when the T1 dermatome was isolated in another. It is suggested that the absence of the first, second and fifth digits from the sheep has permitted the medial and lateral boundaries of each of these dermatomes to approach each other and fuse.

As already noted, the pattern of the distribution of the hindlimb dermatomes is more difficult to resolve, and comparisons with man, the monkey and the cat (the only species for which data is available to the writer) are complicated by differences between species in the numbers of thoracic, lumbar and sacral vertebrae. There is a general correspondence between these last three species in that three dermatomes appear to extend below the tarsus in each case. Kuhn's (1953) diagrams for the cat show the fifth, sixth and seventh lumbar fields to extend to the digits: they thus appear to correspond with the sixth lumbar and the first and second sacral fields in the sheep.

On the plantar surface, the cranial and caudal borders of the sixth and seventh lumbar and the first sacral dermatomes meet at an acute angle: in each case the boundary lies for part of its length along the surface itself. (Figure 17). Since these abrupt junctions are apparently not seen in the other species studied, it seems reasonable to suggest that, as with the eighth cervical and first thoracic dermatomes in the forelimb, the loss of the first, second and fifth metatarsals has permitted the medial and lateral boundaries of the dermatomes to overlap.

One further feature of the forelimb dermatomes in the sheep should be noted. The eighth cervical and the first and second thoracic fields slope cranioventrally from the withers. No such slope is seen in Hekmatpanah's (1961) diagrams of the dermatomes in the cat, or in Keegan and Garrett (1948) maps of the human dermatomes. It is possible that in the sheep the absence of a clavicle has permitted a forward displacement of the shoulder. This is also suggested by the narrowness of the eighth cervical and first thoracic dermatomes dorsally, and by the correspondingly increased width of the second and third thoracic dermatomes.

Figure 16 shows an area of skin in front of the withers which apparently lacks a sensory innervation, and two other areas - one below the shoulder, the other on the croup - which are apparently only supplied by a single spinal nerve. These deficiencies are likely to have appeared because in assembling this compound figure no allowance was made for the possibility of individual variation; as was seen in the first thoracic dermatome, there may be considerable variation between sheep. It is also possible that further study may show the sixth and seventh cervical and the second sacral dermatomes to extend to the dorsal midline of the body.

The Axial Lines.

A fundamental difference exists between the findings of Keegan and Garrett (1948) and those of previous workers. Keegan and Garrett maintain, as a result of their definition of the human dermatomes, that the sensory cutaneous fields spiral along the limbs from the dorsal midline of the body.

The possibility that all of the dermatomes in the sheep extend to the dorsal midline has already been mentioned. The findings in this study would support those of Keegan and Garrett if it is assumed:

(i) That the sixth and seventh cervical and the second sacral fields do reach the dorsal midline, and

(ii) That the compression of the dermatome fields on the front of the shoulder has followed a secondary change in the position of the shoulder-joint.

Keegan and Garrett also maintain that in the limbs there is a ventral but not a dorsal axial line - an axial line being a hypothetical indication of the overlap of dermatomes which are not in regular sequence. In the sheep, however, a dorsal axial line would appear to be present in the forelimb formed by the overlap of cervical and thoracic fields on the shoulder. There does not appear to be a dorsal axial line in the hindlimb.

A ventral axial line would seem likely to exist in the forelimb; formed by an overlap of the sixth cervical dermatome with the third and

and fourth thoracic dermatomes. It is formed in the hindlimb by the medial overlap of the midlumbar and the caudal sacral dermatomes.

Sherrington (1893) noted that the limb dermatomes reached the dorsal midline in the frog, but not in *Macacus*. He remarked that if the limb fields in the monkey were to extend to the dorsal midline, excessive overlap would arise on the shoulder. The dorsal portions of the eighth cervical and first thoracic dermatomes are quite narrow, however, and the same could apply to a dorsal extension of the seventh cervical dermatome. The statement by Herringham (1887) that the central nerves of the limb plexus remain deeply buried in the limb and emerge toward the periphery implies a difference between skin and muscle fields which is difficult to explain on an embryological basis. Sherrington (*loc. cit.*) has commented that the distinction may be related more to a difference between afferent and efferent fields than to a difference between skin and muscles. In this investigation most of the dermatomes supplying the distal portions of the limbs were found to reach the dorsal midline. It therefore seems that there may be no fundamental difference in the dorsal extent of the afferent and efferent fields of a spinal nerve: this is not to imply that they must coincide.

The Head.

The distribution of the branches of the trigeminal nerve in the sheep is similar to that described in man (Bolk, 1898), the monkey (Sherrington, 1898), the horse (Ellenberger-Baum, 1943), the ox (Schaller, 1956) and the cat (Darien-Smith *et al.*, 1965). The limitations imposed by the surgical procedures meant that the sensory innervation of the auriculotemporal region could not be fully mapped. From the limited evidence available, it appears that in the sheep, (Fig. 15) as in other species noted above, the degree of overlap between the divisions of the trigeminal nerve is quite small and comparable with that of other adjacent peripheral fields (Darien-Smith et al., loc, cit.). The multiple innervation of the pinna is also common to other species, including man (Brodal, 1962).

Variation.

When the small number of sheep in which multiple isolations of any one dermatome were made is considered, the extent of the variation seen indicates that appreciable individual variation must be regarded as a common phenomenon.

Variation in overlapping has been considered. Some marked flexures were seen in the dermatome boundaries. These appeared to coincide in position with the zones of overlap between the fields of adjacent cutaneous rami. Some indication of the fields of these rami has been obtained (Kirk, unpublished): they appear to resemble closely those shown for the ox by Schaller (1956). It thus seems probable that the flexures result from differences in the cranio-caudal extent of these fields. A similar explanation is given (Ariëns Kappers et al., 1960) for the displacement between the dorsal and the ventral portion of the trunk dermatomes in man, as mapped by Bolk (1898): no such general displacement was noted in these sheep.

The existence of marked flexures reintroduces the possibility that some parts of the skin in the locality of the flexure may be deprived of part of their normal nerve supply i.e. they may now be supplied by only a single spinal nerve. However, it is likely that when a flexure is present, the extent of the adjacent dermatomes would also be modified. In one sheep in which traumatic damage to the nerves was thought unlikely it was found that the fourth thoracic dermatome did not reach the dorsal midline on one side: on the other side the second and fifth thoracic dermatomes were found to overlap.

Variation in the positions of whole dermatomes was also found. The limited evidence to support a comparison between the lumbar dermatomes in sheep with six and with seven lumbar vertebrae suggests that the "additional" lumbar dermatome is situated, in effect, at the thoracolumbar junction. This is, however, probably an oversimplification, for variations in the origins of the various components of the lumbosacral plexus in the sheep have been recorded. (Linzell, 1959).

Variation in the position of entire dermatomes is particularly obvious in the case of the first thoracic dermatome. It emphasises that when two mappings vary, there is little to indicate which is probably the more normal.

The Fields of the Individual Dorsal Spinal Nerve Rootlets

The limited evidence available from the present study supports Kuhn's (1953) finding that the fields of the individual dorsal spinal nerve rootlets are serially disposed within the dermatome. The variations in the intensity of the responses to stimuli also support the finding by Kuhn that there is a gradation in the intensity of innervation between different portions of a rootlet field. In the present study the fields of the caudal rootlet of the twelve thoracic nerve and of the cranial rootlet of the first sacral nerve were found to be discontinuous.

The fields illustrated by Kuhn, however, do not show an intermediate insensitive areas. It is suggested that the intermediate insensitive areas in the present study may have arisen because there were no fibres from the particular rootlet present in the cutaneous rami supplying these areas.

CONCLUSIONS

1. Each dermatome was a continuous field.

2. The trunk dermatomes were regular serial bands extending between the dorsal and ventral midlines. This pattern was modified on the limbs.

3. The degree of cranio-caudal overlap was approximately one-half. Overlapping across the dorsal and ventral midlines of the body was slight except on the lower lip.

4. The ninth and twelfth thoracic and the first lumbar dermatomes were bilaterally symmetrical.

5. The dermatomes resembled those of the other species studied in their general positions. In the limbs, most of the dermatomes extended from the dorsal midline of the body: they therefore most resembled those recorded in humans by Keegan and Garrett (1948).

6. Three dermatomes supplied the extremities of the fore and the hind limbs. Although the primitive pentadactyl limb is much reduced in the sheep, a close correlation existed between the forelimb dermatomes and those of other species. A less precise correlation was found in the hindlimb.

7. The second to fourth lumbar and the third and fourth sacral dermatomes extended onto the mammary gland. In the ram the third and possibly the fourth sacral dermatome covers the scrotum and prepuce: contributions from lumbar nerves were not investigated.

8. The trigeminal nerve provided the chief cutaneous sensory supply to the skin of the face. The distribution of its three main divisions was similar to that in other species. The overlap between these divisions was much less than that of the dermatomes.

9. Appreciable variations between individuals were common. Flexures in the dermatome boundaries were probably due to variation in skin fields of the individual cutaneous rami.

