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SPINAL NERVE DISTRIBUTIONS IN THE UPPER LIMB: THE ORGANIZATION OF THE DERMATOME AND AFFERENT MYOTOME

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CONTENTS

Discussion

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Single fibres were dissected from the dorsal spinal roots of the nerves serving the brachial plexus in African green monkeys. The dermatomal organization of these spinal nerves was deduced from data concerning the receptive fields of 2834 single afferent fibres. These data were collected in an attempt to reconcile some of the discrepancies that exist in published descriptions of the dermatomes in primates; our results and the literature reviewed suggest that the cutaneous region served by one spinal nerve is actually much wider and much more variable in location than is generally recognized. This makes any summary diagram a misleading indicator of the true complexity of the spinal innervation of the upper limb. In spite of this variability among individuals, within any specific individual there is a regular and orderly progression of innervation which allows prediction of the region served by a particular spinal nerve when information concerning the site of innervation of adjacent nerves is available. The territory of each myotome tended to be larger than the dermatome of the same spinal nerve. Most muscles of the limb received afferent innervation from three to four different spinal nerves. Further, the territory of the myotome did not of necessity coincide with the dermatome of the same spinal nerve. Even those nerves innervating the hand still innervated axial muscles. These observations have important implications for the diagnosis of spinal nerve injuries.

INTRODUCTION

For more than a century investigators have attempted to define the innervation patterns of spinal nerves. Nevertheless, inspection of dermatomal charts prepared by the major contributors to this effort shows inconsistencies (Inouye & Buchthal 1977). Further, experiments by Denny-Brown and his colleagues (Denny-Brown *et al.* 1973; Kirk & Denny-Brown 1970) suggest that spinal mechanisms alter the boundaries of dermatomes obtained by the use of behavioural techniques. Since most published dermatomal maps are derived from behavioural observations there is reason to suspect that some aspects of these maps may be incorrect. We have therefore reinvestigated the problem by means of electrophysiological techniques. To avoid the modifications of the dermatomal boundaries that occur as the result of spinal mechanisms, we have used single fibre recording techniques to study the afferent fibres at the dorsal root entry zone. We have placed particular emphasis upon (i) the variable location of the region served by specific nerves and (ii) the relationship between the muscle and skin regions served by a single dorsal root.

METHODS

The data were obtained from ten African green monkeys (*Cercopithecus aethiops*) of both sexes weighing 2.2 to 3.0 kg. Four squirrel monkeys were used in preliminary studies and three other African green monkeys were only partially studied before they died. Thus, the maps of only one or two spinal nerves were completed in these animals. Data from the earlier nerves could be used as examples of single nerve distribution but could not be used to infer dermatomal sequences.

A single terminal experiment was performed on each animal. Careful attention to the physiological state of the animal was imperative; the mapping of the distribution of a single nerve required 6–8 h and a complete map of all the spinal roots contributing to one brachial plexus required 36–48 h. Thus a tracheostomy was performed and respiration was artificially controlled from the onset of the experiment. Carbon dioxide was continuously monitored and ventilation was adjusted to keep the end-tidal CO_2 around 3 %.

At the beginning of each experiment, the animal was tranquillized with 15 mg/kg of phencyclidine hydrochloride and a venous catheter was placed in the popliteal vein. This provided a route for administering an initial dose of sodium pentobarbital (20 mg/kg), penicillin (potassium G, 1×10^6 units) and supplementary doses of anaesthetic as required to maintain areflexia. Later in the experiment, Ringer solution (containing lactose, 10 g/l) was delivered to maintain fluid volume and to provide an energy source. Prednisolone (25 ng), a glucocorticoid, was injected intramuscularly.

The dissections were performed in a modified spinal apparatus. The animal's body was suspended by a clamp attached to a rod and mounted on a heavy base. The clamp was applied to the spinous process of one of the lumbar vertebrae. A small metal plate was attached to the skull by means of screws and dental acrylic, where it was used to fix the head, in a flexed position, to a post on the other end of the base. A radical laminectomy exposed the spinal cord from C_2 through T_6. Pins were placed in the bodies of the fifth and sixth thoracic vertebrae and the area was covered with dental acrylic, and also fixed to the base to reduce displacement of the spinal column caused by respiratory movements. Following this procedure, the limbs were fixed by pins through the bones near joints, thereby movements which might affect the stability of the recording being prevented. All subsequent work proceeded with the aid of an operating microscope.

After the dura was opened, a small dissecting platform was positioned near the root to be studied and a recording electrode was placed nearby. One dorsal rootlet was cut as proximally as possible, freed of the arachnoidal membranes and reflected onto the platform for further dissection. Bundles of fibres sufficiently small to contain one to three active fibres were teased free and placed on the electrode, where individual units were identified by their spike amplitudes.

The action potentials were amplified in two stages, first × 1000 with a differential amplifier (Princeton Applied Research model 113) having a bandpass of 30 to 10 kHz, and then × 10 to × 20 by a Tektronix 2A63 amplifier. The output of the second amplifier was connected to a custom-built differential amplitude discriminator containing logic circuitry that generated pulses on one output whenever action potentials crossed one voltage threshold and not a second, higher threshold. These pulses were counted electronically to obtain the mean frequency of discharge for a single fibre and were led to an audio amplifier to provide an auditory cue while the receptive field was mapped.

Even though, in some cases, several spikes appeared in the recording from a small fascicle, each fibre was identified as an individual unit on the basis of spike amplitude. If the presence of other fibres prevented a detailed inspection and characterization of the unit under study, the amplitude discriminator was used to exclude the discharges from the other fibres. In this way a detailed qualitative description of each fibre was quickly obtained. In each instance the description included: (i) the modality that activated the fibre (skin, muscles, joint, deep, unknown); (ii) the spontaneous discharge rate; (iii) the location of the receptive field on the forelimb (by drawing on photographs of the upper limb the muscle, joint or skin region that produced a discharge).

The criteria used to make the modality and submodality assignments were subjective. Afferent fibres from skin were those whose receptors could be activated best by brushing over, or pressing on, the skin. That they were located in the skin was made obvious by moving the skin to a new position or lifting it to demonstrate that the effective region shifted with

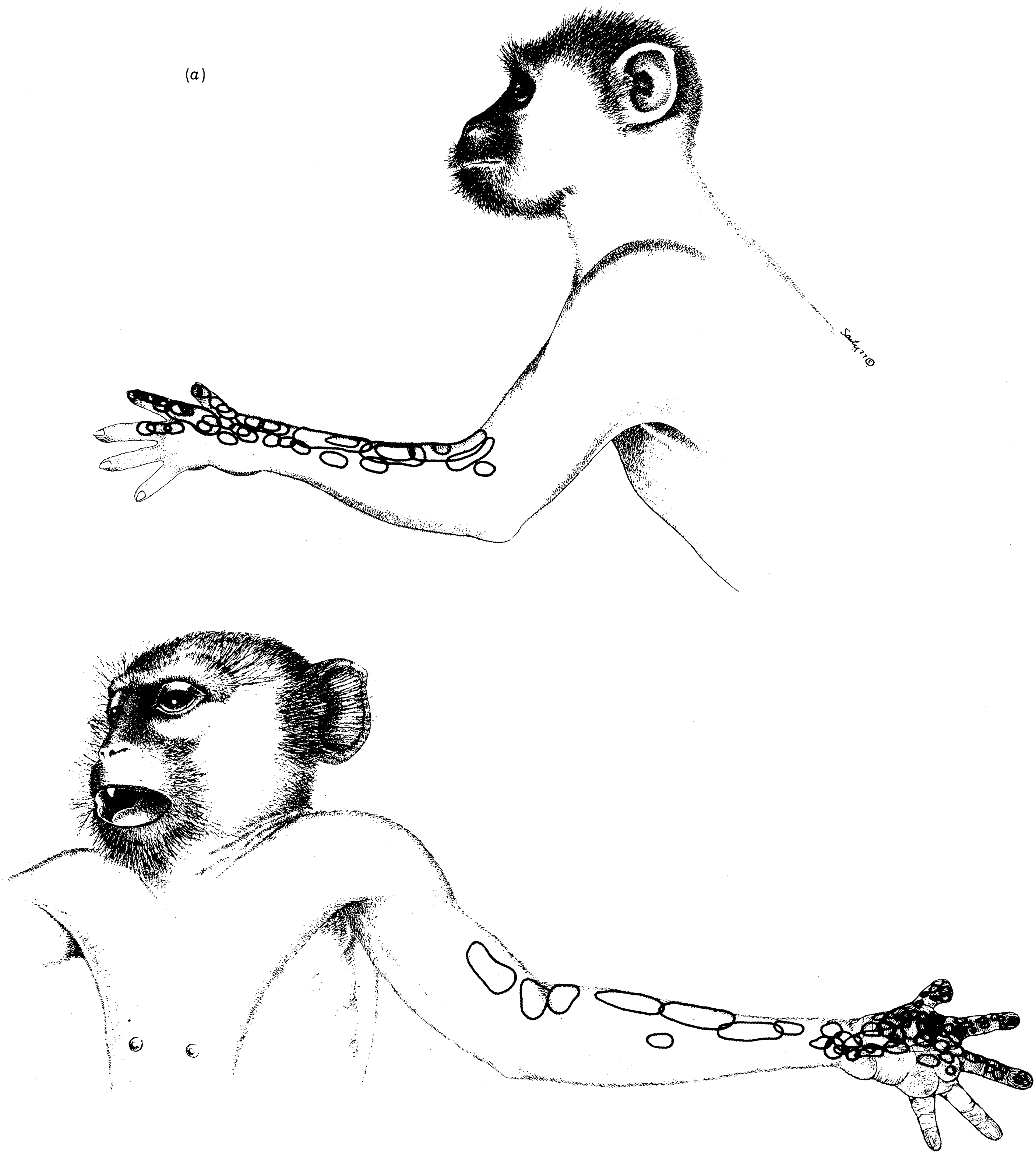


Figure 1. (*a*) An example of the manner in which data were summarized. Cutaneous receptive fields were drawn around that skin region which activated an individual fibre. All receptive fields from one spinal nerve were transferred to these two views of a prototypical animal. The particular spinal nerve illustrated here is the seventh cervical.

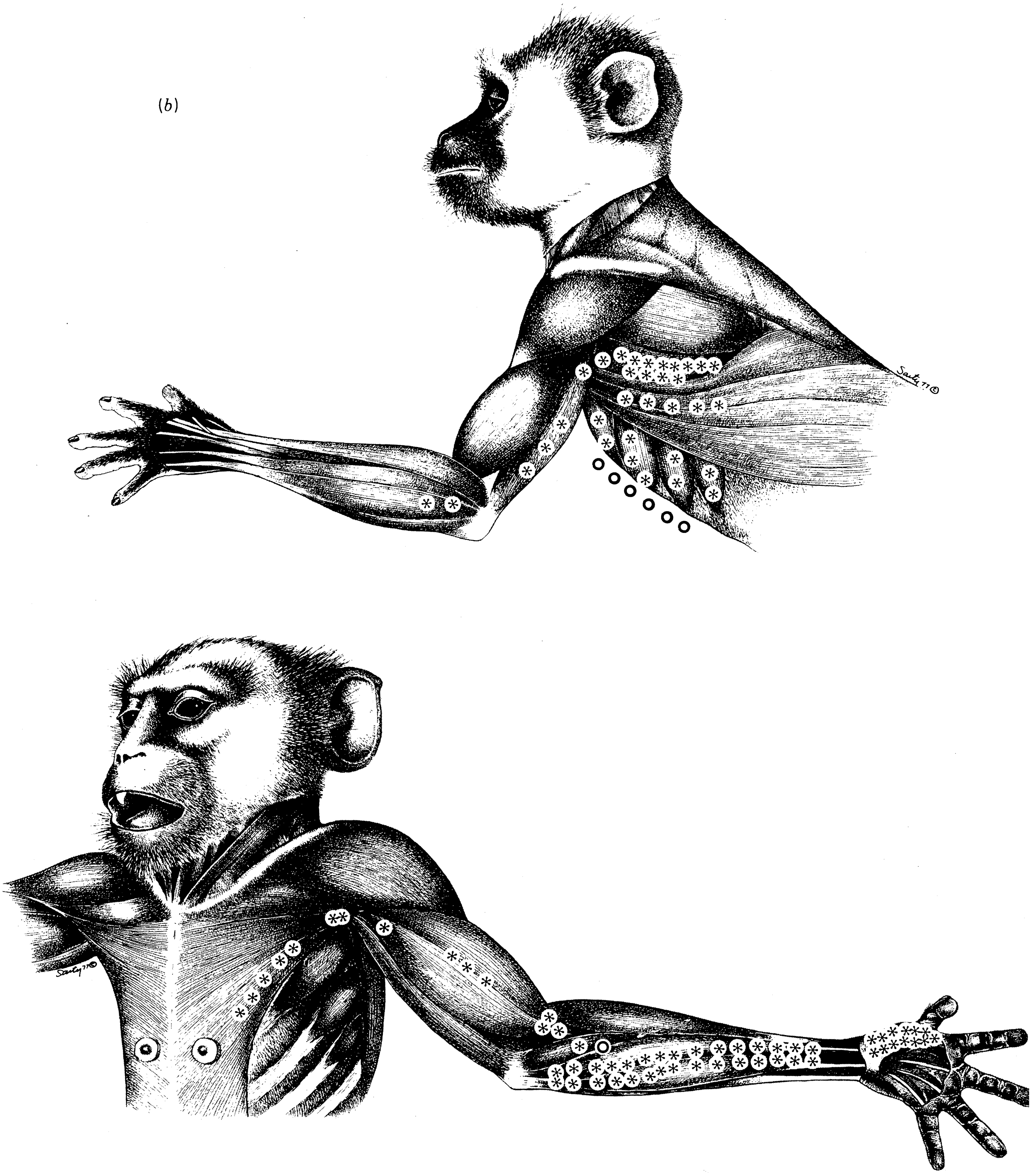


Figure 1. (*b*) Afferent fibres from muscles were identified by an asterisk on that region of the muscle where manipulation activated the fibre. Open circles below the animal were afferents driven by respiration, that presumably served intercostal muscles but were difficult to localize.

the skin. In the same nerves from these animals, afferent fibres from muscle were identified by their location beneath the skin and by being activated with the stretching of a tendon through flexing or extending a joint *and* by pressure over the belly of the muscle. Often these fibres had a regular spontaneous discharge. Afferent fibres serving joints were excited by flexion or extension of a specific joint and pressure at some point over the joint capsule, while pressure on the muscle did not cause a response.

Afferent fibres from deep tissues produced discharge with firm pressure on subcutaneous structures. They were generally difficult to localize precisely but could be differentiated from the other categories by the tests described above. Obviously ambiguity arises when an afferent fibre is activated by pressure near a tendinous insertion of a muscle near a joint. In such instances mistaken classifications probably occurred. Such situations were infrequent. However, if errors in classification were random they should have cancelled one another. Afferent fibres were assigned to the unknown category when they were characterized by (i) spontaneous rates that could not be modified by stimulation of the forearm and thorax, or (ii) one or few discharges produced by manipulation of the limb in a manner that defied further classification.

For cutaneous afferent fibres, the responses were divided into a rapidly and a slowly adapting submodality depending upon the rate with which the fibre adapted to a sustained stimulus. Any fibre that continued to discharge, above its resting level, for more than 1 s after application of a steady stimulus was termed slowly adapting.

Data summaries were prepared separately for cutaneous afferent fibres and for afferent fibres from muscles. The receptive fields of afferent fibres serving skin were drawn on one of two standard drawings (figure 1) as a line enclosing the skin region that activated the fibre. The cutaneous region served by one spinal nerve, the dermatome, was defined as that region that encompassed all the cutaneous receptive fields observed in the recordings from that spinal nerve. For the afferent fibres from muscle, the equivalent region was termed the afferent myotome. This is consistent with the use of this term in embryology and allows us to readily discuss the differences between the cutaneous afferent and muscular afferent innervation arising from one spinal nerve.

For the myotome, the data for one spinal nerve was transferred to one pair of figures, that depicted the muscles of the upper limb and torso. The receptive field of each afferent fibre from muscle was represented by an asterisk placed on the appropriate muscle. When information was present concerning the location of the receptor within the muscle, the symbol was positioned accordingly. In a small number of cases afferent fibres were driven by the respiratory movements of the animal. Manipulation of the intercostal spaces suggested that these fibres were afferent fibres from intercostal muscles. Such fibres have been indicated on the figures with an open circle.

There was no attempt to differentiate the several types of afferent fibres serving muscles. Presumably fibres of groups Ia, Ib and II were all encountered and classed as fibres responding to the mechanical manipulation of muscle tissue. Some of the fibres activated by points very close to joints may have been erroneously classified as afferents from joints. However, since the number of joint afferents per spinal root never exceeded 11.4 % of the number of fibres studied in that root, we estimate that such an error is unlikely to exceed 1–2 % of the fibre sample.

Fibres classified as deep might also have been associated with muscle. However, this category contains only those fibres that could not be assigned to muscle or joint groups and thus represents afferent fibres of non-cutaneous origin that did not respond to pressure over muscles or joint capsules and were not activated by muscle stretch. Because there were few of them per spinal root, no summary figures were prepared for joint or deep afferent fibres.

Results

The afferent fibre sample consisted of 2834 fibres from ten animals. In five of these animals all of the nerves serving the brachial plexus were studied. In the others only selected spinal roots were studied, but these were documented in more detail.

Table 1. Fibres studied

spinal root ... monkey†	C_3	C_4	C_5	C_6	C_7	C_8	T_1	T_2	T_3	T_4	total
1	—	47	61	64	27	29	5	—	—	—	233
2	—	13	25	63	102	55	27	21	13	20	339
3	—	40	16	49	47	67	20	—	—	—	239
4	—	—	—	—	252	33	—	—	—	—	285
5	—	—	—	—	259	—	121	23	—	—	403
7	—	—	62	83	84	111	100	77	46	—	563
8	—	—	—	48	—	—	—	—	—	—	48
9	63	5	—	—	—	—	—	—	—	—	68
10	—	—	—	39	—	—	—	—	—	—	39
11	—	91	65	99	150	124	67	—	21	—	617
total	63	196	229	445	921	419	340	121	80	20	2834

† The sixth animal died before any data were collected.

