Mathematical Modelling of Intra- and Extracellular Potentials Generated by Active Structures: Effects of a Step Change in Structure Diameter

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Abstract. A mathematical model developed in our laboratory is used to estimate and analyse extracellular potentials generated in a volume conductor by a geometrically inhomogeneous structure with a step increase or a step decrease in its diameter. The transmembrane potentials were calculated using the model of Hodgkin and Huxley (1952) and the method of Joyner et al. (1978). Variations in waveforms of the transmembrane and extracellular potentials were described and discussed. Differences in waveforms of the extracellular potentials and in declines of their components are due to changes in the source which generates these potentials. In case of a propagation block the peak-to-peak amplitude of the extracellular potentials calculated over the area of the block may be higher than that over the area of propagation of action potentials. The possible applications of the results to the analysis of extracellular potentials recorded around actual motoneurons during their orthodromic or antidromic activation are discussed.

Introduction

The model of Hodgkin and Huxley (1952) gives a fair description of transmembrane processes occurring in active excitable fibres. Owing to the development of methods for solving the system of equations describing the above model, the latter has become a basis for theoretical and experimental investigations of geometrically or functionally more complex structures.

Cooley and Dodge (1966) were the first to solve this system of equations numerically without assuming a constancy of the excitation propagation velocity along the fibre, as done by Hodgkin and Huxley (1952). Khodorov et al. (1969) extended the method of Cooley and Dodge (1966) for the case of geometrical inhomogeneity — a step widening of the fibre; Moore et al. (1975) used the Crank-Nicholson method to solve the equations which describe a

cylindrical cell, while Joyner et al. (1975) extended this method for structures with an arbitrary number of bifurcations and different diameters. The development of computing methods has brought a number of publications which have contributed to the understanding of the mechanisms of impulse conduction along such structures. Dodge and Cooley (1973) modelled a motoneuron and sought combinations of the functional properties of its different regions, that would yield transmembrane potentials close to those actually recorded; Ramon et al. (1975) studied theoretically and experimentally action potentials for some geometrical and functional inhomogeneities in an axon, while Parnas and Segev (1979) analysed conduction of action potentials along branching axons. Timin and Khodorov (1971), Miller and Rinzel (1981), Stephanova and Dimitrov (1983) studied changes in the propagation velocity of the action potential at different time intervals after a preceding stimulus; Scriven (1981) modelled action potentials in a thin unmyelinated fibre. Joyner and Westerfield (1982) studied the synaptic activity; Moore and Westerfield (1983) showed experimentally and theoretically the dynamics of the threshold characteristic in inhomogeneous areas; Moore et al. (1983) modeled a neuron and studied the site of the impulse initiation in it upon changing the functional properties of its parts, etc.

In clinical practice, mesurements of extracellular potentials are fundamental, their interpretation is however, difficult. Even with a bell-shaped transmembrane potential, which propagates with a constant velocity along a homogeneous striated muscle fibre, the extracellular potentials may have different numbers of components (from two to five). Their waveforms led of near and far from a structure may be quite different. This has been shown experimentally (Gydikov and Kosarov 1972a, b; 1973) and in theoretical studies (Dimitrova 1974; Dimitrova and Dimitrov 1974; Dimitrov and Dimitrova 1974b). The picture is even more complicated for geometrically and functionally inhomogeneous structures, such as branching axons and dendrites or an initial segment-soma area of a neuron. The waveforms of transmembrane potentials and the velocity of the propagation of excitation along such structures are quite different. The transmembrane potential profile continuously changes and considerably complicates the interpretation of the potentials recorded. Due to this, the spatial distribution of membrane excitability was estimated differently by different authors (Brock et al. 1953; Fatt 1957; Freygang 1958; Terzuolo and Araki 1961; Nelson and Frank 1964; Rosenthal 1971; Grace and Bunney 1983). For example, Freygang (1958) assumed that the dendrite membrane together with the main part of the soma was passive, while Fatt (1957), and Terzuolo and Araki (1961) believed that the somatic membrane and the proximal part of the dendrites were active.