10. The skin fields of the individual dorsal rootlets were serially disposed within the dermatome, but some were discontinuous: and have been taken to account for one apparent case of discontinuity.

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CHAPTER V

EFFECTS OF DORSAL ROOT SECTION OTHER THAN LOSS OF CUTANEOUS SENSATION

Section of the dorsal root of a spinal nerve not only interrupts sensory fibres from the skin, it affects similar fibres from other somatic structures and from the viscera. For this reason, the rhizotomies performed in isolating the dermatomes were followed by changes involving inflammatory responses, the musculoskeletal, alimentary, urogenital, respiratory and circulatory systems, and the behaviour of the animals. Few sheep were kept for more than ten days after operation, and to reduce nursing difficulties and the risk of damage to the skin, most were held in a sling for several days at least. The observations of these concurrent effects were therefore restricted. They, and the effects of section of branches of some of the cranial nerves, are summarised below.

The Musculoskeletal System

(a) Effects of Trauma to the Spinal Cord.

In the earlier laminectomies accidental damage to the spinal cord occurred: this amounted to a partial transection of the neuraxis. The following observations were made in the animals involved.

(i) Rigid extension of both hindlimbs followed damage to the lumbar region of the spinal cord, and persisted until the animals were destroyed up to a week later. Sheep supported in a sling extended the hindlimbs forward beneath the abdomen: at times the feet were held clear of the ground. If either hindlimb was forcibly returned to a more normal position, it was re-extended immediately the restraint was removed. There was no apparent abnormality of the forelimbs.

(ii) Extensor rigidity in both forelimbs followed damage to the mid-thoracic region of the spinal cord. The extension persisted when the sheep were held with their feet off the ground. If either forelimb was returned to a more normal position and then released, it was immediately re-extended. There was less resistance to flexion of the limb than was the case with the rigid hind limbs seen in (i) above.

(iii) Flaccidity of the muscles of the hindlimbs and perineum followed lesser damage to the thoracolumbar spinal cord in other sheep. It developed in the animal in which the suction tube was applied - with less care than was exercised in later operations - to several segments of the lumbar region of the spinal cord.

(iv) In sheep in which the lumbar spinal nerves were exposed bilaterally and their dorsal roots handled but not sectioned, some sensory nerve fibres were possibly damaged: slight flexion of both rear fetlocks was seen on the first day postoperatively.

(v) The spinal cord, within the dura mater, could be displaced toward one side of the vertebral canal without apparent permanent effect. In some sheep, however, such a manipulation in the cervical region was followed by intermittent cessation of respiration during the remainder of the operation and, in some instances, during the first hour after the anaesthetic apparatus was disconnected.

(b) Muscle Flaccidity.

In the absence of gross damage to the spinal cord, section of the dorsal roots of all of the spinal nerves concerned in the innervation of a limb was followed by a loss of tone in the muscles of that limb. The flaccidity was evident even before the animal had recovered from anaesthesia. There was no resistance to passive movement of the limb: if unsupported, it hung loosely in full extension. This effect was less obvious in the forelimb, because the position of the upper portion of the limb was largely maintained by the muscles attaching the limb to the trunk. The fetlock flexed passively when the foot rested on the ground. Because of the mechanical rigidity which remained in the stifle and hock joints, a sheep could support some weight on the dorsal aspects of the pastern of a hind limb.

When deafferentation of the limb was incomplete, lesser degrees of flaccidity were observed. Irrespective of whether the limb was held in flexion or in extension, there did not appear to be any increased muscular resistance to manipulation of the limb. The support afforded by a plaster cast applied to the fetlock was often sufficient to enable these sheep to make use of the limb. Some animals repeatedly performed manoeuvres in which they moved backwards until a flexed fetlock joint extended passively and then placed weight on the relatively stable limb.

Flaccidity was apparent in muscles other than those of the limbs. The ram in which the second sacral dermatome was isolated developed a permanent partial prolapse of the penis. In sheep in which the facial nerve was sectioned, the lower lip and cheek on that side bulged outward, and the ipsilateral ear was not held fully erect.

(c) Flexure of the Vertebral Column.

Unilateral section of a group of dorsal spinal nerve roots was followed in most instances by flexion of the vertebral column towards the opposite side. This flexion was particularly obvious in the cervical and lumbar regions, but did not follow rhizotomies confined to the anterior thoracic region. Lateral flexion of the thoracolumbar column was not seen after bilateral operations in which the regional dorsal nerve roots were cut symmetrically; if operations in this region were extensive, lordosis appeared.

When the dorsal roots of the cervical nerves were divided on one side, the neck and the head were turned to the opposite side. After four or five days, the sheep turned its head to face forward again; the neck remained flexed, and bowed considerably to the ipsilateral side. In contrast, when the dorsal capitis muscles on one side were detached from the atlas and the epistropheus, the head was held permanently rotated on its longitudinal axis, toward the opposite side.

Unilateral section of the coccygeal nerves was followed by deflection of what remained of the (docked) tail to the opposite side.

(d) Posture.

When a limb was largely or completely deafferentated, the sheep stood with the contralateral limb closer to the midline. If a forelimb was affected, the animal tended to stand with its back arched and with more weight placed on the hindlimbs. When a hindlimb was deafferentated the hock of the opposite limb was abducted and the foot of the limb was turned inward. In these latter sheep, the pelvis was also rotated to the opposite side; an effect augmented by lumbar flexion.

When sheep held in a portable crate attempted to stand, the crate moved slightly. The animals seemed to be considerably embarrassed by these small movements: they had great difficulty in gaining their feet and maintaining their balance, and would stand much more easily if the crates were firmly held, or if they were removed from the crates and placed on the ground.

(e) The Innervation of Separate Muscle Groups.

Muscles of the Forelimb.

The following details were recorded:

(i) Unilateral section of the dorsal roots of the first five cervical spinal nerves had no obvious effect on a sheep's ability to use either forelimb.

(ii) The animal in which the seventh cervical dermatome was isolated on one side stood the next day, with some assistance; thereafter it habitually kept the ipsilateral forelimb extended.

(iii) The two sheep in which the eighth cervical dermatome was isolated could not extend the ipsilateral fetlock. Sheep in which the seventh and eighth cervical spinal nerves were both sectioned could not support any weight on the forelimb.

(iv) When the seventh cervical dorsal spinal nerve root above was cut on one side, the animal concerned seemed to be able to use the limb normally. The assessment of its use of the limb was complicated, however, by a concurrent partial deafferentation of the other forelimb.

Muscles of the Hindlimb.

Representative changes in hindlimb action are recorded in Table 8. When the sixth lumbar and first sacral spinal nerves were intact, good use could be made of the limb and flexion of the fetlock was not seen. Flexion of the fetlock followed section of the dorsal roots of the sacral spinal nerves.

TABLE 8

Dermatome isolated	Dorsal roots sectioned	Effect
L4	L1-L6, S1	Stood next day; could support hindquarters fully on fifth day. Ipsilateral hindlimb extended backwards.
L6	L1-L5, S1-S4	Stood next day. Difficulty in stepping backwards for the three weeks kept alive.
S1	L3-L6, S2-Cc2	Stood evenly next day, with support from ipsilateral hindlimb.
S2	L5-S1, S3-S4	Ipsilateral fetlock flexed, even when limb extended. No attempt to stand without support.
S3	L4-S2, S4-Cc1	Stood on second day, with ipsilateral hindlimb flaccid.
S4	L1-S3, Cc1	Stood next day. Ipsilateral limb abducted, and fetlock flexed.

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(f) Changes in Muscles.

Sheep given their liberty after being slung for a week or more could not stand and walk freely until the second day after their release. This observation was taken to indicate that such slinging might retard an animal's recovery. Where possible, sheep were kept in a sling for only a day or two.

In those sheep which were kept alive for several weeks, the volume of the flaccid muscles decreased: this was particularly obvious in the upper limbs. As a result of such changes, the lateral processes of the cervical vertebrae were more easily palpated, and the individual ribs became more prominent. Wasting of the masseter muscle followed section of the mandibular nerve.

DISCUSSION

Loss of muscle tone was the most dramatic consequence of dorsal root section, and was particularly obvious in the limbs. In the forelimb, as Sherrington (1893) has commented, the group of muscles which attaches the upper portion of the limb to the trunk tends to maintain the scapula and the humerus in more or less fixed positions: the flaccidity in the muscles of the upper limb itself is therefore masked. The disposition of the joints and their associated ligaments restricts the main movements of the limbs of the sheep to a sagittal plane and permits a partially deafferentated limb, once positioned appropriately, to support appreciable weight. This was well illustrated by use made of a limb when the fetlock joint was supported in a plaster cast.

