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CONDUCTION VELOCITY ALONG THE AFFERENT VAGAL DENDRITES: A NEW TYPE OF FIBRE

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SUMMARY

1. We systematically calculated the conduction velocity along the peripheral extensions of sensory vagal neurones in cats (the dendrites). In addition, a study of excitability cycle and light microscopic investigation were also conducted on these neurones.

2. The conduction velocity of the three known types of fibres (A, B and C) remains uniform along the dendrites.

3. Another mixed type of fibres exists with a C conduction velocity (mean value 1·5 m/sec) along its distal pathway and a B conduction velocity (mean value 6 m/sec) along its proximal pathway. The change in conduction velocity progressively occurs in the thoraco-cervical portion of the vagus nerve at least 20 mm from the receptor and at least 40 mm from the T cell.

4. The mixed fibres exhibited a C type excitability cycle in their peripheral pathway and a B type excitability cycle in their central pathway.

5. The histological study using the teasing method demonstrated the existence of unmyelinated fibres, in the thoraco-cervical region of the vagus nerve, becoming progressively myelinated from the periphery to the nodose ganglion. These fibres are likely to be the ones showing mixed electrophysiological properties. They represent (approximately) 10% of the vagal nerve population.

6. We propose to call the mixed fibres BC because they present electrophysiological and morphological properties of C fibres in their distal part and properties of B fibres in their proximal part.

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INTRODUCTION

Traditionally it was thought that nerve impulses spread at a constant velocity along the entire primary afferent neurone which would imply that the morphological and functional properties of nerve fibres are comparable along nerves. Recent electrophysiological and histological studies (Mei, 1970; Mei, Boyer & Condamin, 1971; Mei, Ranieri & Crousillat, 1974) have indicated that this proposal should be treated with extreme caution. Indeed, the two processes of the vagal sensory neurone, i.e. the peripheral branch corresponding to the dendrite and the central branch corresponding to the axon, are not identical; the former has a diameter and a conduction velocity far greater than those of the latter.

Regarding the conduction velocity in the dendrite itself, the following two hypotheses can be made.

(1) Impulses are transmitted at a constant velocity along the dendrite; this presupposes that the morphological properties (the diameter in particular) remain constant from the receptor up to the sensory cell.

(2) Conduction velocity varies along the dendrite. Two results relating to a few vagal and cutaneous fibres (Iggo, 1958; Iggo & Ogawa, 1971) suggested that the conduction velocity of impulses could increase from the periphery to the central nervous system.

In this study, we verified these two hypotheses through the systematic study of the conduction velocity along a relatively large number of vagal dendrites using the extracellular micro-electrode method (Mei, 1962 and 1970).

METHODS

Electrophysiological experiments were performed on fifteen healthy, domestically bred adult cats. The cats were anaesthetized with sodium pentobarbitone (15 mg/kg, I.V., after halothane induction), immobilized with Flaxedil and artificially ventilated.

(1) *Stimulation of vagal dendrites*

Five pairs of stimulation electrodes were placed along the vagus nerve, always at the same distance from the nodose ganglion. Two are situated at the cervical level: C1 and C2, and three at the thoracic level: T1, T2 and T3 (Text-fig. 1). These electrodes were made up of either plain silver hooks or Plexiglas grooves with two silver or platinum wires in the bottom. The former were especially used at the cervical level, whereas the latter better suited the thoracic level (more difficult nerve access, necessity of closing off the thorax). Whatever the type of electrodes used, the temperature of the tissues bordering on the nerve was maintained at the normal rectal value (37–38° C).

Electrical stimulation was produced by a Grass-type neurostimulator. The parameters varied according to the type of fibre studied (duration between 0·1 and 1 msec, voltage between 0·1 and 30 V).

(2) *Recording of unitary vagal potentials*

Action potentials produced by electrical stimulations were recorded by extracellular glass micro-electrodes implanted in the nodose ganglion, according to the method previously described (Mei, 1970). In our experiments, only perfectly unitary, or if necessary, slightly pluri-unitary recordings (two to three action potentials) were taken into consideration. In all cases we systematically applied traditional identification criteria (polarity, amplitude, duration and shape of different phases of action potentials) so as to be sure that the responses evoked from the different stimulation points (C1, C2, T1, T2 and T3) occurred in the same neurone.

(3) *Typical experimental procedure*

After obtaining a unitary response through a test stimulation (C1 in general), we successively stimulated the vagus nerve at C2, T1, T2 and eventually at T3. The responses were observed on an oscillograph screen and recorded on film.