Some attempts were also made to solve these problems using mathematical models. Rall (1962a) examined a particular case of a passive soma-dendrite complex with a fixed geometry. Dvořák and Srch (1977) suggested a way of the

calculation of extracellular potentials around an active cell which consisted of a long unmyelinated axon and ellipsoidal soma without any dendrites. Dimitrova (1985) studied influences of different geometric relations between an active short soma and dendrites on the extracellular potentials. However, there has been no attempt to systematically examine the influence of different geometrical parameters on the profile of transmembrane potentials and hence on extracellular potentials around a structure.

The large number of papers which describe transmembrane processes are a good basis for calculations of extracellular potentials around inhomogeneous structures.

The purpose of the present paper was to study changes in transmembrane and extracellular potentials in a case of the most simple geometric inhomogeneity, namely, a step change in the diameters of a structure.

Methods

The Hodgkin-Huxley (1952) model was used to calculate transmembrane potentials in the time and distance domain. The system of differential equations was solved according to Joyner et al. (1978). The structure studied was presented as two interconnected cables having different diameters. The diameter of the initial part of the cable (the site of the stimulus application) was of the order of that of a motoneuron soma (50 μ m). The structure was long (1–2.5 cm) in order to eliminate the effect of its boundaries on the potentials studied. The resistance of the extracellular volume conductor was assumed to be zero, the time step was 10 μ s, the temperature was 20 °C. Boundary conditions: $V_{-1} = V_1$ (the stimulus was applied to the zero segment), $V_{L+1} = 0$. The remaining parameters were the same as reported by Hodgkin and Huxley (1952).

The extracellular potentials $V_e(x, y)$ were calculated on the basis of the distribution of the transmembrane potential profile along the structure at a moment *t* (Plonsey 1969, 1977; Pattle 1971; Dimitrova 1985):

$$V_{\rm e}(x, y) = K \int_{z_1}^{z_2} -\frac{\partial V_{\rm m}}{\partial z} a^2(z) \frac{x-z}{[(x-z)^2 + K_{\rm an}y^2]^{3/2}} dz \tag{1}$$

where x, y are coordinates of the point at which the extracellular potentials were calculated; z is the coordinate of the respective segment along the structure; a(z) is the radius of the structure in segment z; $V_m(z)$ is the transmembrane potential in segment z; z_1 , z_2 are coordinates of the structure ends; and K_{an} is the anisotropy coefficient of the volume conductor.

Only one wave of the potential profile was considered, namely that right to the site of stimulation.

In the present paper, results of calculations of transmembrane and extracellular potentials for a homogeneous fibre and for structures with a 2; 4; 5; and 0.25 — fold step change in the diameters are described. The radial distances from the structure axis were 0.5; 1; and 2 mm, the anisotropy coefficient of the volume conductor was 1.

Results

Figure 1 represents a reference pattern for transmembrane (A) and extracellular (B) potentials generated by a geometrically homogeneous fibre. The ex-

tracellular potentials are triphasic. Upon increasing the radial distance, the duration of the negative phases increases, and the amplitudes of the first and the second positive phase become equal, as described earlier (Dimitrov and Dimitrova 1974c). In all cases considered, at sites remote from the geometrical inhomogeneities and from the fibre ends, the transmembrane potentials, as a function of time, do not depend on the fibre diameter (see, e. g., Figs. 1 A, 2A)



Fig. 1. Transmembrane (A) and extracellular (B) potentials generated by a geometrically homogeneous fibre. The radial distances (y) of the points of observation from the fibre axis were 0.5; 1; and 2 mm (B1, B2, B3).

I. Step Increase in the diameter

a) Below the critical value (Fig. 2)

When the diameter increased twice, which is far below the critical value at which a propagation block occurs, an approximately 10 % decrease of the transmembrane potential amplitude, slowing down of the depolarization processes and an increased total duration of the potential were observed in the narrow part of the structure in the vicinity of the diameter increase (Fig. 2 A1). In the thicker part, the amplitude and the velocity of propagation stabilized at a value typical of a homogeneous fibre with the larger diameter. The relatively small changes in the waveforms of the transmembrane potentials, together with the clearly observed changes in their propagation velocity, resulted in a considerable widening of the transmembrane potential profile in the thicker part of the structure (Fig. 2 A2).

A thickening of the structure had different effects on extracellular potentials

above the thinner and thicker part. An additional negative-positive potential was generated above the thinner part and above the site of diameter change, as a result of the thickening. Depending on the location of the point of recording, this additional potential appeared on the background of the negative or the second positive phase (Fig. 2 B). At any radial distance this may increase the duration of the negative phase of the extracellular potential as compared with the respective values for a homogeneous thin fibre (Fig. 1 B).