When a limb was partially deafferentated, varying degrees of flexion or extension of the limb were seen; but in the absence of damage which constituted a partial transection of the spinal cord, the degree of tone in the active muscles did not seem excessive when the limb was manipulated. This suggests that when one group of muscles is deafferentated, the "antagonistic" group of muscles does not exhibit increased tone: more critical studies may show otherwise. In the immediate post-operative period there was little resistance to passive straightening of the flexures in the vertebral column: the resistance increased with the development of ankylosis. It was considered, therefore, that the flexion was due primarily to a loss of tone in the ipsilateral muscles. The considerable flexion of the lumbar column reflects the great mobility possible in this region. The changes in posture after deafferentation of the limbs were similar to those seen in sheep after partial chordotomy (Tietz, 1964).

This loss of muscle tone contrasted sharply with the extensor rigidity which followed severe damage to the spinal cord. Extensor rigidity is regarded as a characteristic sign of an incomplete division of the spinal cord, and is thought to follow damage to the corticospinal and vestibulospinal tracts (Fulton, 1949). The latter tract is probably the only one involved since the extent of the corticospinal tract in the sheep is uncertain and probably limited (Ariens Kappers et al., (1960): King (1911) has stated that it does not extend beyond the first cervical segment.

The extension of the forelimbs after damage to the thoracic region of the spinal cord - the Schiff - Sherrington phenomenon - is thought to result from a cephalad release of function after the loss of inhibitory afferent impulses from the more caudal regions of the body (Moruzzi, 1950). Reid (1962) noted that after portions of the spinal cord between the seventh cervical and the first thoracic segments and, more particularly, between the third and seventh thoracic segments were extirpated, the forelimbs were thrust backward and turned outward, and the digits were abducted.

The unexpected degree to which slight movements of the portable crates embarrassed sheep in their efforts to stand suggests a major interference in these animals with the passage of impulses concerned in the maintenance of equilibrium. This is consistent with the location of proprioceptive fibres in the dorsal columns of the spinal cord (Ariens, K ppers et al. (1960); a site in which they are more likely to be damaged during surgery. It also emphasises the importance of proprioceptive impulses in the maintenance of equilibrium.

Sherrington (1893) found the motor activity of a spinal nerve to be largely dependent on the afferent impulses which enter the dorsal root of the same segments. In the present study, digital extension was still present when, among the dorsal spinal nerve roots contributing to hindlimb innervation, only those of the last lumbar and the first sacral spinal nerves were left intact.

From this it was deduced that the action of the digital extensor muscles depended on the integrity of the dorsal roots of the last lumbar and first sacral spinal nerves. The sciatic nerve, which supplies the digital extensor and flexor muscles in the hindlimb, is formed from the last lumbar and the first two sacral spinal nerves.

Two further examples were noted in support of the idea that muscle tone depends on the integrity of sensory pathways. Prolapse of the penis occurred in a ram in which the second sacral dermatome was isolated. Definition of this dermatome involves section of, among others, the third and fourth sacral dorsal spinal nerve roots, both of which convey many of the sensory fibres of the pudental nerve into the spinal cord (Larson & Kitchell, 1959).

The animal in which the seventh cervical dermatome was isolated could make good use of the corresponding forelimb: sheep in which both the seventh and the eighth dorsal spinal nerve roots were cut, could not. The extensor muscles of the forelimb are supplied by the radial nerve: in the sheep this is formed by contributions from the seventh and eighth cervical and the first thoracic spinal nerves (May, 1964). It thus appears that the seventh cervical spinal nerve carries a large proportion of the fibres of the radial nerve in the sheep.

When the disposition of the extensor and flexor muscle groups in the limbs is compared with that of the dermatomes, it is apparent that the skin and muscle fields of a spinal nerve which innervates a limb do not correspond. This lack of correspondence has been deduced, from much more detailed evidence, by Sherrington (1893, 1898): it is also shown in the diagrams of Inman and Saunders (1944), as reproduced by Wolff and Wolf (1948).

CONCLUSIONS

1. Extensor rigidity in the limbs followed damage to the spinal cord which amounted to partial transection. Forward extension of the forelimbs followed damage to the thoracic segments of the spinal cord: similar extension of the hindlimbs followed damage to the lumbar regions of the spinal cord.
2. Section of all of the dorsal roots of the spinal nerves supplying a muscle was followed by flaccidity of that muscle. This was followed in turn by atrophy.
3. In partially deafferentated limbs, varying degrees of extension and flexion were seen: there did not appear to be any gross increase in the tone of the muscles which remained active.
4. Proprioceptive impulses transmitted through the dorsal columns of the spinal cord appear to be of great significance in the maintenance of equilibrium.
5. Some evidence was obtained to support the conclusion that the motor activity of a spinal nerve is greatly dependent on afferent impulses entering the dorsal root of the same segment.
6. In the limbs, the skin and the muscle fields of the spinal nerves do not correspond.

The Digestive System

The following observations were recorded:

(i). Prehension.

Most sheep ate and drank within eight hours of the completion of surgery. Immediately after operation some sheep were much more interested in food than in water: in others, the opposite applied. Animals in the former group would often take their first drink within five to ten minutes of micturating for the first time.

Following unilateral section of the mandibular division of the trigeminal nerve, sheep had great difficulty initially in taking food or water: after being assisted in their first attempts, they would eat apparently normally within ten minutes.

Several sheep did not seek to eat immediately. It was thought that some of these were generally discomforted: if kept alive, they ate after their discomfort was thought to have disappeared.

Apart from the one animal in which the thirteenth thoracic dermatome was isolated all of the operations to isolate thoracic dermatomes involved bilateral rhizotomies, as did several of the lumbar dermatomes. Five of the sheep involved in these bilateral operations made no attempt to take food or water for themselves in the first few days. These animals vigorously chewed any food placed in their mouths, swallowed it readily, and did not resist force-feeding. They appeared to be interested in the whereabouts of food, and would nuzzle the contents of their feed tins. Details of the operations on these sheep are recorded in Table 9; the corresponding details for the eight sheep which did not show any reluctance to eat are recorded in Table 10.

TABLE 9

OPERATIONS FOLLOWED BY TEMPORARY FAILURE TO PREHEND

Sheep Code No.	Dermatomes isolated		Dorsal roots sectioned	Effect
27	T1	RS	C4-C8, T2-T5	Had to be force-fed for 1 day
	T2	LS	C5-T1, T3-T5	
16	T4,T7	RS	T2,3,5,6,8,9	Had to be force-fed for 2 days
	T5,T8	LS	T3,4,6,7,9,10	
4	T12	RS	T10,11,13,L1	Had to be force-fed for 2 days
	T12	LS	T10,11,13,L1	
15	L2	RS	T13,L1,3,4,5	Had to be force-fed for 3 days
	L3	LS	L1,2,4,5,6	
41	L2	RS	T13,L1,3,4,5	Had to be force-fed for 3 days*
	L3	LS	L1,2,4,5,6	

* - prehension first occurred during a "hyperaesthetic response" to contact with electric clippers. RS - right side LS = left side.

No persistent failure to prehend was recorded after any of the cervical or lumbo sacral operations. Some other sheep showed some reluctance to eat during the first day, but began eating while making the biting or nibbling movements associated with a hyperaethetic response, and showed no further reluctance thenceforth. Prehension in one of the five animals discussed above (No. 41, Table 9) was initiated on the third day during such a hyperaesthetic episode.

TABLE 10

OPERATIONS NOT FOLLOWED BY FAILURE TO PREHEND

Sheep Code No.	Dermatomes isolated		Dorsal roots sectioned.
54	T1	RS	C4-C8, T2-T4
	T3	LS	C5-T2, T4-T5
9	T3,T6	RS	T1,2,4,5,7,8
	T5	LS	T3,4,6,7
28	T3	RS	C4-T2, T4-T6
	T4	LS	T1-T3, T5-T7
48	T11	RS	T9,10,12,13
	T11	LS	T9,10,12,13
51	T10	RS	T9,10,11,12
	T6,T11	LS	T4,5,7-10, 12,13,L1
53	T12	RS	T10,11,13, L1
	T12	LS	T10,11,13, L1
3	L1	RS	T12-T14,L2-L4
		LS	T12-T14,L2-L4
39	L4	RS	L1-L3,L5-L6
	L3	LS	L1-L2,L4-L5

(ii) Mastication and Deglutition.

Unilateral section of the divisions of the trigeminal nerve had little obvious effect in the ability of a sheep to chew and swallow, although the ability to take up food was impaired. Similarly, unilateral section of the dorsal roots of the cervical spinal nerves did not appear to affect mastication or deglutition. Flaccidity of the lower lip on one side after the facial nerve was sectioned was observed to be associated with a failure to prevent food from falling from its mouth.

In one sheep in which the ninth and tenth cranial nerves, the rostral branches of the seventh cranial nerve, and the maxillary and mandibular divisions of the fifth cranial nerve were cut on the right side, and the cranial cervical sympathetic ganglion on the same side extirpated, difficulties in chewing and swallowing occurred. Food accumulated in the ipsilateral cheek and between the dorsal eminence of the tongue and the hard palate: some fell from between the lips. The sheep appeared to salivate profusely, but this impression may have resulted from an impairment of swallowing. Some boluses were swallowed unaided. In most cases it was necessary to push a bolus over the dorsum of the tongue before it could be swallowed. Occasionally the animal would cough during this procedure, and then fail to swallow.

