THE ELECTRICAL PROPERTIES OF A CRUSTACEAN SENSORY DENDRITE

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SUMMARY

1. The input properties and the response to stretch of a coxal receptor, the S fibre of the crab *Scylla serrata*, were studied using two and three intracellular microelectrodes.

2. In the relaxed receptor the transmembrane potential ranged from about —60 to —70 mV, and the input resistance, $R_T$, from 1 to 3 MΩ. The input $IV$ relationship, studied by injecting slow-rising current ramps, was not linear either in the hyperpolarizing or in the depolarizing quadrants.

3. Low values of $R_T$ and a linear $IV$ relationship were associated with a large leakage of the microelectrodes.

4. The response to step stretches was complex, consisting of an initial depolarizing transient, $V_a$, and a steady-state depolarizing plateau, $V_e$. Both $V_a$ and $V_e$ propagated with decrement in the fibre which was about 9 mm long. The spatial decrement of $V_a$ and $V_e$ was equal to that of the response to distally injected current pulses of comparable duration and amplitude.

5. On the basis of the spatial decrement of both $V_a$ and $V_e$ the dendrite can be considered equivalent, for current flowing from its distal to its proximal end, to a semi-infinite cable having a length constant of between 4 and 6 cm.

6. The voltage transients recorded in response to long current pulses reached 84% of their final value in a time ($t_{84\%}$) ranging from 150 to 180 ms in fibres in which $R_T$ was 2 MΩ or larger. $t_{84\%}$ was smaller in fibres having a lower $R_T$.

7. The time course of the transients recorded in response to injected current pulses deviated from the semi-infinite cable model in a manner suggesting the presence of a partial short circuit. For this reason the membrane time constant of the fibre is considered larger (by an undetermined amount) than $t_{84\%}$.

8. The fibre presented less resistance to current flowing from its proximal to its distal end than to current flowing in the opposite direction. For this reason, and also because of the time course of the voltage transient, it is concluded that the distal sensory endings of the fibre have the properties of a leaky end termination, even in the non-stimulated receptors.
M. Mirolli

INTRODUCTION

The occurrence of neurones which transmit information without generating action potentials is now well documented (Pearson, 1976). This phenomenon, which seems particularly common among primary sensory neurones (same reference), was first documented by Ripley, Bush & Roberts (1968) for the crustacean coxal muscle receptors (Alexandrowicz & Whitear, 1957; Bush, 1976). In these cells the graded receptor potentials, resulting from the mechanical stimulation of peripheral sensory endings, appear to directly affect the synaptic activity of the intraganglionic parts (Bush & Roberts, 1968). The dendrites, or fibres, in which the receptor potentials propagate, can be over a centimetre long (Bush, 1976), and since propagation is thought to be passive (Bush & Roberts, 1968), it seems likely that these fibres must have unusual cable properties. In a preliminary study Roberts & Bush (1971) have examined the electrical properties of the two largest among these fibres, called S and T (Whitear, 1965). In their study, done on young specimens of Carcinus, Roberts & Bush assumed an infinite cable model, and, on this basis, estimated a length constant of several millimetres. More recently, however, Cannone (1974) working with the same material and on the same assumption calculated that the length constant was, in two exceptional cases, as large as 11 (S fibre) and 16 mm (T fibre). In the opinion of Bush (1976) these two large values are more representative of the actual properties of the cells, while the lower ones, previously obtained, may reflect injury of the preparation during the experiments. Though incomplete, these data suggest that transmission of information in the peripheral dendrites of the coxal receptor may indeed depend on specialized cable properties, and that a more systematic study of these properties would be of interest for the understanding of the physiology of these sensory neurones.

Following this idea, I have studied the electrical properties of the coxal muscle receptors in the Pacific mud crab Scylla serrata (Forskål). The large size of the dendrites of these cells has made possible the insertion of two or three microelectrodes, thus allowing a direct comparison between the spatial decrement of the response to stretch and the decrement of the transmembrane potential changes resulting from injected current. Two major conclusions can be drawn from the results obtained. The first is that both the high frequency and the low frequency components of the response to stretch propagate passively in the fibre with an extremely low attenuation. The second is that the efficiency of passive propagation of the response to stretch depends not only on the properties of the dendrites, but also on the electrical and the geometrical characteristics of the distal and proximal endings.

MATERIALS AND METHODS

Morphology of the dendrites

Most of the experiments reported in this paper were done on the S fibre of Scylla serrata; however, some observations on the T fibre will also be discussed. The dendrites of the several sensory cells which monitor the movement of the coxa in the Brachyura are held together by a common connective tissue sheath to form
Electrical properties of a dendrite

Fig. 1. (A) Semi-schematic drawing of the S and T fibres and their topographical relation to the receptor muscle (RM) and the endosternite (E). (B) Stereogram showing a transverse section of one of the S fibre terminal branches cut approximately at the level of the arrow in A. F, dendritic fingers.

sensory nerve which bridges, for each pereiopod, the distance from the thoracic ganglion where the somata of the cells are found, to the mesial edge of the endosternite (Alexandrowicz & Whitear, 1957). The S fibre divides at its distal end into two branches which are embedded in the specialized connectival strands flanking the proximal part of a small receptor muscle (Fig. 1 A). The proximal tendon of this muscle is attached to the mesial edge of the endosternite, and the distal tendon to the inferior margin of the coxa. The more numerous branches of the T fibre terminate in the proximal tendon of the muscle (Fig. 1 A).

The fine structure of the endings are similar in both the S and the T fibres (Whitear, 1965). Fig. 1 B offers a schematic view of the endings of the S fibre. The numerous small tubular fingers shown in the Figure are deformed during stretch and are thought to be the sites of electromechanical transduction (Krauhs & Mirolli, 1975; Whitear, 1965). In contrast to the complicated geometry of the sensory endings, the surface of the fibres and of the proximal part of their branches has only minor indentations. Dendrites and branches are surrounded by a sheath formed by concentric
layers of flattened glial cells alternated with lamellae of dense extracellular matrix similar to that found in other crustacean nerve preparations (Abbott, 1971; Heuser & Doggenweiler, 1966). This sheath is permeable to ionic lanthanum (Krauhs & Mirolli, 1975), at least in the region where the dendritic fingers are located.

Both the S and T fibres are smallest at their origin in the ganglion, increase in diameter in their most proximal third, then remain approximately constant in dimensions up to their bifurcation into the distal branches. Thus a tapered and a cylindrical part can be distinguished in the fibres. The length and the diameter of these two parts were measured under a high power dissecting microscope, in a sample of 12 S fibres, dissected from adult crabs of the same size as those used for the electrophysiology (carapace width from 14 to 18 cm). The results (average ± standard deviation) were the following. The total length of the dendrite (minus the distal branches) was 0.87 ± 0.1 cm. The middle part of the dendrite, where the cross-section is apparently uniform, measured 0.57 ± 0.08 cm in length and 87 ± 7.5 μm in diameter; the more proximal part was 0.29 ± 0.05 cm long and tapered to 34 μm at its entry into the ganglion. The diameter of the T fibre is larger than that of the S fibre in the cylindrical and the tapered part, but the length is about the same.

