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Projection of forelimb nerve afferents to external cuneate nucleus of the rat as revealed by intraneural injection of a neurotoxic lectin, *Ricinus communis* agglutinin

S.W. Cha and C.K. Tan
Department of Anatomy, National University of Singapore, Kent Ridge, Singapore

Summary. This study seeks to extend the observations of previous studies of projection of primary afferent fibres from the forelimb nerves and muscles to the external cuneate nucleus (ECN) of mammals using a neurotoxic lectin, *Ricinus communis* agglutinin (RCA) to achieve chemical ganglionectomy of the dorsal root ganglia. Following intraneural injection of RCA into the three main forelimb nerves, namely the radial, ulnar and median nerves, terminal degeneration of the primary afferent fibres in the ECN was studied under the light microscope by means of the Fink-Heimer method. The results show that the primary afferent fibres from these three nerves project to the medial part of the ECN. The field of terminal degeneration take a crescentic form. The projection from the median nerve was most dorsally located whereas that from the radial nerve was the most ventral with extensive overlaps between them. Of the three nerves, the projection from the radial nerve was the most dense. Rostrocaudally, the three nerves also show extensive overlaps. The rostrocaudal extent of maximum terminal degeneration was greatest for the radial nerve and least for the median nerve. Analysis of variance showed that these differences were statistically significant. This suggests that the radial nerve has the most extensive projection to the ECN and the median nerve the least.

Key words: External cuneate nucleus, Forelimb nerve afferents, Ricinus communis agglutinin, Rat

Introduction

The external cuneate nucleus (ECN) relays proprioceptive information from the forelimb, upper trunk and neck to the cerebellum (Hand, 1966; Tracey, 1982) and some of its efferent fibres also terminate in the somatosensory thalamus (Boivie et al., 1975; Tracey et al., 1980). Studies using electrophysiological techniques have demonstrated that the ECN receives both primary and secondary muscle afferents via the cervical and thoracic dorsal roots in the rat (Campbell et al., 1974), cat (Rosen, 1969; Cooke et al., 1971a,b; Rosen and Sjolund, 1973), raccoon (Johnson et al., 1968) and monkey (Hummelsheim et al., 1985). Terminal degeneration has also been reported in the ECN following dorsal rhizotomy of the cervical and thoracic dorsal roots in the rat (Basbaum and Hand, 1973; Rosenstein et al., 1977), cat (Liu, 1956; Rustioni and Macchi, 1968), brush-tailed possum (Culberson, 1987) and monkey (Shriver et al., 1968).

With the technique of transganglionic transport of horseradish peroxidase (HRP) and its conjugates (Grant et al., 1979; Mesulam and Brushart, 1979), afferents from muscles (Amman et al., 1983; Nyberg and Blomqvist, 1984; Bakker et al., 1985; Jasmin et al., 1985; Wild, 1985; Edney and Porter, 1986; Lan et al., 1994), muscle nerves (Beck, 1981; Mysicka and Zenker, 1981; Nyberg and Blomqvist, 1982; Hummelsheim et al., 1985; Jasmin et al., 1985; Abrahams and Swett, 1986; Ygge, 1989; LaMotte et al., 1991), spinal nerves (Abrahams et al., 1984; Liu and Hu, 1988) and dorsal root ganglia (Jasmin et al., 1985; Imamura et al., 1986; Pfaller and Arvidsson, 1988; Arvidsson and Pfaller, 1990) have been traced to their terminations in the ECN.

HRP, though widely used as a histochemical method to label primary afferent terminals, has drawbacks especially in its lack of sensitivity (Mesulam and Brushart, 1979). In a comparative study using not only HRP but also cytotoxic lectins, Leong and Tan (1987) have shown that the latter method gave a more consistent and better localisation of the primary afferent terminals in the rat gracile nucleus. The rationale for using cytotoxic lectins is that when they are injected into a peripheral nerve, they are transported retrogradely to the dorsal root ganglion cells which they destroy, thereby effecting a chemical ganglionectomy; this results in the degeneration of the primary afferent terminals in the central nervous system (Yamamoto et al., 1983, 1984).