Three days later, the dorsal roots of the second, third and fourth cervical spinal nerves were severed on the same side. Although its ability to swallow was still impaired, the sheep chewed vigorously, displayed strong rumen movements, and micturated and defecated normally. On the third day after the second operation, the sheep was unexpectedly found dead. Fresh green grass packed the entire length of the oesophagus and the entrance to the larynx: none was present in the stomach.

(iii) Defecation

The inclusion of quantities of green grass in the feed was believed to have increased the volume of the faeces and reduced the possibility of post-operative intestinal stasis.

Mucus usually coated the faeces for the first day post-operatively. The only animals which failed to produce pelletted faeces were those fed appreciable quantities of green grass, those in which the sacral spinal cord was damaged, and three animals fed chaff and listed in Table 11. The Table also notes the four animals in which blood appeared in the faeces.

TABLE 11

OPERATION FOLLOWED BY ABNORMALITIES ON DEFECATION

Dermatome isolated		Dorsal roots sectioned	Effect
T4,T7	RS	T2,3,5,6,8,9	Faeces pelletted, but pellets small (0.7 cm diameter) for the 21 days the sheep was kept alive.
T5,T8	LS	T3,4,6,7,9,10	
L2*	RS	T13,L1,3,4,5	Faeces pelleted, but black and tarry until the fourth day (indicative of gastric or high alimentary tract bleeding).
S1*	LS	T12-L6, S2-S4	Faeces unformed until third day, and slightly tinged with fresh blood.
S2*	LS	T12-S1, S3-S4	Faeces unformed for the five days kept alive, with much fresh blood.
S3*	LS	L4-S2, S4-Ccl	Faeces pelletted, slightly tinged with fresh blood.
L6,S3	LS	L4-L5, S1-S2, S4-Ccl	Faeces unformed until fifth day.

* Each of these dermatomes was isolated in at least one other sheep without consequent haemorrhage.

RS = right side   LS = Left side.

DISCUSSION

The transient inability to take food displayed by sheep in which the mandibular division of the trigeminal nerve on one side had been severed, probably resulted from a reduction in the sensory information received from the lower lip.

A clear distinction between the motor control of chewing and of swallowing was found. As in man (Brodal, 1952), effective mastication appears to depend on the integrity of the fifth cranial nerve, while swallowing is controlled by the ninth and tenth cranial nerves.

The finding that one sheep died with its oesophagus impacted with grass suggests that relaxation of the caudal oesophageal spincter is at least partially dependent on the integrity of afferent fibres which enter the spinal cord between the second and fourth cervical segments on the right side: it may also depend partially on the integrity of the right vagus nerve, which in this experiment had been severed earlier.

The data in Table 9 indicates that afferent impulses entering the thoracolumbar segments of the spinal cord may be significant in feeding behaviour. Bott, Denton and Weller (1965) state that sensory impulses arising from the passage of water through the lower oesophagus and its entry into the rumen are one of several components determining the degree of satiation. Hazarika, Coote and Downman (1964) have shown, in the cat, that afferent impulses from the lower oesophagus, stomach and small intestine enter the spinal cord between the third thoracic and the second lumbar segments. Afferent fibres from the abomasum of the sheep traverse the splanchnic as well as the vagus nerves (Titchen, 1953; Titchen and Reid, 1964). It seems probable that the conduction of afferent information from the gut was impaired in the sheep referred to in Table 9. The initiation of feeding during a hyperaesthetic reaction suggests that the latter triggered a release from inhibition. However, hyperaesthetic reactions did not in themselves induce feeding unless the sheep actually picked up food during its frenzied, undirected nibbling.

The passage of uniformed faeces for up to five days suggests an alteration in the activity of the musculature of the colon or of its absorptive function. A depression of colon motility has been reported in man during the period of spinal shock (Denny-Brown and Robertson, 1935).

A marked reduction in the size of the faecal pellets in one sheep is difficult to explain. It is possible that the particular dorsal spinal nerve root sections in this animal were followed by increased activity in some direction of a significant length of the intestine.

The appearance of black tarry faeces in one animal is also difficult to explain, but is consistent with an upper intestinal origin of the blood (Hunter & Bomford, 1965). The fresh blood seen after sacral operations is most likely to have arisen from the lower intestine. The mucus which commonly coated the faeces for the first one to two days post operatively also appeared to have originated in the lower intestine. It is clear that there is need for a great deal of work to define the contributions sensory fibres which take a course into the spinal cord make in the regulation of gut activity. It is possible that one such contribution will come from a study of the defects which follow dorsal root sections at various levels of the spinal cord.

CONCLUSIONS

1. Unilateral division of the fifth cranial nerve produced little permanent impairment of chewing and swallowing.
2. A major effect on food intake was detected. Some sheep subjected to extensive bilateral section of thoracolumbar dorsal spinal nerve roots went as long as three days before first consuming food post-operatively.
3. Effective mastication depends on the integrity of the fifth cranial nerve; when the ninth and tenth cranial nerves are sectioned, swallowing is also impaired.
4. The passage of unformed faeces may follow section of the dorsal roots of the sacral spinal nerves.

Micturition

The following observations were made:

Posturing to micturate followed repeated delivery of pinch-stimuli to the skin of the caudal half of the body, as recorded in Chapter IV. The response was particularly brisk when the skin of the 3rd and 4th sacral dermatomes was stimulated.

Sheep seemed unable to void urine voluntarily unless they assumed the appropriate stance, with the back arched and the hindlimbs partially flexed. Loosening of the caudal straps of the sling and allowing the hindquarters to sag would often be sufficient to initiate micturition. Most animals retained voluntary control over the passage of urine. An animal which was swaying considerably while micturating (because of motor disturbances following a lumbosacral rhizotomy) would abruptly cease to void when its hindquarters were touched. After the first day, the sheep would not react in this way, but would place considerable weight on the hand providing support, and micturate freely.

Sheep in which the dorsal root sections were confined to the cervical and anterior thoracic regions exhibted no abnormality of micturition. Urinary retention with or without overflow followed some more caudal interferences. Most of the animals in which lumbar dermatomes were isolated micturated next day if given some help in supporting their hindquarters; by the third or fourth day they no longer required assistance. They frequently exhibited stronger and more brisk reactions to cutaneous stimulation after the bladder had been partly emptied.

Retention with overflow followed gross trauma to the lumbar spinal cord; in one sheep it followed upon damage to the cervical cord.

The sheep made no attempt to micturate; urine dribbled continually and large volumes could be expressed readily by compression of the bladder through the ventral abdominal wall. The dribbling of urine became intermittent after the fourth or fifth day, rhythmic voiding commenced when the bladder was compressed, and further control was regained progressively over the next three or four days. In another sheep unilateral section of the dorsal roots of the third and fourth spinal nerves was followed by urinary retention, with overflow.

DISCUSSION

The initiation of micturition by cutaneous stimulation over a wide area of the trunk suggests the importance of sensory impulses other than those which arise in the urinary bladder itself. There appeared to be a close association between the adoption of a particular stance - a somatic event - and the passage of urine - largely a visceral event. The adopting of the particular stance would appear to alter the relative positions of the bladder and urethra (Kuru, 1965), and to allow the perineal musculature to relax. Some of these reactions are probably co-ordinated at quite a low level in the spinal cord: Sherrington (1906) observed nettoyage to follow defecation in dogs in which the spinal cord was transected.

Sheep have considerable voluntary control over the voiding of urine. This direct control is also prominent in other animals (Learmouth, 1931). In man, cessation of voiding can be produced by voluntary closure of the external sphincter of the bladder (Denny-Brown and Robertson, 1933). In many cases of urinary retention the sheep made no apparent attempt to micturate. In humans, the desire to micturate depends on impulses evoked by the distension of the bladder and urethra:

(Denny-Brown and Robertson, 1933): trauma to the sacral region of the spinal cord abolishes this desire. Barrington (1928) recorded that after division of the sacral dorsal spinal nerve roots in dogs and cats, urinary retention with overflow resulted without apparent discomfort to the animals. Similar observations were made in the present study: the interpretation of the present findings is complicated by the large extent of the lumbosacral rhizotomies and by the possibility of concurrent damage to some of the ventral spinal nerve roots as well - there was no evidence of the latter however.

The fourth day was found to be a common time at which voiding in spurts became apparent with manual pressure on the bladder. The effect was probably due to the appearance of autonomous contractions of the urethra (Barrington, 1928).

The Respiratory System

The following observations were made:

(i) In several anaesthetised sheep moderate digital pressure applied over the lateral midside between the ribs caudal to the forelimb produced an immediate cessation of respiration. A regular respiratory rhythm was restored after a single forced inspiration, i.e. a single squeeze of the rebreathing bag.