In some cases (eight experiments) the excitability cycle of the fibres was studied at different levels of stimulation. The traditional double shock method was then used (see Mei, 1970; Ranieri, Crousillat & Mei, 1975).

(4) *Analysis of results*

On the recordings, we determined latencies of action potentials produced by the different stimulations. Then by subtraction, latencies corresponding to the different nerve portions (R–C1, C1–C2, C2–T1, T1–T2 and T2–T3) could be calculated. Finally we calculated the conduction velocities in these nerve portions, the length of which is known (Text-fig. 1).

Histological experiments were performed on two additional animals. The cervico-thoracic portion of vagal nerves was removed and after treatment with glycerol solution, individual fibres were separated using teasing method (Vizozzo & Young, 1948). Fibres are isolated under a Zeiss operation microscope (× 50) and observed under a light microscope (× 400).

RESULTS

Electrophysiological data

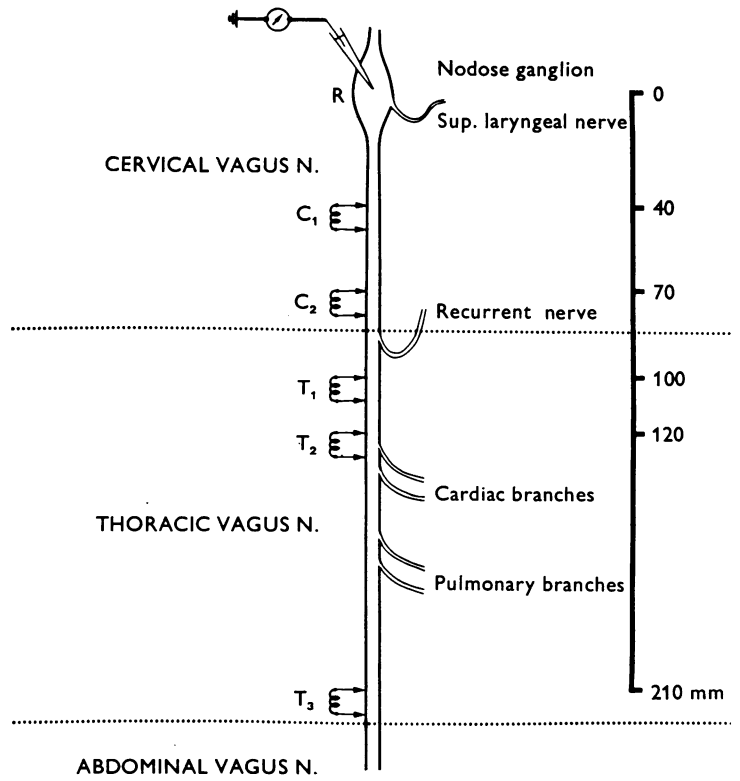
Conduction velocity

The conduction velocity in the different portions of the vagus nerve was calculated for eighty fibres.

Sixty fibres had a conduction velocity that did not significantly vary along the dendrite (Text-figs. 2 and 3). These fibres belonged to the three types of fibres A, B and C described in the afferent vagal component (Paintal, 1963; Mei, 1970) with mean conduction velocity of respectively 24, 7·5 and 1·1 m/sec in the R-C1 nerve portions. Text-fig. 2 sums the results in the form of histograms of mean values.

Twenty fibres had a significatively different conduction velocity along the dendrites (Text-figs. 2, 3 and 4). These are fibres with C fibre conduction velocity (mean = 1·5 m/sec) along their distal pathway (below T1 or C2 depending on the fibre) and B fibre conduction velocity (mean = 6 m/sec) along their proximal pathway. The histogram of mean values

(Text-fig. 2), like the specific cases shown in Text-figs. 3 and 4, clearly demonstrated the mixed type of these fibres which are called BC for this reason. In Table 1, the conduction velocity of the BC fibres is compared to the conduction velocity of A, B and C fibres. The increase of conduction velocity in the BC fibres occurred at a distance of at least 20 mm from the



Text-fig. 1. Scheme showing the position of stimulating electrodes on the vagus nerve. R: recording site of the micro-electrode in the nodose ganglion.