Electrophysiological techniques

Receptors of the fifth and third legs were used for electrophysiology. The preparations were isolated by first cutting all the nerves originating from the thoracic ganglia, except for the sensory nerve in which the S and T fibres are found; next, the corresponding receptor muscle was cut to a length of about 1.5 cm. The part of the endosternite to which both the sensory nerve and the muscle are attached was then cut out and the preparation transferred to a thin plate of clear Sylgard (Dow Corning) in a Petri dish. The fragment of endosternite was firmly fastened to the Sylgard by means of fine stainless steel needles. The common connectival sheath of the sensory nerve was opened, and the S or the T fibres carefully freed from the other nervous elements. The fibre selected for study was then attached to the Sylgard plate throughout its entire length by pinning its sheath to the plate with fine cactus spines. During this phase of the procedure dendrites could be easily damaged; however, injuries at this stage could be recognized because the clear cytoplasm of the dendrites became granular at the point of damage. In addition, no response to stretch could be recorded from the part of the dendrite proximal to the injured region. The standard preparations included the ganglia.

During the experiments the preparation was continuously perfused with saline flowing at a rate of about 1.5-2 ml/min. Temperature of the inflowing saline was kept at 20-21°C with a thermoelectric device. The saline used, artificial sea water (ASW), was that suggested by Dalton (1958) except that morpholinepropanesulfonic acid (MOPS) was used instead of boric acid to buffer the solution to pH 7.2. Its composition, in mM, was as follows: Na 0.460; K 0.011; Mg 0.017; Ca 0.024; SO₄ 0.0191; Cl 0.516; MOPS 0.005. In some experiments the K content was reduced to 10⁻⁴ M (10⁻⁴ M-K ASW).

Recording techniques were conventional. Current was injected via a feedback circuit. Ground was provided by connecting the saline to the negative input of a
Electrical properties of a dendrite

high input impedance amplifier whose positive input was grounded, and whose output was used to monitor current. The electrodes were equilibrated pairs of platinized Ag/AgCl pellets embedded in a jelly of 1% agar in 4-3 M-KCl saturated with AgCl. The micropipettes were initially fashioned to have a tip resistance, in sea water, of 40 MΩ or more when filled with 3 M-KCl. These pipettes had a tip potential of between —10 to over —20 mV; in addition, they exhibited hysteresis and rectified when used to pass current. The electrical properties of the micropipettes were considerably improved when their tips were broken (Adrian, 1956) by gently touching them with a small strip of fine lapping paper (Imperial Lapping Film, 3M Company, 0.3 µm grade). In about half of the cases the tip resistance was reduced to between 10 and 20 MΩ, and the tip potential to —5 to —10 mV. These pipettes could pass a current of up to 10⁻⁷ A in either direction without gross rectification. In addition, breaking of the tip also facilitated a clean penetration of the sheath surrounding the dendrites, thus reducing the effects of the injury during insertion. Micropipettes with lower tip resistances (less than 10 MΩ) had much better electrical properties and, apparently, penetrated the sheath without damage. However, the values for the input resistance of the dendrite, obtained with these pipettes, were consistently lower than those obtained with micropipettes having higher tip resistances, and for this reason these pipettes were not used.

Mechanical stimuli were applied by stretching the receptor muscle. For this purpose the cut end of the muscle was ligated and attached to a small glass hook which was rigidly connected to the coil of an electromagnetic vibrator (Ling, Inc.) whose movement was controlled by voltage pulses of variable amplitudes. The vibrator was mounted on a micromanipulator so that it was possible to adjust manually the length of the muscle to slightly below its relaxed length in vivo.

The sudden displacement of the muscle due to the stretch pulses resulted in some turbulence of the flowing saline which could affect the stability of the microelectrodes. To minimize the possibility of microelectrode movement, stretch was usually applied in two equal steps.

RESULTS

Measurements taken and the effect of the microelectrode shunt

The types of experiments and the measurements taken are illustrated in Figs. 2–4. In the simplest type of experiment two microelectrodes were inserted in the fibre, each at a different distance from the bifurcation, to record the response to stretch and to measure the spatial decrement of the response in the fibre. In the example of Fig. 2 the first electrode was inserted at 0.7 mm from the bifurcation. Fig. 2A shows the response to a test stretch recorded about 1 h after the insertion of this electrode. Stretch was applied in two equal steps, each one resulting in a fast transient ($V_a$) followed by a steady-state plateau ($V_s$). The amplitude of $V_a$ remained approximately constant as long as the stretch was maintained. Fig. 2B shows the effects seen when the second electrode was inserted 4.2 mm more proximally. There was a small hyperpolarization of the fibre, and a small decrease of the amplitude of the steady-state component of the response to stretch (recorded at the distal site) from 22 to 19.5 mV. As shown in the Figure, the amplitude of both $V_a$
Fig. 2. Characteristics of the response to step stretch stimuli in the S fibre recorded simultaneously at 0.7 mm (lower trace) and at 4.9 mm (upper trace) from the bifurcation. Stretch was applied in two steps of equal amplitude, each step resulting in a fast transient, \( T_o \), followed by a steady-state plateau, \( V_s \) (see labels in the Figure). (A) Response recorded at the distal electrode just before the insertion of the proximal electrode. (B) Effect of the insertion of the second electrode; note, in lower trace the slight hyperpolarization of the fibre and the decrease in the amplitude of the steady-state response to stretch. The steady-state components of the response recorded at the distal site are labelled \( V_{rd} \) and \( V_{sd} \), and the same quantities recorded at the proximal site are labelled \( V_{sp} \) and \( V_{sd} \). (Subscripts \( p \) and \( d \) are used throughout this paper to indicate the relative positions in the fibre of the recording electrodes with respect to the sensory endings.) (C) Response to stretch recorded by the distal and the proximal electrodes about 1 h after B. The amplitude of both \( V_{rd} \) and \( V_{sd} \) at each recording point, is significantly larger; also larger are the ratios \( V_{rd}/V_{sd} \) and \( V_{sp}/V_{sd} \), whose magnitudes are inversely proportional to the spatial decrement of the response considered. In this and in the following Figures the transmembrane potential of the non-stimulated fibre is indicated, in mV, above the experimental traces. The two time scales correspond to the two speeds at which the chart recorder was run during the experiments. The portion of the records obtained at the slower speed can be recognized from the thicker trace.

and \( V_s \) was considerably smaller at the proximal than at the distal recording point. Using \( p \) and \( d \) as subscripts to indicate the relative positions of the recording electrodes, the ratio measuring the spatial decrement of the fast component can be indicated as \( V_{sp}/V_{rd} \) and the ratio for the decrement of the steady-state components as \( V_{sp}/V_{rd} \). In Fig. 2B these two ratios were 0.75 and 0.82, respectively. Fig. 2C shows the response to the same test stretch 1 h after the insertion of the proximal electrode. The amplitude of each component had significantly increased, especially at the proximal point, the ratios measuring the spatial decrement of the two components of the response being \( V_{sp}/V_{rd} = 0.90 \) and \( V_{sp}/V_{rd} = 0.93 \). The resting potential had decreased to \(-63 \) mV.

The data suggest that the insertion of each electrode was accompanied by a local injury which resulted in a leakage shunt (Hodgkin & Nakajima, 1972). The leakage associated with each electrode was large enough to seriously affect the amplitude of the response to stretch. However, the leakage was, at least partially, sealed with time, as witnessed by the marked increase of both \( V_{sp} \) and \( V_{sd} \) recorded 1 h after the insertion of the proximal electrode, with respect to the values recorded immediately after the electrode entry. \( V_m \) was also affected by the microelectrode leakage, but, at least in this experiment, only to a minimal extent.