(ii) Following the cessation of the administration of the anaesthetic agent, respiration was stimulated by light external pressure on the larynx.

(iii) In the immediate post-operative period, several sheep breathed freely when placed in a sitting position on the ground, but ceased breathing several minutes after being placed in a sling. It was thought that the cessation of respiration was caused by pressure of the sling on the thoracic walls.

(iv) Some sheep in which the cervical spinal cord had been damaged during operation respired intermittently; these animals required supervision for up to an hour after the anaesthetic apparatus was disconnected. The accidental application of pressure to the thoracic or lumbar regions of the spinal cord - the pressure being much less than that which produced any permanent effects on the musculature - was, in many instances, followed immediately by irregularities in the respiratory rhythm of the anaesthetised sheep. These irregularities did not persist for more than a few minutes.

(v) Sheep in which every third thoracolumbar spinal nerve was left intact displayed irregular chest movements in place of the normal smooth respiratory rhythm. The excursions of the abdominal wall were exaggerated. In two of these sheep the respiratory rate increased threefold when the animals were made to walk.

(vi) In one animal the ventral as well as the dorsal roots of the last five cervical spinal nerves were cut on the right side. From the second day, the walls of the thorax and abdomen were seen to move alternately during each respiration. This thoracolumbar respiratory rhythm was not present in animals in which the ventral roots of these nerves had been left intact. There was no perceptible change in the respiratory rhythm in anaesthetised sheep during the sectioning of the dorsal roots of these nerves.

DISCUSSION

Pressure over the lateral chest wall inhibited respiration in the anaesthetised sheep, and in some animals inhibition of respiration appeared to be associated with the pressure of a sling on the sternum and the ventral portions of the walls of the thorax. No previous reference to this observation has been found. In fact the converse observation has been recorded: Stein (1966) for example, reported that in anaesthetised dogs pressure on the cranial part of the sternum will stimulate respiration. The observation reported here may be suggestive of the presence of chest wall receptors terminating inspiratory activity.

The alternating movements of the thorax and abdomen seen after the last five cervical ventral roots were sectioned on one side suggests that contraction of the diaphragm was impaired. This would be consistent with interruption of the motor supply to the diaphragm i.e. of the phrenic nerves: in the sheep these nerves arise from the fifth to seventh cervical spinal nerves, and occasionally from the fourth cervical spinal nerve. (May, 1964). Some proprioceptive afferent fibres are to be found in the phrenic nerves (Corda, von Euler and Lennerstrand, 1965). The absence of any apparent disturbance to the respiratory rhythm on sectioning the cervical dorsal spinal nerve roots may indicate that either no great number of impulses from the diaphragm traverse the right phrenic nerve in the sheep in quiet respiration <u>or</u> that compensatory mechanisms allow a rapid adjustment to a sudden decrease in the number of afferent impulses from this organ. Irregular chest movements observed after section of a number of thoracic dorsal spinal nerve roots indicate the importance of co-ordinated activity of the thoraric muscles, particularly those associated with the ribs, in the maintenance of a smooth respiratory rhythm. Sheep in which were cut lumbar as well as thoracic dorsal spinal nerve roots indicate the importance of coordinated activity of the thoracic muscles, particularly those associated with the ribs, in the maintenace of a smooth respiratory rhythm. Sheep in which lumbar as well as thoracic dorsal spinal nerve roots had been sectioned exhibited respiratory embarrassment on exercise. This may indicate that they were relying almost entirely on diaphragmatic respiratory movements, and could not make adequate supplementary movements of the body wall.

The Circulatory System

Two sheep developed swellings of the tissues of the lips and the upper neck region after cervical laminectomy. The first animal was found dead: it was thought that the extensive swellings had occluded the airway through the nostrils and pharynx. The swelling in the second sheep regressed rapidly after the animal's head was raised. Care was taken thereafter to ensure that for the first day, sheep in which cervical operations had been performed could not lower their heads below the level of their shoulders. No further swellings occurred.

That sheep in which the first thoracic dermatome was isolated on one side and the second thoracic dermatome isolated on the other, developed similar swellings in the limbs while it was held in a sling. When the animal was placed in ventral recumbency, the swelling lessened during the next day, and then disappeared.

A fourth sheep developed a soft swelling of the pastern of a partially deafferentated hindlimb: it persisted for two days.

The swellings were thought to have resulted from lack of movement of the affected part. This would have led to venous stasis and an increased formation of interstitial fluid. Had the swellings been due to a primary effect on blood vessels, they would have been expected to have appeared more frequently, especially in dependent parts of the limbs. The site of the swellings indicated that fluid accumulated in the most dependent parts, and that the degree of swelling was influenced by the extent to which the subcutaneous tissues could be readily distended.

The Healing of Wounds

Incisions in normal skin healed sufficiently within 5-6 days to permit the removal of most of the skin sutures. Sutures closing dorsal midline incisions in front of the withers had to be left much longer, because movements of the neck tended to pull the skin edges apart. Where the skin of the edges of the wound had been deafferentated, healing was much slower: if the sutures were removed at 7-8 days the wound gaped open once even only moderate tension developed in the surrounding skin. Similarly, abrasions of the skin in deafferentated areas healed slowly. The time taken for wound repair in normal skin in the sheep is thus similar to that required in man (Douglas, 1963). The integrity of sensory nerve fibres seems a pre-requisite for normal healing.

In sheep kept for more than two weeks after laminectomy, the connective tissues which had formed in the operation zone was found to be firmly adherent to the dorsal surface of the dura mater. This union of tissues made it difficult to avoid damage to the spinal cord during a second operation at the same level after this time. Fibrous adhesions also made it difficult to decide which dorsal rootlets were still intact, unless a small section of each severed rootlet had been removed initially. It is possible that studies over a longer time would be complicated by constriction of this fibrous tissue producing compression of the spinal cord, as has been reported in dogs (Funkquist & Schautz, 1962).

The Behaviour of the Sheep

It was considered that most sheep were more disturbed by their initial confinement in indoor crates than by any of the subsequent procedures, and that their post-operative progress was often related directly to the readiness with which they had accepted their new environment. Some considerable differences between individuals and between breeds were observed. As already noted by von Borstel (1952), Cheviots generally reacted more than did Romneys against the initial restraints, but then responded more quickly to training. The Cheviots also made more vigorous efforts to stand and walk after operation.

In the training period, each sheep had to be prevented from violent jumping each time a pinch-stimulus was delivered. If this was not done, the animals soon began making extreme reactions to even weak stimuli. A number of "dummy" approaches had to be made to prevent the sheep from moving away each time the forceps were brought towards it. Similarly sheep reacted violently when the skin was simply touched with the forceps if a pinch-stimulus consistently followed this contact. While in a hyperaesthetic state, several sheep became restless when electric clippers were switched on, even though the blades were not touching the skin. One animal continued to turn and nibble at the forceps whenever its skin was pinched or touched, long after other signs usually associated with hyperaesthesia had disappeared. Conditioned reflexes thus appeared to be readily established. No signs of experimental neurosis was seen (Anderson and Liddell, 1935), and no attempt was made to provoke it be increasing the frequency of repetition of the stimulation. Individual eccentricity was also encountered: one sheep preferred chaffed hay to green grass, and made good progress once this preference had been detected and catered for.

It was thought that sheep made a greater effort to stand and walk after an operation if they were helped even briefly into a standing position once or twice a day. They were also thought to be encouraged by adjustments to the sling which resulted in the sheep being held in a more normal posture, by the expression of urine from a distended bladder, and by the presence of other sheep. The animals rapidly learned to use the side of the crate for support when attempting to stand. Once a sheep had achieved some success, it persisted in its attempts to stand unaided.

Ready adaptation to new surroundings and variation in individual responses to experimental procedures have been found in previous investigations in which sheep have been used. (Anderson and Liddell, 1935). Many of the changes in behaviour probably resulted from the laminectomy procedures, and not from the rhizotomies themselves. The ease with which conditioned reflexes may be established emphasises the need for repeated evaluation of the extent to which central effects may have modified the responses to any particular stimulus.

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CHAPTER VI

SENSORY TRACTS IN THE SPINAL CORD

When a nerve axon is divided, the portion separated from the nerve cell body degenerates (Ranson, 1959). Since the cell bodies of the afferent fibres in a dorsal spinal nerve root are located in the dorsal root ganglion (Ranson, *loc. cit.*), dorsal root section will be followed by the degeneration of the portion of each of these fibres which lies within the spinal cord. The Marchi technique was applied in an attempt to reveal the degeneration of myelinated fibres and to obtain some indication of the positions of the primary afferent pathways in the spinal cord of the sheep.

Procedure.

The sheep were exsanguinated under Nembutal anaesthesia and perfused with either buffered or neutral formalin (Gurr, 1962). Each cadaver was then left for 12-18 hours before the neuraxis was removed. This partial fixation *in situ* gave the nervous tissue an additional firmness and rigidity which allowed its removal with less possibility of damage, and was presumed also to reduce the extent of autolytic changes.