The origin of the fibres in the sample is shown in table 1. The predominance of fibres from the nerves in the central portion of the brachial plexus reflects the larger size of these nerves. The spinal roots in the centre of the brachial plexus had more rootlets than had the adjacent roots. Consequently, even when the sample per rootlet was limited to 45 fibres, more fibres were taken from the central roots because these roots contained more rootlets. With this procedure, however, the number of fibres sampled per spinal root is roughly proportional to the number of fibres present in that root (figure 2).

Table 2 summarizes data concerning root of origin and modality. To avoid bias due to differential sampling of the roots, the data are presented as percentages of the numbers of fibres studied in each root. The final column presents the overall percentages for the total sample.

The percentage of cutaneous afferent fibres in each root varied considerably, being greatest in the most rostral and most caudal dermatomes studied (figure 3). Conversely, the percentage of afferent fibres from muscle exceeded the percentage from skin by an average of 20 % with the largest values occurring in the central nerves of the brachial plexus. The data of table 2 show that for a specific spinal nerve the ratio of skin to muscle could vary from 1:4 to 4:1. By determining confidence limits for proportions in a sample of 45 fibres, it was possible to infer that these ratios were not due to sampling errors but instead reflected actual differences in the relative proportions of modalities in the underlying fibre populations. For C_3 the cutaneous proportion in table 2 is high. Although this may be related to an actual predominance of cutaneous innervation, there is a possibility that muscle input is under-represented because some innervation of the cervical neck muscles may have been interrupted by the laminectomy

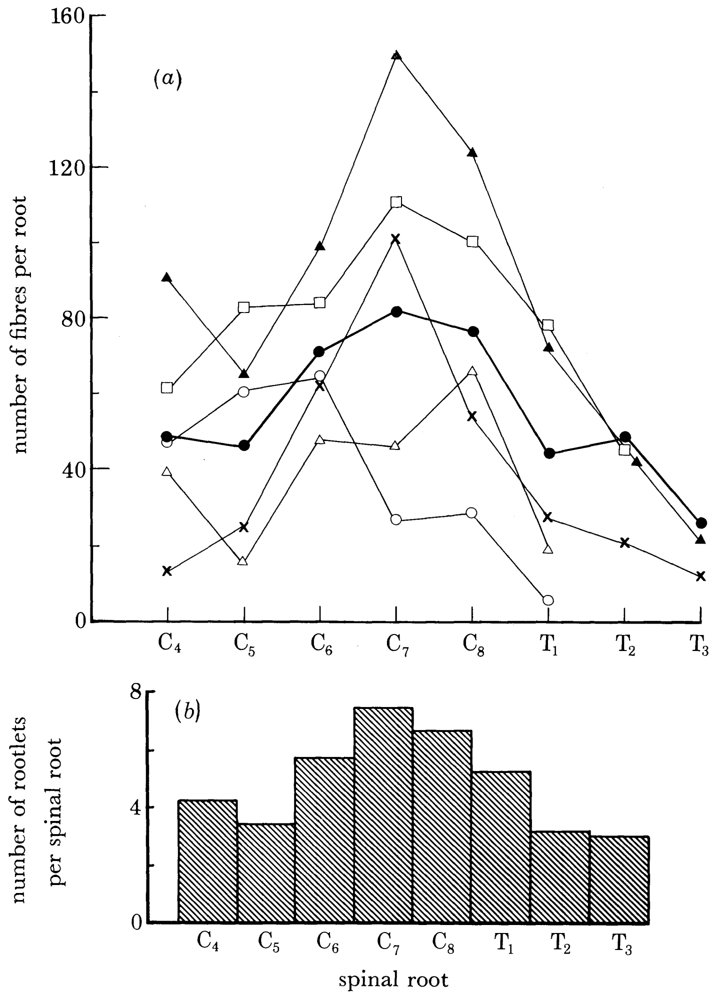


FIGURE 2. (*a*) The number of afferent fibres per spinal root varied with the root studied. Since the number of fibres studied was a proportion of the total number present, it reflected the magnitude of this difference among spinal roots. (*b*) The larger number of afferent fibres found in the central nerves of the brachial plexus was also reflected in the number of rootlets contributing to these nerves.

TABLE 2. PERCENTAGE OF FIBRES IN EACH MODALITY

($n = 2834$)

spinal root ...	C_3	C_4	C_5	C_6	C_7	C_8	T_1	T_2	T_3	T_4
modality										
skin	69.8	39.3	14.0	14.6	31.9	32.2	28.2	38.0	36.2	70.0
muscle	22.2	45.4	56.8	62.0	50.1	49.4	49.7	38.8	41.2	30.0
joint	1.6	0	11.4	7.9	10.0	7.9	5.6	0.8	1.2	0
deep	0	3.6	3.5	5.2	3.4	5.0	2.6	2.5	8.8	0
unknown	6.3	11.7	14.4	10.3	4.7	5.5	13.8	19.8	12.5	0

procedures. The proportion of cutaneous afferent fibres decreased progressively in C_4, C_5 and C_6. These nerves served primarily the shoulder and upper arm and seemed to consist predominantly of afferent fibres from muscles of the shoulder girdle. Then in the cervical nerves serving the hand (C_7, C_8 and T_1) the percentage of cutaneous fibres increased and remained at about 35 % of the sample until T_5. The value of 70 % afferent fibres from skin in T_4 may be spuriously high since only a few fibres ($n = 20$) were studied and only in one animal.

Potential sampling problems

The dissection technique used in these experiments did not produce records of unmyelinated fibres. Single fibre recording techniques are known to bias the sample towards the larger fibres, leaving the smallest (1–6 μm) myelinated fibres under-represented (Brown & Iggo 1967). Since the afferent fibres serving the mechanosensory modalities are all of a relatively large diameter (6–14 μm; Boyd & Davey 1968), the bias against the lightly myelinated and unmyelinated fibres was ignored. Potentially, another factor could affect the sample. The afferent fibres within the dorsal rootlets appear to be segregated according to modality.

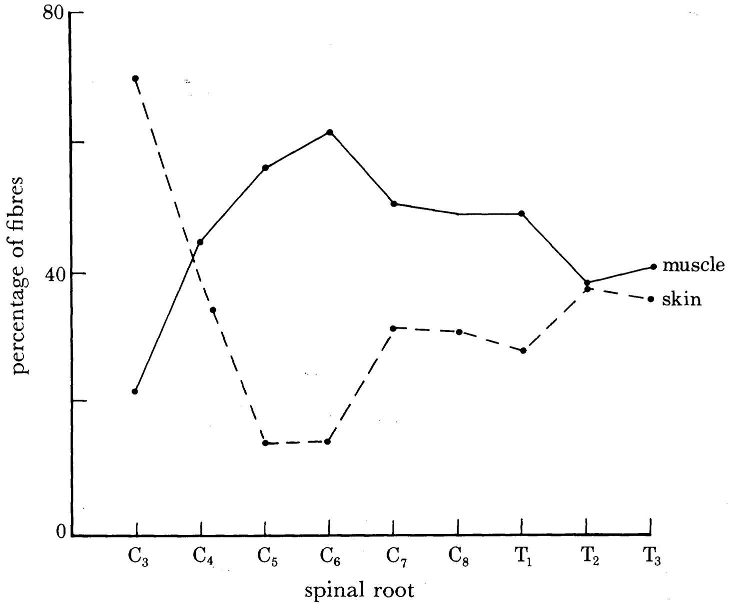


FIGURE 3. The percentage of cutaneous afferent fibres per root varied as a function of the root studied. This may reflect a functional specialization of particular spinal roots.

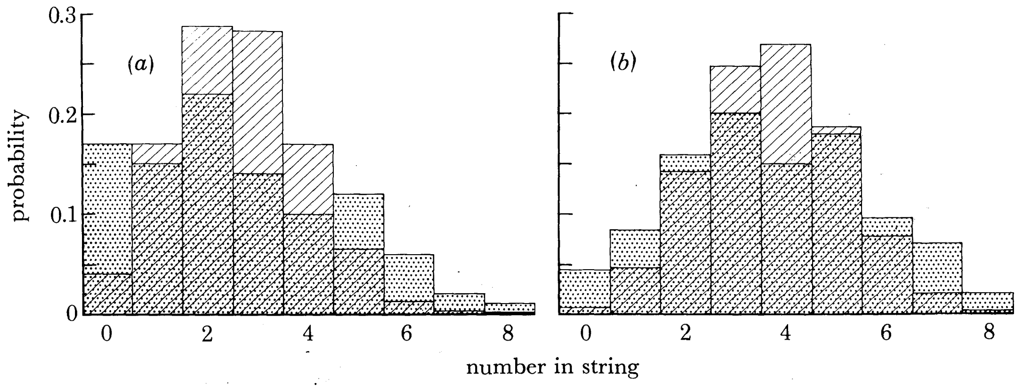


FIGURE 4. When any sample of eight afferent fibres was analysed, clustering of fibres by modalities and submodalities was observed. This phenomenon was reflected in the probability distribution for the proportion of (*a*) skin or (*b*) slowly adapting fibres found in any sample. Both distributions differ significantly from a binomial distribution generated on the assumption of no clustering of the fibres.

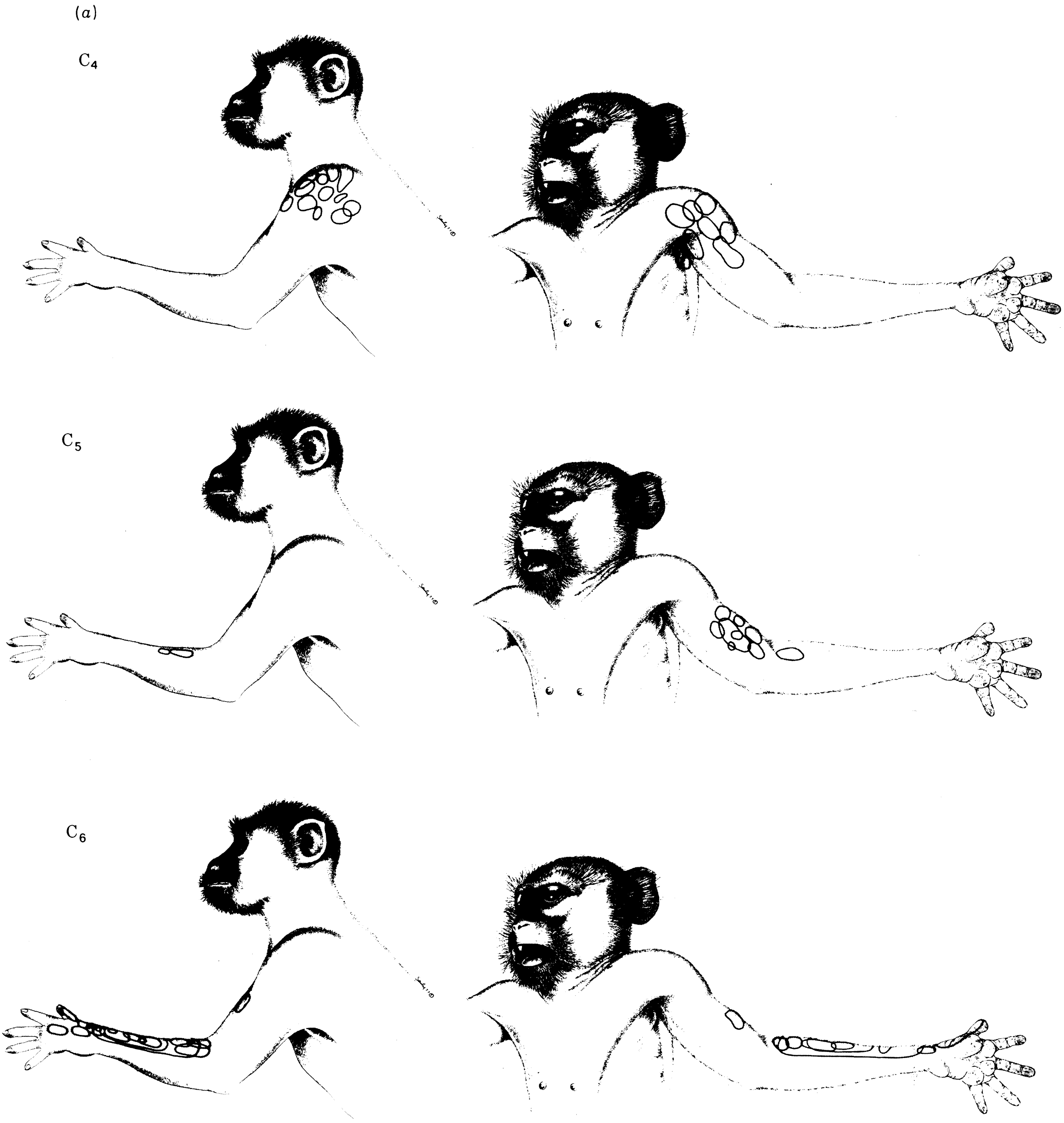
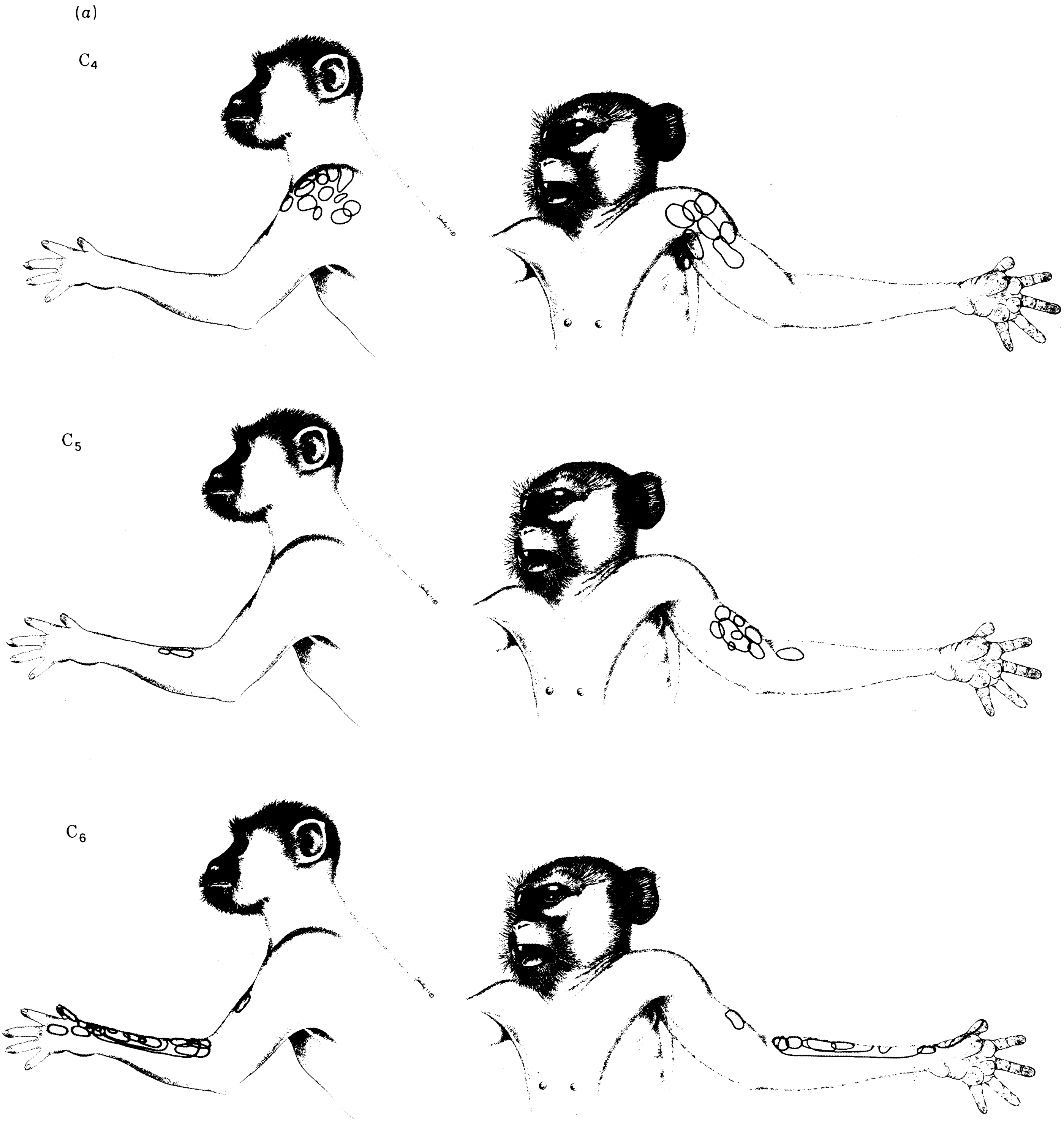


FIGURE 5. The receptive fields of cutaneous afferent fibres studied in animal 11 are shown. Each pair of figures shows the distribution for the indicated spinal nerve.