Fig. 3 illustrates the second type of experiment. In this case two microelectrodes
Electrical properties of a dendrite

Fig. 3. Effects of the microelectrode shunt on the transmembrane potential and on the input resistance of the S fibre. Two electrodes were inserted at about 1.8 mm from the bifurcation, one to record the membrane potential (trace shown) and the second to inject current (trace not shown). A, B and C are consecutive records. Note in A (arrow) the large depolarization and the decrease in the amplitude of the response to a test stretch produced by the insertion of the second electrode. Response to stretch marked by an asterisk. During the recovery (B and C) the fibre hyperpolarized to about $-73$ mV and then depolarized to $-60$ mV. The input resistance, $R_I$, was monitored during the recovery by a current pulse of $9$ nA, 1 s in duration, repeated every 15 s. Note that $R_I$ was only $0.8$ MΩ when $V_m$ was $-74$ mV (arrow in trace C) but increased to $2.4$ MΩ after recovery. (D) Response to stretch and to a current pulse of $5.4$ nA recorded after recovery.

were both inserted close to the bifurcation of the S fibre, the interelectrode distance being slightly less than 0.3 mm. One of the electrodes was used to inject current. Thus the input resistance of the fibre, $R_I$, could be measured as the ratio between the steady-state transmembrane potential changes, $V_m$, and the current injected, $I$. Only the trace of the voltage recording electrode (inserted first) is shown in the Figure. In this case the entry of the second electrode resulted in a severe injury as shown by the large depolarization and by the drastic reduction of the amplitude of the response to stretch (see legend to the Figure). The input resistance, measured shortly after the entry of the current electrode, was less than 0.5 MΩ (Fig. 3A, see legend). Recovery took more than 3 h; the final value recorded for $R_I$ was 2.4 MΩ. In the same time interval $V_m$ increased from less than 3 mV to 24 mV.

The experiment illustrated in Fig. 3 is an extreme case, and, as a rule, the injury produced by the microelectrode entry was much less obvious, as in the example of Fig. 2. The results of Fig. 3 are worth discussing, however, because they demonstrate quite clearly that in the coxal receptors the value of the resting potential alone could not be used as a criterion to judge the status of the preparation, and hence the
validity of the data. This finding is in marked contrast with what has been observed in muscle fibres, the only other preparation in which the effect of the leakage associated with the microelectrode has been studied (Hodgkin & Nakajima, 1972; Stefani & Steinbach, 1969). Thus, the S fibre hyperpolarized during recovery from the injury produced by the microelectrode insertion, and the highest values for the transmembrane potential, $V_m$ (−74 mV) was recorded when $R_T$ was only 0·8 MΩ (see arrow in Fig. 3 B). By contrast, when $R_T$ reached its maximum, $V_m$ was reduced to −60 mV.

In the third type of experiment, illustrated in Fig. 4, three microelectrodes were used. Two of them were inserted close together (0·3 mm or less) to measure $R_T$, as in the experiment discussed in Fig. 3, while the third electrode was inserted several millimetres or more away from the first pair. In this manner it was possible to measure the amplitude of the response to injected current at the locus of current injection, $x = 0$, and also $x$ mm away. Using 0 and $x$ as subscripts to indicate the position of the two recording electrodes, the responses recorded at the two points can be indicated as $V_{io}$ and $V_{ix}$. The ratio $V_{ix}/V_{io}$ is a measure of the spatial distribution of the charges resulting from the flow of injected current. The third electrode could be positioned either proximally, with respect to the pair used to measure $R_T$, or distally; when the third electrode was proximal, the ratio $V_{ix}/V_{io}$ was dependent on the same input parameters as the ratio $V_{sp}/V_{sd}$ measuring the decrement of the response to stretch. In this case both ratios resulted from the gradient of an axial current flowing from a distal position in the fibre into the fibre’s proximal end. By contrast, when
Electrical properties of a dendrite

the third electrode was distal with respect to the electrode pair used to measure \( R_T \) then the magnitude of \( V_{ts}/V_{t0} \) depended on the gradient of an axial current flowing from a proximal point into the distal moiety of the fibre. Thus with the three-electrode experiments it was possible not only to compare the spatial decrement of the response to stretch with the decrement of the response to injected current, but also to explore, to a limited extent, the input properties of the proximal end of the neurone and those of its distal end.

Before examining the results obtained in more detail, a few more words on the leakage associated with the microelectrodes are necessary. The effects of this shunt were seen in all the experiments done, although their magnitudes differed greatly from case to case, as shown by the examples discussed. They were most obvious immediately after a microelectrode was inserted and were progressively reduced with time (Figs. 2-4). Because of the long recovery times involved, it was not practical to study the spatial decrement of the responses to stretch and to injected current by inserting an electrode in succession at different points in the same fibre. Instead the problem had to be studied on a statistical basis by using data obtained in different experiments. For the same reason it was not possible to estimate directly the magnitude of the shunt associated with the microelectrodes after recovery. Since values as high as 2·5-3 M\( \Omega \) were measured for the combined resistances of the fibre plus the leakage (\( R_T \), Table 1), even when three microelectrodes were used, it is clear that the shunt resistance must have been quite large after recovery. The average shunt resistance associated with each microelectrode, after recovery, was estimated to be at least 20 M\( \Omega \). This estimate is based on a comparison between the characteristics of the observed spatial decrement of the response to stretch and those expected on the assumption that no leakage shunt was present. The theoretical treatment of this problem is given in the Appendix to this paper; the data are shown and discussed in the legend to Fig. 7.

Input properties of the S fibre

As already stated the input resistance, \( R_T \), was measured by injecting small current pulses. In all of the 11 cases studied \( R_T \) was 1 M\( \Omega \) or less at the beginning of the experiments but increased progressively over the next several hours reaching, ultimately, values as high as 2-3 M\( \Omega \) (Table 1). In the same cells the transmembrane potential, \( V_m \), ranged from -58 to -73 mV. Undoubtedly much more of the variability of \( V_m \) and \( R_T \) reflects causes which could not be properly controlled, such as the condition of the animals and injuries to the preparation during the dissection. Part of it, however, seems due to the different degrees of recovery from the damage produced by the microelectrode entry; this is particularly true for the experiments in which low values for the input resistance were measured. There was no clear correlation between the magnitude of \( R_T \) and the position of the electrodes in the fibres (Table 1).

Small inward and outward current steps of equal intensity resulted in potential changes of approximately equal amplitude (Fig. 5); with larger current, however, the responses were distinctly asymmetrical, indicating that the input resistance of the S fibre was voltage dependent.

The \( IV \) relationship was studied using slow-rising triangular current ramps (Marmor, 1971, 1975), since the micropipettes rectified when attempts were made to use current steps of high intensity. Electrode rectification and hysteresis were
Table 1. *Input properties of the S fibre*

<table>
<thead>
<tr>
<th>Expt no.</th>
<th>x (mm)</th>
<th>$V_m$ [mV]</th>
<th>$R_T$ [MΩ]</th>
<th>$t_{84%}$ (ms)</th>
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Average

<table>
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<tr>
<th>± standard deviation</th>
<th>$V_m$</th>
<th>$R_T$</th>
<th>$t_{84%}$</th>
</tr>
</thead>
<tbody>
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<td></td>
<td>-63</td>
<td>2.1</td>
<td>139</td>
</tr>
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</table>

$x$, point, in mm, from the distal bifurcation of the fibres, at which the voltage recording electrode was inserted. Current injecting electrode was inserted within 0.3 mm from the recording electrode.