Fig. 2. Transmembrane (A) and extracellular (B) potentials generated by a structure with a twofold step increase in diameter. The transmembrane potentials are shown for segments J = 40; 80; 120; 160; 200 (A1) and for times t = 1; 2; 3; 4; 5 ms (A2). The coordinates of the points of observation were x = 0.6; 0.8; 1; 1.2; 1.4 cm, and y = 0.5; 1; 2 mm (B1, B2, B3). The geometry of the structure is shown schematically in the right upper corner. The diameter change is at x = 1 cm (segment 80). The arrow indicates the direction of the propagation of excitation along the structure.

The amplitudes of the first positive and the negative phase gradually increase above the thicker part to reach stationary values characteristic of a homogeneous fibre with a diameter equal to that of the larger part. Close to the structure the duration of the negative phase of the extracellular potentials remained practically unchanged, whereas at longer distances, it was shorter as compared with that generated by a homogeneous thin fibre (compare Figs. 2 B and 1 B for identical radial distances). Potential amplitudes above the thicker part were higher than those above the thinner part.

An increase in the radial distance resulted in an extension of the area above the structure, where the influence of an increased diameter could be observed.

b) Nearly the critical value, but below it (Fig. 3)

In this case, at a fourfold increase in the diameter, a more than a twofold decrease in the transmembrane potential amplitude, a decrease in the velocity of the depolarization processes and a decremental reverse conduction were observed in the thinner part (Fig. 3A1). In the thicker part, close to the site of the diameter change, there was a substantial delay in the development of the initial part of the depolarization phase and a subsequent fast restoration of the transmembrane potential amplitude.



Fig. 3. Transmembrane (A) and extracellular (B) potentials generated by a structure with a fourfold increase in diameter. Transmembrane potentials in the time domain are shown for segments 65 ± 92 at every 3 (A1). Transmembrane potentials in the distance domain are shown for times $1 \pm 2.8 \text{ ms}$ at every 0.2 ms (A2). For other conditions see Fig. 2.

The delay in the development of depolarization resulted in a substantial decrease in the amplitude of the transmembrane potential profile and in a change in the steepness of the depolarization front (Fig. 3A2). When the excitation wave approached the point where the structure became thickened, the depolarization front became steeper in the thin part of the structure. When the excitation wave entered the thicker part, the depolarization front sharply became initially less steep, and subsequently both its slope and amplitude increased first gradually and then sharply, to reach values characteristic of a thicker fibre. The peak was simultaneously rounded up. Also, the propagation velocity of the excitation changed, to reach values characteristic of a thicker fibre. As a result, the profile was much more extended in this part of the structure than in a fibre with a twofold diameter.

The more pronounced changes in the profile and in the power of elementary sources (proportional to a^2), as compared with those in a structure with a twofold diameter, were reflected in the extracellular potentials (Fig. 3). The long delay in the development of the depolarization phase, during the spread of excitation through the inhomogeneous section resulted in a substantial prolongation of the phases of extracellular potentials generated during this period. These phases (negative above the thinner part of the structure and above the inhomogeneity, and the first positive above the thicker part) had a complex configuration which changed upon shifting the position of the recording point. This reflects the above described dynamics in the development of the depolarization phase. The development of the repolarization phase in the thicker part of the structure and the propagation of excitation along it gave rise to a second positive phase above the thinner part of the structure, considerably greater than those observed with a twofold diameter. At longer radial distances the extracellular potentials above the thin part, as well as those above the inhomogeneity, became practically biphasic, negative-positive, with a complex negative phase. Above the thicker part, the potentials were triphasic. Upon increasing the distance axially from the site of the inhomogeneity, the amplitudes of the first positive and the negative phase increased to reach values characteristic of a thick fibre. At long radial distances (Fig. 3 B3) the shortening of the negative phase of the extracellular potential above the thicker part, as compared with the negative phase generated by a homogeneous thin fibre (Fig. 1 B), was more marked than with a twofold diameter.

c) Above the critical value (Fig. 4)