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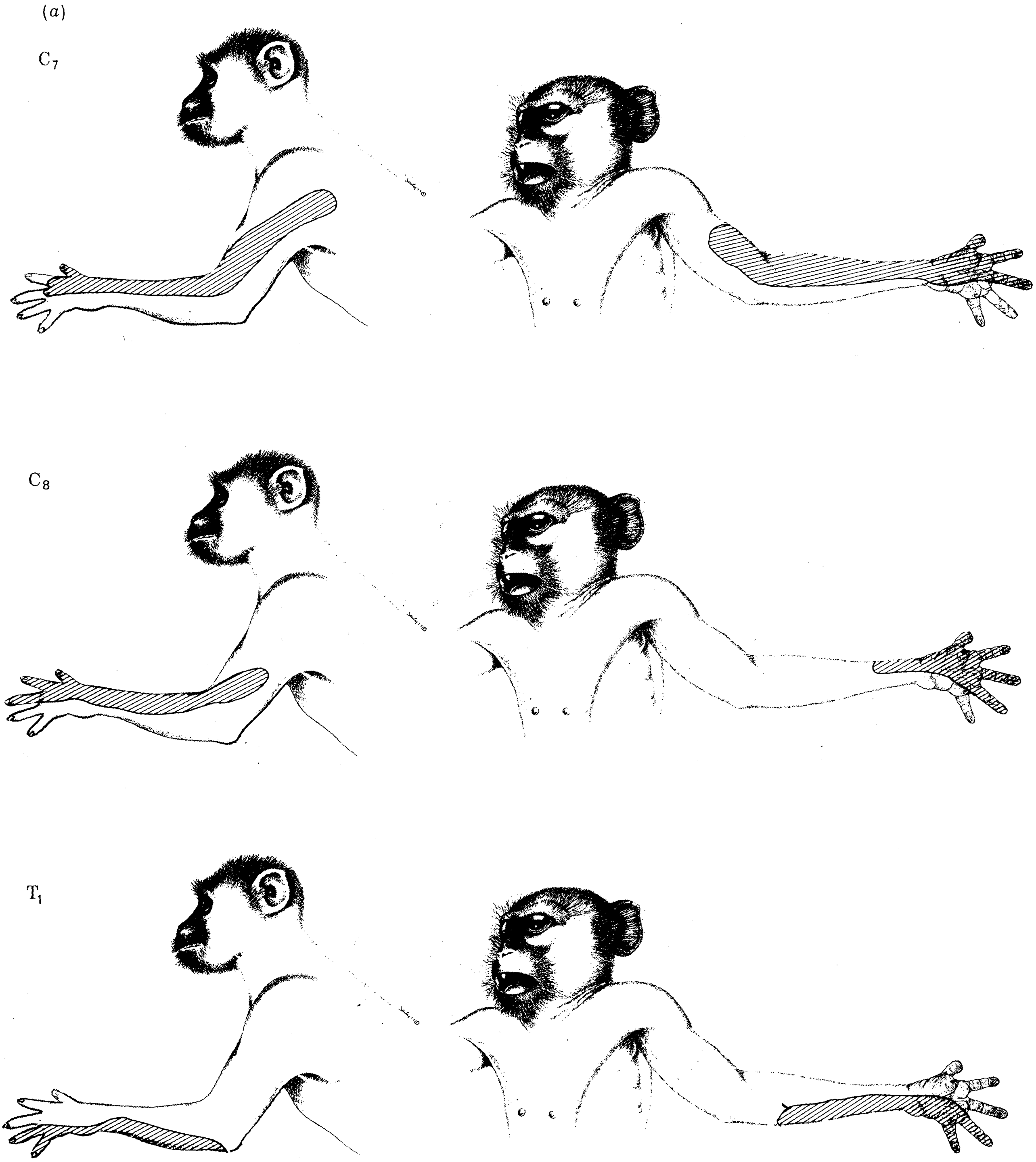


FIGURE 6. Two examples of the innervation of the glabrous skin and dorsum of the hand. Contrary to the usual assumption that C_6 serves the hand it does not do so in these two animals. (*a*) Animal 2. Note the extent of C_7, the width of C_8 and the presence of T_1 on the hand. (*b*) Animal 7. Note the difference from animal 2 and again the width of the dermatomes.

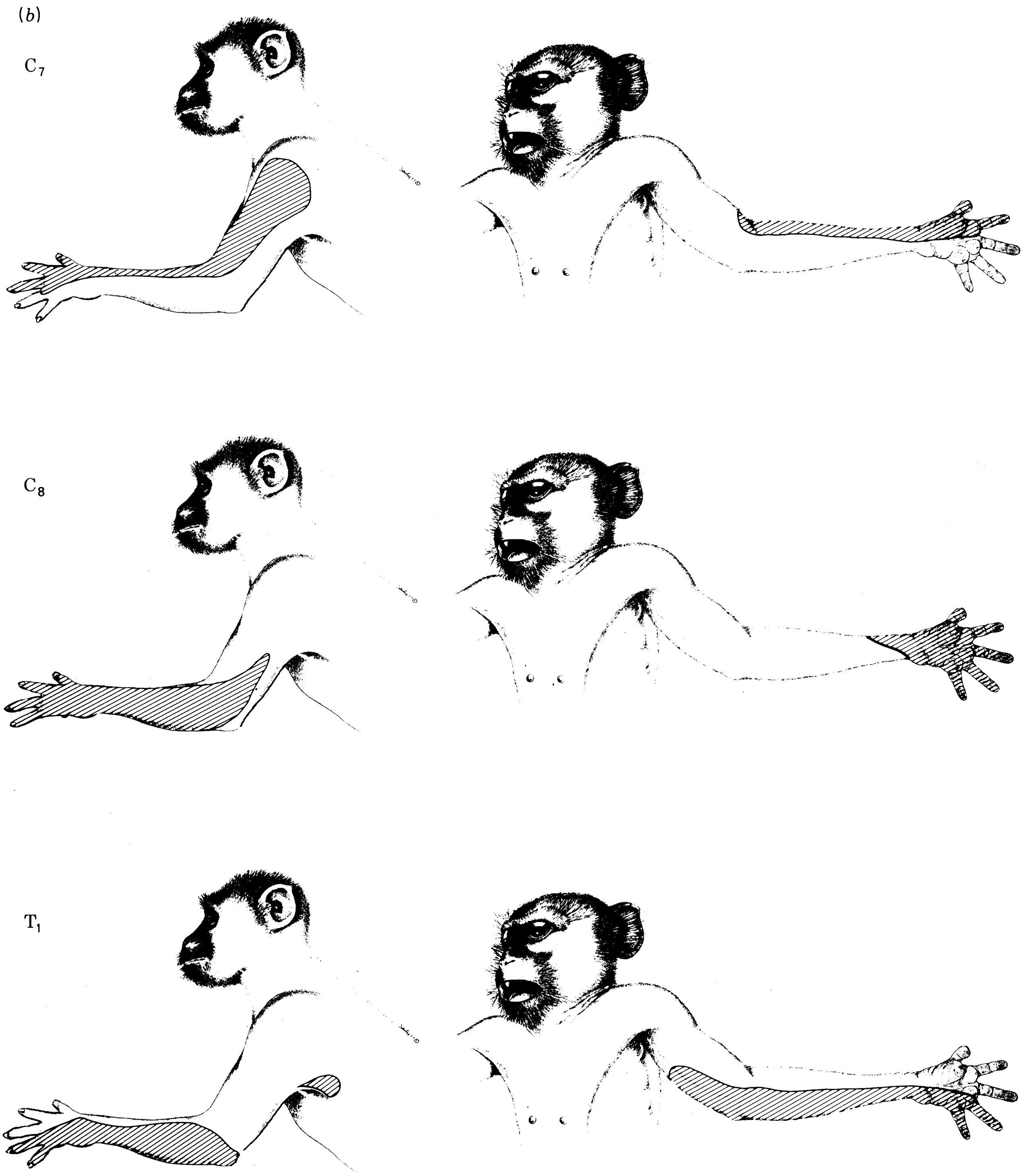


Figure 6. For description see opposite.

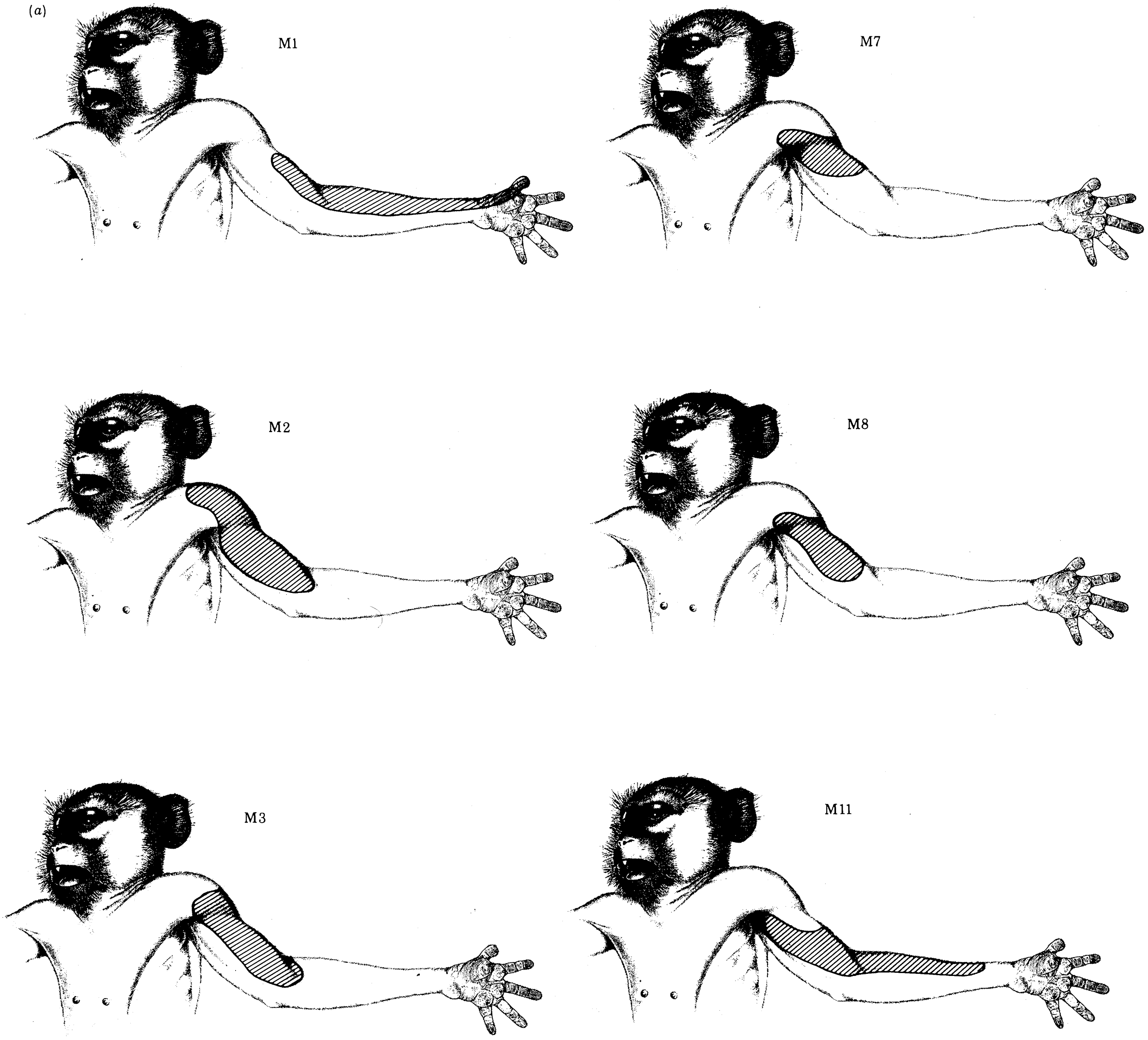


FIGURE 7. The variations in dermatomal distributions: six examples of C_6 illustrate the range of innervation patterns seen for this dermatome. (*a*) Anterior aspect; (*b*) posterior aspect.

Figure 4 illustrates the frequency with which strings of the same modality were encountered in samples of eight sequentially isolated fibres. During the experiments it became apparent that the frequency with which strings of the same modality were observed was greater than chance. When the data were compared to the expected probabilities of finding strings in a series of random samples of a population having the proportions of table 2, a χ^2 test indicated significant deviation from the predicted distribution ($p < 0.01$). This non-random distribution

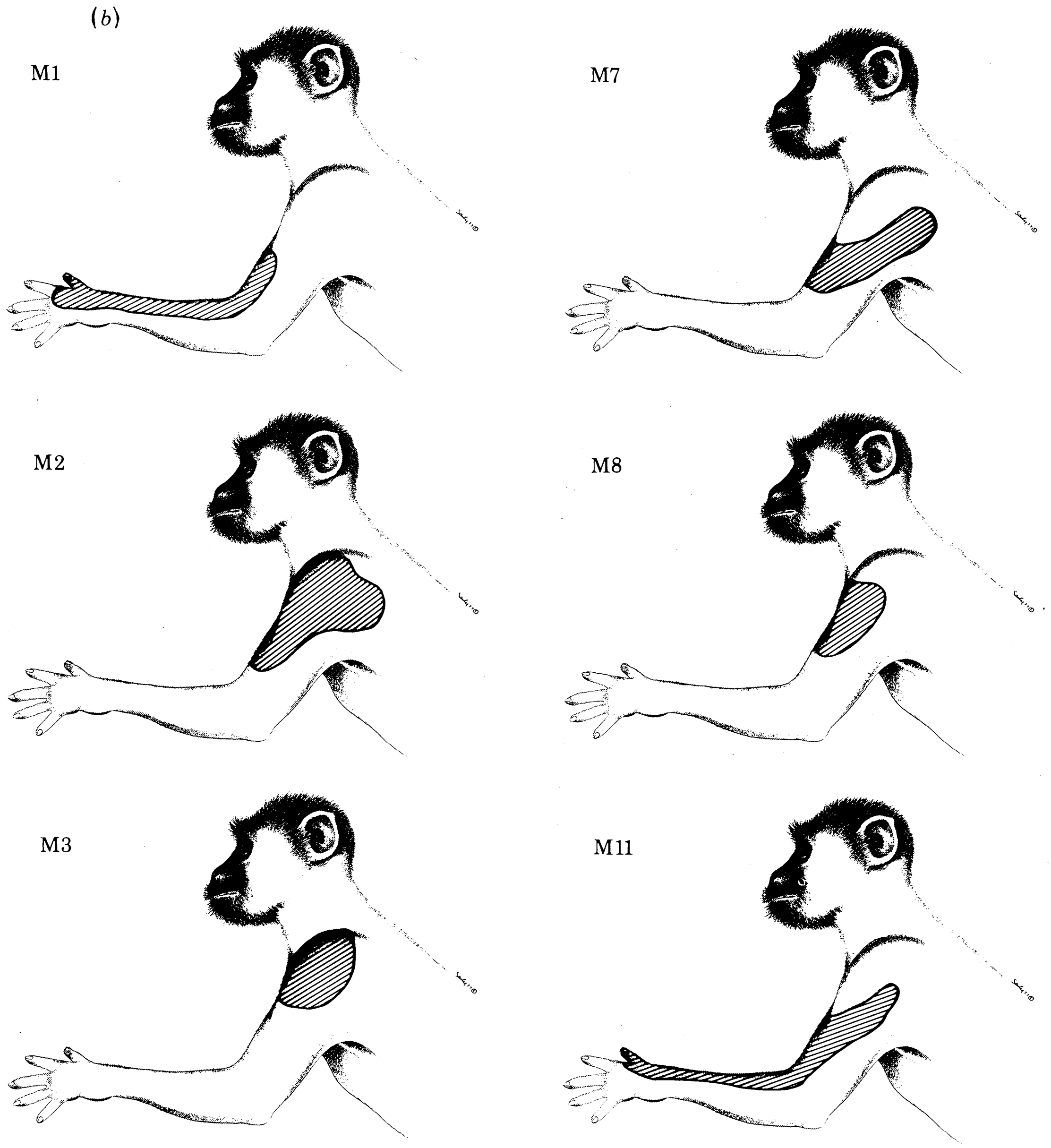


Figure 7. For description see opposite.

appeared whether the test was for skin and muscle modalities or just for the two cutaneous submodalities. Fortunately, although such grouping by function is present, it does not affect the results presented here, because the sample size per root (about 60 fibres) is large relative to the average length of the string of a particular modality (length of strings, $\bar{x} = 4$).

A typical case

Figure 5*a*, *b* illustrates the data from monkey II. The receptive field of each cutaneous afferent fibre isolated from one spinal nerve is drawn on one of two views. The three most rostral spinal nerves are illustrated in figure 5*a* and the three most caudal in figure 5*b*. The individual receptive fields are illustrated to emphasize that there was a very distinct region

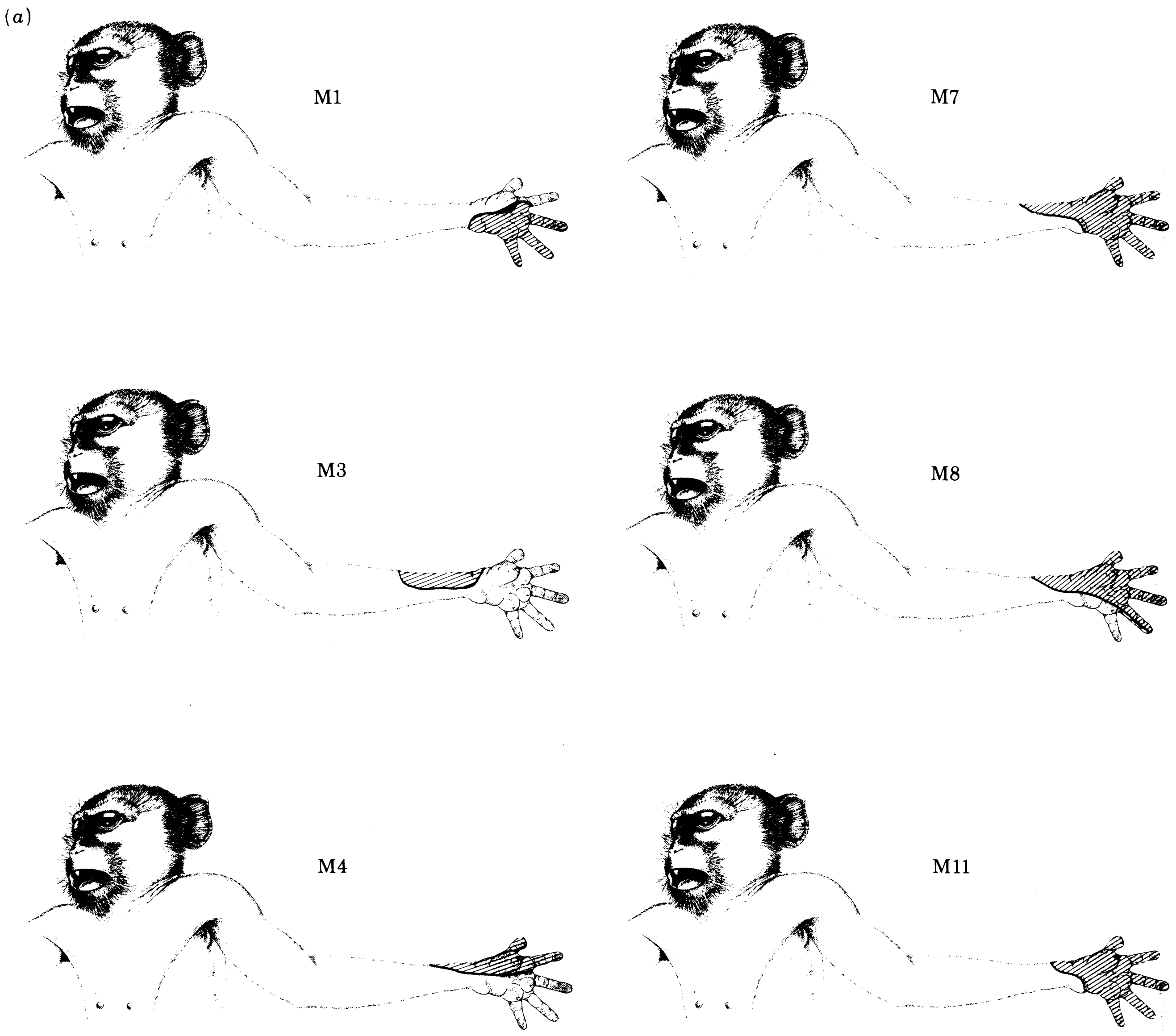


FIGURE 8. The variations in dermatomal distributions: six examples of C_8 illustrate the range of innervation patterns seen for this dermatome. (*a*) Anterior aspect; (*b*) posterior aspect.

of innervation for each spinal nerve, with little evidence of a gradient of innervation density. C_4 supplied the skin over the deltoid. C_5 supplied the skin covering the biceps and cubital fossa. C_6 covered the forearm on the radial side and extended onto the thumb. C_7 involved the first three digits and part of the palm, C_8 covered both the last three digits and the ulnar forearm, while T_1 covered the skin over the posterior aspect of the triceps.