$V_m$, transmembrane potential of the unstimulated fibres.

$R_T$, input resistance, as determined by small hyperpolarizing current pulses.

$t_{84\%}$, time at which the voltage transient, resulting from injecting current pulses, reached 84% of their final value ($V_m$).

The values for $R_T$ and $t_{84\%}$, reported in the Table, are the averages of the three highest values measured for these quantities in each experiment. Value of $V_m$ reported corresponds to when $R_T$ was measured.

Fig. 5. Transmembrane potential changes (lower trace) recorded at about 1 mm from the bifurcation in response to a hyperpolarizing and a depolarizing current pulse. Current (upper trace) was a 4.4 nA pulse, 4.5 s in duration. The time ($t_{84\%}$) at which the voltage transients reached 84% of the value recorded at the end of the pulse ($V_m$) was about 160 ms for both the hyperpolarizing and the depolarizing pulses.

Fig. 6. The IV curves thus obtained were practically linear when $R_T$ was 1 MΩ or lower, but revealed a complex series of rectifying processes when $R_T$ was larger. Rectification was present in both the hyperpolarizing and depolarizing quadrants. In the hyperpolarizing quadrant the ramp IV relationships were approximately linear up to about -100 mV; inward-going rectification became evident around -130 mV, and for more negative
Electrical properties of a dendrite

Fig. 6. IV relationship recorded in the proximal part of the S fibre using current ramps. Both current (I) and voltage (V_m) traces are shown. Note voltage dependence of the steady-state input resistance, complex sequence of rectification in the depolarizing quadrant, and high conductance state in the extreme of the hyperpolarizing quadrant. On cessation of both inward and outward current ramps, the fibres remained depolarized (hysteresis). Voltage calibration shown on vertical scale; horizontal bar: 50 s, 25 nA.

values of V_m, the relationships were characterized by a ‘high conductance state’ (Marmor, 1971, 1975) during which the transmembrane potential became unstable, as has been shown in molluscan neurones (Marmor, 1971, 1975). In the depolarizing quadrant rectification was outward-going up to about —20 mV, inward-going between —20 and +10 mV, and again outward-going above +10 mV. The limits given for these rectification ranges are approximate, and some variability was found among the different cells examined. Injection of current resulted in a hysteresis, particularly when long-lasting ramps were used (Fig. 6, see legend).
Table 2. Spatial decrement of the responses to stretch and to current pulses in the S fibre. Data obtained in three-electrode experiments

<table>
<thead>
<tr>
<th>Expt no.</th>
<th>Δx (mm)</th>
<th>$V_{ps}/V_{pd}$</th>
<th>$V_{sp}/V_{pd}$</th>
<th>$V_{ts}/V_{to}$</th>
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<td>Average</td>
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<td>0.75</td>
<td>0.91</td>
<td>0.80</td>
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</tbody>
</table>

A. Current electrode proximal

| 5        | 7.0     | 0.41            | 0.86            | 0.87            |
| 6        | 6.9     | 0.44            | 0.86            | 0.91            |
| 7        | 3.6     | 0.89            | 0.94            | 0.94            |
| 8        | 4.8     | 0.89            | 0.94            | 0.93            |
| Average  | 5.6     | 0.66            | 0.90            | 0.91            |

B. Current electrode distal

Experiment 6 was done on the same fibre as Expt 2, and Expt 8 on the same fibre as Expt 4.

Δx, distance between recording electrodes.

$V_{ps}/V_{pd}$ and $V_{sp}/V_{pd}$, ratios between the amplitudes of the fast transient ($V_p$) and of the steady-state component ($V_s$) of the response to stretch, recorded at the proximal (p) and the distal points (d).

$V_{ts}/V_{to}$, ratio between the amplitude of the steady-state transmembrane potential changes recorded when a current pulse was injected at $x = 0$; $V_{ts}$ is the response recorded at the site of current injection; $V_{to}$ is the response recorded $Δx$ mm away.

Values given for $V_{ps}/V_{pd}$, $V_{sp}/V_{pd}$ and $V_{ts}/V_{to}$ are averages for the three highest values recorded for each ratio during the experiment.

**Spatial decrement of the steady state response to stretch and to injected current**

Table 2A and B summarizes the results obtained in the eight experiments in which the spatial decrement of the response to stretch and to injected current were studied. It is evident, by inspection of the data, that the decrement of $V_s$ was quite small: this quantity was reduced, on average, by only 9% over a mean distance, Δx, of 5.6 mm. For this reason alone it would be reasonable to suspect that the response to stretch propagates, at least in part, through an active response. However, an equally small spatial decrement characterized the propagation of the steady-state response to current steps in those cases where the current-injecting electrode was distal (Table 2). In considering the spatial decrement of the response to injected currents, the involvement of an active response could be excluded because the value of the ratio $V_{ts}/V_{to}$ was about the same when hyperpolarizing or depolarizing current steps were used, provided that current was of small intensity. With larger currents $V_{ts}/V_{to}$ was larger with hyperpolarizing currents than with depolarizing ones, as would be expected on the basis of the $IV$ relationship.

Since the S fibre is a little less than 1 cm long, the small spatial decrement of $V_s$ and of $V_t$ could suggest that the fibre may be equivalent, for currents flowing from its distal to its proximal end, to a short closed cable (Shaw, 1972; Weidman, 1952). However, the results of a graphical analysis of the data (Fig. 7) do not support this interpretation, and suggest that the dendrite could also be equivalent to a semi-infinite cable characterized by a length constant of about 6 cm. The analysis was done by adjusting to the experimental points curves calculated from the equations of monodimensional cable theory (Jack, Noble & Tsien, 1975; Rall, 1959). The data could be reasonably fitted by only two of the mathematical models considered (see
Electrical properties of a dendrite

Fig. 7. Spatial decrement of the steady-state response to stretch in the S fibre. The data plotted (points) are those reported in Table 2 plus those obtained in 11 additional experiments in which only two microelectrodes were used. The two straight lines drawn through that data both correspond to a semi-infinite cable model (\( V_{sd}/V_{ad} = -\Delta x/\lambda \)), while the two curves labelled \( L = 0.5 \) and \( L = 0.4 \) correspond to the model of a short cable of length \( l = 1 \) cm, terminated at \( x = l \) by an open circuit.

\[
\ln \frac{V_{sd}}{V_{ad}} = \frac{\Delta x}{\lambda} \left( \frac{\cosh \frac{x}{\lambda}}{\cosh \frac{1}{\lambda}} \right).
\]

The best fitting to the data is given by the dashed line which was calculated by the least squares method; the slope of this line corresponds to a \( \lambda \) of 7.2 cm. Note, however, that this line intercepts the vertical axis well below the origin. This deviation can be explained as being due to the systematic error introduced by the leakage shunt associated with the microelectrodes. A quantitative analysis of this problem is given in the Appendix. The dotted line was drawn, taking this error into account, through the origin and through the centre of mass of the points corresponding to \( \Delta x \geq 4 \) mm, which should be less affected by the microelectrode shunt (see Appendix for further explanation). The slope of this line corresponds to a \( \lambda \) of 5.8 cm. The curve labelled \( L = 0.5 \) corresponds to a closed cable of length constant \( \lambda = 2 \) cm (\( L = l/\lambda \)); this curve fits the data reasonably well except for the points at or near the origin and for the two points corresponding to \( \Delta x > 6 \) mm. Other curves drawn using the equation of the closed cable model but significantly different values of \( \lambda \) and \( l \) did not fit the data at all (the curve labelled \( L = 0.4 \), calculated for \( l = 1 \) cm and \( \lambda = 2.5 \) cm, is an example of the poor fitting obtained).

