The Electrical Properties of Metal Microelectrodes

DAVID A. ROBINSON, MEMBER, IEEE

Abstract—The electrical properties of metal microelectrodes for single-unit recording are reviewed. An equivalent circuit is presented, the elements of which are discussed. The most important element is the electrolytic capacitor formed by the metal-electrolyte interface. Its value is about $0.2~\mathrm{pF}/\mu^2$ at 1 kHz. The effects of exposed metallic area at the tip and platinization are described, and some consideration is given to problems peculiar to the operation of these electrodes in neural tissue.

INTRODUCTION

THE USE of metal microelectrodes for extracellular recording of single-unit activity in nervous tissue is widespread, since it is one of the principal tools of the neurophysiologist interested in nervous organization at the cellular level. Despite this prevalence there remains a good deal of mystery about how best to make these electrodes and how to interpret the extracellular potentials that they record. The attitude of many practical users is the sensibly pragmatic one of the biological assay. When one finds some method of making microelectrodes that successfully isolate units in a given neural structure, one "freezes the design" and attends to the more important task of collecting neural data. The attitude is very much one of not looking a gift horse in the mouth, and it must appear particularly frustrating to the beginner in this field who naturally enough wishes to understand the characteristics of that tool on which he would like to rely for the collection of his data.

The subject of metal microelectrodes may be considered in three parts: the techniques of their manufacture, their electrical characteristics in a conducting medium such as isotonic saline, and their ability to isolate and record from fibers and cell bodies in various parts of the central nervous system. The extreme difficulties of understanding the last aspect account for much of the mystery in the use of metal microelectrodes. Those characteristics that permit a tip to isolate and record from a large number of single units along an electrode track are not yet understood, and the inability to regulate manufacturing processes to make reproducible tip sizes and shapes makes it difficult to do controlled experiments on the subject. It is not the purpose of this paper to discuss the performance of microelectrodes in tissue. Neither is it intended to discuss manufacturing techniques which are described in a number of papers. [1]-[5] It is characteristic of fabrication methods that each investigator adds something of his own to each process and each process responds differently in the hands of each in-

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The author is with the Department of Medicine, Division of Biomedical Engineering, The Johns Hopkins School of Medicine, Baltimore, Md.

vestigator. All the techniques described to date suffer by containing at least one step, invariably involving the amount of uninsulated metal exposed at the tip, which remains an art and which leads to lack of reproducibility. The best strategy for the beginner is to adopt any one method (which one is probably not important) and stay with it until it produces results in his hands.

However, the electrical characteristics of electrode tips in a homogeneous conducting medium such as isotonic saline are amenable to study and quantitative description. Consequently, it seems worthwhile to investigate these characteristics to provide a basis for subsequent investigations into the more difficult subject of electrode behavior in neural tissue. Although an understanding of the electrical characteristics is not necessary for the pragmatist in single-unit recording, it should be of value in a more rational approach to the fabrication and use of metal microelectrodes. Although some of the measurements that follow have been substantiated at the Division of Biomedical Engineering of The Johns Hopkins School of Medicine, most of the information on this subject already exists widely scattered among books and journals in electrochemistry, electrophysiology, and neurophysiology. Consequently, the following represents a bringing together of this information which is presented from the standpoint of the investigator interested in single-unit recording in the hope that it may help the beginning user of metal microelectrodes.

EQUIVALENT CIRCUIT

The equivalent circuit of a metal microelectrode is shown in Fig. 1. The physical origins of the components are as follows.

 Z_a is the input impedance of the amplifier. Most amplifiers, either commercial or homemade, that use either vacuum tubes or field-effect transistors have input impedances (at 1 kHz) in excess of 10 M Ω so that Z_a is seldom a problem in recording single-unit activity.

 C_s is all the shunt capacitance to ground from the tip to the input of the amplifier. This includes the capacitance from the metal of the electrode to the bath through the insulation as well as the accumulated capacitance of all the connectors and (shielded) wires leading from the preparation to the amplifier.