The progressive shift of the region served, so that it only overlaps partially the previous spinal nerve territory, is apparent from the figure. This partially shifted overlap has been noted by all observers since the first experiments by Sherrington (1893, 1898). Two other observations are less consistent with published data: (i) the width of the skin area served

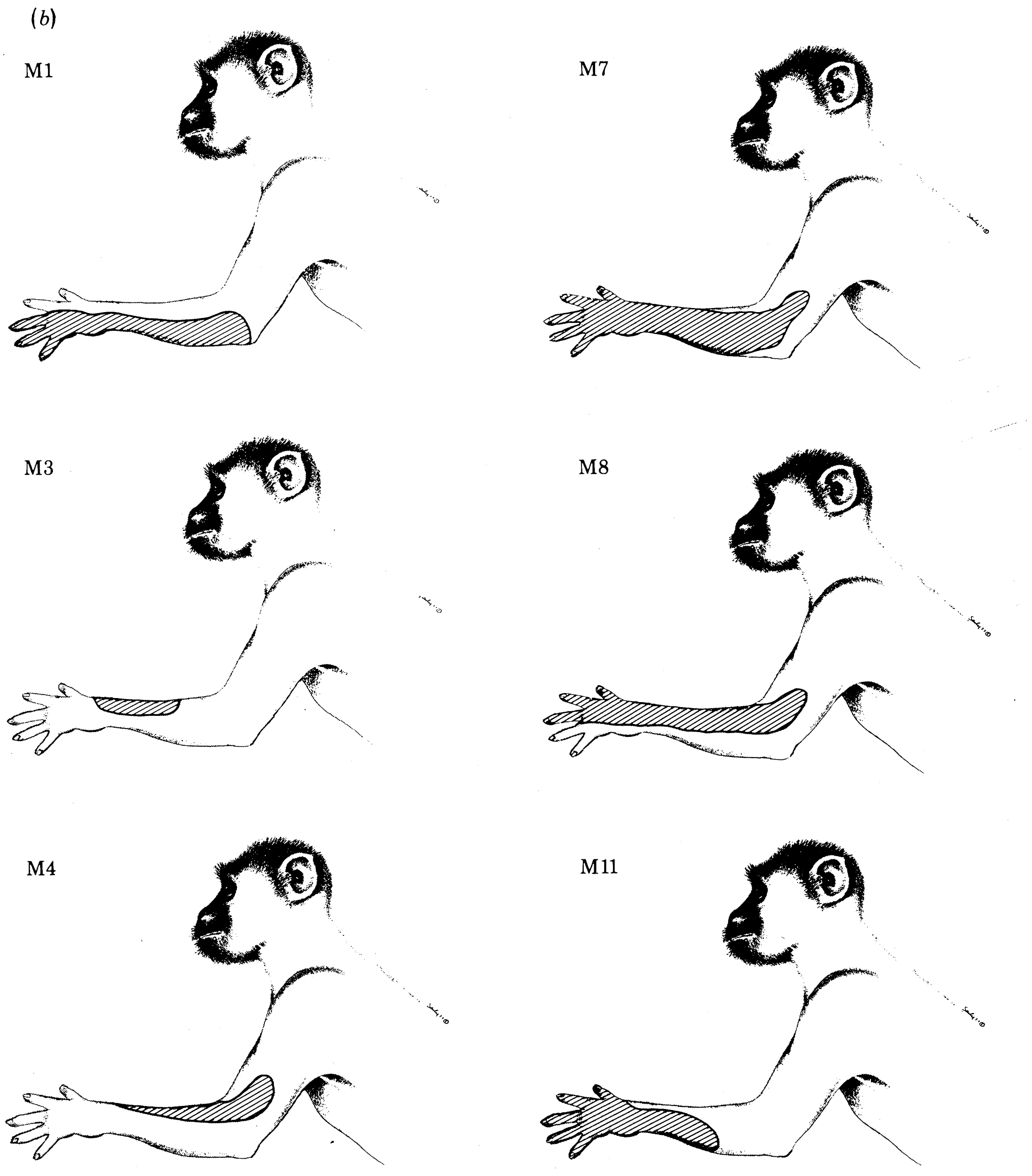


Figure 8. For description see opposite.

by one spinal nerve is circumscribed but wider than that illustrated in most textbooks (see, for example: Anderson 1978; Gray 1965); and (ii) the proximal boundary of a dermatome does not necessarily connect to the midline as these same publications suggest.

Innervation of the skin of the hand

Figure 6 illustrates the innervation of the skin of the hand. Generally this region is said to be served by C_6, C_7 and C_8 in both man and monkey (Gray 1965; Netter 1962). Figure 6*a* shows the data from monkey 2. In this animal the hand is innervated by C_7, C_8 and T_1. The dermatome from C_7 extends from the shoulder down onto the hand, but on the dorsum serves only the hand and not the dorsal aspect of the first three digits. C_8 serves the radial side of the palm, the back of the hand and the digits. This dermatome is much wider than is generally illustrated for C_8 and does not extend up the length of the arm on the preaxial side (Gray 1965). T_1 serves the radial two digits and extends only part way up the forearm.

Figure 6*b* illustrates the data from the same three spinal roots (C_7, C_8, T_1) for monkey 7. The same points with minor variations are apparent: (i) C_6 did not serve the hand (instead C_7 reached the radial aspect of the thumb) (ii) only the C_7 dermatome approached the midline, (iii) C_8 and T_1 served the majority of the hand, and (iv) the dermatomes were much wider than those illustrated in current texts. The absence of C_6 innervation of the hand in these two animals was not the result of a post-fixed plexus in this species; it simply represents a generally unrecognized degree of variability: in the animal illustrated in figure 4, C_6 served the hand.

Dermatome variability

The degree to which the dermatomal distributions varied among individuals is remarkable. Some indication of this is seen by comparing figure 4, 5 and 6*a*, *b*. To make this point more forcefully, six examples of the distribution of the C_6 dermatome are illustrated in figure 7. Figure 7*a* illustrates the innervation of skin on the posterior aspect of the arm, while figure 7*b* illustrates the anterior aspect of the arm for those same animals. The variability is equally obvious from either view. The location of the C_6 dermatome ranged from an oval region on the shoulder centred over the deltoid in two animals, to, in two animals, extending onto the hand on the radial side, where, in one of these cases, the thumb was served by this spinal root.

Figure 8 illustrates the degree of variability observed in the C_8 dermatome. Figure 8*a* shows that C_8 could innervate an area ranging from the radial side of the lower forearm in animal M_1 to, in animal M11, the entire glabrous skin of the hand and part of the ulnar forearm. Figure 8*b* illustrates the posterior aspect of these animals and shows that the C_8 dermatome can range from a patch on the radial forearm to a band extending from the third, fourth and fifth digits up along the ulnar side of the forearm.

These two spinal nerves were selected for detailed analysis because they are important nerves traditionally serving the upper arm (figure 7) and hand (figure 8) respectively. However, an equivalent degree of variability was seen in each of the other spinal nerves studied.

Overlap of dermatomes and the dermatomal sequence

The degree of overlap of the sequential dermatomes varied with the spinal nerve being studied and with the individual. The overlap was sufficient in each case, however, to suggest that any point of skin was served by at least three dermatomes. Figure 9 illustrates the pattern of this overlap for monkey 2. Because of the extensive overlap, the figure illustrates only every other dermatome; for each dermatome there was another dermatome positioned over an area intermediate between the ones illustrated.

The progression of dermatomes is apparent from this figure; although there was a large amount of variability among individuals, there was always a regular, sequential progression of dermatomes within any one individual.

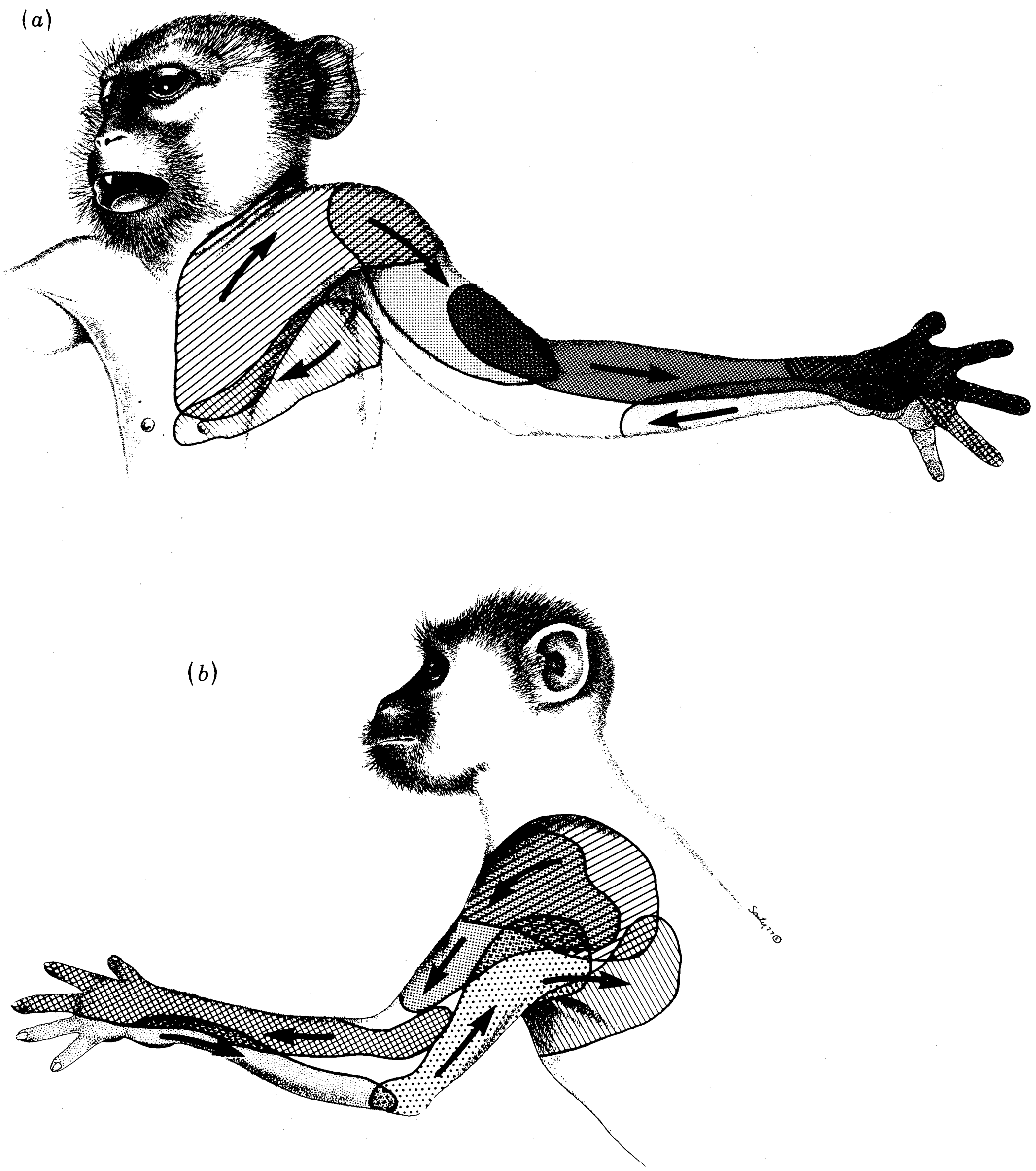


Figure 9. The partially shifted overlap of sequential dermatomes is illustrated for animal 2. Because of the extensive overlap, only every other dermatome is shown. (*a*) Dermatomes C_4, C_6, C_8, T_1 and T_4; (*b*) dermatomes C_4, C_6, C_8, T_1, T_2 and T_4.

The afferent fibres from muscles

Of the 2834 fibres studied, 1433 (50.6%) were activated by manipulation of muscles (table 3). The proportion per spinal root varied from 22.2 to 62.0% of the fibres studied, in a pattern that was approximately an inverse of the proportion of fibres serving skin (see figure 3).

The highest average value for muscle afferents was found in spinal root C_6 (62%) but the proportions for individual animals varied greatly and were not always maximum at C_6

(figure 10). The overall proportion of afferent fibres from muscle was 50.6 %. Even though the majority of nerves had lower values, the mean value was 50.6 % because the spinal nerves in the mid-portion of the brachial plexus contained more nerve fibres than those on the rostral or caudal border of the plexus.

Table 3. Afferent fibres serving muscle spinal root

spinal root … animal	C_3	C_4	C_5	C_6	C_7	C_8	T_1	T_2	T_3	T_4	total
1	—	39	41	29	13	8	0	—	—	—	130
2	—	5	6	48	41	16	8	7	3	6	140
3	—	6	4	20	13	34	12	—	—	—	89
4	—	—	—	—	108	29	—	—	—	—	137
5	—	—	—	—	148	—	64	4	—	—	216
7	—	—	42	60	51	59	56	36	18	—	322
8	—	—	—	26	—	—	—	—	—	—	26
9	14	2	—	—	—	—	—	—	—	—	16
10	—	—	—	23	—	—	—	—	—	—	23
11	—	37	37	70	87	61	29	—	12	—	333
total	14	89	130	276	461	207	169	47	33	6	1432

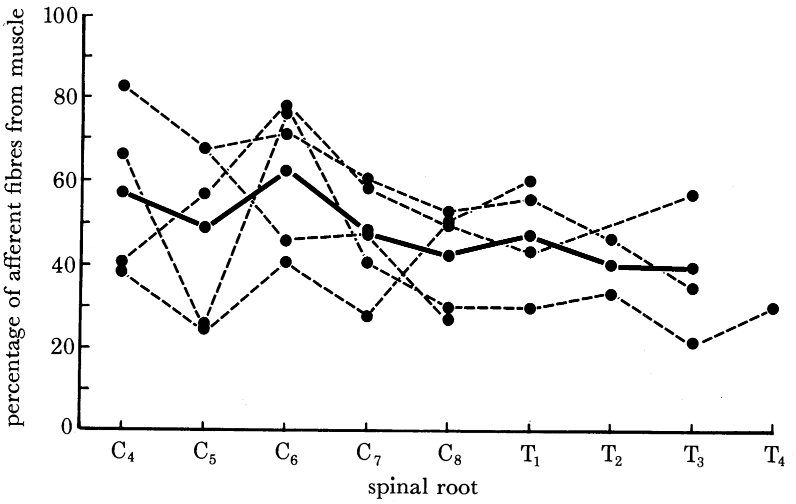


Figure 10. The proportion of afferent fibres serving muscles varied among the spinal roots. The mean (——) was highest at C_6 but there were wide fluctuations in different animals (----), making generalizations difficult.

Patterns of innervation

Figure 11 illustrates the muscle afferent fibres obtained from monkey 11. The peripheral distributions of these fibres, in sum, represent the distribution of the myotomes of the spinal nerves contributing to the brachial plexus. Each pair of figures shows the muscles served by one dorsal spinal root. From any one spinal root seldom were there more than 12 afferent fibres serving any single muscle. Generally, however, one muscle was innervated by several roots and one spinal root served a number of muscles. Figure 11 shows that there is a regular progression to the patterns of innervation of this animal, the fourth cervical nerve innervated the musculature of the neck and suprascapular region; the fifth cervical nerve innervated the muscles of the shoulder girdle; and the sixth innervated the shoulder girdle and upper arm. The following figures illustrate the innervation pattern for the subsequent nerve roots; the forearm and hand were innervated by C_7 and C_8, and T_1, T_2 and T_3 served regions located progressively more proximal on the arm until, for T_3, again the region of innervation was limited to the torso.

The relationship of the dermatome to the afferent myotome

In contrast to the distribution of the dermatomes, where the entire region served by a particular spinal nerve might be located distally on the limb and completely separated from the trunk, for each myotome there were always a few fibres of each spinal root that innervated trunk muscles; each afferent myotome remained in continuity with the trunk.

Also, afferent myotomes appeared wider than the corresponding dermatomes; the same spinal nerve that served the biceps might also serve the triceps or serve both the forearm extensors and flexors simultaneously. This contrasts with the dermatomal pattern, where a nerve serving pre-axial or radial skin area seldom served the post-axial or ulnar region simultaneously.

A particularly important relationship is that existing between the dermatome and myotome of the same spinal root. The distribution of the afferent myotome could not be predicted from the distribution of the dermatome of the same nerve. Figure 12 illustrates the dermatome and myotome of spinal nerve C_7 of animal 5. This dermatome served the skin of the pre-axial upper arm, forearm and first three digits of the hand, covering the pre-axial musculature of the biceps, brachioradialis, forearm extensors and some of the intrinsic muscles of the hand. However, instead of serving the underlying muscles, the myotome for the seventh spinal nerve consisted of fibres serving the post-axial musculature and musculature of the lower part of the shoulder girdle. The only regions where the skin innervated by C_7 overlaid the muscles served by C_7 was in the region of the forearm extensors. And, even in this region, the forearm extensors were only partially innervated by C_7; the distal portions of these muscles were innervated by C_6.

Figure 12*b* illustrates the dermatome and afferent myotome of T_1 in another animal. Again the dermatome was positioned over only a few of the muscles served by T_1; the dermatome of T_1 served the post-axial skin of the upper arm, and forearm. It also covered the fifth and half of the fourth digit, but notably did not reach the midline of the torso. In contrast, the myotome of T_1 innervated the lower portion of the pectoralis, the forearm flexors, and the upper end of the forearm extensors, the triceps, the serratus anterior and the teres major. Only the forearm flexors, forearm extensors and the triceps were located beneath skin served by the same spinal nerves. Similar results were observed in nearly every case where the dermatome and myotome of a given spinal nerve were compared. Generally the afferent myotome served a wider region than the dermatome. However, this greater extent was not sufficient to account for the discrepancy between dermatomal and myotomal boundaries. In many instances one was displaced from the other. The distance by which the myotomal boundary was separated from the dermatomal boundary seemed to be related to the body region innervated by that spinal root; those nerves serving either skin or muscle in the hand or forearm were the nerves most likely to have myotomes and dermatomes with a large discrepancy in their respective boundaries.