Legend to Fig. 7 for more details): a semi-infinite cable of length constant \( \lambda = 5.8 \) cm (dotted line) and a short cable of length \( l = 1 \) cm and length constant \( \lambda = 2.0 \) cm, terminated at one end (\( x = l \)) by an open circuit (closed cable; curve labelled \( L = 0.5 \)). Both the straight line corresponding to a semi-infinite cable and the curve describing the closed cable deviate from the experimental points at or near the
Fig. 8. (A, B) Oscilloscope records of the initial transient response to a step stretch ($V_d$) recorded simultaneously at two different points in the S fibre. (A) Recording points at 1.1 and 5.9 mm from the bifurcation; the ratio $V_{as}/V_{sd}$ is 0.88. (B) Recording points at 7.7 and 0.8 mm from the bifurcation; the ratio $V_{as}/V_{sd}$ is 0.44. In both A and B the upper trace is that of the distal recording electrode. Note in B that the shape of the response is considerably slower at the proximal than at the distal recording point. (C) Response to a brief current pulse injected near the distal electrode in the same experiment as A. Upper trace—current; middle trace—response recorded at the distal electrode; lower trace—response recorded at the proximal electrode. Calibration: A, 5 mV per division for both traces; B, 10 mV for upper trace and 5 mV for lower trace; C, 5 mV, both voltage traces; Current trace: $10^{-7}$ A per division; time 20 ms per division in A, B and C.
Electrical properties of a dendrite

Fig. 9. Responses to progressively larger stretches applied in a single step (upper row) or in two steps (lower row). Stretch strength is indicated below each record as percentage increase in the length of the receptor muscle. The amplitude of the steady-state response ($V_s$) increased gradually with stretch strength, but the initial transient ($V_t$) was graded only for stretches of small strength and became all-or-none with larger stretches. Peak of $V_t$ indicated by a dot in each record. Membrane potential was $-62$ mV.

origin. As shown in the Appendix this deviation is to be expected on the basis of a systematic error introduced by the microelectrode shunt (see legend to Fig. 7). In addition, the short cable model deviates from the experimental data in the extreme right of the range. In this case the deviation cannot be explained as being due to a systematic error, and suggests a genuine discrepancy between this model and the experimental points. However, the data considered are subject to a considerable variability since they were obtained in different experiments. By themselves, therefore, the results discussed in this section are not sufficient to discriminate between the two models considered.

Spatial decrement of the initial transient of the response to stretch

A more complete description of the cable properties of the S fibre was obtained by also considering the propagation of the fast component of the response, $V_a$. The basic datum is that $V_a$ propagated with a larger loss in amplitude than the steady-state component, $V_s$. Fig. 8 A and B gives a qualitative illustration of the phenomenon which is documented quantitively in Table 2. In all the cases examined the ratio $V_{sp}/V_{ad}$ was smaller than the ratio $V_{ap}/V_{sd}$, the difference between the two average
ratios being highly significant (see Table 2 legend). Since $V_a$ propagated according to the passive cable properties of the fibre, it follows, a fortiori, that $V_a$ should also have been propagated passively and not by an active response. Other characteristics of the propagation of the initial fast transient which supports this conclusion may be summarized as follows: first, the difference between $V_{ap}/V_{ad}$ and $V_{ep}/V_{ed}$ was larger, the larger was the distance between the recording electrodes (Fig. 8A and B; Table 2); second, the time course of the transient became distinctly slower the more proximal was the recording point (same Fig.). These results are in qualitative agreement with those expected in the case of the passive propagation, in a cable, of the transient response to a brief current pulse (Jack, Noble & Tsien, 1975, pp. 46–57).

It should be stressed that this conclusion does not contradict the results obtained by Roberts & Bush (1971) who have shown that in Carcinus coxal receptors the initial fast transient originates as a partial Na$^+$ action potential. In fact the all-or-none character of $V_a$ can be clearly demonstrated also in Scylla (Fig. 9, see legend). However, in the Scylla preparation only the most distal region of the dendrite could generate an active response (Fig. 10).

$V_a$ propagates passively in the S fibre with the same decrement as that of the response to very brief current pulses (compare Fig. 9A and C). Therefore, the functional dependence of $V_{ap}/V_{ad}$ on the interelectrode distance, $\Delta x$, and on the fibre's length constant, $\lambda$, should be described by one of the curves of the graph.
given by Jack et al. (1975, p. 76). One of these curves describes the case of an infinite cable while the others apply to short cables of different lengths terminating in closed ends. The experimental values of $V_{ap}/V_{ad}$ measured from oscilloscope records were between 0.32 and 0.90, the corresponding value of $\Delta x$ lying between 7 and 3.5 mm (Table 2). For this range of values of $V_{ap}/V_{ad}$ the influence of the end conditions is negligible, and all the curves superimpose. Thus $\lambda$ can be obtained directly from the value of $\Delta x/\lambda$ corresponding to the ratio $V_{ap}/V_{ad}$ measured. $\lambda$ thus calculated ranges from 3.2 to 5.3 cm (Table 2), the average being 4.3 cm.

None of the data obtained in this analysis support the hypothesis that the S fibre is equivalent to a closed cable, for current flowing from its distal to its proximal end, unless a large value of $\lambda$ is assumed (at least 3.2 cm). However, as shown in the graph of Figure 7, the curves corresponding to a closed cable calculated for a value of $\lambda$ larger than 2 cm grossly deviate from the experimental points (see in Fig. 7 the curve labelled $L = 0.4$). Thus when the results of the analysis of the spatial decrement of both components of the response to stretch are considered together, the closed cable model must be rejected. By exclusion, therefore, the semi-infinite cable should be considered as the one which provides the best fitting to the data. The value of 5.8 cm calculated for $\lambda$ from the graphical analysis of the decrement of $V_{ap}$, assuming a semi-infinite cable model, is about 25% larger than the average (4.3 cm) obtained from the decrement of $V_{ap}$. However, the difference is not large enough to provide a serious objection to this interpretation. Both sets of data are subjected to considerable error, as already observed; moreover, the function calculated by Jack et al. converges rapidly, when $V_{ap}/V_{ad}$ approaches 0.85, toward a value of $\Delta x/\lambda$ equal to 0.1, so that for values of $V_{ap}/V_{ad} \geq 0.85$, $\lambda$, calculated from the decrement in the peak amplitude of the fast transient, is systematically underestimated.