The spinal cord was freed by cutting through the dorsal and ventral roots of each spinal nerve outside the dura mater. A single transverse cut was made through the dura and the spinal cord midway between each successive pair of spinal nerves. The most ventral part of the dura mater was, however, left intact: this permitted the whole spinal cord to be folded into a vessel of buffered or neutral formalin without pulling it apart.

After fixation for an additional 48 hours sections approximately 3 mm wide were taken by cutting parallel to the exposed face of each segment. A small sliver cut from its cranial face allowed each section to be orientated subsequently with the left side of its caudal (intact) face to the observer's left. The sections were then placed in the chlorate-osmic-formalin solution of Swank and Davenport (1935), or in the modifications of this solution recommended by Mara and Yoss (1952) and Poirier, Ayotte & Gauthier, (1954).

RESULTS

(a) Variation in Staining.

Considerable variation was found in the intensity of the staining of the spinal cord sections. Some of this variation appeared to be due to the particular staining solutions used. Spinal cord sections placed in the Swank-Davenport solution usually stained within 4-5 days: in several instances differential staining of the areas of degeneration was apparent within 6 hours ! Most of the sections placed in the "rapid modification" solution of Mara and Yoss (1952) became uniformly black, while most of those placed in the solution recommended by Poirier *et al*. (1954) failed to darken. There was no apparent difference between sections fixed in buffered or in neutral formalin.

Excellent staining occurred in various sections from seven sheep. These sections were taken between 7 and 30 days after dorsal root section. 7 days was the shortest post-operative interval tested: sections taken from a sheep 60 days after operation failed to stain. However, sections taken from other sheep within 7-30 days after operation did not stain satisfactorily; even when processed together with sections which stained well.

When successfully stained sections were kept in the staining solution for three to four months, the unstained background lightened

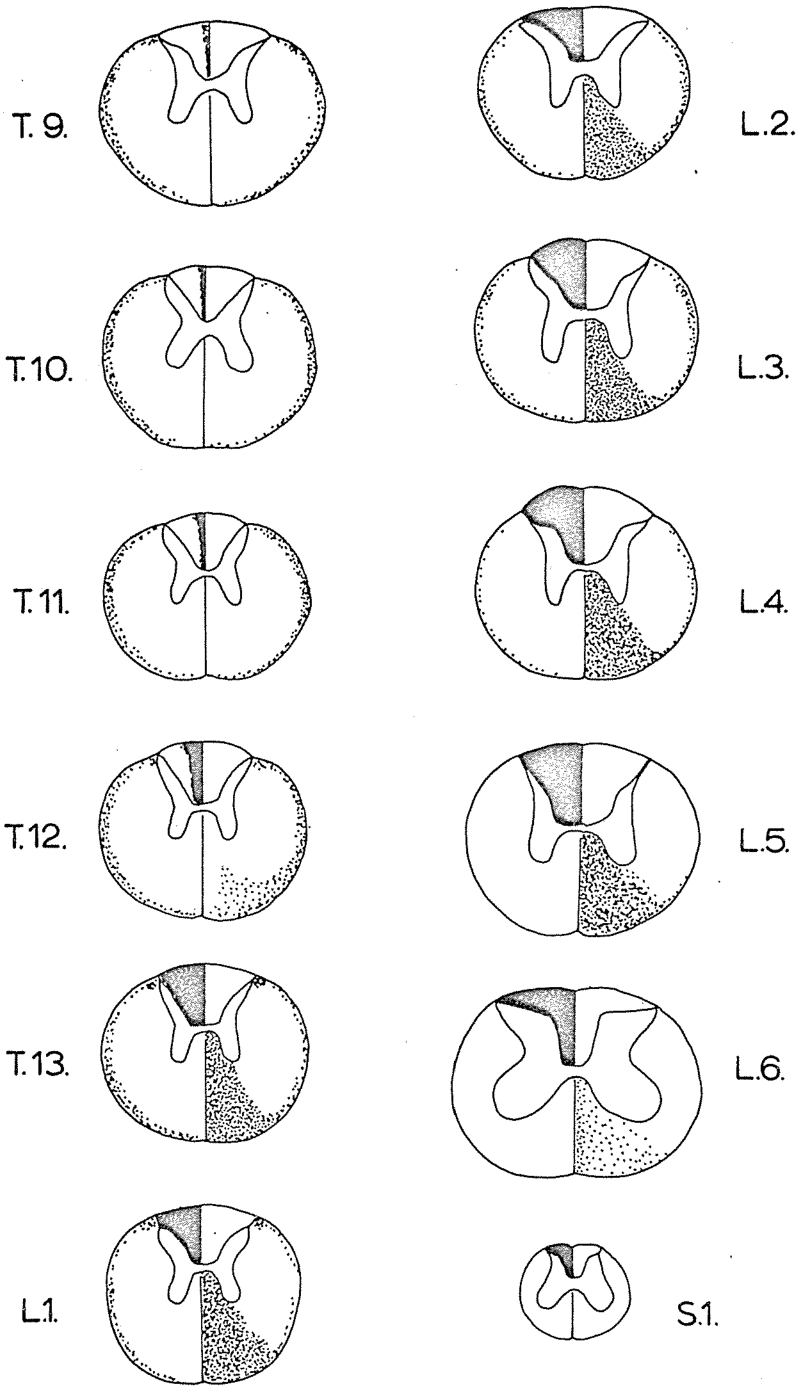

Fig. 18: Marchi stain obtained after section of the first sacral dorsal spinal nerve root and all of the lumbar dorsal spinal nerve roots apart from that of the fourth lumbar spinal nerve. The left side of each section is towards the left side of the figure.

in colour in some cases: the stained areas were then more easily seen.

(b) Fibre Tracts.

The differential staining was not shown satisfactorily on photographic prints. Figure 18 was therefore produced by projecting the film negative onto a screen and tracing the outlines of the magnified sections. The outlines were modified slightly to make them symmetrical, and the stained areas were marked in by referring to the sections themselves.

Figure 18 illustrates the degeneration seen in the spinal cords of two sheep after unilateral lumbosacral dorsal root section. Staining occurred in three main areas:

(i) In the segments in which the dorsal roots were severed, the staining in the dorsal white matter was intense, but restricted to the ipsilateral side of the spinal cord. Cranially, the extent of this staining diminished rapidly in successive sections; before it disappeared completely it was restricted to a zone immediately adjacent to the median septum.

(ii) In the lumbar and the last thoracic segments, staining appeared in the contralateral ventral white matter. This staining was less intense than that in the ipsilateral dorsal columns. In the caudal lumbar sections it lay close to the median fissure of the spinal cord; cranially, it became displaced progressively toward the lateral margin of the sections.

(iii) Staining also appeared in the lateral white matter on each side of the more cranial sections. The extent of this staining diminished rapidly in the thoracic region. Staining was not seen in sections taken from the cranial thoracic and the cervical segments of the spinal cord of these sheep.

It was not possible to obtain a consecutive group of sections to show degeneration in the cervical and anterior thoracic regions of the spinal cord. For this reason no definite indication of the relative positions of the fasciculus gracilis and the fasciculus cuneatus was obtained.

It was observed that after a series of dorsal roots were sectioned staining did not extend for more than one segment caudal to the level of the most caudal dorsal root sectioned.

(iv) Intense staining often developed in a small peripheral area immediately below the extremity of the dorsal horn, on one or both sides. In some instances this staining appeared in isolated segments well caudal to the laminectomy zone. In one case the spinal cord was folded sharply at the first lumbar segment during its removal from the cadaver. Subsequently, a section from this segment was the only one to stain, and it blackened completely.

DISCUSSION

The Marchi Stain.

The Marchi technique depends on the selective reduction of osmic acid by the products of myelin degeneration: it therefore reveals only "myelinated" fibres, and can only be used in the period between the first appearance of appreciable degeneration products and the removal of the material by phagocytosis (Baker, 1958). Swank and Davenport (1935) found that a post-operative degeneration time of 14-20 days gave optimal staining in cats: in rabbits the optimum period was 10 days. In this investigation, excellent differential staining was obtained of sections taken at 7 days in one case, and at 8 days in another. This success may have been partly due to the short fixation time: Glees (1954) states that if the post-operative survival period is short, the fixation period should also be short. It is possible that good staining might have been obtained with survival periods of less than 7 or greater than 30 days. The demonstration that the Marchi technique could be applied within 7 days of dorsal root section and after a 2 day fixation period offers the chance of a rather more expeditious application of the technique than might have been thought possible.

It is felt that the limited amount of information available from this investigation precludes any assessment of the relative merits of the three staining solutions used. The tendency to overstain is a recognised fault of the Marchi technique (Walker, 1949): it might well be that some slight modifications to the procedure used in this investigation would have corrected this tendency.