At a temperature of 20 °C and with a fivefold increase in the structure diameter, the excitation wave failed to propagate through the inhomogeneity. The amplitude of the transmembrane potential in the thin part of the structure decreased when the excitation wave approached the thickening, and was not restored (Fig. 4A) unlike the case of the structure with a fourfold diameter (Fig. 3 A). This is why the extracellular potential lacked components corresponding to the restoration of the amplitude and to the development of the repolarizatin phase in the thicker part. Above the thinner part, the thickening did not result in the generation of additional negative-positive potentials, as in the previous cases; negative potentials were only generated. The extracellular potentials before and above the site of diameter change were positive-negative, with small positive phases, and negative phases of complex configurations, with practically no second positive phases. Above the thicker part, the extracellular potentials were positive-negative, the positive phase being greater than the negative one. The latter rapidly decreased with increasing axial distance from the site of the inhomogeneity (Fig. 4B). In spite of the propagation block, the amplitudes of the extracellular potentials (of the positive component and the peak-to-peak amplitude) above the thicker part, close to the widening, were greater than those above the thinner part.



Fig. 4. Transmembrane (A) and extracellular (B) potentials generated by a structure with a fivefold increase in diameter. For details see Fig. 3.

II. Step Decrease in the Diameter (Fig. 5)

When the structure diameter was abruptly decreased (four times), an approximately 10 % increase in the amplitude of the transmembrane potential, a decrease of the depolarization time and of the total duration of the transmembrane potential before the area of the diameter change were observed. In the thinner part, the transmembrane potential was rapidly restored to values characteristic of a homogeneous thin fibre (Fig. 5A1). The spatial profile changed in accordance with shape changes of the transmembrane potential and changes in its propagation velocity along the structure (Fig. 5A2). When the point of registration was moved closer to the site where the fibre became narrower, the extracellular potential became biphasic, positive-negative (Fig. 5B). The first positive phase was similar to that observed with homogeneous structures. The negative phase initially increased, when the depolarization front entered the thinner part, and substantially decreased thereafter, when the repolarization processes started in the thinner part. This resulted in a prolongation of the negative phase above the thicker part of the structure.

Above the thinner part of the fibre, small triphasic potentials generated by it developed on the background of higher positive-negative potentials generated by the thicker part of the structure (Fig. 5 C). The latter potentials were similar to those generated beyond the fibre end (Dimitrova 1974; Dimitrova and Dimitrov 1974). Upon increasing the radial distance, the extracellular potentials around the inhomogeneity (Fig. 5 B, C) became similar to those recorded in the area near the end of the fibre (Dimitrova 1974; Dimitrova 1974).



Fig. 5. Transmembrane (A) and extracellular (B and C) potentials generated by a structure with a fourfold decrease in diameter. Transmembrane potentials in the time domain are shown for segments 35 + 62 at every 3 (A1). Transmembrane potentials in the distance domain are shown for times 1 + 2.8 ms at every 0.2 ms (A2). The diameter changes at segment 50 (x = 0.625 cm). The coordinates of the points of observation: B, x = 0.4; 0.5; 0.6; 0.7; 0.8 cm; y = 0.5; 1; 2 mm; C, x = 0.7; 0.75; 0.8; 0.85; 0.9 cm; y = 0.5; 1; 2 mm.

III. Effects of the Transmembrane Potential Profile and Power of the Elementary Generators on the Extracellular Potentials

a) Effect of the transmembrane potential profile

Let us consider extracellular potentials (Fig. 6 A) generated by a hypothetical fibre. At any moment its potential profile is the same as that in a case of a structure with a fourfold increase in diameter but its radius is constant and equal to that of the initial part of the structure. The nature of the extracellular potentials generator is quasi-quadrupole in this case, similarly as in the homogeneous fibres (Dimitrov and Dimitrova 1974a). In both parts of the structure, at long distances from the inhomogeneity, the lengths of the depolarized zones are proportional to the propagation velocities of the excitation along these parts, since the duration of the transmembrane potentials in homogeneous parts of the structure does not depend on the structure diameter (Figs. 1A, 2A and Goldstein and Rall 1974). The differences in the amplitudes of the potentials above the parts with shorter and longer profile respectively, and change in their ratio upon increasing the radial distance, result from the non-monotonous dependence of the amplitudes of the extracellular potentials on the length of the depolarized zone (Dimitrova 1973). Changes in the ratios of the different potential components (Fig. 6A), which, in the case of a quasi-quadrupole nature of the generator, reflect also changes in the amplitude and asymmetry of the potential profile (Dimitrov and Dimitrova 1974a), differ from those shown in Fig. 3 B. The conditions of the generation of these potentials are also different. Let us, therefore, consider another possibility.

b) Effect of the power of the elementary generators

Our studies have shown that when the excitation wave approaches the site of the diameter change, the power of the elementary sources $\left(\sim \frac{\partial V_m}{\partial z} a^2(z)\right)$ increases as compared with that typical of the homogeneous thin fibre. It continues to increase in the region of increased diameter where it reaches its maximal values. The values are substantially larger than those in the long thin fibre.