Electrotonic asymmetry of the S fibre

In four of the eight experiments in which three electrodes were used, the current electrode was placed in a proximal position. In this case the attenuation of the response to an injected step current depended on the input properties of the distal branches. The results reported in Table 2 show that $V_{ix}/V_{io}$ was significantly smaller with this configuration of the electrodes than in the case where the current electrode was distal. When the current electrode was proximal, $V_{ix}/V_{io}$ was, on average, 0.80 for a mean interelectrode distance of 5.7 mm; by contrast, with the opposite electrode configuration the value of this ratio was 0.91 for the same mean interelectrode distance (5.6 mm). This difference could not be due to a systematically larger shunt of the electrodes because the input resistance ($R_T$) was, if anything, larger when the current electrode was proximal than when it was distal (Table 1). Although the number of data is too small to allow a quantitative analysis, they suggest that the non-stimulated S dendrite has asymmetric electrotonic properties, with its distal end having a smaller input resistance than its proximal end. The results discussed in the previous sections suggest that the dendrite is equivalent to a semi-infinite cable for current flowing from its proximal to its distal end. It follows that the distal moiety of the S fibre should be equivalent to a short cable terminated by a leaky end. Additional support for this conclusion has also been obtained by an analysis of the time course of the transient responses to injected currents, discussed next.
Voltage transients recorded in response to current pulses

The properties of the S dendrite as a passive cable should also be reflected in the time course of the charging curves recorded when current pulses are injected. The voltage transients recorded at the point of current injection were all characterized by a noticeable creeping, with the voltage increasing continuously, albeit by minimal increments, even when current pulses several seconds long were used (Fig. 5). The first part of these transients could be fitted, with good approximation, using theoretical curves describing the behaviour of an infinite cable (Hodgkin & Rushton, 1946). Assuming this model, the time constant of the membrane should be equal to the time \( t_{84\%} \) at which the transmembrane potential reached 84\% of its final value \( V_\infty \). The values for \( t_{84\%} \) thus determined ranged from 85 to 190 ms (Table 1). However, if the latter portion of the transients was also considered, then the infinite cable model resulted in a poor fitting, with the experimental data being, for most of the range, significantly smaller than the corresponding values calculated from the equations of Hodgkin and Rushton.

A satisfactory interpretation of these results can be given assuming that the S fibre is equivalent to a semi-infinite cable terminated by a short circuit. The theoretical analysis of the problem is shown in Fig. 11 and was done by first calculating the charging curves corresponding to a semi-infinite cable terminated with an open circuit (closed end termination), and those corresponding to a semi-infinite cable terminated in a short circuit. These curves were calculated using the method of reflexion (Hodgkin & Nakajima, 1972; Jack et al. 1975). Next, the time scale of each theoretical curve was normalized, using as a unit, the time at which, in each case, the calculated function reached 84\% of its final value. The results of this procedure (Fig. 11) show that for a closed cable (for which \( t_{84\%} \) is larger than the membrane time constant), the points of \( V/V_\infty \) lag with respect to the corresponding points in the curve for an infinite cable for times smaller than \( t_{84\%} \) (Fig. 11 A). For the cable terminated in a short circuit, for which the \( t_{84\%} \) is smaller than the circuit time constant, the reverse is true (Fig. 11 B).

All the experimental traces deviated from the infinite cable model in the manner characteristic of a shorted cable (Fig. 12). This result could have arisen either because of the passive cable properties of the fibre or because of a time and/or voltage dependence of the membrane resistance or, finally, as a consequence of the shunt associated with the microelectrodes. In all of these cases (or combinations thereof) the input admittance of the equivalent circuit of the dendrite plus the microelectrode shunt would be expected to increase during a current pulse, relative to the admittance of an infinite cable. However, although both changes in the membrane resistance and microelectrode shunt may have influenced the results, their effect was probably minor. First, the transients analysed were obtained with small hyperpolarizing currents and thus in the linear range of the \( IV \) relationship. Secondly, the transients conformed to the short cable model even when \( R_T \) was larger than 2.5 M\( \Omega \) and when, therefore, the microelectrode shunt was relatively small. Finally, the deviation characteristic of a cable terminated in a short circuit, though present, was considerably reduced when the fibres were exposed to saline containing only \( 10^{-4} \) M-K in spite of the fact that the input resistance of the fibre was considerably increase.
Fig. 11. Theoretical analysis of the deviation from the infinite cable model of semi-infinite cables terminated in an open circuit (A) or in a short circuit (B). In both graphs the smooth curve was drawn from the equation $V/V_\infty = \text{erf}\sqrt{T}$, describing the time course of the voltage transients expected in an infinite cable at the point of current injection when current pulses were injected. $V_\infty$ is the final (steady-state) value of $V$; $T$ is the time normalized in terms of the time constant, $\tau$ ($T = t/\tau$), and the abbreviation erf stands for error function. The points in Fig. 11A were obtained by first drawing the curve of the equation

$$\frac{V}{V_\infty} = 2 \text{ erf}\sqrt{\tau'} + \exp(-2L) \text{ erf c} \left(\frac{L}{\sqrt{\tau}} - \sqrt{\tau'}\right) - \exp(2L) \text{ erf c} \left(\frac{L}{\sqrt{\tau}} + \sqrt{\tau'}\right),$$

describing the time course of voltage transients in a cable terminated by an open circuit (closed cable). In the equation $\tau' = t/\tau$, $L$ is the distance, $l$, between the closed end termination and the point of current injection and voltage recording, divided by the cable length constant, $\lambda$; the abbreviation erf c stands for error function complement. Selected points of this curve were then redrawn as dots in the Figure, after dividing $\tau'$ by the value $\tau'_{\text{open}}$ for which $V = 84\% V_\infty$. The points in Fig. 11B were obtained in the same manner, except that the equation considered was

$$\frac{V}{V_\infty} = 2 \text{ erf}\sqrt{\tau'} - \exp(-2L) \text{ erf c} \left(\frac{L}{\sqrt{\tau}} - \sqrt{\tau'}\right) + \exp(2L) \text{ erf c} \left(\frac{L}{\sqrt{\tau}} + \sqrt{\tau'}\right),$$

describing a cable terminated in a short circuit. For both cases $L$ was assumed to be 0.25. However, the deviation of the points corresponding to the two semi-infinite cables from the curve of the infinite cable would be of the same sign even if other values of $L$ are considered.
Electrical properties of a dendrite

when the extracellular K was reduced (Fig. 12A and B). If the deviation from the infinite cable model were due simply to the shunt, then it should have become more marked in low K saline. The fact that the opposite was observed suggests that the shape of the transient was not due to the recording conditions, but reflects instead the intrinsic properties of the fibre.

The time course of voltage transients in a short cable depends on the resistance load of both terminations. There is evidence, as already argued, that the distal part of the S fibre is equivalent to a leaky ending, and this fact alone could explain the characteristic deviation of the transient from the infinite cable model. Since the input resistances of the proximal and of the distal end of the S fibre are not known with any reliable approximation, a quantitative interpretation of the data is not possible. On a qualitative basis, however, it is safe to conclude that the time constant of the surface membrane of the S dendrite is larger (by an undetermined amount) than the $t_{44\%}$ calculated from the voltage transients reported in Table 1. This conclusion may be stated in a manner which has more immediate physiological significance: the voltage transients in the S fibre have a time course which is faster (albeit by an undetermined amount) than that expected if the fibre were an infinite cable.