Although previous studies have involved intraneural or intraganglionic injection of HRP or HRP conjugates into one or more of the forelimb nerves in the rat and

Offprint requests to: Dr. S.W. Cha, Department of Anatomy, National University of Singapore, Kent Ridge, Singapore 0511

other mammals, studies involving intraneural injection of neurotoxic lectins into the radial, ulnar and median nerves concurrently have not been reported previously. The present study aims to reinvestigate the afferent projections of the three main forelimb nerves of the rat into the ECN following intraneural injection of a lectin, *Ricinus communis* agglutinin 60 (RCA 60). It aims to determine more accurately 1) the sites of termination of primary afferent fibres from the three nerves in the ECN, 2) the location of maximum degeneration, 3) the rostrocaudal extent of degeneration and 4) whether the differences in projection amongst the three nerves are statistically significant.

Materials and methods

A total of 32 adult male albino rats of the Wistar strain weighing between 150g and 180g were used in this study. All rats were anaesthetized by an intraperitoneal injection of 0.8-1.0 ml of 7% chloral hydrate solution both for surgery and perfusion.

Exposure of the radial, ulnar and median nerves

Dissection of the rat upper limb was carried out with the aid of an anatomical manual prepared by Hebel and Stromberg (1976). For 8 animals, a longitudinal incision was made in the skin over the posterior pat of the upper right arm. The triceps muscle was then separated with iris scissors along the direction of its fibres to expose as much of the right radial nerve as possible. For another 12 animals, a longitudinal incision was made in the skin over the anterior part of the upper right arm. The tensor fasciae antebrachii muscle was then separated with iris scissors from the medial head of the triceps muscle in order to expose as much as possible of the right ulnar nerve. The procedure to expose the right median nerve in the last 12 animals was smilar to the procedure for the ulnar nerve as these two nerves lie in close proximity to each other in the upper arm.

Intraneural injection of RCA 60

First, each nerve was isolated from the surrounding muscle and lifted up with a glass hook. A second glass hook was used to hold up the nerve so that about 1.5 cm of its length at the mid-arm level was clearly isolated. This length of nerve was crushed with a pair of Halsted artery forceps for about 5 seconds. 3 µl of 0.1% of RCA 60 (Seikagaku Kogyo, Tokyo, Japan) were then injected into the nerve at the site of crush using a Hamilton syringe to which a glass micropipette was attached. This method was adapted from a method described by Yamamoto et al. (1983, 1984) and Leong and Tan (1987).

Perfusion, fixation and staining

Seven days later, the animals were perfused intracardially with 100ml of 0.9% saline solution followed by 500 ml of 10% formalin. The brainstem and thoracic segments of the spinal cord were dissected out and kept in formalin overnight. Frozen sections of 30 µm thickness were then cut serially in the transverse plane and stained for degenerating fibres and terminals according to the method of Fink and Heimer (1967). Briefly, this method involves firstly the suppression of normal fibres by potassium permanganate solution followed by bleaching in a mixture of oxalic acid and hydroquinone. The sections were then stained with a mixture of uranyl nitrate and silver nitrate followed by reduction in a mixture of alcohol, formalin and citric acid. Finally they were developed in a solution of sodium thiosulphate before they were mounted on gelatinised slides.

Analysis of results

Terminal degeneration in the ECN was observed using a Zeiss binocular microscope fitted with a drawing tube. The rostral and caudal extents of degeneration for each nerve was measured by numerically adding the thickness of the respective 30 µm sections of the brainstem which stained positively for degenerating fibres and terminals. The means and standard deviations of the rostral limits, caudal limits and total rostrocadual extents of degeneration for each forelimb nerve were then calculated and subjected to an analysis of variance.

Results

The present study has shown that *Ricinus communis* agglutinin when injected into the three main forelimb nerves, viz. radial, ulnar and median nerves, was transganglionically transported up the spinal cord to terminate in the ipsilateral main and external cuneate nuclei. In the latter, the dust-like silver deposits characteristic of the Fink-Heimer method showed that the primary afferent fibres carried by these three nerves terminated in a crescent-shaped distribution in the medial part of the nucleus (Fig. 1a-c).

Along the rostrocaudal axis of the ECN, degeneration was observed to be most heavy in its middle and caudal parts following injection of RCA into the three nerves. The region of maximum degeneration for the radial nerve was located more caudally (Fig. 1a) than those for the ulnar and median nerves (Fig. 1b,c). No degeneration was observed in the most rostral part of the nucleus for all the three nerves (Fig. 1a-c). There was also no degeneration in the contralateral ECN.

Rostral and caudal limits of degeneration

The mean caudal limits of the degeneration in the ECN following RCA injection into the radial, ulnar and median nerves showed distinct differences; these were found to be 330.0±62.0 µm, 435.7±87.3 µm and 518.0±78.2 µm, respectively caudal to the obex (Table

1). Analysis of variance showed that this variability in the caudal limits of degeneration was statistically highly significant ($p<0.01$).