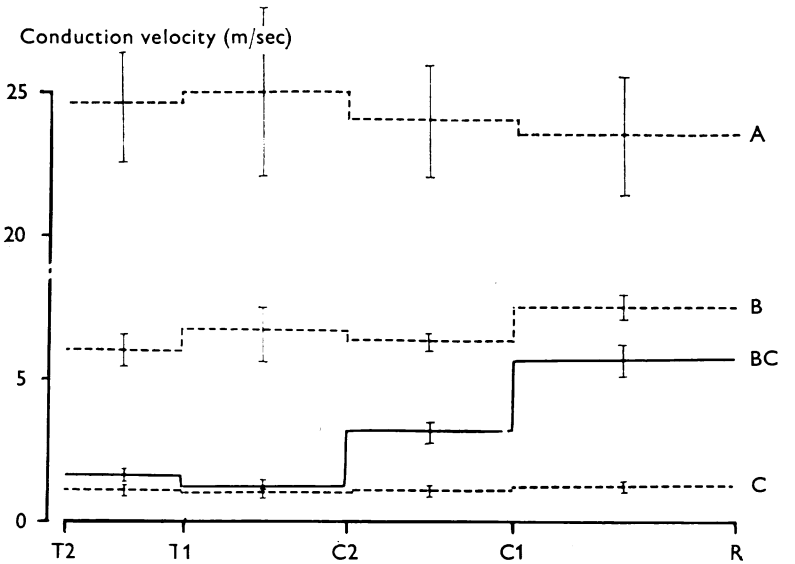
receptor site and 40 mm from the nodose ganglion and was progressive as shown in Text-fig. 4. For two fibres an additional pair of electrodes was placed between points T1 and C2 at I; intermediary values for conduction velocity were found (Text-fig. 5).

Excitability cycle

The mixed BC fibres had a C excitability cycle (no supernormal period, relatively long subnormal period) along their distal pathway and a B excitability cycle (no supernormal period, relatively short subnormal

period) along their proximal pathway. In the intermediary region of the nerve (between T1 and C2), the excitability cycle was intermediate (Text-fig. 5). A comparison between the excitability cycles of A, B, C and BC fibres is shown in Table 1.

The afferent vagal component contains the two known types of C fibres: dorsal root C fibres which have not a supernormal period and sympathetic C fibres which have a complete excitability cycle (Mei, 1970). Here, we are concerned only with the former.



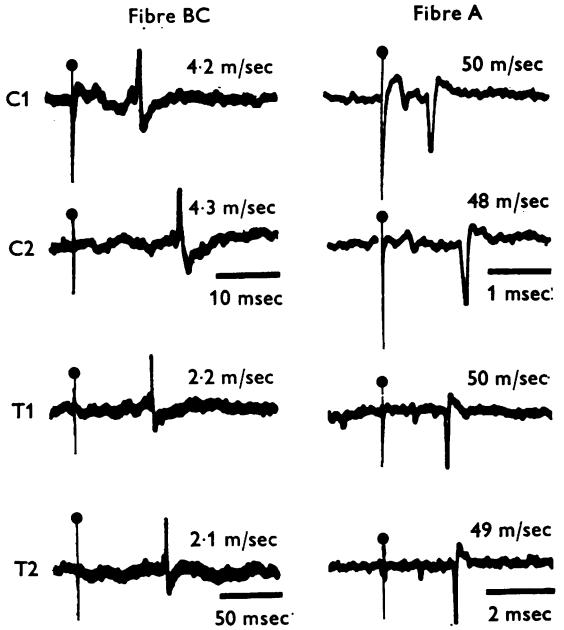
Text-fig. 2. Conduction velocities along the vagal dendrites of the A, B and C types (dashed histograms) and of BC type (continuous histogram). Mean values are plotted for the different nerve portions (R–C1, C1–C2, C2–T1 and T1–T2). Standard errors are also indicated. Note that the conduction velocity is similar in the different nerve portions for the A, B and C fibres and much greater in R–C1 portion than in C1–T2 portion for the BC fibres.

Light microscopy data

The teasing method made it possible to observe unmyelinated fibres that became progressively myelinated as they approached the nodose ganglion (Pl. 1). These fibres are not uncommon as they represented about 10 % of the small diameter myelinated fibres we dissected.