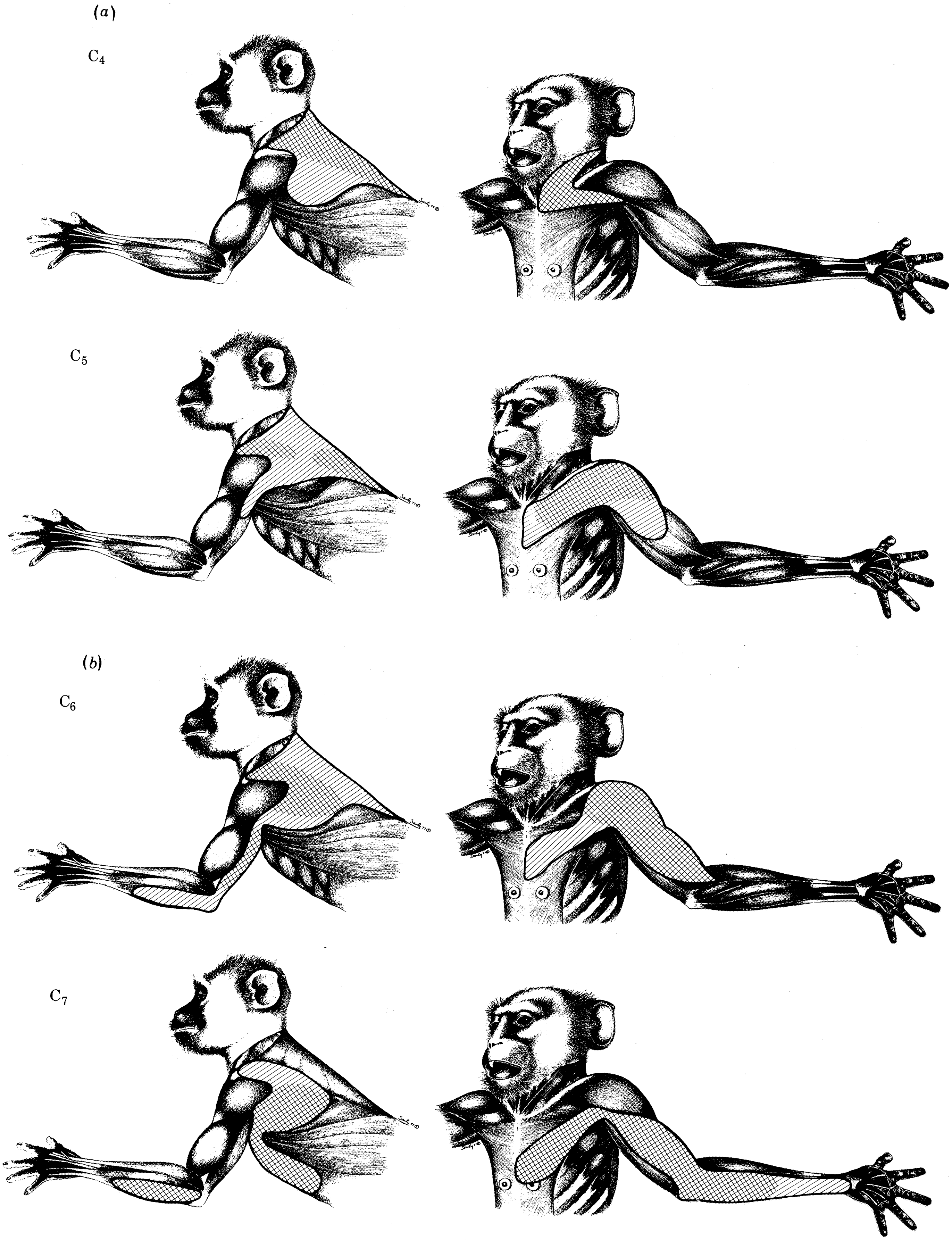


FIGURE 11. For description see opposite.

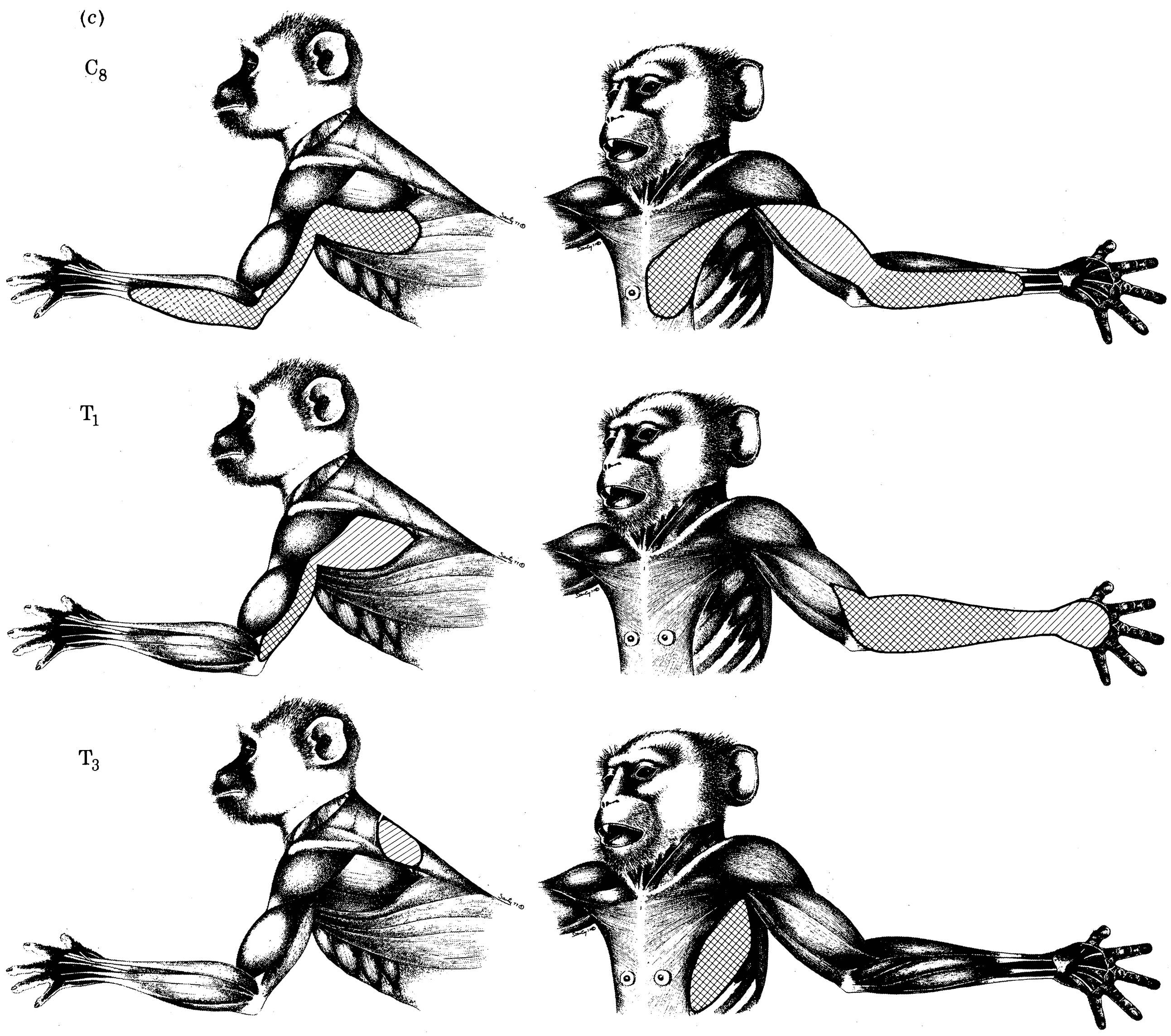


FIGURE 11. The pattern of muscle innervation by afferent fibres of successive spinal roots is displayed for animal 11. The region served by each nerve is a white area outlined in black. The area with the highest innervation density is doubly cross-hatched. Regions containing fewer endings of afferent fibres are only singly cross-hatched.

Multiple innervation of specific muscles

The afferent fibres from one spinal nerve served a large number of muscles. Conversely, any one muscle was innervated by a large number of different spinal roots. Figure 13 illustrates this phenomenon for three different muscle groups in animal 7. Figure 13*a* shows the innervation of both heads of the biceps. In this example, C_5 provided only one afferent fibre to the biceps, C_6 provided 21, C_7 provided 12 and C_8 provided 4. Figure 13*b* illustrates the same phenomenon for the triceps. In this case, C_7, C_8, T_1 and T_2 provided the innervation of the triceps and the heaviest contribution came from C_8 and T_1. Figure 13*c* illustrates the multiple innervation of the extensors of the forearm, by C_7, C_8, T_1, and T_2.


(a)
C7
C7

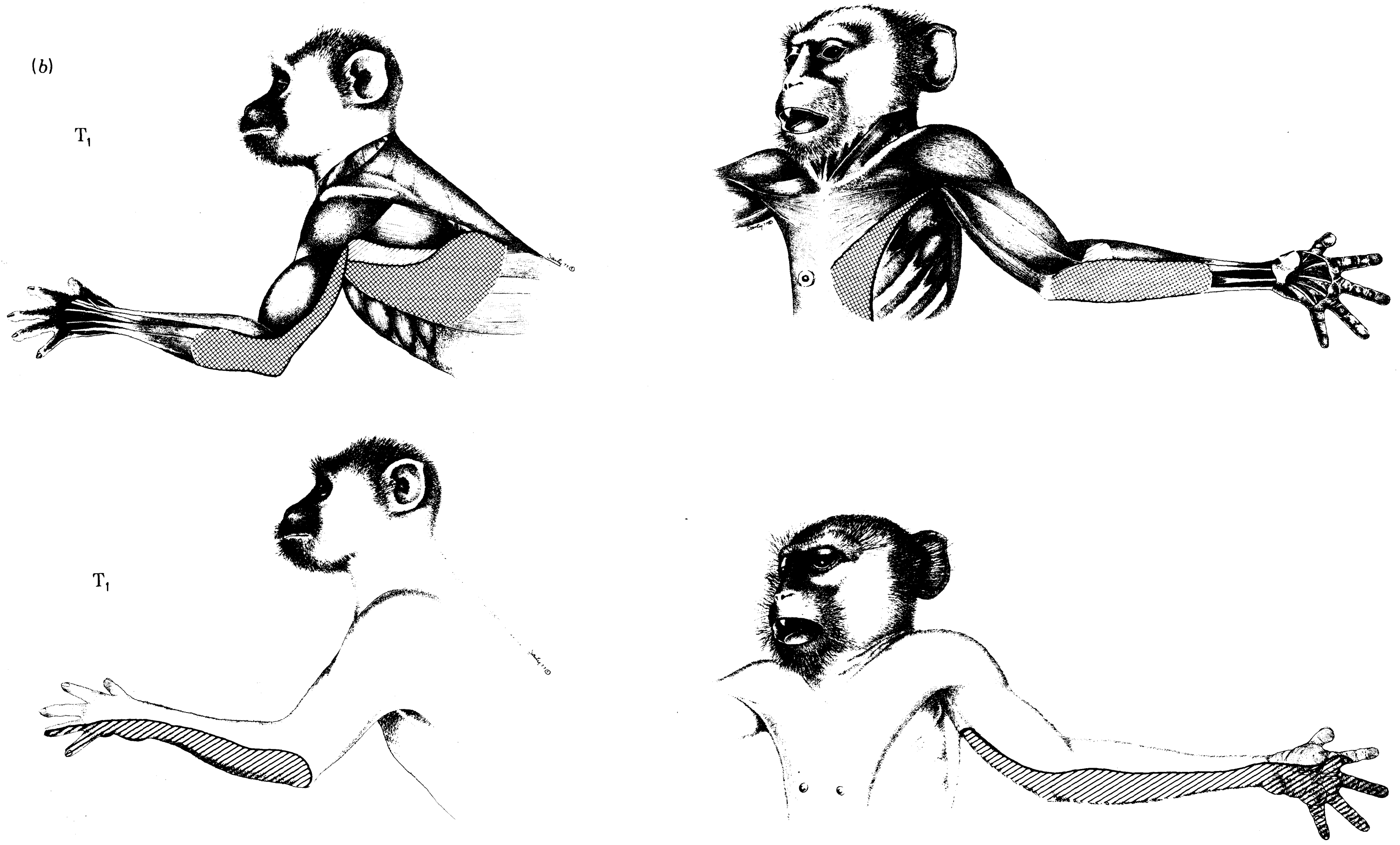
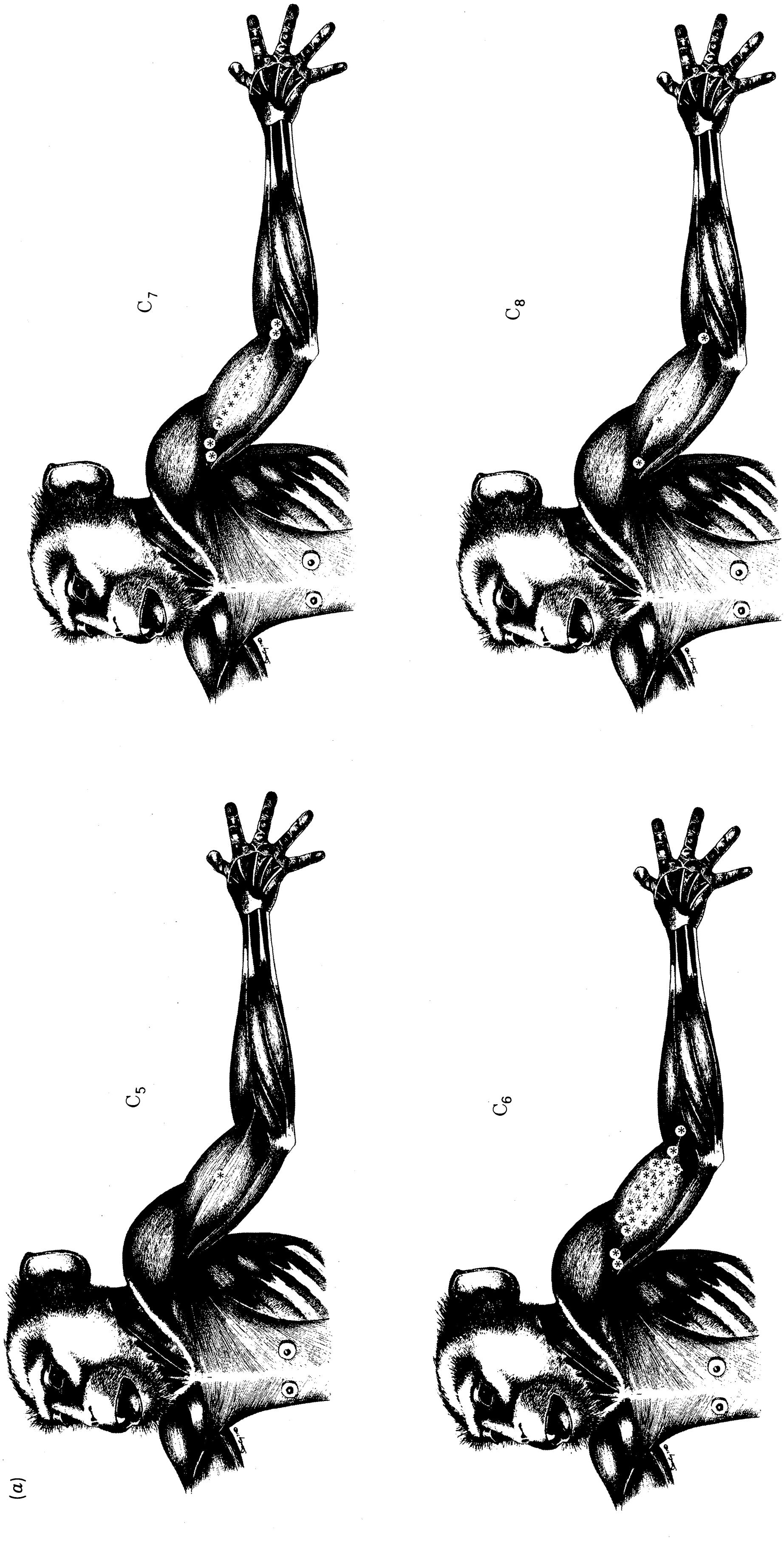


FIGURE 12. The dermatome and myotome for the same spinal nerve in the same animal are compared. Generally the myotome extended over a greater area than the dermatome: the dermatome could be separated from the midline but the myotome always served some of the midline musculature. (*a*) The myotome and dermatome of C_7 spinal nerve for animal M_5. (*b*) The myotome and dermatome for T_1 in the same animal.