Therefore, let us consider extracellular potentials generated by the thicker part of the fibre only (Fig. 6 *B*). The ratios of the components of the negative phases change during the development of the profile in the thicker part of the structure adjacent to the region where the diameter is changed. During the initial period of this development the depolarization front changes from very slightly inclined to steeper, and its amplitude rises. The steepest region of the profile is near the position where the diameter is changed (Fig. 3 A2). Therefore, close to the structure, the maximum of the negative potential is near the place where the

diameter changes (Fig. 6 B). At longer radial distances the negative maximum of the extracellular potentials shifts axially to the thinner part of the structure, approximately at 0.7y (Dimitrova 1985). Thus, at longer radial distances the potentials aside the position where the diameter changes may exceed those above that position (Fig. 6 B3). During subsequent periods of the development of the depolarization front the profile peak becomes rounded up and the steepest sections of the profile and the negative maxima of the extracellular potentials are shifted towards the thicker part of the structure. Consequently, the ratio changes of the different components of the extracellular potentials, imposing a different declines of these components with the distance from the structure, may be a reflection of the dynamics in the development of the distributed source. Analogous considerations also concern the first positive phase of the extracellular potentials in the area of the site of the diameter change.



Fig. 6. Extracellular potentials generated by structures having the same profile of the transmembrane potentials as that calculated for the fourfold step increase in the structure diameter. A: the radius of the structure is constant along the entire structure length and is the same as in its initial part; B: extracellular potentials generated by the thicker part of the structure only. For coordinates of the points of observation see Fig. 2.

The amplitudes of the negative phase of the extracellular potentials grow upon increasing the axial distance from the inhomogeneity. This growth continues until the profile no longer contributes by further expansion to the amplitude increase ($x \approx 1.4$ cm). Far from the structure, the duration of the negative phase decreases (Figs. 6 B3, 2 B3, 3 B3, x = 1.4 cm) as compared with a homogeneous thin fibre (Fig. 1 B3), due to the fact that the potential profile in the thicker part of the structure is prolonged at the expense of an increase in the propagation velocity of the excitation along the structure (Dimitrov 1987).

For other ratios of diameters of the two parts of the structure the regularities in the development of the extracellular potential are similar to those discussed above. Differences only occur in the actual ratios of different components. They are determined by the amplitude and asymmetry of the transmembrane potential profile, as well as by the dynamics of the development of the distributed source which generates the extracellular potentials.

In geometric inhomogeneities examined in the present paper the effects of the parameters which characterize the generator and its power in the thicker part of the structure, are more pronounced than those of the whole profile of the transmembrane potentials and its asymmetry. Consequently, the peak-to-peak amplitude of the extracellular potentials above the thicker part of the structure may be greater than that above the thinner one (Fig. 4 B), even when a propagation block occurs.

Discussion

Brock et al. (1953), Freygang (1958), Terzuolo and Araki (1961), Nelson and Frank (1964), Rosenthal (1971), Grace and Bunney (1983) proposed different interpretations of the intra- and extracellular potentials recorded in experiments on single neurons. This multiplicity of views is due to our poor understanding of the processes, as well as to numerous parameters which seem to play a role in the generation of the potentials studied. Simulations described in the present paper show that a change of even one geometric parameter may be of importance for transmembrane and extracellular potentials. In addition to alterations of transmembrane potentials as described for some geometric inhomogeneities by Cooley and Dodge (1966), Khodorov et al. (1969), Dodge and Cooley (1973), Goldstein and Rall (1974), Joyner et al. (1978), and Moore et al. (1983), the nature of the distributed source generating extracellular potentials also undergoes changes. Our data have shown that this results in a shift of the maxima of the extracellular potential components, in differences in the decline of these components and, consequently, in changes in the waveforms of the extracellular potentials. Potentials calculated for points above the inhomogeneity may show a negative plateau and a peak which decline in different ways. These potentials resemble those recorded by Fatt (1957), Terzuolo and Araki (1961), Nelson and Frank (1964) around motoneurons. To what extent, however, does the analogy between motoneurons and the structures examined by us hold?