Observations on the $T$ fibre

A number of experiments were also made on the T fibre, and Fig. 13 illustrates some of these results. The response to step stretches was similar to that of the S fibre, being characterized by both an initial fast transient and a steady-state response. The release after-potential was a large hyperpolarization, even when the resting potential was about $-60$ mV, and its time course was considerably faster than that of the after potential of the S fibre. The ratios measuring the spatial decrement of the steady-state response to stretch and to injected current were of the same order of magnitude, for comparable interelectrode distances, as those measured for the S fibre. An asymmetry between the axial potential gradients resulting from a proximal and a distal position of the current source was also evident (see legend to Fig. 13). The time course of the voltage responses to injected current pulses appeared to be faster than that seen in the S fibre ($t_{44\%} \approx 120$ ms in the example), even when there was, apparently, a good sealing of the microelectrode shunt as judged by the input resistance. The transients were characterized by a pronounced deviation from the infinite cable model, a deviation which, even in this case, was the one expected for that of a short cable terminated in a leaky ending. The $IV$ relationship was similar to

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Fig. 12. Comparison of the time course of the transients recorded in the S fibre in response to a current pulse with the time course expected in the case of an infinite cable. The transients analysed were recorded from the same fibre: (A) in control ASW ($1.1 \times 10^{-4}$ M-K); (B) in low K ASW ($1 \times 10^{-4}$ M-K). In both cases the current injected was a $45 \text{nA}$ pulse, $3.5$ s long. The voltage recording electrode was at $5.5$ mm from the bifurcation, and the current injecting electrode was $0.3$ mm more proximal. The analysis was done according to the procedure outlined in the text and in the legend to Fig. 11 using the chart records shown in the insets and also oscilloscope records of the initial part taken on a faster time base. In both control ASW and low K ASW the points calculated from the traces (dots) deviate from the curve describing the behaviour of an infinite cable in the manner expected of a short cable terminated by a short circuit. Note that in low K ASW the fibre depolarized (from $-60$ mV to $-48$ mV) while its input resistance increased from $2.5$ to $3.5 \text{M}\Omega$. More comments on the effects of low K + saline are found in the following paper (Mirolli, 1979).
Fig. 13. Responses of a T fibre to stretch and to current pulses recorded at 1 mm from the bifurcation (upper trace) and 5.3 mm more proximally (lower trace). Current was injected by a third microelectrode inserted about 0.2 mm from the proximal one (trace not shown). Note hyperpolarization on release of stretch and also the different spatial decrement of the response to stretch and to injected current ($V_{SP} / V_{SD} = 0.90; V_{IS} / V_{IA} = 0.86$). Note large decrease in the input resistance during stretch. Further comments in text.

that obtained in the S fibre in the hyperpolarizing quadrant and also in the depolarizing quadrant up to $-20 \text{ mV}$. No data were obtained for the remainder of the depolarizing range.

DISCUSSION

The results presented in this paper confirm, in general, the earlier results obtained by Roberts & Bush (1971), Bush & Roberts (1971) and Cannone (1974). In both Scylla and Carcinus mechanical stimulation of the sensory endings of the coxal receptors resulted in graded potentials which propagated with decrement in the fibres. Because of the unusually low spatial attenuation of these potentials, it was legitimate to question whether their propagation was entirely dependent on the passive cable properties of the fibres. The results obtained in Scylla clarify this point. Propagation of the response to stretch is passive since an equally low spatial attenuation was measured when the responses to either hyperpolarizing or depolarizing current pulses were studied.

According to the measurements taken, the middle part of the dendrite of the S fibre of Scylla can be considered equivalent, for its passive electrical properties, to a semi-infinite cable terminated at one end by a partial short circuit (leaky end termination). The presence of a leaky end termination is suggested by the time course of the voltage responses to current pulses. In addition, a comparison between the axial potential gradients, resulting from currents injected either proximally or distally, suggest that the leaky end should be associated with the distal part of the fibre. These results are of intrinsic interest because they illustrate different aspects
of the remarkable adaptation of the coxal receptors for the transmission of graded potentials.

Since both components of the response to a step stretch, the fast initial transient \(V_a\) and the steady state plateau \(V_t\), propagate passively in the S fibre, two independent estimates for the length constant \(\lambda\) were obtained. The estimate based on \(V_s\), namely 5.8 cm, is larger than the 4.3 cm obtained from the measurements of \(V_e\) (Table 2) although, as already made clear in the Results section, the latter is probably an underestimate. In any case, irrespective of which of these two values is chosen, the length constant of the S fibre of Scylla is larger than any other value thus far calculated for a nerve cell: Hodgkin & Rushton (1946) measured a length constant of only 1.61 mm for large lobster axons, 75 \(\mu\)m in diameter; Mellon & Kaars (1974) estimated \(\lambda\) to be 0.858 mm in the axons of a crayfish sensory neurone, 18 \(\mu\)m in diameter; Shaw (1972), assuming a closed cable model, estimated that the \(\lambda\) of Balanus photoreceptor axons (15 \(\mu\)m in diameter) was 4.9 mm. Much closer to the values measured in Scylla is the value of 16 mm which Cannone (1974) has calculated for the T fibre of Carcinus. The \(\lambda\) found in the Scylla preparation is very large even when compared to the giant fibres of the cephalopods: the axons of Sepia (about 200 \(\mu\)m in diameter) have a length constant of up to 1 cm (Weidman, 1951); slightly smaller values may be computed for the larger fibres of Loligo from the values of the diameter and the surface and internal resistivity of these axons (Hodgkin, Huxley & Katz, 1952; Hodgkin & Huxley, 1952). A value of 2.0 cm was estimated for the giant axon of Anisodoris, a gastropod (Gorman & Mirolli, 1972).

From the values of \(\lambda\) found it is possible to calculate the specific membrane resistance of the fibre, \(R_m\), or, more precisely, a range of values of this quantity. In a semi-infinite cable, \(R_m\) and \(\lambda\) are related by the equation \(R_m = 2\lambda^2R_t/a\), where \(a\) [cm] is the radius of the fibre and \(R_t\) [\(\Omega\cdot\text{cm}\)] is the specific resistance of the axoplasm. The cylindrical part of the S fibre has an approximately circular cross-section of radius 43.5 \(\times\) 10^{-4} cm. No direct measurements of \(R_t\) are available for Scylla, but it is fair to assume that the value of this quantity should lie between the extreme values measured in other nerve cells: 50 \(\Omega\) cm (Carpenter, Hovey & Bak, 1975; Cole, 1975) and 90 \(\Omega\) cm (Hodgkin, 1947). Accordingly, the \(R_m\) corresponding to the lower estimate of \(\lambda\) (4.3 cm) should be between 0.25 and 0.76 M\(\Omega\) cm^2. Larger figures are obtained if the upper estimate of \(\lambda\) is used. These values of \(R_m\) are high but not unreasonably so, and comparable ones have been reported for other biological membranes (Carpenter, 1973; Gorman & Mirolli, 1972; Marmor, 1975; Millecchia & Mauro, 1969; Weidman, 1951).

It should be emphasized that these estimates of \(\lambda\) and of \(R_m\) are only valid for the cylindrical part of the S fibre and not for the remainder of the cell. The response to stretch decrements in the fibre as if the input resistance of the tapered part and of the intraganglionic region were equivalent to that of an infinite extension of the fibre. It follows that if the intraganglionic portion of the neurone had the same specific membrane resistance calculated for the fibre, its total surface area should be that of a cylinder 80 \(\mu\)m in diameter and as long as about twice the calculated \(\lambda\), or 8–13 cm (Rall, 1959). Since the intraganglionic portion of the S neurone is only a few millimetres long, and has a diameter distinctly smaller than that of the fibre itself (Bush, 1976), it is clear that its input conductance depends either on a value of \(R_m\) consider-
ably lower than that calculated for the fibre, or on a profuse branching (Rall, 1959), or a combination of both factors.