The mean rostral limits of the degeneration in the ECN following RCA injection into the radial, ulnar and median nerves were found to be 1075.0±1551.0 µm, 1051±99.1 µm and 104.2±150.9 µm, respectively rostral to the obex (Table 1). However, analysis of variance

Table 1. Mean ($\bar{X}$), standard deviation (s) and analysis of variance of the rostral limits, caudal limits and total rostrocaudal extents of degeneration in the ECN following intraneural injection of RCA into the right radial (RRN), ulnar (RUN) and median (RMN) nerves.

DEGENERATION IN THE ECN	FOREARM NERVE	$\bar{X}$	s	ANALYSIS OF VARIANCE
Caudal limit (µm)	RRN	-330.0	62.0	
	RUN	-435.7	87.3	p<0.01
	RMN	-518.0	78.2	
Rostral limit (µm)	RRN	+1075.0	155.0	
	RUN	+1051.4	99.1	p>0.05
	RMN	+1042.0	150.9	
Total rostrocaudal extent (µm)	RRN	1405.0	153.5	
	RUN	1487.1	128.3	p<0.05
	RMN	1560.0	118.1	

-: caudal to obex; +: rostral to obex.

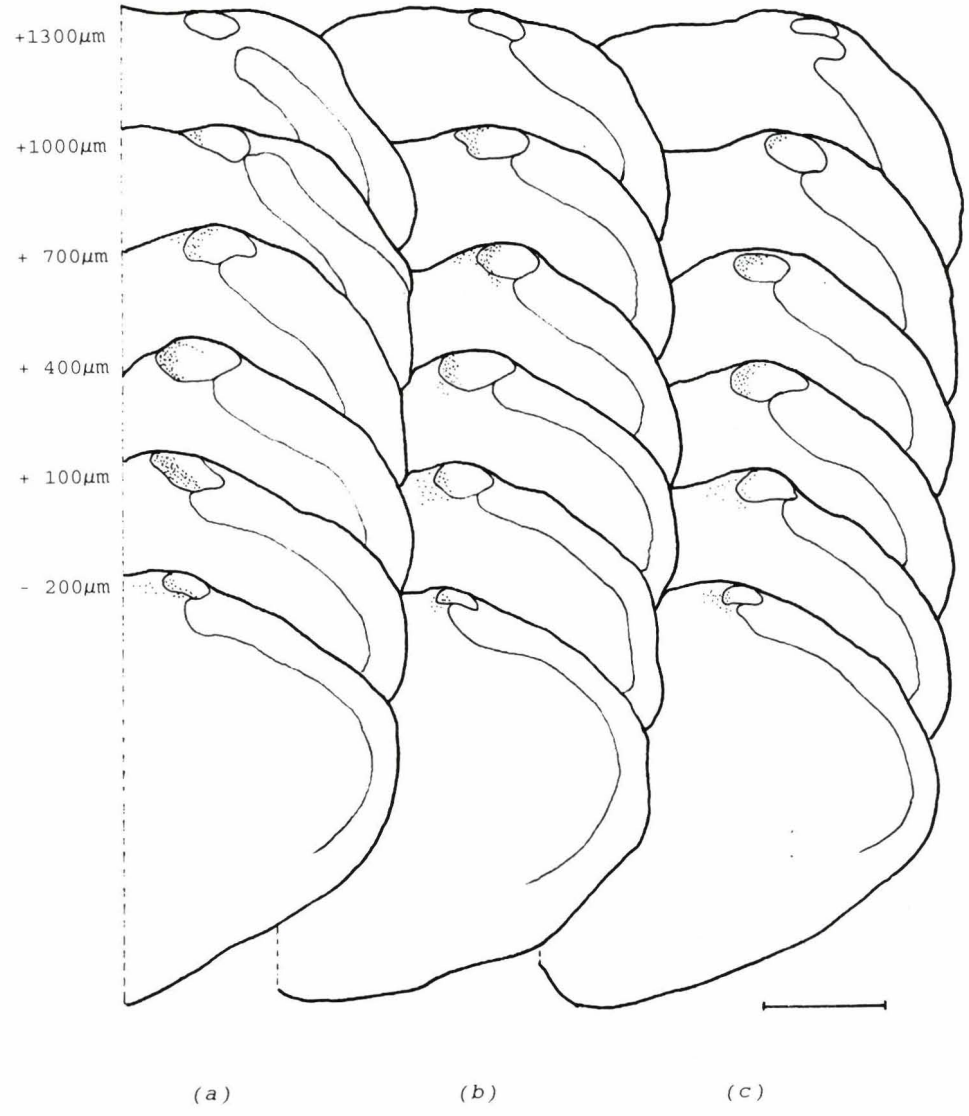

Fig. 1. Degeneration of afferent terminals in the ECN following intraneural injection of RCA 60 into the **(a)** right radial nerve (RNN), **(b)** right ulnar nerve (RUN) and **(c)** right median nerve (RMN). Bar: 0.1 µm.

showed that these differences were not statistically significant ($p>0.05$).