They were observed only in the lower cervical and in the upper thoracic regions of the vagus nerve. Such mixed fibres were never seen in the opposite direction, that is, from the nodose ganglion to the periphery. It thus seems likely that the BC fibres shown in this study are indeed mixed afferent fibres that are unmyelinated at the periphery and that become

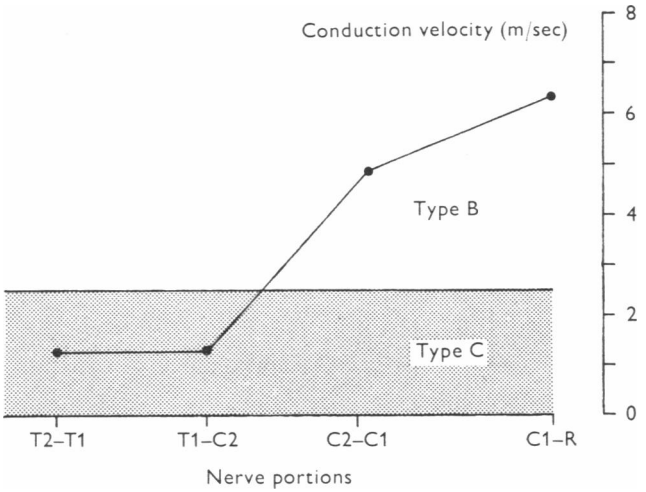
progressively medullated nearing the nodose ganglion. Morphological properties of A, B, C and BC fibres in the vagus nerve are compared in Table 1.



Text-fig. 3. Conduction velocity along a BC and an A vagal dendrites. Action potential recordings. Unitary action potentials were elicited by electrical vagal stimulation at C1, C2, T1 and T2. The numbers indicate the values of the conduction velocities corresponding to nerve portions (R–C1, C1–C2, C2–T1 and T1–T2 respectively). The dots show the situation of the stimulation artifacts.

DISCUSSION

This study shows that the conduction velocity of nerve impulses varies very little along the dendrites corresponding to the three types of afferent vagal fibres A, B and C. However, there are fibres that conduct nerve impulses much more rapidly along their proximal pathway than along their distal pathway. This velocity change concerns a well determined portion of the vagus nerve, the thoraco-cervical region located between 40 and 100 mm from the nodose ganglion and occurs progressively. We called these fibres BC because they have a conduction velocity, an excitability cycle and morphological characteristics of the C fibres along their distal pathway and of the B fibres along their proximal pathway. The phenomenon does not seem to be pathological in origin, since (1) it was found



Text-fig. 4. Increase of the conduction velocity along a BC vagal dendrite. Graphic study. Values of the conduction velocity are indicated for the different nerve regions (R–C1, C1–C2, C2–T1, T1–T2). The grey area on the graph concerns non-medullated fibres (conduction velocity < 2·5 m/sec. The fibre has a C conduction velocity in its distal portions (T1–T2 and C2–T1), and a B conduction velocity in its proximal portions (C1–C2 and R–C1). Note that the conduction velocity increase is progressive from the periphery to the nodose ganglion.

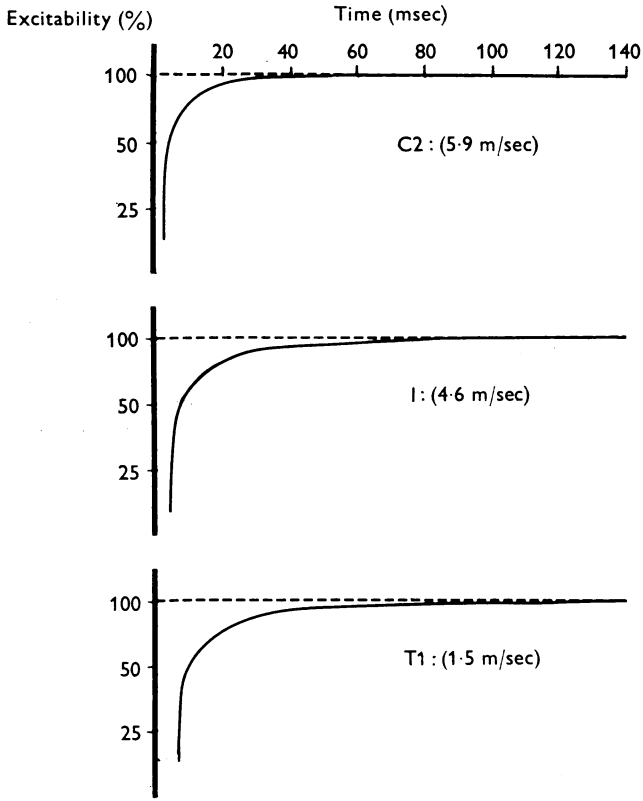
TABLE 1. Comparison between the properties of A, B, C and BC vagal afferent dendrites

	Properties			
	Conduction velocity (mean value and S.E. m/sec)	Excitability cycle		
		Supernormal period (mean value msec)	Subnormal period (mean value msec)	
Type of fibres				Diameter (μm)
A	24 ± 4·2 n = 17	20	100	3–10*
B	7·5 ± 0·8 n = 18	None	55	1·5–3*
C	1·1 ± 0·3 n = 25	None	110	0·5–2*
BC				
Distal part	1·5 ± 0·4 n = 20	None	110	< 2
Proximal part	7 ± 0·8 n = 20	None	45	2–3

* According to our histological observations (Mei *et al.* 1971 and unpublished data). n indicates the number of fibres.

in healthy adult cats and (2) it concerned only one given type of fibres and one well delimited nerve region.