On two occasions, two sheep with very similar case histories were destroyed at the same time, and the spinal cord sections from both were all processed together: sections from one animal stained well, those from the other did not. Differences between individual sheep thus seem to be significant. Other variables must also be considered. Deposits of Marchi dust are likely to arise if the anaesthesia during operation is prolonged (Glees, 1954). Section of the blood vessels accompanying a series of dorsal spinal nerve roots may result in local changes in the spinal cord due to ischaemia (Suh and Alexander, 1939).

The isolated appearance of blackening in the region of Lissauer's tract was probably due to damage to dorsal root fibres which occurred during the removal of the spinal cord from the cadaver. The staining of the section of the lumbar spinal cord subjected to trauma in another sheep, and the progressive lightening of the background in some stored sections indicates that chemical reaction within the cord continues for a long period.

The Fibre Tracts.

The staining has revealed two main sensory pathways in the spinal cord; one in the ipsilateral dorsal columns, the other in the contralateral ventral and lateral white matter. The intense staining in the dorsal columns is consistent with the presence of coarse myelinated fibres which conduct impulses concerned with special tactile sensibility and proprioception (Ariens Kappers et al., 1960). The rapid reduction in the extent of staining in the dorsal columns in the midthoracic region which is found in sheep which have undergone a lumbosacral rhizotomy indicates that most fibres entering a dorsal root formed relays with other fibres in the dorsal columns. Because the reduction in staining dorsally was not accompanied by a proportionate increase in the staining on the contralateral side, it is considered that few, if any of the fibres had crossed to the opposite side. Cranially, the staining in the dorsal columns in these sheep was limited to the vicinity of the median septum. This illustrates the lamination in the dorsal columns; the fibres which originate in the more caudal parts of the body occupy a more medial position and so on.

The progressive lateral displacement in the ventral white matter of the crossed fibres indicates that in the sheep, as in man (Ranson, 1959), lamination also occurs in this region: this time the fibres which originate in the more caudal parts of the body fibres are laterally placed.

The aggregation of sensory fibres in the dorsal columns explains why the appearance of disturbances in equilibrium and of hyperaethetic reactions is likely to be a result of surgical trauma to the dorsal columns. There was no direct evidence available to indicate which sensations were transmitted by each pathway, but, as recorded in the previous chapter, damage to the dorsal columns seemed to affect particularly position-sense and vibratory impulses.

The restriction of staining in the dorsal columns to one side of the spinal cord can be taken to indicate that a normal laminectomy was not followed by any appreciable degeneration of dorsal column fibres. Gross damage to the cord was, however, followed by degeneration within the dorsal columns.

The results of this investigation reveal a basic pattern of afferent pathways in the spinal cord of the sheep which is similar to that in primates and the other domestic mammals.

CONCLUSIONS

1. Marchi staining proved a variable technique.
2. Some artifacts may arise from post-mortem trauma to the spinal cord.
3. Excellent staining has been obtained in the sheep between 7 and 30 days after operation: the time limits may be wider than this.
4. It is possible to produce sections showing degeneration clearly, within ten days of dorsal root section (7 days degeneration, with 2 days fixation and with 1 day staining).
5. Two main sensory pathways in the spinal cord of the sheep have

been found by this method: one in the ipsilateral dorsal columns, the other in the contralateral ventral and lateral regions of the cord.

6. Primary afferent fibres were not detected descending for more than one segment.

7. Lamination is apparent in both the dorsal columns and the ventrolateral tracts.

8. There was no evidence that in the absence of gross damage to the spinal cord, either at operation or during post-mortem procedures, laminectomy produced degenerative changes within the dorsal columns of the cord.

9. The general pattern of the sensory pathways appears similar to that in other higher animals.

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CHAPTER VII

FINAL DISCUSSION

The present study has been concerned primarily with the definition of the segmental basis of the innervation of the skin of the sheep. This definition has been based on the use of the "remaining sensibility" technique - the technique used by Sherrington in his now classical study of the dermatomes in macaque and rhesus monkeys, and by Foerster in his important study of the human dermatomes. Many of the disadvantages of this technique have been encountered in the course of this present investigation: these have been considered in the discussions in earlier chapters. It is therefore appropriate that the particular advantages to be gained from the use of this method should now be considered.

The "remaining sensibility" technique is the only one available by which the cutaneous sensory field of any one spinal nerve can be isolated for study in chronic preparations. This means that the responses obtained will not be modified by the effects of anaesthetic agents and other drugs on the nervous system. It is thus possible to assess the responses likely to be encountered in the normal conscious animal.

The importance of being able to make such an assessment has been shown by the great variation in the responses obtained. For example, distension of the urinary bladder was accompanied by a general reduction in reactivity; the intensity of the responses were also found to depend on whether the sheep studied was standing or recumbent. In particular, the present study afforded a good opportunity to define hyperaesthetic responses in sheep.

The technique also allows some assessment of changes in dermatome boundaries between successive tests and over periods of several weeks or more to be made. The use of chronic preparations also permits subsequent histological examination of the extent of nerve fibre degenerations within the central nervous system.

The stimuli applied in this study were largely restricted to pinch and touch. Pinch stimuli were presumed to comprise a combination of pain and pressure stimuli: the dermatomes therefore show the areas of "total response" (Kuhn, 1953). Although responses to heat and cold stimuli were not investigated, a study of these modalities would assist in offering explanations of the means by which temperature changes affect reproductive performances (Smith, 1962) and wool growth (Ferguson, Carter and Hardy, 1949). Although the general pattern of the innervation of wool fibres appeared to be similar to that of human hair, a more complete study may show significant differences. An indication of the likelihood of this being the case might be obtained by comparing the hairy skin of Drysdale with that of, say, Merino sheep.

A further study of the distribution of the individual rootlets of the dorsal spinal nerve roots may help to resolve some of the differences in the intensities of reaction between different parts of the one dermatome. Some evidence has been obtained (Kuhn, 1953) to suggest that the fibres of certain sensory modalities are limited to specific rootlets. With a greater knowledge of dorsal root fibre compositions, it may be possible, for example, to relieve pain in specific areas by sectioning particular rootlets instead of entire dorsal roots. The likelihood that in some instances the fibres of particular sensory modalities are largely confined to particular dorsal rootlets also suggests that it might be possible to study these fibres without the responses being complicated by the receptors of other modalities.

The recording of impulses from dorsal root filaments, as used by Kuhn (1953), Pubols et al. (1965) and Darien-Smith (1965) offers more precise evidence as to whether afferent impulses are being conducted from the cutaneous receptors, and the extent and duration of the responses can be more accurately recorded. Different sensory modalities can be tested, and multiple recordings obtained from the one preparation. The necessity remains to keep the stimuli applied within normal physiological limits.

In all such investigations the problem of ascertaining what sensations a sheep is experiencing remains. Hensel and Bowman (1960) have made some attempt to relate specific stimuli to specific sensations in man: it still has to be assumed that such stimuli evoke the same or corresponding sensations in other species.

The sheep is a convenient experimental animal because it is of moderate size, is easily handled, and with little training will accept human company and imposed restraints. It is particularly useful as a "representative" ruminant. The evidence from this study suggests that there is a close correspondence between the dermatomes of cattle, sheep and goats (Schreiber, 1955: Linzell, 1959), at least in the lumbar region, and that information to be gained from studies in sheep is likely to be largely applicable to the other two species. The sheep is not an aggressive beast, and the meekness with which it submits to restraints seems to be accompanied by a profound change in its responses to cutaneous stimuli. When compared with a primate or a carnivore, the sheep exhibits a limited range of motor activities. In some cases this could restrict the usefulness of the animal in studies involving efferent systems: in others the reduced range of possible reactions could simplify assessments of motor reactions. The variation between individual sheep in their responses to an experimental environment has revealed a useful potential for further behavioural studies.

The cutaneous sensory fields in the sheep have a general disposition similar to that in other animals. The features of the individual dermatomes correlate closely with the known details of embryological development. The sheep shows a greater reduction from the pentadactyl limb than any other of the species studied so far. It would be of particular interest to obtain confirmation of the disposition of the hindlimb dermatomes in the sheep: the angular flexures in the boundaries on the plantar surface seem peculiar to this animal. Such flexures might, however, be more conspicuous in the limb dermatomes of a soliped.

The results of this study are believed to offer much support for the claim by Keegan and Garrett (1948) that the limb dermatomes spiral from the dorsal midline. As Fulton (1955) remarked, it is rather strange that disagreement should still exist on such an apparently fundamental issue. It would appear from the Keegan and Garrett findings that the skin and muscle fields of a spinal nerve both extend to the dorsal midline. This embodies a consistency in disposition which is comparable to the finding that the cutaneous fields of the individual rootlets overlap in a serial manner in the same way as the dermatomes themselves. Yet this study has revealed what is apparently a new inconsistency: the fields of some dorsal rootlets appeared to be discontinuous, at least in respect of sensitivity to pinch and touch stimuli. It is possible that these discontinuities arise because the fibres in any one dorsal rootlet are not distributed through each of the cutaneous rami of the spinal nerve. It is probable that similar variations would also be found in the innervation of the myotomes and sclerotomes, and of the viscerotomes.