(a)
C_5
C_6
C_7
C_8

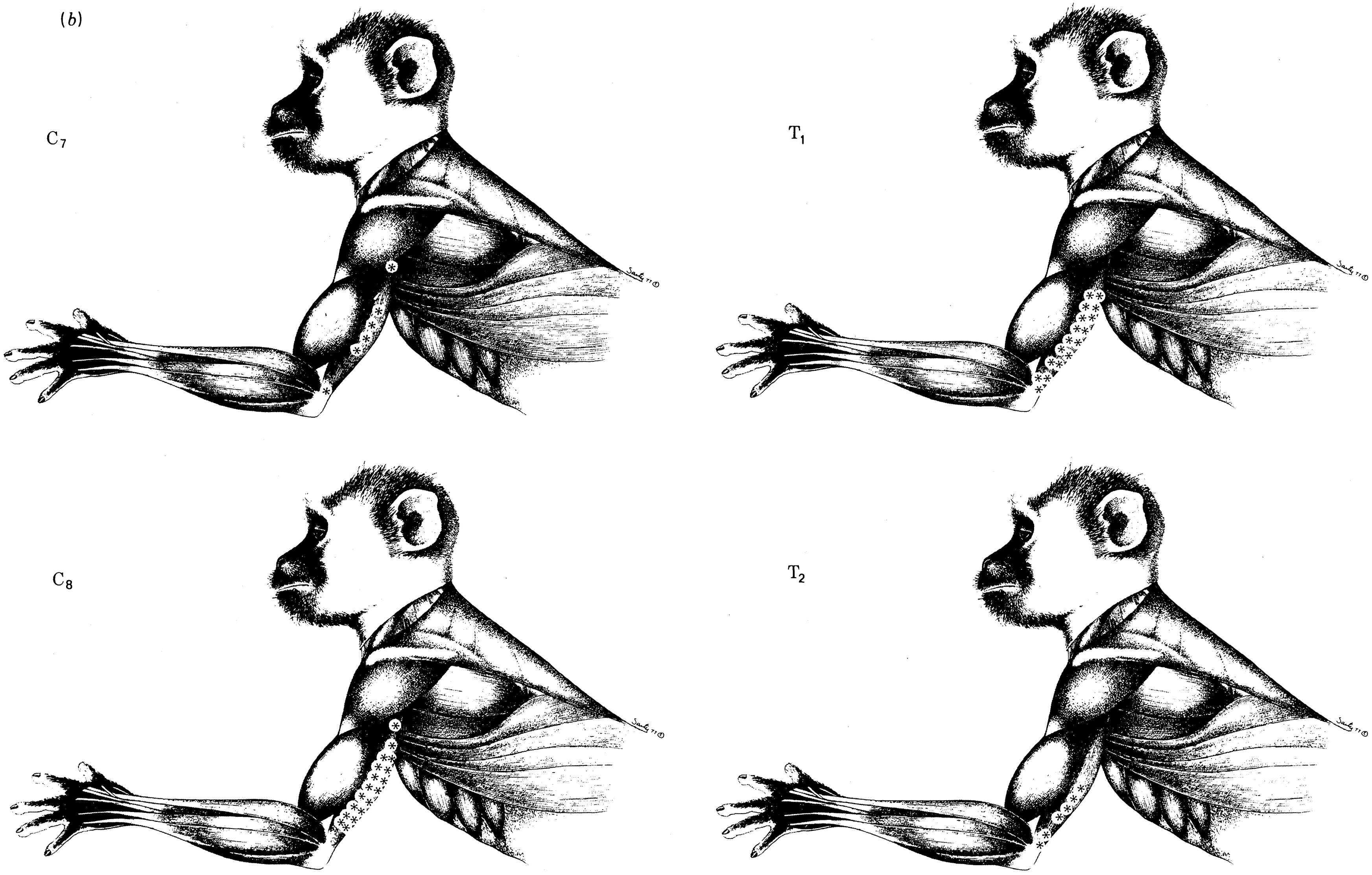


FIGURE 13*b*. For description see p. 536.

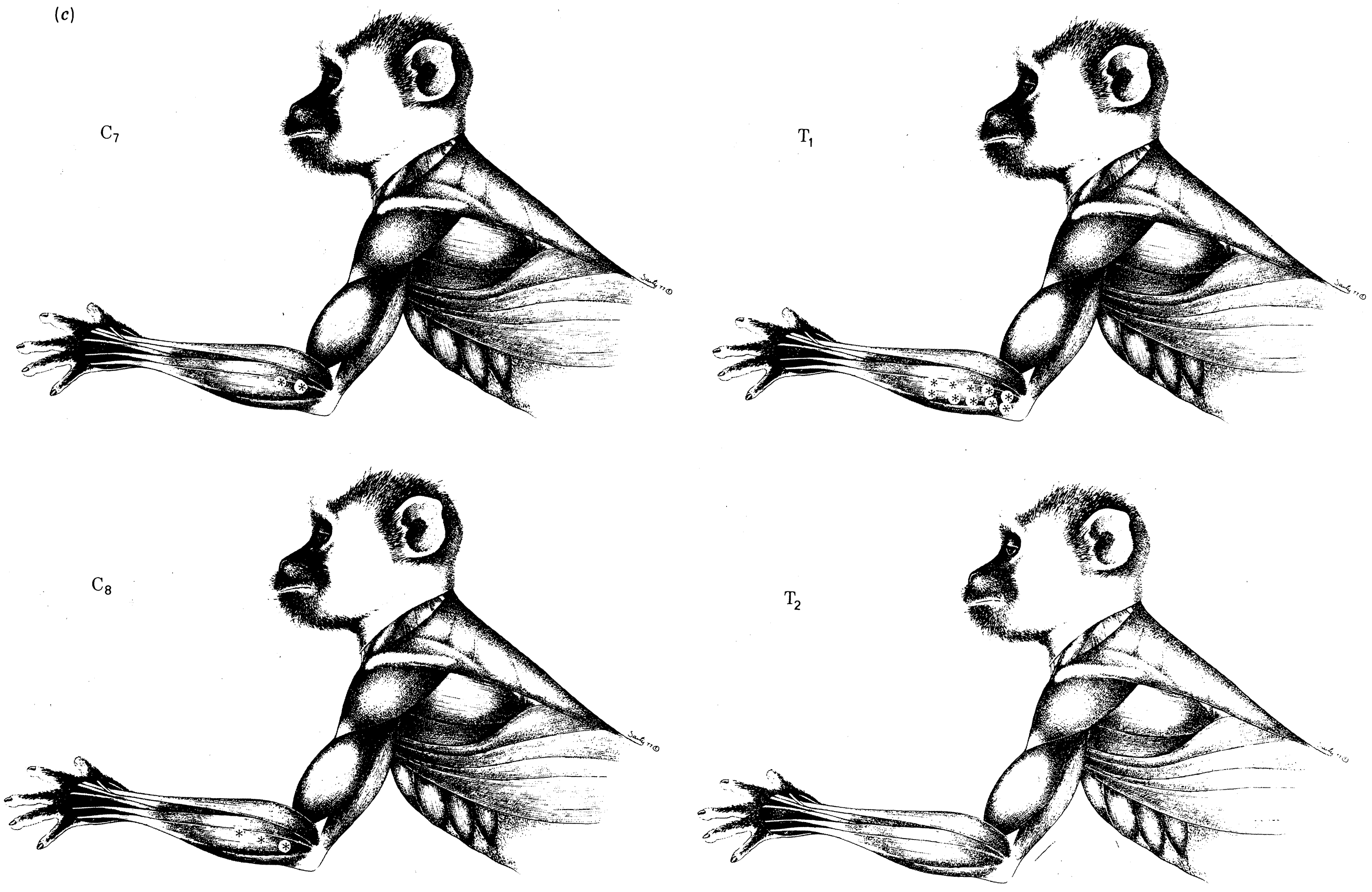


FIGURE 13. Most muscles received afferent fibres from several spinal nerves. In animal 7 this multiple innervation is illustrated for (a) the biceps, (b) the triceps, and (c) the forearm extensors.

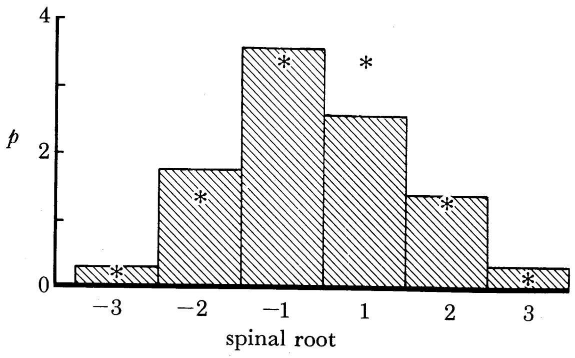
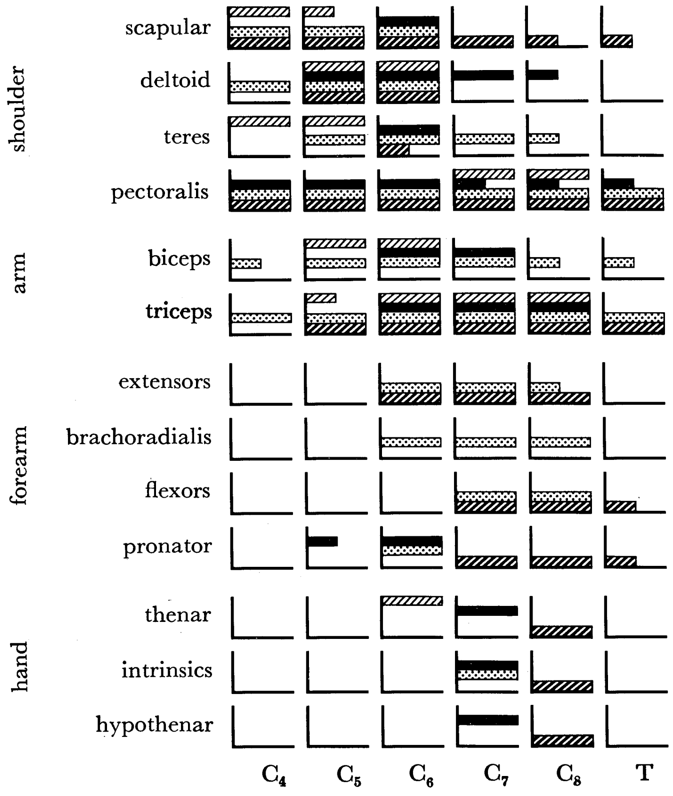


FIGURE 14. The probability of occurrence of afferent fibres in roots adjacent to the major innervation of either the triceps or the biceps. Adjacent roots contained decreasing numbers of fibres. The asterisks indicate the values of a histogram based on the normal distribution. These values produced a histogram not significantly different from the one obtained from the actual data (χ^2 test) and thus suggest that the distribution of innervation for these muscles is adequately described by a normal distribution.

TABLE 4. AFFERENT SUPPLY TO MAJOR MUSCLE GROUPS IN FOUR ANIMALS



Despite this widespread distribution, there was a focus to the innervation of most muscles so that the predominate innervation of any one muscle came from one or at most two spinal nerves. For example, even though the biceps or triceps were each innervated by afferents from five or six spinal nerves, the predominant contribution was only from one nerve and the magnitude of the contribution from adjacent nerves was smaller. This was so for most muscles;

only an occasional muscle is served almost equally by two adjacent spinal nerves. This distribution was described by combining data from several animals.

Figure 14 illustrates the probability of occurrence of afferent fibres in spinal roots adjacent to the root primarily responsible for serving either the triceps or biceps. Usually five or six roots served each of these muscles and an occasional fibre was found as far as four roots away from the principal root. The data were taken from eight animals in which sampling occurred in at least three roots above and below the principal root to the triceps or biceps. The distribution of the fibres serving these two muscles is approximated by a normal distribution ($p < 0.01$) and each successive spinal root is about one standard deviation further from the centre; the sample from three spinal roots contains about 65% of the fibres and five spinal roots contain 97% of the sample. The breadth of this distribution (standard deviation) depended on the location of the muscles. The number of spinal roots that provided afferent fibres to a muscle decreased in more distal muscles in the limb. Muscles of the shoulder girdle were often served by all the nerves of the brachial plexus while the intrinsic muscles of the hand were often served by only one spinal root. This point is apparent from table 4, which shows the source of innervation for selected muscles of the limb in four different animals. The muscles of the shoulder are innervated by the majority of the nerves in the brachial plexus. In the forearm the average number of spinal nerves innervating a muscle is three, and in the hand generally only one spinal nerve innervates all of the muscles in any given individual.

The variable distribution of the myotome

Table 4 also documents the remarkable degree to which innervation patterns are unique to the individual. This is seen most clearly in the muscles of the hand. It is apparent that these muscles are served by only one spinal nerve, but in different individuals this may be cervical nerve 6, 7 or 8.

With the hand innervation as a reference, it can be seen that there is a pattern to the innervation of each individual. The first animal appears prefixed in all muscle groups while the fourth animal appears postfixed.

Figure 15 provides more details of this individuality for the muscles innervated by C_5 in three individuals. In the first animal (figure 15*a*), the biceps were the focus of innervation; the deltoid and forearm flexors were only lightly innervated. In the second animal (figure 15*b*), innervation was approximately evenly distributed around the shoulder girdle. Only one afferent fibre was located in the scapular origin of the biceps. In the third animal (figure 15*c*), the pectoralis received the major innervation with lighter innervation of the deltoid and biceps. Such variability was a consistent finding throughout our experiments; the region of major innervation by a particular spinal nerve could differ widely in both location and function from one animal to the next.

Size of the myotome

The size of the myotome varied with the position of its nerve in the brachial plexus. Those dorsal roots at the upper and lower ends of the plexus served muscles over an area smaller than the area served by the myotomes of the midportion of the plexus. In the centre of the plexus the spinal roots served muscles throughout a large portion of the arm. Figure 16 shows the C_7 myotome in animal 5 as an example. This myotome was one from the centre of the plexus and contained afferent fibres from muscles over most of the forearm. The area covered

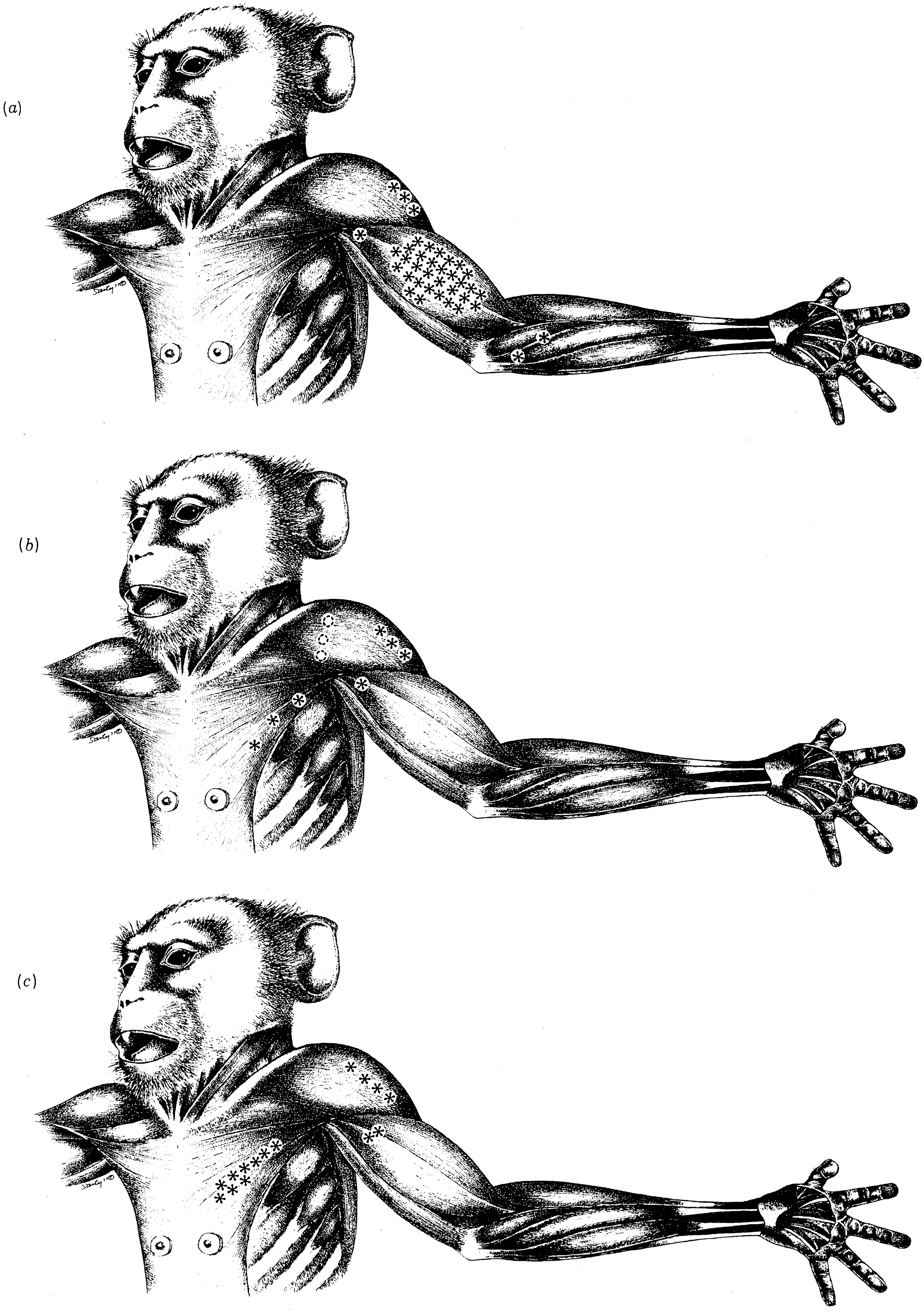


FIGURE 15. Variability in the muscles innervated by a particular spinal nerve was not limited to those nerves serving the forearm and hand. Even spinal nerves serving axial muscles displayed variability. Displayed are three examples of the muscles served by the C_5 spinal nerve.

and the number of muscles served by this myotome are in striking contrast to the C_7 afferent myotome innervating the shoulder of the same animal (figure 15*c*).

Partially shifting overlap of the myotomes

One of the classic concepts of dermatomal organization is the idea of the overlapping nerve territories that shift progressively more caudally with successively lower spinal nerves (Sherrington 1893). Since the afferent myotomes are located in such disparate regions in different animals (figure 15) and since the focus of the myotomal innervation is not necessarily coincident with the dermatome (Figure 12), it is not logically necessary that the myotomes show the same progression of innervation across the body that is characteristic of the dermatome. However, the data on muscle afferents show evidence of the same partially shifted overlap for muscle innervation that is characteristic of the dermatomes. The pattern is less apparent because the myotomes have a wider distribution than the dermatomes and their boundaries are often indistinct because they include elongated muscles that may be only partially innervated by one spinal nerve. However, an attempt was made in figure 17 to provide an example of the partially shifted overlap for afferent myotomes. The regions of innervation have been shaded to emphasize the territory of each spinal root. Within this territory some muscles received heavier innervation than others, but these variations have been ignored in this summary figure, which attempts to show the general pattern.