Total rostrocaudal extents of degeneration

Fig. 2 shows schematically the rostrocaudal extents of degeneration in the ECN. The mean total extent of degeneration in the ECN following RCA injection in the radial, ulnar and median nerves were found to be 1405.0±153.5 µm, 1487.1±128.3 µm and 1560.0±118.1 µm, respectively (Table 1). Analysis of variance showed that these differences were statistically significant ($p<0.05$).

Rostrocaudal extents of maximum degeneration

The mean caudal limit of maximum degeneration in the ECN (Fig. 2) following RCA injection into the radial

Table 1. Mean ($\bar{X}$), standard deviation (s) and analysis of variance of the rostral limits, caudal limits and rostrocaudal extents of maximun degeneration in the ECN following intraneural injection of RCA into the right radial (RRN), ulnar (RUN) and median (RMN) nerves.

DEGENERATION IN THE ECN	FOREARM NERVE	$\bar{X}$	s	ANALYSIS OF VARIANCE
Caudal limit of maximum degeneration (µm)	RRN	-70.0	45.2	
	RUN	+14.3	11.3	p<0.01
	RMN	+106.0	93.4	
Rostral limit of maximum degeneration (µm)	RRN	+370.0	123.0	
	RUN	+425.7	53.2	p>0.05
	RMN	+400.0	106.1	
Rostrocaudal extent of maximum degeneration (µm)	RRN	440.0	129.6	
	RUN	411.4	54.0	p<0.05
	RMN	294.0	57.7	

-: caudal to obex; +: rostral to obex.