The regular conus ascendens of the spinal cord of man has not been found in the ungulates studied. The changes in the directions of the rootlets suggest that there have been appreciable local variations in growth rate in development. In ungulates, too, the spinal cord extends further caudad than in the other species studied. This could have some relevance to the likelihood that the caudal dermatomes all reach the dorsal midline in the sheep. A greater knowledge of details of embryological development in the sheep would seem to be of considerable value in the understanding of the disposition of the spinal nerves and their cutaneous sensory fields. A knowledge of the disposition of the cutaneous sensory fields can be applied in the study of many visceral events. Responses to cutaneous stimuli have been shown to influence the visceral events in micturition; hyperaesthetic responses, in particular, have been related to changes in feeding behaviour and to the clinical signs of a scrapie infection. Many of the observations made in these present study cannot be fully explained. Sensory impulses from the chest wall were found in some instances to inhibit respiration, and irregularities in respiratory rhythm were a common sequel to thoracolumbar rhizotomoies. A study of the interrelations between sensory impulses from the skin and from deeper structures of the chest wall may reveal the precise mechanism by which these changes in respiration are produced. Other studies of visceral events may explain why faeces should be coated with mucus or blood.

The Marchi technique was shown to be a useful means of defining sensory pathways in the spinal cord. If the technique was standardised to give reasonably consistent results under conditions such as obtained in the present study - and this might not be at all difficult to achieve - the short post-operative degeneration time necessary would permit a rapid assessment of the results of section of various nerve fibres. Such staining could be used to trace demyelination in diseases such as swayback or in cases of injury to the spinal cord.

The definitions of the dermatomes made by Head, Foerster and Sherrington have been used as the basis for comparative studies in other species. The close general correspondence between man and the various animal species indicates that information gained in either man himself or his domestic animals, will find useful application in both human and veterinary medicine.

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APPENDIX

The Tables which follow give details of the dorsal spinal nerve roots sectioned and, where applicable, the branches of the cranial nerves divided, in isolating the dermatomes.

The code numbers of the sheep are included to indicate the animals in which more than one dermatome was isolated. In some cases trunk dermatomes were isolated on both sides of the body: symmetrical isolations are specifically noted. As has been noted in Chapter V, partial definitions of individual boundaries have only been included when almost all of the boundary had been mapped.

Some discrepancies exist between the dorsal root sections recorded for an individual animal in the isolation of a dermatome, and those recorded for the same animal in the consideration, in Capter V, of the effects of dorsal root section other than a loss of cutaneous sensitivity. They arise because in some instances the particular side effects were recorded after a first-stage operation and before the dermatome was completely isolated.

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TABLE 12

CRANIAL NERVES/DORSAL ROOTS SECTIONED IN ISOLATING CERVICAL DERMATOMES

Dermatome	Sheep Code No.	Cranial Nerve branches/ Spinal Dorsal Roots sectioned	Other dermatome boundaries defined
C1	55	Pinna branches of VII Oph & Mand divs of V C2-C5	- -
C2	44	Pinna branches of VII Oph & Mand divs of V C1, C3-C5	- -
C3	40	Oph & Mand divs of V C1-C2, C4-C5	- -
C4	37	C2-C3, C5-C7	- -
C5	35	C1-C4, C6-T3	Ant. border T4
C6	25	C3-C5, C7-T4	- -
C7	19	C4-C6, C8-T4	Ant. border T5 Post. border C3
C8	23	C4-C7, T1-T5	Post. border C3
	57	C4-C7, T1-T4	Ant. border T5

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TABLE 13

DORSAL ROOTS SECTIONED TO ISOLATE THORACIC DERMATOMES

Dermatome	Sheep Code No.	Th/L*	Dorsal Roots sectioned	Other dermatome boundaries defined
T1	27	13/6	C4-C8, T2-T5	Post. border C3 Ant. border T6
	54	12/7	C4-C8, T2-T4	Ant. border T5
T2	27	13/6	C5-T1, T3-T5	Post. border C4
T3	28	13/7	C4-T2, T4-T6	- -
	54	12/7	C5-T2, T4-T5	Ant. border T6
T4	16	13/6	T2-T3, T5-T6	Post. border T1 (P)
	28	13/7	T1-T3, T5-T7	Ant. border T8
T5	9	13/7	T3-T4, T6-T7	Ant. border T8
	16	13/6	T3-T4, T6-T7	Post. border T2 (P)
T6	51	13/6	T4-T5, T7-T10	Post. border T3
T7	16	13/6	T5-T6, T8-T9	Ant. border T10
T8	16	13/6	T6-T7, T9-T10	Ant. border T11
T9	4 B	13/6	T7-T8, T10-T11	Post. border T6
T10	51	13/6	T8-T9, T11-T12	Post. border T7 Ant. border T13
T11	48 BN	14/6	T9-T10, T12-T13	- -
	51	13/6	T7-T10, T12-L1	- -
T12	4 B	13/6	T10-T11, T13-L1	Ant. border L2
T13	24	13/6	T9-T12, L1-L2	- -
T14	--		Not isolated	- -

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* - Number of Thoracic/Lumbar vertebrae

B - Dermatome isolated bilaterally

N - No insensitive areas appeared

(P)- Dermatome boundary only partially defined

TABLE 14

DORSAL ROOTS SECTIONED TO ISOLATE LUMBAR DERMATOMES

Dermatome	Sheep Code No.	Th/L*	Dorsal Roots sectioned	Other dermatome boundaries defined
L1	3**	14/6	T12-T14, L2-L4	- -
L2	15	13/6	T13-L1, L3-L4	Post. border T12 Ant. border L5
	51	13/6	T12-L1, L3-L5	- -
L3	15	13/6	L1-L2, L4-L5	Post. border T13 Ant. border L6 (P)
	39	13/6	L1-L2, L4-L5	- -
	41	13/6	L1-L2, L4-L6	- -
	42	13/6	T13-L2, L4-S1	Post. border T12 Ant. border S2 (P)
	56	13/6	T13-L2, L4-S2	- -
L4	39	13/6	L1-L3, L5-L6	Ant. border S1
	50	13/6	L1-L3, L5-S1	Ant. border S2 (P)
L5	20	13/7	L3-L4, L6-S4	Post. border L2 Ant. border Cc1
	49	13/6	T13-L4, L6-S2	Post. border T12 Ant. border S3 (P)
	53	14/6	T13-L4, L6-Cc2	- -
L6	34 R (P)	13/6	T12-L5, S1-S4	Post. border T11 (P)
	51	13/6	L3-L5, S1-S4	- -
L7	36	13/7	T13-L6, S1-S4	- -

* - Number of Thoracic/Lumbar vertebrae

** - Dermatome isolated bilaterally

(P) - Dermatome boundary only partially defined

R - Ram

TABLE 15

DORSAL ROOTS SECTIONED TO ISOLATE SACRAL AND COCCYGEAL DERMATOMES

Dermatome	Sheep Code No.	Th/L*	Dorsal Roots sectioned	Other dermatome boundaries defined
S1	33 R (P)	13/6	T12-L6, S2-S4	Post.border T11
	43	13/6	L3-L6, S2-Cc2	- -
S2	31 R	13/6	T12-S1, S3-Cc1,cord	Post.border T11 (P)
S3	18	13/6	L4-S2, S4-Cc1,cord	Post.border L3
	29 R	13/6	L1-S2, S4-Cc1,cord	- -
	47	13/6	L5-S2, S4-Cc2,cord	- -
	56	13/6	L4-S2, S4-Cc1,cord	- -
S4	30 R	13/6	L2-S3, Cc1,cord	- -
	32 R	13/6	T12-S3, Cc1-Cc3,cord	Post.border T11 (P)
	50	13/6	L5-S3, Cc1,cord	- -
Cc1	48	14/6	S3-S4, Cc2,cord	- -
	51	13/6	S1-S4, Cc2,cord	- -
	54	12/7	S2-S4, Cc2,cord	- -
Cc2	58	13/7	S2-Cc1, Cc3,cord	- -

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* - Number of Thoracic/Lumbar vertebrae

** - Spinal cord was transected caudal to last-named nerve

(P) - Dermatome boundary only partially defined

R - Ram

TABLE 16

SUPPLEMENTARY ISOLATIONS OF SINGLE DERMATOME BOUNDARIES

Sheep Code No.	Number of Thoracic/Lumbar Vertebrae	Dorsal Roots sectioned	Dermatome boundary isolated
1	13/6	T11-T13	Post. border T10 Ant. border L1
10	13/6	L4-L5	Ant. border L6 (P)
22	13/6	L2-L5	Post. border L1
26	13/7	L3-S3	Post. border L2 Ant. border S4
54	12/7	L3-L6	Post. border L2
58	13/7 B	T10-L1	Post. border T9 Ant. border L2

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B - Bilateral operation

(P) - Dermatome boundary only partially defined.

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