A similar problem arises upon consideration of the conductance of the distal end of the fibre, except that in this case the input resistance to be considered should be less than that of the proximal end because the distal part of the fibre seems to have the properties of a leaky end termination. Although the distal branches of the S fibre are only 1–2 mm long, their surface area can be many times larger than that of a simple cylinder of equal diameter and length. This is due to the presence of surface infoldings and of numerous small tubular structures, called dendritic ‘fingers’ by Whitman (1965), which are thought to be the sites of electromechanical transduction (Krauhs & Mirolli, 1975). It remains to be seen whether the surface of the branches, when corrected for the foldings and the fingers, is sufficiently large to account for the electrical properties of this part of the cell.

The large $\lambda$ found for the S dendrites of *Scylla* has an obvious adaptive value, since these receptor neurones are specialized for transmitting analogue signals (Ripley, Bush & Roberts, 1968). The loss of the ability to produce spikes can also be interpreted as a consequence of this specialization, and it is interesting to note that this loss is limited to the fibre and to the proximal parts of the neurone. Pearson (1976) has suggested that the use of analogue signalling may have evolutionary advantages, when a given variable is being monitored by a single cell (or by a small number of cells), because it eliminates discontinuity in the transmitted information which could be present if a spike train coding were used. A more general advantage of analogue signalling can be appreciated by first considering that in any chain of neurones, spike trains, when present, are interposed between two analogue signals since, in any member of the chain, information is first received and later transmitted as a graded potential (receptor or synaptic potentials). It follows at once that wherever feasible analogue signalling would be of advantage simply because it reduces the inevitable distortions and non-linearities resulting from the encoding in and subsequent decoding from a digital form of a continuous function.

Some of the disadvantages of analogue signalling – bulky size and efficiency limited to short distances – are well recognized. Another, perhaps equally important, disadvantage is that the information contained in the time course of the stimulus may be either totally or partially lost. This condition would necessarily occur were the signal propagated even over moderate distances in an infinite cable, because the requirement for a large length constant implies a large value for the membrane resistance and consequently for the time constant. However, the time course of voltage perturbations propagated in a cable depends not only on the membrane time constant itself but also on the nature of the cable terminations. In particular, when the termination at which the signal originates has an input conductance lower than that expected if the cable were infinitely extended, then the time course of the perturbation will depend on a set of different time constants, each one of which is smaller than the membrane time constant itself (Rall, 1969). Therefore a faster and more faithful transmission of the time course of the original signal is possible. This situation is found in the *Scylla* coxal receptors which thus would appear, even on this score, to be a good example of the adaptive properties possibly present in non-spiking neurones.

The discussion has been focused thus far on the data obtained with the S fibre,
but similar conclusions seem also valid for the T fibre of *Scylla* (Fig. 13, see legend). A comparison with the results obtained with other mechanoreceptors is more difficult because of the lack of comparable data. The major differences between the properties of the coxal receptors of *Scylla* and of those of *Carcinus*, studied by Bush and collaborators, are quantitative, the estimates obtained for the *Carcinus* receptors being several times smaller than those calculated for *Scylla*. In the present work a low value for the input resistance, a small ratio for the spatial decrement of the responses to stretch and to injected current, and a small $t_{94\%}$ were all found to be invariably associated with a large leakage shunt. Thus, it is possible that the quantitative differences between the *Carcinus* and the *Scylla* preparations are mainly artifactual, reflecting more a difference in the techniques used than in the intrinsic properties of the coxal receptors in the two species (see also Bush, 1976).

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**APPENDIX**

*Error introduced by the leakage associated with the microelectrode in the determination of the length constant of cable-like cells*

The space constant of a nerve fibre can be determined with intracellular microelectrodes by measuring at different points the amplitude of the electrotonic potential, $V_s$, resulting from the steady-state flow of an axial current. When $V_s$ is recorded simultaneously at two points, $p$ and $d$, the latter being nearer to the position of the current source, the ratio $V_{sp}/V_{sd}$ is a measure of the spatial decrement of this current in the fibre. Both $V_{sd}$ and $V_{sp}$ will be affected by the leakage shunt associated with the recording electrodes. However, since $V_{sd}$ is taken as reference, only the leakage associated with the microelectrode at $p$ will affect the magnitude of the ratio $V_{sp}/V_{sd}$. Moreover, this ratio will be reduced proportionally more the closer are the recording electrodes.

Quantitatively the error affecting the measurements can be estimated as follows. Assume that the equations of monodimensional cable theory (Rall, 1959) apply, and indicate the electrotonic potential at $p$ in absence of the shunt as $V'_{sp}$; this quantity is equal to the product of the input resistance of the proximal part of the fibre, $R_p$, times the axial current at $p$, $I_{p}$, $I_{p}$, in turn, is equal to the axial current at $d$, $I_d$, minus the current lost through the fibre membrane in the segment $dp$, $\Delta I_d$. Thus, if the fibre is equivalent to a semi-infinite cable, then:

$$V'_{sp} = R_p(I_d - \Delta I_d) = \lambda r_d(I_d - \Delta I_d),$$

where $\lambda [\text{cm}]$ is the (actual) space constant of the fibre, and $r_d [\Omega \text{ cm}^{-1}]$ is the core resistance per unit length of the fibre. If there is a leak, $R_L$, around the microelectrode, its effect will be a further loss of axial current, $I_L$. Therefore, the voltage measured, $V_{sp}$, is:

$$V_{sp} = \lambda r_d(I_d - \Delta I_d - I_L).$$
The magnitude of the ratio between the measured voltage and that expected in absence of a leak, tends to one for $A/d > I_L$. Since $A/d$ is proportional to the distance, $\Delta x$, between the two recording points, $p$ and $d$, it follows that the quantity measured, $V_{sp}$, will be smaller than the quantity to be estimated, $V'^{sp}$, in inverse proportion to $\Delta x$.

Because of the systematic error introduced by $R_L$, the distribution of the values of the function $\ln V_{sp}/V_{ad} = f(\Delta x)$ will be different from the distribution of the function $\ln V'^{sp}/V'^{ad} = f'(\Delta x)$. If a straight line is fitted by the least squares method to the experimental data, the slope of the line will be smaller than the slope of the line which would be calculated if the data were not affected by $R_L$. Hence, the estimated $\lambda$ will be larger than the actual space constant of the fibre. Also, the line fitted to the experimental points will cross the vertical axis below the origin.

In the case examined in this paper, a second line was drawn to the data, passing through the origin of the graph, as explained in the legend to Fig. 7. On the basis of the considerations presented above, the estimate for the length constant calculated from the slope of this line, 5.8 cm, should be less affected by the error due to the shunt, than the estimate of 7.2 cm, which corresponds to the slope of the line calculated by the least squares method. The average value of the shunt associated with the microelectrodes, $R_L$, can then be calculated as the difference between the estimate of the input conductance of the proximal part of the fibre ($G_p = 1/\lambda r_i$) corresponding to the two estimates of the length constant. The magnitude of this difference depends on the value of the specific resistance, $R_i [\Omega \cdot cm]$ of the fibre's cytoplasm, and on the radius, $a$, of the fibre ($r_i = R_i/[\pi a^2]$). Using the average radius of the S fibre ($43.5 \times 10^{-4} \text{ cm}$) and assuming the lowest value of $R_i$ reported in the literature, about 30 $\Omega \cdot cm$ (Carpenter et al. 1975; Cole, 1975), $R_L$ is about 20 M$\Omega$. $R_L$ estimated would be larger if larger values of $R_i$ were assumed.

The same conclusion and the same estimate of $R_L$ (approximately) are also reached if the equation corresponding to a closed cable (Rall, 1959) are used instead of that for an infinite cable.

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Electrical properties of a dendrite