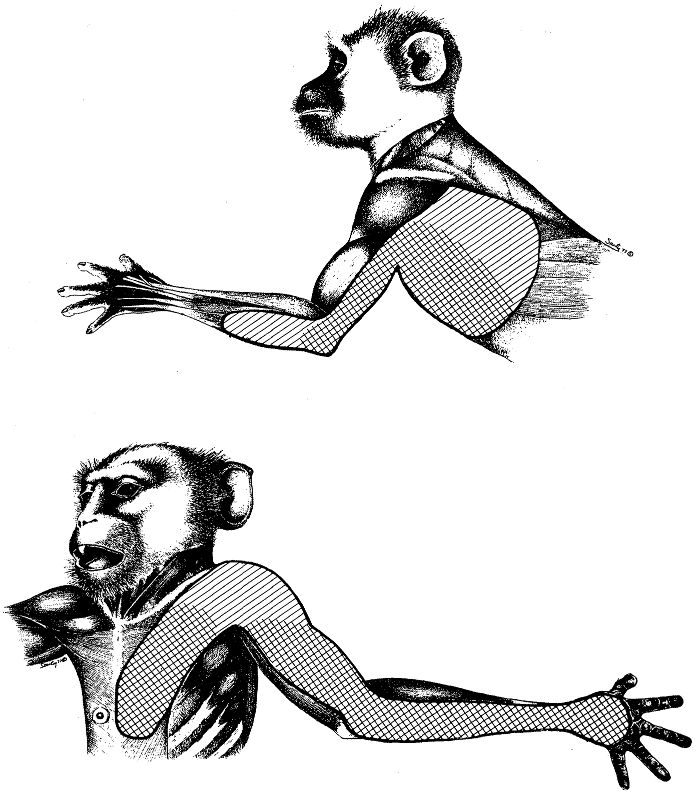


FIGURE 16. The variation in the size of the myotome is emphasized by the C_7 myotome, which innervated axial musculature, arm and forearm. This contrasts with the more limited region served by C_5 shown in figure 8.

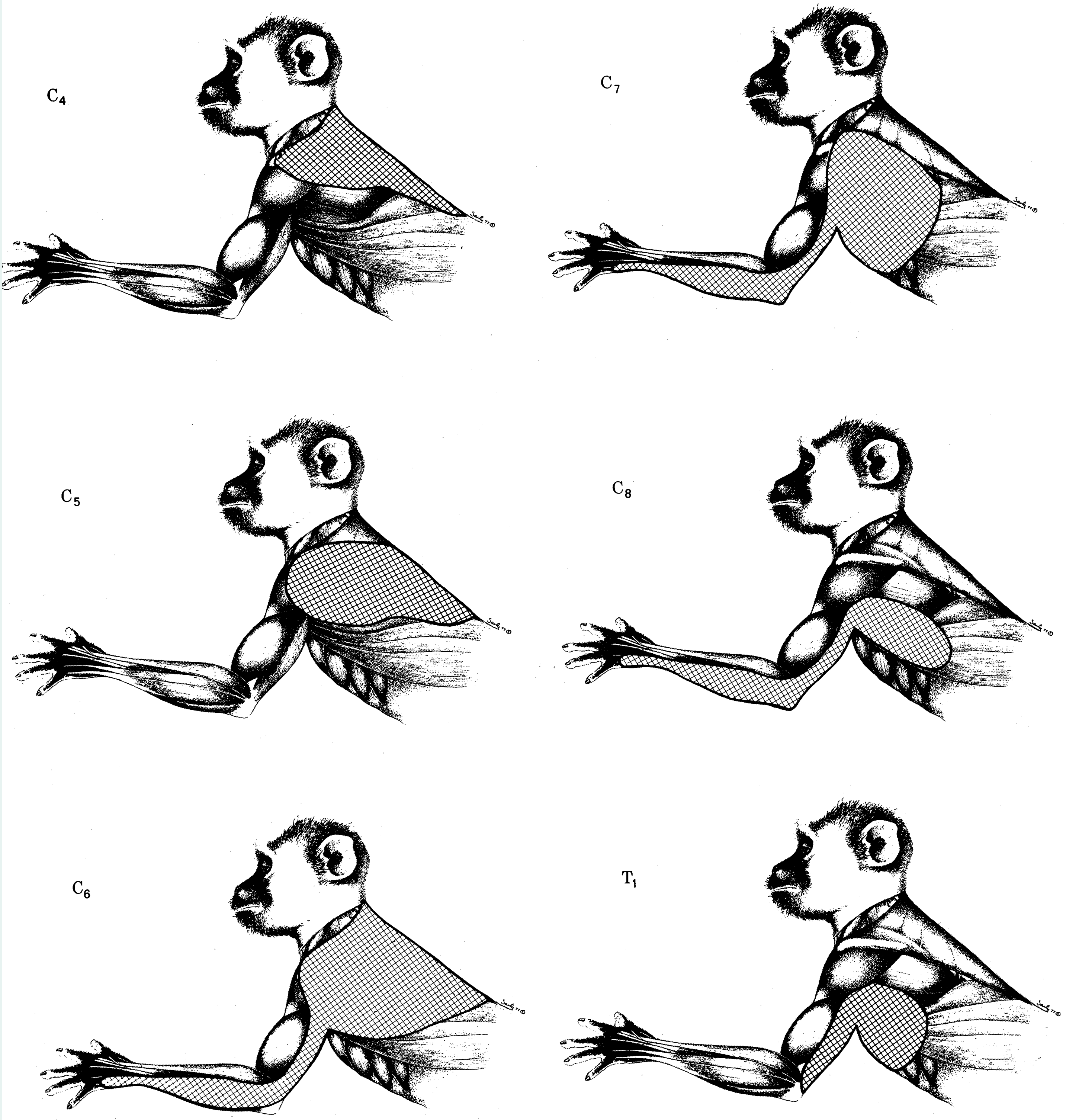


FIGURE 17. The Sherringtonian partially shifted overlap is present in muscle innervation also. The large area served by each afferent myotome makes this more difficult to visualize, but inspection of the juxtaposed figures displaying the innervation of spinal nerves in this animal provides evidence for a regular progression from C_4 to T_1.

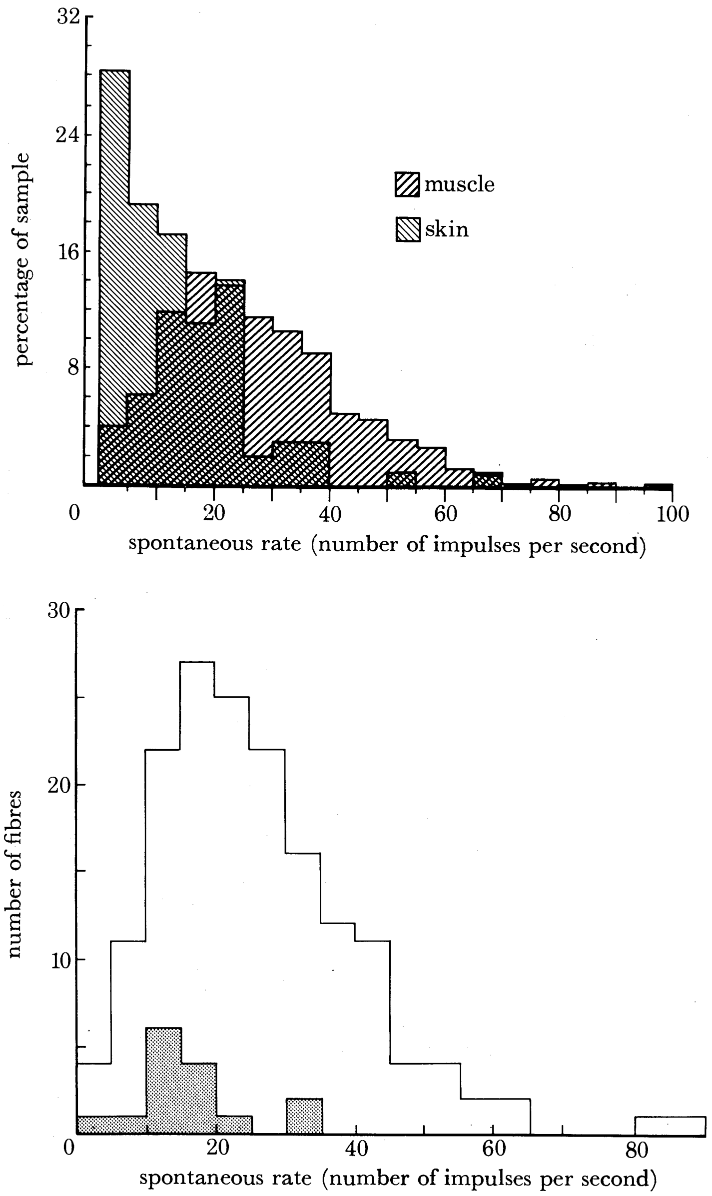


FIGURE 18. (*a*) Spontaneous activity was much more common in muscle afferents than in afferents from skin. Further, the mean discharge rate from active muscle afferents was higher than that from cutaneous afferents. (*b*) The muscle afferents from the intrinsic muscles of the hand (shaded histogram) has a significantly lower ($p < 0.05$) mean rate than active fibres from the biceps and triceps.

It is also apparent from this figure as well as from figure 11 that there is overlap of successive myotomes from at least three adjacent spinal roots and generally from four. For paraspinal muscles, the scapular muscles, the triceps, the forearm extensors and the muscles over the posterior trunk, the overlap is at least four spinal roots.

Spontaneous activity of afferent fibres serving muscles

Spontaneous discharges were much more common in afferent fibres serving muscle than in fibres serving skin. For those fibres in which the relevant data were collected, 83% of the afferent fibres from muscle (736 of 888 fibres) had a spontaneous rate greater than one impulse per second while only 27.1% of the fibres from skin (99 of 365 fibres) were spontaneously active. Also, the mean discharge rate was significantly higher in the spontaneously active muscle afferent fibres than in spontaneously active fibres from skin (figure 18*a*); the rate for skin was 14.3 impulses per second (s.e. = 1.6) whereas for muscle it was 28.4 impulses per second (s.e. = 0.6).

Upon inspection of the spontaneous activity arising from different muscles, it was noted that the intrinsic muscles of the hand had significantly lower spontaneous rates of discharge than had the afferent fibres serving the biceps and triceps (29.4 and 22.4 compared with 16.3 impulses per second; $p < 0.05$; figure 18*b*). No other muscle group could be shown to have spontaneous rates different from the average, nor did the proportion of spontaneously active muscle afferent fibres vary significantly among the different muscle groups studied. Since the muscles were essentially deafferented by the dissection procedure and were essentially flaccid under the barbiturate anaesthesia, it is doubtful that these differences are due to limb position or to tonic gamma-fibre activity.

Discussion

Historical perspective: the dermatome

For more than a century scientists have attempted to define the region served by one spinal nerve. In these experiments the afferent distribution has been studied more consistently than has the efferent distribution. However, even for the distribution of the cutaneous afferent regions served by one nerve, the results have been clearly inconsistent. A brief history of previous experiments on dermatomal organization and muscle innervation follows. It emphasizes the recurring lack of consensus about the size and location of specific dermatomes. Since some of the discrepancies appear to be attributable to the methods used to define the dermatome, they will be listed at the outset. Most of these methods have been used since the late 19th century or early twentieth century (cf. Foerster 1933).

(i) *Anatomical dissection* of the distribution of a spinal nerve is the oldest procedure used. It is of limited value for studying nerve plexuses and the finer branches of nerves since only gross patterns can be deduced. Sherrington (1893), however, credits Herringham (1887) with gaining major insight into the pattern of dermatomal distribution in the upper limb from a series of careful anatomical dissections.

(ii) *Degeneration methods* require cutting of one spinal root and checking of peripheral nerves four to five weeks later for degenerated axons. This method can be used to follow minor contributions through a plexus. In 1865, Krause, and, in 1869 Meyer used these methods to define areas served by one spinal root (cf. Sherrington 1893).

(iii) *The zone of remaining sensibility* was introduced by Peyer to map the cervical roots in rabbits in 1854 (cf. Sherrington 1893). This method requires surgical transection of the roots above and below the one under study to produce an island of remaining sensibility. The boundaries of this island are defined by watching for a behavioural response when that area is stimulated (Foerster 1933; Sherrington 1893, 1898). It appears that animals consistently orient to tactile as well as noxious stimuli.

(iv) *Strychnine application*. When applied to the posterior roots strychnine produces an area of hypoaesthesia similar to the zone of remaining sensibility. Again reflex responses are recorded.

(v) *Herpes zoster eruptions* can be informative when herpes viruses afflict single dorsal root ganglia. The virus particles are transported to the skin, where they produce cutaneous eruptions that, at least in part, outline the area of the dermatome (Head 1920).

(vi) *Faradic stimulation* was used by Foerster (1933). High frequency electrical stimuli applied to the distal end of a divided root produce cutaneous vasodilation by a mechanism still unclear today. This area is assumed to be coextensive with the dermatome.

(vii) *Ruptured intervertebral discs*. The central pulp of the intervertebral disc may be ejected through the vertebral ligaments to press upon a single spinal root. The resulting pressure may cause a partial or complete block of that spinal nerve, resulting in an area of hypoaesthesia, which can be detected by careful testing in a cooperative patient (Spurling & Scoville 1944; Keegan 1943; Keegan & Garrett 1948; Davis *et al.* 1952).

(viii) *Multi-unit recording of rootlets*. More recently electrophysiological methods have been used to record multi-fibre activity from individual rootlets of one spinal nerve. The area served by each rootlet is obtained by stroking the skin and recording those areas that cause neural activity. The dermatome is the sum of the areas obtained by recording from all of the rootlets (Fletcher & Kitchell 1966; Hekmatpanah 1961; Kuhn 1953).

(ix) *Single fibre recordings*. With microelectrodes or single fibre dissection methods, action potentials of individual fibres can be recorded at the root entry zone. The area encompassing all of their receptive fields is the dermatome (Pubols *et al.* 1965; Pubols & Pubols 1969; Brown & Koerber 1978).

The use of the *method of remaining sensibility* as the method of choice for obtaining dermatomal maps has resulted in the emphasis being placed upon the cutaneous distribution of spinal nerves. This method depends upon the observation of behaviours indicating stimulus detection when tactile stimuli are applied to an island of innervated skin and obviously provides little information about subcutaneous or muscle innervation. Sherrington popularized this method in his classic studies of 1893 and 1898, and Sir Henry Head provided the eponym that it carries today. Sherrington (1893) acknowledged the work of Turck in 1856, published posthumously in 1869, describing experiments in which Turck sectioned one spinal root in dogs and looked for an area of hypoaesthesia. His dermatomes, drawn as bands around the limb, provided Sherrington with the idea that possibly some dermatomes became separated from the midline as the limb bud developed in the embryo. Turck also noted a large degree of individual variability, a fact that has been lost in modern descriptions of the dermatome.

Using degeneration methods, Meyer found dermatomal overlap in 1869 and suggested that any skin region was served by at least two spinal nerves. In 1868 Koschewnikoff made similar observations using the method of remaining sensibility and noted the marked variation in innervation patterns among individuals (cf. Sherrington 1893).

Thorburn (1889) collected and reviewed the nineteenth century clinical data, but the major work on the dermatome in primates consisted of Sherrington's two papers (1893, 1898) on the spinal nerves of the upper and lower limbs. In fact, the general ideas in the clinical literature today were first observed in frogs. In his first paper Sherrington reviewed the literature, described his methods and reported some preliminary experiments on several dozen decerebrate frogs wherein he elucidated the major principles of dermatomal organization as they exist today. He observed that: (i) the field of one root is continuous; (ii) adjacent nerves overlap extensively (he later estimated three nerves overlap any one point); (iii) the dermatomes meet at the dorsal and ventral midline but overlap there is limited; (iv) the front (posterior) side of the limb is served by more rostral spinal nerves than the back; (v) the distribution of nerve fibres is less abundant near the edge of the dermatome than in the centre. In 1893 he coined the terms prefixed and postfixed to describe variations in the spinal root pattern contributing to the brachial plexus.

Then, in two series of experiments on both cats ($n = 29$) and monkeys (*Macaca rhesus* and *Macaca speciosus*; $n = 21$), Sherrington found essentially the same general principles of organization that he first saw in frogs. His 1893 paper included a map of the dermatomes of the lower leg of monkey, with comments in the text indicating that there is significant variability among individuals.

In 1898, Sherrington published his dermatomal map of the upper limb of the monkey. There had been no previous work on the nerves of the upper limb of monkeys, and Sherrington's paper is still the only major experimental study. He examined each spinal nerve in 2–4 animals. He described and tabulated the skin and the muscle distribution of each nerve, and noted that both were variable. Sherrington showed results similar to those that he reported for the lower limb, including an overlap of about three spinal nerves, a variability of the dermatomal distribution, a different location for the motor and sensory areas, and the distortion of the essentially metameric organization of the torso by the embryonic growth of the limbs. In both papers, however, Sherrington's summary diagrams did not indicate the degree of variation among individuals that he noted in the text; each of his figures depicted a typical case whose demarcations had sharp boundaries with long continuous contours. It is the ideas expressed in those summary diagrams that are still seen in the figures reproduced in textbooks today (Gray 1965; Netter 1962; Anderson 1978).

In 1920 Head presented the first map of the dermatomes in man. This diagram was a composite of the skin regions affected by herpes zoster in a large clinical series. The boundaries of Head's dermatomes obtained in this way were more irregular and wider than those of Sherrington. In many cases they did not reach the midline. Since there was no *a priori* reason to expect every neuron of a ganglion to be infected or to produce viral eruptions within its skin field, these dermatomes were given less credence than those obtained by the method of remaining sensibility.

In 1933 a chart obtained by the method of remaining sensibility was published for man. Foerster (1933) sectioned various spinal roots in man for the relief of pain and deduced dermatomal boundaries for the nerves of the upper limb. His data were extensive (93 published examples) and led to several general conclusions: (i) the dermatomes in man overlap as do those in monkey; (ii) tactile dermatomes are larger than those for temperature and pain; (iii) vasodilation following stimulation of the sectioned nerve showed a similar but not identical distribution to the tactile dermatome reported by the patient before section; (iv) each rootlet encompassed the whole dermatome. Foerster said that it was possible to section as many as two-thirds of the rootlets of one spinal nerve without sensory loss in the dermatomal area.

Although the dermatomal charts presented by Sherrington, Head and Foerster all differ, these three charts remained in the literature without challenge until 1943, when Keegan first published a map of dermatomes obtained by mapping the area of hypoaesthesia found subsequent to rupture of an intervertebral disc in patients. His chart showed long, narrow dermatomal lines for nerves S_5 through L_1 stretching from midline to periphery of the lower limb. Although Keegan (1943) reported 185 cases, 90 of which were said to be verified by surgery, he provided no illustrations of the actual data nor any case histories. He noted that it was not always possible to map the complete dermatome because 'nerve-root function is not completely interrupted'. However, he gave no indication of how it is possible, in a specific situation, to ascertain whether or not the dermatome mapped was the entire distribution of the affected nerve.

Although Keegan's aesthetically pleasing charts have remained in textbooks until today (Netter 1962; Anderson 1978), even in the 1940s there was evidence that the dermatomal pattern was not as clear as his published figures suggested. First, Keegan's dermatomes contradicted the patterns presented by Head (1920), Foerster (1933) and Sherrington (1893, 1898). Secondly, both Semmes & Murphy (1943; four cases) and Michelsen & Mexter (1944; eight cases) reported that the rupture of a disc produced zones of hypoaesthesia that did not extend over the entire limb but were localized generally in the extremity, and that the location affected by a particular disc was quite variable.