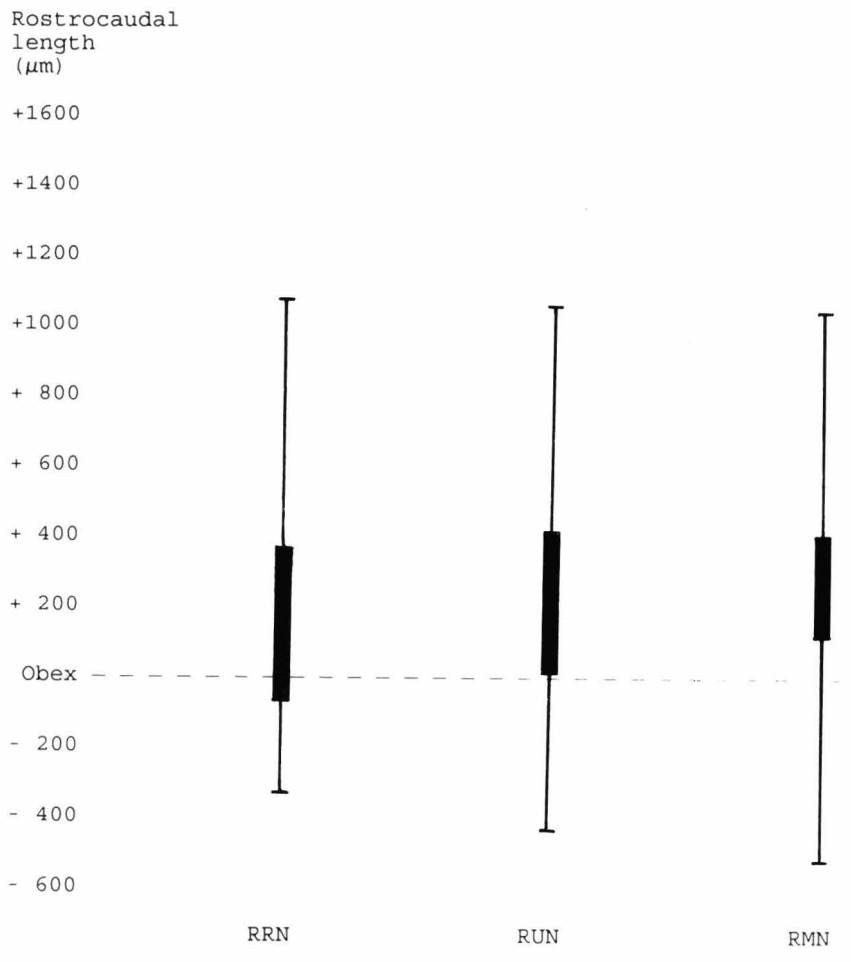

Fig. 2. Mean rostrocaudal extents of degeneration (single line) and regions of maximum degeneration (shaded columns) in the ECN following injection of RCA 60 into the right radial (RRN), ulnar (RUN) and median (RMN) nerves.

nerve measured 70.0±45.2 μm caudal to the obex whereas the mean caudal limit of maximum degeneration in the ECN following RCA injection into the ulnar and median nerves measured 14.3±11.3 μm and 106.0±93.4 μm, respectively rostral to the obex (Table 2). Analysis of variance showed that these differences were statistically highly significant ($p<0.01$).

The mean rostral limits of maximum degeneration in the ECN following RCA injection into the radial, ulnar and median nerves (Fig. 2) measured 370.0±123.0 μm, 427.5±53.2 μm and 400.0±106.1 μm, respectively rostral to the obex (Table 2). Analysis of variance showed that these differences were, statistically, not significantly different ($p<0.05$).

The mean rostrocaudal extent of maximum degeneration for the radial, ulnar and median nerves (Fig. 2) were found to be 440.0±129.6 μm, 411±54.0 μm and 294.0±57.7 μm (Table 2). Analysis of variance showed that these differences were statistically significant ($p<0.05$).

Discussion

Use of RCA 60 in chemical ganglionectomy

The lectin, *Ricinus communis* agglutinin (RCA 60), is a highly toxic protein which interferes with ribosomal functions of many cells (Nicolson and Blanstein, 1972). It is also known to bind with specific membrane glycoproteins. Wiley et al. (1982) had shown that when RCA was injected into the rat vagus nerve it was retrogradely transported to the cell bodies in the nodose ganglia and dorsal motor nucleus, causing neuronal death. When the same lectin was injected into the rat sciatic nerve, Yamamoto et al. (1983) reported that the L_4-L_6 dorsal root ganglia cells showed loss of Nissl substance as early as after 24 hours followed by karyorrhexis and vacuolation of the perikarya after a survival period of 3 days. Leong and Tan (1987) later injected RCA into the same nerve and showed that degenerating fibres were observed in the ipsilateral fasciculus gracilis and dorsal horn in the spinal cord, caudal pole of the gracile nucleus, ventral and central regions of the cuneate nucleus at the level of the obex, dorsomedial corner of the inferior cerebellar peduncle and in the medial tip of the ECN almost to its rostral pole after a postoperative survival period of 5 days.

In the present study, RCA has been used to achieve chemical ganglionectomy of the dorsal root ganglion following its injection into the radial, ulnar and median nerves. This has permitted the study of terminal degeneration in the ECN following the injection of RCA into the radial, ulnar and median nerves.

Mediolateral projection of primary afferent fibres of the forelimb to the ECN

Beck (1981) has shown that when the rat forelimb peripheral nerves were soaked in HRP, more reaction product was observed in ECN following the application of the tracer to the deep branch of the radial nerve than that of the ulnar and median nerves. This has been confirmed in the present study using intraneural injection of RCA. In addition, the present study has also shown that the afferent projections from the radial, ulnar and median nerves to the ECN showed a crescent-shaped distribution in the medial part of the ECN (Fig. 1) with extensive overlaps. This was not emphasised by Beck (1981).

In a previous HRP study on the radial nerve of the rat, Ygge (1989) has reported that the reaction products showed a mediolateral distribution. This is in contrast to the present study in which degeneration was confined to the medial aspect of the ECN in transverse sections of the brainstem. The present observation is accord with the finding of Nyberg and Blomqvist (1984) who also reported that the reaction product following HRP injection into the deep branch of the ulnar nerve of the cat was located in the medialmost part of the nucleus. In addition, Nyberg and Blomqvist (1984) also showed that there was a musculotopic organization in the ECN in which the forearm, arm and shoulder was represented progressively more laterally.