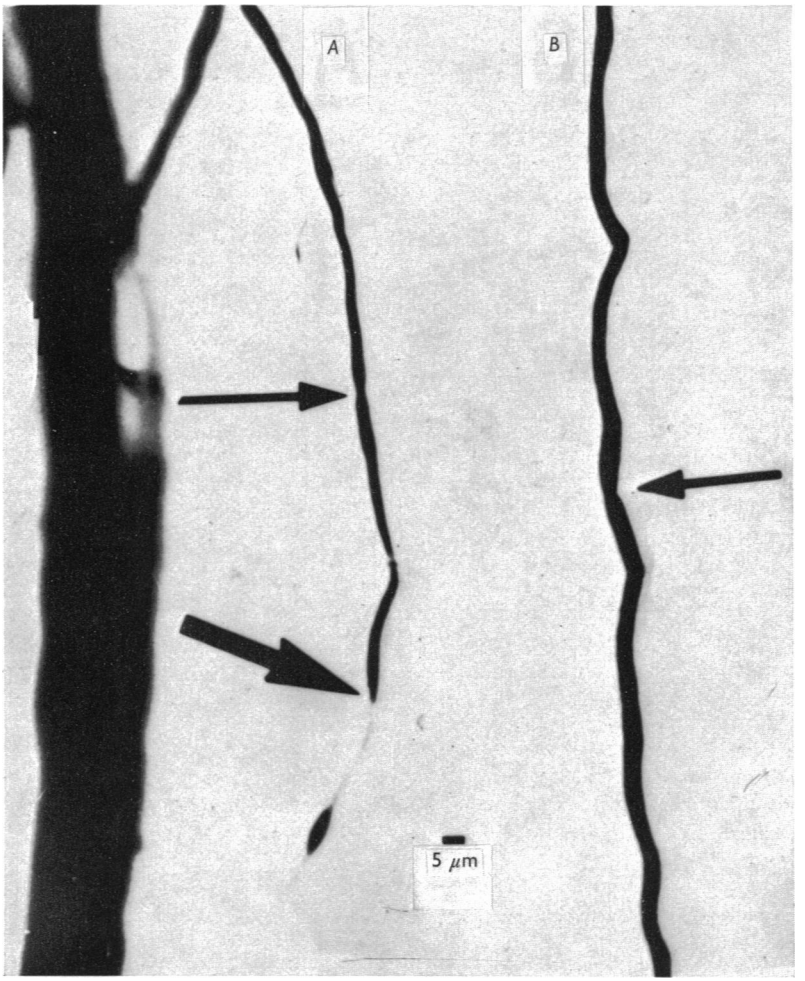
Thus, the myelinization of afferent fibres does not take place exclusively in the immediate proximity of the receptors as might be thought since all the endings are totally lacking in myelin. As we have shown in the vagus nerve, myelinization can occur higher up in the nerve. If our results are



Text-fig. 5. Excitability cycles of a BC vagal dendrite studied at C2, T1 and I levels. Explanations in the text.

considered in light of an observation made by Iggo & Ogawa (1971) in some fibres of cutaneous origin, it could be thought that the presence of such fibres is not uncommon in somatic and visceral nerves.

It may be that BC fibres are essentially oesophageal in origin. Indeed, previous studies have demonstrated that the oesophagus is essentially innervated by myelinated fibres belonging to B type at the cervical level (Mei, 1965, 1970). Possibly some of these fibres are unmyelinated below this level.


A
B
5 μm

The phenomenon described in this study as well as previous results (Mei, 1970), demonstrating the existence of morphological and functional differences between the peripheral and central extensions of vagal and dorsal root cells, prove that conduction velocity can vary considerably along an afferent nerve fibre.

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EXPLANATION OF PLATE

Histological aspect of BC vagal dendrite. In *A*: a BC fibre. The large arrow shows the area where the fibre becomes medullated. In *B*: a typical A fibre. The small arrows indicate Ranvier nodes.