By 1948, Keegan & Garrett (1948) reported that they had collected 1264 cases of root compression in the lower limb and 165 cases in the upper limb. Of these 754 were shown by surgical means to be related to a compressed nerve. In addition, Keegan (1947) had performed ten anaesthetic blocks of a given cervical nerve that were verified by X-rays. Of these numerous cases only 12 examples of lower limb dermatomes and nine of the upper extremity were ever published.

In none of his publications did Keegan discuss the problem of variability between individuals except to report that the area served by a spinal nerve is highly reproducible and did not vary by more than a centimetre, nor did he discuss how he excluded those cases with incomplete nerve block that 'may show hyposensitivity only in the more distal portion of the limb' (Keegan & Garrett 1948).

In 1952 Davis *et al.* presented more data contradicting the idea that dermatomal maps are highly regular narrow bands stretching out from the midline; in a series of 500 patients they found no correlation between the level of a ruptured intervertebral disc and the pattern of sensory alteration.

The role of spinal inhibition

In addition to giving an incorrect impression of uniformity, our present conception of the dermatome is distorted by neglecting neural mechanisms residing in the spinal cord. Denny-Brown and his colleagues (Kirk & Denny-Brown 1970; Denny-Brown *et al.* 1973) demonstrated the effect of spinal inhibitory mechanisms by repeating Sherrington's monkey experiments, exposing seven spinal roots and sectioning three above and three below the one being investigated. When tested behaviourally, the resulting dermatomes were very stable; the borders remained within ± 1–2 mm for several months. However, if two additional roots on each side of the isolated root were cut, the dermatomal area increased to a new stable size nearly twice its previous size. Thus, the size of an isolated dermatome from which reflexes can be elicited is not entirely determined by anatomy, but is due in part to a prolonged, stable influence from adjacent portions of the spinal cord.

With additional lesions of the spinal cord or spinal roots, Denny-Brown *et al.* (1973) showed that each point on the skin is represented in at least five spinal roots, and that the effect of input from one spinal root is conveyed up and down the cord in Lissauer's tract for five or more segments. These experiments imply that any dermatomal map that relies on behavioural measures will be influenced by the inhibitory mechanisms of the spinal cord. To avoid this effect the distribution of one spinal root must be assessed before it reaches the dorsal horn. Thus, only electrophysiological methods can obtain undistorted information concerning the distribution of spinal nerves.

The discovery of the suppressive effects of spinal mechanisms does not invalidate previous observations. It does, however, change some of the conclusions drawn from the data. Since the effective locus is less than the entire dermatome, the behaviourally obtained dermatome may actually provide a better clinical indicator of the locus of a lesion than would a map of the full extent of the dermatome. However, since such an area is only part of the entire dermatome, other techniques must be used to define its full extent. Input from this undisclosed portion of the dermatome, which appears not to be available to consciousness, may play a role in phenomena such as paraesthesia, phantom limb pain, acupuncture and electroanalgesia. In this context it is important to mention that (i) the small myelinated fibres may play an important role in these mechanisms and (ii) no dermatomal maps have ever been created for the small myelinated fibres and so it is impossible to describe their spatial relationship to the dermatome of the larger myelinated fibres.

There are only a few electrophysiological studies of dermatomes. All but one of these (Inouye & Buchthal 1977) have been performed on subhuman mammals by means of either gross electrodes (Fletcher & Kitchell 1966; Hekmatpanah 1961; Kuhn 1953) or microelectrodes (Pubols *et al.* 1965; Pubols & Pubols 1969; Brown & Koerber 1978). Kuhn (1953) used evoked potentials to investigate the cutaneous regions served by single filaments of the lumbosacral dorsal roots of cats and monkeys. He reported that the skin areas served by individual rootlets were arranged in an orderly sequence within the dermatome in a pattern resembling the shifting overlap noticed by others for whole dermatomes. He also reported that some spinal root filaments had little skin representation but could be activated by stimulating muscle or joints. Each cutaneous field had a central area producing a strong response and a peripheral zone yielding weaker responses. The degree of overlap was up to four dermatomes in the cat but the data for monkey showed little overlap. Inouye & Buchthal (1977) showed in man that stimulation of a single digit evoked activity in four spinal nerves and thus that overlap in this primate can extend over at least four roots. The location of dermatomal borders was noted to vary between individuals for cats and monkeys (Kuhn 1953) and also man (Inouye & Buchthal 1977).

A study of the dermatomes C_1 through C_4 in the cat (Hekmatpanah 1961) by similar methods produced comparable results for the upper part of the body. The degree of overlap again was noted to be extensive. Variability could not be documented since most dermatomes were mapped on only one animal. For dogs, the only study with sufficient data to describe variability of dermatomal distribution is the study of Fletcher & Kitchell (1966). These investigators mapped the dermatomes L_1 through Co_5 using 35 dogs. They obtained data from six to 12 dogs for each spinal root tested and made a major point to the variability observed among individuals. Overlap ranged from two to four dermatomes.

The only other study on a large number of animals that might provide evidence of variability is that of Werner & Whitsel (1968), who mapped the coccygeal, sacral, and lumbar dermatomes in 22 squirrel monkeys. Using Kuhn's method they mapped only the regions producing maximal activity so that the progression of dermatomes could be observed without the confusion produced by the overlap. However, no mention was made of variability and only one summary map was produced. This map showed the skin surface unfolded along the ventroaxial line, a line along the inner thigh running down to the foot. Werner & Whitsel claimed that this was the 'only natural axis of dermatomal organization'. The dermatomes of this study do not correspond to those reported by Kuhn (1953); they were much smaller and postfixed by about one dermatome. Since Werner & Whitsel (1967) used squirrel monkeys and Kuhn's animals were of an unspecified genus and species; this latter difference might be a species variation.

The only single fibre data bearing on the problem of dermatomal distributions come from the work of Pubols *et al.* (1965), Pubols & Pubols (1969) and Brown & Koerber (1978). In 1965 Pubols *et al.* described the spinal nerves of the forelimb of racoon, coatimundi and cat showing that a single root may receive input from all five digits and one digit may contribute input to four spinal roots. Thus, overlap of dermatomes was considerable and some individual variability was noted. Their data were pooled, however, to make very wide composite dermatomes for each species. In 1969 Pubols & Pubols studied 1006 fibres from spinal roots of the forelimb, hindlimb and tail of 12 monkeys. Again the data were pooled across animals so that it was not possible to discuss variability among individuals. In a subset of the data gross electrode recordings from the S_2 dermatome in three animals indicated that at least this dermatome varied by the equivalent of one to two spinal segments. The dermatomal maps of the pooled data appeared wider than those obtained by Sherrington (1893, 1898).

Brown & Koerber (1978) studied 452 fibres from six spinal nerves serving the hindlimb of cats. They studied each spinal nerve in at least two cats and concluded that the dermatomes were smaller than those reported in earlier studies. This finding of small dermatomes is the opposite of our experience with monkeys as well as the electrophysiological data in the literature. It can be explained only by a remarkable species difference between cats and monkeys or by a sampling problem arising from the limited number of fibres (average = 75 per root) sampled from the cats.

Other aspects of their data supported the observations presented here: (i) innervation density was much greater in the distal portion of the limb; (ii) those dermatomes serving the distal limb were not connected to the trunk; and (iii) the dermatomes were ovoid instead of being long narrow strips. They also remarked that their results were sufficiently discrepant from the published data to merit a re-examination of dermatomal distribution. Our own data are sufficient to make certain generalization concerning the composition, distribution and variability of the dermatomes of primates.

Inspection of the data presented here permit three generalizations that are consistent with the preceding literature review. As a unit of the peripheral nervous system, the dermatome appears to be (i) extremely variable in location and thus in the body part served, (ii) wider than previously thought, and (iii) composed of spatially distinct muscle and cutaneous afferent fibre components.

Variability

The variability in the locus of a particular dermatome is not due to an absence of organization to the dermatomal pattern. An orderly sequence of innervation is apparent from the progression of dermatomal areas within any one individual; in each case a gradually shifting overlap exists so that each spinal nerve follows in its sequence just as described by Sherrington (1893, 1898) (figure 9). There is, however, extreme variability among individuals as to which body site is innervated by a particular spinal nerve. From our data it appears that the area served by one dermatome can shift up or down the body so that the skin region in one animal can be served by a spinal nerve as much as three spinal roots away from the one that serves this region in another animal.

Since the nerves on the contralateral side of the body were never studied in the same animal it is not possible to state whether there was a bilateral symmetry or any other type of correlation between the pattern on the two sides of the body.

Width

In most cases, the width of the dermatomes recorded in these experiments was approximately twice that which would be expected, based on predictions from behavioural studies. The explanation of the wide dermatome appears to be that the behaviourally determined dermatomes of previous investigators were restricted in lateral extent to some fraction of the total innervation area because they were viewed subsequently to the actions of spinal inhibitory mechanisms that prevented neural activity from the edge of the dermatomes from either reaching consciousness or producing any reflex activity. Thus our data are consistent with the work of Denny-Brown *et al.* (1973) and Kirk & Denny-Brown (1970). Since the spinal suppression of the activity at the edge of the dermatome does not confound our data, they should display the entire width of the dermatome just as do the data of Kirk & Denny-Brown (1970) following section of many adjacent roots or section of Lissaur's tract (Denny-Brown *et al.* 1973).

The data from previous electrophysiological studies which showed relatively narrow dermatomes came from studies where (i) only the maximum response was recorded or, (ii) the sample size was small. In those cases we believe that the narrow dermatomal bands may be only the area of maximum response. Often with multi-unit recording, the weaker activity from the fringe areas is lost in the noise of the recording.

Thus, although the dermatome is a unit of the nervous system that is discussed as if it is well defined, the available literature shows a remarkable lack of agreement concerning its basic description. The published dermatomal maps show major differences in the region said to be innervated by specific spinal roots. In those few reports where sufficient data are available, the dermatome is shown to be so highly variable that it is difficult to see how any dermatome chart can be constructed without some indication of variability. The demonstration, by Denny-Brown & colleagues, that spinal inhibitory mechanisms restrict the apparent size of the dermatome to an area as small as 50 % of the true area further confounds the description of the dermatome.

Partially shifted overlap

One undisputed observation of all workers in the past century is the progressive shift of the locus of the dermatomes of successive spinal nerves. Even though a specific individual may have a particular spinal nerve innervating an area far removed from the area served by the same nerve in another individual, in both cases adjacent nerves will serve adjacent skin regions. With successively lower spinal nerves the body region served shifts successively lower. In the upper limb, this progression follows a particular pattern. The sequences of dermatomes passes from the neck, over the shoulder, down the lateral aspect of the arm, across the radial forearm and hand to return on the ulnar side of the hand and forearm and the medial arm to the chest. The regularity of this sequence provides a clinically useful tool for diagnosis of nerve injuries.

Even though it is no longer possible to unequivocally assert that C_6 serves the skin over the deltoid, it is possible to infer that, whichever nerve does serve the deltoid, the next lower nerve probably serves the thumb, and the second lower nerve serves the skin over the majority of the hand.

Historical perspective: the afferent myotome

A review of the literature concerning the innervation of the muscles serving the upper limb has emphasized that: (i) little original work has been done on this subject in this century (ii) the textbooks of anatomy, neurology, surgery and physiotherapy that form the basis of modern diagnosis and treatment are remarkably out of date; relevant clinical documentation is frequently over fifty years old; (iii) the schemes of peripheral innervation and accompanying muscle charts presented in these texts give the impression of being firmly established and invariant. Seldom is there an indication of how the data were acquired, what methods were employed, or the frequency with which variations occur.

Conceptions of a segmental body architecture can be traced to Goethe & Oken (cf. Sherrington 1898), who first conceived of the body as being composed of a series of similar structural units. The obvious segmental character of the vertebrae and ribs directed early investigators to study the limb for evidence of segmentation in an attempt to extend the segmental theory to the extremities. Goodsir (1857) suggested that the peripheral nerve distribution might be used to determine the segmental origin of the limbs, but tests of Goodsir's beliefs were hampered by difficulties faced in determining the intricate course of nerve fibres at the level of the limb plexuses.

The first attempt to study innervation of the muscles of an extremity were carried out by Eckhard (1849) using the 'reflex' method. Eckhard cut all the posterior roots in the hindlimb of decapitated frogs except the one that he was studying and watched for the presence or absence of movement secondary to cutaneous stimuli. Movement was taken as an index of segmental innervation. The conclusions he drew correlating skin and muscle innervation were quite accurate: 'The field of skin to which a sensory root goes is not exactly that which overlies the muscles which are supplied by the corresponding motor root'.

Four years later, Peyer (1853) investigated the distribution of the cervicothoracic spinal nerves in the rabbit by applying mechanical and thermal stimuli to the skin and watching for reflex activity in those spinal nerves he left intact. Some of his findings on cutaneous innervation were accurate and have been reviewed above. However, his conclusion that the skin overlying a muscle in the limb is supplied with sensory fibres of the same spinal nerve that contributes fibres to the underlying muscle conflicted with Eckhard's work. Krause (1865) used the reflex method in rabbits and also employed techniques allowing him to detect Wallerian degeneration. He concluded incorrectly, but in support of Peyer, that a muscle is supplied with nerve fibres by the same spinal nerve that innervated the overlying skin. He also believed incorrectly that the proximal and distal termination of the motor and sensory nerve supply of the upper limb are fixed and not subject to individual variation. This position was rebutted in subsequent years by the works of Koschewnikoff (1868), Meyer (1869) and Sherrington (1893, 1898).

From work on 55 cadavers Herringham (1886) provided the first extensive anatomical scheme of innervation of the musculature of the upper limb. He formulated three rules of innervation:

(i) 'Of two muscles, or of two parts of a muscle, that which is nearer the head-end of the body tends to be supplied by the higher, that which is nearer the tail-end by the lower nerve';

(ii) 'Of two muscles, that which is nearer the long axis of the body tends to be supplied by the higher, that which is nearer the periphery by the lower nerve';

(iii) 'Of two muscles, that which is nearer the surface tends to be supplied by the higher, that which is further from it by the lower nerve'.

Sherrington's data were in complete agreement with Herringham's first two formulations; however, the third rule was shown to be in error (Sherrington 1898, p. 121).

Sherrington (1898) employed two procedures in his meticulous studies of the distribution of the motor roots of the monkey. First, he resected a series of spinal nerves above and below the one to be investigated. Then, after allowing 28 days for degeneration, he electrically excited the various peripheral muscle nerves. If a muscle contracted it was taken as evidence that this particular muscle received a nerve supply from the undamaged spinal root.

Secondly, by means of Wallerian degeneration, only the spinal nerve being studied was transected. After allowing sufficient time for degeneration to begin, the nerves of the upper extremity were fixed and stained with osmic acid and exhaustively searched for degenerating fibres. Using these relatively crude techniques, Sherrington obtained a description of the distribution of motor nerves in the upper limb, which forms the basis for our current picture of muscle innervation. Some of his conclusions concerning the innervation of the muscles of the upper limb are:

(i) Although dermatomes in the mid-portion of the brachial plexus become separated from the midline, the muscle efferents do not;

(ii) the size and location of the motor and sensory (cutaneous) spinal roots are widely dissimilar, especially for nerves in the mid-portion of the brachial plexus;

(iii) afferent fibres from muscle pass through the same spinal nerve, as do the afferents to the muscles in question;

(iv) the muscles are 'plurisegmental' in their innervation and considerable overlap of innervation occurs;

(v) in the variability among individuals, each myotome is displaced absolutely but not relative to its neighbours.

Thus, with the exception of the third observation on efferent innervation, for which we have no data, our conclusions are consistent with, and support, those of Sherrington (1893, 1898).

Spatial separation of muscle and skin areas served by a spinal root

Actually the observation of different sites of termination for the skin and muscle components of a spinal nerve was first made in 1849 by Eckard and was confirmed by Sherrington (1893, 1898). It has not been discussed in publications since that time but the original observations are confirmed by our data. Figure 12 presents several examples of the degree of separation that can arise between skin and muscle. For any single nerve the magnitude of separation was variable; in this animal there was a complete separation of the dermatome and myotome, with the dermatome being located distally on the limb and the myotome being located in the shoulder girdle. In other cases for the same nerve, the myotome and dermatome were nearly coextensive; in several instances the skin and muscle afferent fibres both innervated the shoulder area.

The explanation for these results may exist in the embryological history of the individual. As the limb bud develops in the embryo, the time of innervation may vary sufficiently so that significantly different degrees of migration of skin and/or muscle may occur subsequent to the attachment of nerve fibres. Thus, in the animal shown in figure 12, the cutaneous nerves may have innervated the skin in the embryological stages before migration of skin onto the limb bud. Whether such a hypothesis is tenable depends upon embryological processes that are still very poorly understood (Bradley & Mistretta 1975; Zelena 1964). One aspect that has recently been clarified is that motoneurons are not 'intrinsically' specified to seek certain targets but that during embryogenesis they will even innervate novel targets that they happen to contact (Morris 1978). This suggests that some of the specificity seen in the adult may arise from subsequent interactions with the target tissue.

To account for differences between individuals one must simply note that there are differences in the rate of growth of nerves in different embryos and even on opposite sides within the same embryo. Also, the target organ at this stage may be rather non-specific (Arey 1962, p. 463), with any ectodermal derivative being able to act as a target, so that whichever portion of the limb bud ectoderm happens to be passing by in its phase of rapid elongation at the time the nerves arrive at the skin will become the ultimate site of the dermatome for that nerve. If contact is made early, the dermatome may be dragged towards the tip of the limb, but if the nerve arrives later a more proximal site will be all that is left. Further, if contact is relatively non-specific, the geometry of the limb bud at the time of contact will be very important.

That the afferent myotomal distribution should be different from the dermatomal distribution is consistent with the observation that the sensory fibres grow out to their target organs at a time when the limb bud is relatively immature, the long bones do not exist and the muscles have only begun to take shape as clusters of mesodermal cells. Thus, whereas the cutaneous nerves maintain contact with a two-dimensional epithetical sheet which may become elongated and transported distally, the sensory fibres to muscle must follow their target tissues through smaller spatial displacements but through greater three-dimensional changes that lead to functionally different muscle groups being compartmentalized by bones and fascial planes.

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