In the present paper geometrically inhomogeneous structures were presented as two interconnected cables of different diameters. The structures were long, their initial diameters were of the order of that of a striated muscle fibre or a motoneuron soma. According to Rall (1962a) dendrites load the soma of a motoneuron in such a way that the soma-dendrite complex may be presented as an equivalent cylinder with a diameter equal to that of the soma. As for their shapes, the structures examined in the present paper may thus represent an analog of the branching axons (Parnas and Segev 1979) or dendrites (Rall 1962b; Goldstein and Rall 1974) and an approximation of the axon-soma--dendrite complex of a motoneuron as well. It is an approximation, since the extension of a nerve cell from its initial segment to its soma is gradual. When the diameter changes gradually the transmembrane processes are analogous to those observed with step changes. However, these processes not only depend on the ratio of the diameters in the homogeneous parts but also on the length (1)of the region between these parts (Joyner et al. 1978). Thus, at a given stage, the number of parameters examined can be reduced. We therefore assume the length (1) to be zero. In their models of a motoneuron, Dodge and Cooley (1973) and Moore et al. (1983) used structures similar in their shapes to those considered in our simulations.

In addition to their shape, structures are also characterized by their size. In the time domain the transmembrane processes depend on the shape of the structure only (Goldstein and Rall 1974; Jovner et al. 1978; the present paper -see Fig. 2 A1), but in the distance domain they are strongly affected by the actual values of the diameter. The latter determines the propagation velocity of excitation and, hence, the length of the potential profile. According to the cable theory, when the diameter of a structure changes N-times, this involves \sqrt{N} --times scale change in the distance domain (z). In this case, the extracellular potentials maintain their waveforms at points with coordinates $x_1 = x/\sqrt{N}$ and $y_1 = y/\sqrt{N}$, but their magnitudes are proportionally changed N-times at these points (see formula 1). Keeping in mind this possibility of the transformation of the calculation results for any value of the initial diameter of the structure, we may conclude that all our results may be used to analyse transmembrane and extracellular potentials recorded in experiments on structures of real sizes. The only pre-condition is a similarity between the shape of the real structures and those of the model. Taking into account the similarity between the waveforms of transmembrane potentials recorded in actual experiments (Fatt 1957; Terzuolo and Araki 1961) and those calculated for the case of a nearly critical increase of the diameter (Fig. 3 A1), as well as the considerable length of the structures examined in the present paper, we may consider that the structures used in our model may represent a geometrical analog of both branching axons or dendrites of some nerve cells and the region between the initial segment and the soma of a motoneuron. Then, a step increase in or a decrease of a structure diameter would correspond to an antidromic or orthodromic excitation of a motoneuron respectively.

Using the results of our study, in should be taken into account that, at a given stage, a branching thin axon or dendrites are entirely set equal to an equivalent thick cylinder. This is absolutely correct for the time domain, but not for the distance domain. The potential profile in a thick cylinder is longer than that in thin dendrites connected to the soma. This is reflected in specific values of the amplitudes (Dimitrova 1973) and in shifts of the maxima of different potential components at different radial distances (Dimitrov and Dimitrova 1974a, c) and in the duration (Dimitrov 1987) of the extracellular potentials calculated. However, the dynamics of the transmembrane potential profile and the reasons for differences in the degree of radial decline of the extracellular potential potential components will remain unchanged.

Our studies have shown that changes in the geometry of the excitable structures should always be considered when intra- and extracellular potentials generated by such structures are to be interpreted. Changes in geometry may explain alterations in the waveforms of the extracellular potentials recorded at different distances from the structure, changes in the degree of the decline of different components, higher potentials above regions of block, and differences in the waveforms of extracellular potentials recorded during antidromic or orthodromic activation.

The present results are however insufficient to allow a detailed interpretation of potentials generated by actual inhomogeneous structures. Influence of a short soma, that of the finite length of the dendrites, of their branching, of differences in functional properties of individual parts of a structure, etc., on the transmembrane and extracellular potentials, should also be investigated.

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