The medial distribution of the three forelimb nerves in the rat ECN has also been described by Rosentein et al. (1977) following dorsal rhizotomy. Similar observation was also made in the monkey (Shriver et al., 1968). This medial distribution is also in accordance with the results of studies using HRP to trace forelimb nerve and muscle afferents of the cat (Nyberg and Blomqvist, 1984; Bakker et al., 1985; Jasmin et al., 1985; Abrahams and Swett, 1986) and gerbil (Lan et al., 1994) and electrophysiological studies of forelimb nerve and muscle afferents in the rat (Campbell et al., 1974) and cat (Rosen, 1969).

A combined electrophysiological and anatomical mapping study has reported that the primary muscle afferents from the deep radial nerve projected to a ventromedial segment in the monkey ECN (Hummelsheim et al., 1985). In another anatomical study involving implantation of HRP-immersed gelfoam into forelimb muscles of the gerbil, Lan et al. (1994) reported that upper arm muscle afferents projected to the ventrolateral portion of the caudal two thirds of the nucleus whereas forearm muscle afferents projected to the ventromedial portion from the caudal pole to the midpoint of the nucleus. The same study has also shown that afferent fibres from the forepaws projected to the medial site in the caudal part of the ECN. The projection of the radial nerve into the ventromedial region of the caudal and middle parts of the ECN as observed in the present study has, however, not been reported previously in the rat.

The dorsomedial projection of the median nerve and the medial projection of the ulnar nerve into the ECN as observed in the present study has also been observed in a study involving intraneural injection of HRP into the median and ulnar nerves of the rat (LaMotte et al.,

1991). In this study, it was reported that the afferent terminals from the median nerve were located in a wide band along the dorsomedial border which reached its peak width and intensity midlength in the nucleus. The afferents from the ulnar nerve terminated in a smaller medial and central area in the nucleus.

In a study involving rhizotomy of the dorsal roots C_1 through T_2 in the rat (Basbaum and Hand, 1973) it was observed that all the roots studied projected heavily and topographically to the ECN with extensive overlaps. In other studies involving dorsal rhizotomy of roots C_3 throughC_8 in the rat (Rosenstein et al., 1977) and roots C_1 through T_7 in the monkey (Shriver et al., 1968), the degeneration observed in the ECN was also extensive and topographically organised in the medial and central parts of the nucleus. This would explain the projection of primary afferent fibres coursing in the three major forelimb nerves to the medial part of the ECN as shown in the present study since the dorsal root ganglia of C_5 to T_1 would be associated with these nerves.

Rostrocaudal distribution of terminal degeneration in the ECN

In the earlier study by Beck (1981), no attempt was made to establish the rostrocaudal distribution of primary afferent terminals in the ECN. However, Rosenstein et al. (1977) and LaMotte et al. (1991) have also reported that the forelimb nerve afferent terminals were found along the whole of the rostrocaudal length of the ECN in the rat. Shriver et al. (1968) had reported a similar finding in the monkey. But in an HRP study on the radial nerve of the rat, Ygge (1989) had reported that the terminal labelling in the ECN showed a distinct rostrocaudal distribution. This has also been observed by Nyberg and Blomqvist (1984) following injection of WGA-HRP into the forelimb muscles of the cat. LaMotte et al. (1991) have also reported that the rostrocaudal extent of the ulnar nerve projection was greater than that of the median nerve projection in the spinal cord. Similar differential rostrocaudal distribution of primary afferent terminals in the ECN has been confirmed in the present study. In addition, the present study has provided statistical evidence that such a variability in extent of primary afferents from the three nerves was significant. This was confirmed by an analysis of variance which showed that the variabilites in the caudal limits and the total rostrocaudal extents of the terminal degeneration in the ECN were statistically significant. But the variability in the rostral limits amongst the three nerves was not statistically significant. Such an analysis of variance in the ECN have not been reported previously.

Rostrocaudal distribution of fields of maximum degeneration

It is obvious from the present observations that for each nerve studied, the field of terminal degeneration in the ECN was not uniform throughout the rostrocaudal extent but showed, in each instant, an area of dense degeneration which was termed «maximum degeneration» in the present study. This has not been emphasized by other workers. Analysis of variance in the present study has shown that the variabilities in the caudal limits and the rostrocaudal extents of the fields of maximum degeneration in the ECN following intraneural injection of RCA into the radial, ulnar and median nerves in the ECN was statistically significant but the variability in the rostral limits was not. This finding has also not been reported previously.

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