 R_m is the resistance of the metallic portion of the microelectrode.

 C_e is the capacitance of the electric double layer at the interface of the metal tip and the electrolyte solution.

 R_e is the leakage resistance due to charge carriers crossing the electric double layer.

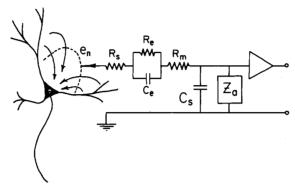


Fig. 1. The equivalent circuit of a metal microelectrode recording from the isopotential line e_n of a neuron in a volume conductor. The bases of the elements shown are discussed in the text.

 R_s is the resistance of the saline bath between the metallic interface and infinity (the indifferent or ground electrode). This is sometimes called the spreading resistance.

 e_n is the potential created in the volume conductor with respect to a point at infinity by the extracellular currents flowing about a neuron during an action potential. It is the potential that would exist at the electrode tip if the tip were present but had no net current flowing into it (i.e., if C_s were zero and Z_a infinite).

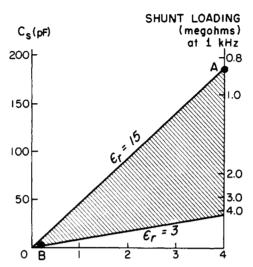
Each of these parameters will now be discussed more fully.

 C_{s}

The formula for the capacitance across an insulating material of relative dielectric constant ε , between a center conductor (the electrode metal) of diameter d and a concentric outer conductor (the electrolyte bath) of diameter D is

$$C_s = \frac{0.245\varepsilon_r}{\log_{10}\left(\frac{D}{d}\right)} \text{pF/cm}.$$

Since the insulation is always thinner near the tip where the metal also becomes thinner, the ratio D/d is roughly constant, and this formula is approximately correct even though the electrode is tapered. As a typical calculation, assume that the thickness of the insulation coating is 10 percent of the electrode diameter so that D/d is equal to 1.2. Dielectric constants range from 3 for many varnish-like materials to 15 for low-melting-point lead solder glass. Putting these numbers into the equation, one can plot C_s as a function of immersion depth for the two dielectric constants mentioned (Fig. 2). Since 1 pF at 1 kHz represents an impedance of 157 M Ω , one can also plot in Fig. 2, on the ordinate at the right, the shunt impedance of this capacitance to ground. Two extreme examples are shown. Point A represents a lead solder glass electrode reaching into deep structures through a saline-filled implanted chamber so that the total immersion depth is 4 cm. The resulting capacitance is 184 pF with a consequent shunt impedance of $0.85 \text{ M}\Omega$ at 1 kHz. Clearly the recordings from an electrode whose tip impedance was, say, 2 M Ω would be severely attenuated. At the other extreme is point B representing a



DEPTH OF IMMERSION IN CONDUCTING MEDIUM (cm)

Fig. 2. The shunt capacitance C_s (left ordinate) and the shunt loading that it represents at 1 kHz in megohms (right ordinate) for various immersion depths. The two boundaries represent the extremes of common dielectric constants from 3 (lower line) to 15 (upper line).

varnish-insulated electrode immersed 2 mm into cortex in a mineral-oil-filled chamber. In this case the capacitance is only 1.84 pF, representing a shunt impedance of 85.4 $M\Omega$. These examples are given to indicate that while electrode shunting due to C_s is usually not a problem, it can be a problem if the structure is deep and the insulating material has a high dielectric constant. This observation is, of course, especially true if the electrode tip impedance is large.

Connecting the microelectrode to the amplifier by means of a shielded cable is usually a dangerous procedure and is unnecessary if the experiments can be done in a shielded room. Most coaxial cables are noisy (electrostatically induced by mechanical vibrations). Microdot Mininoise cable, which is reasonably free of such noise, has a capacitance of 28 pF/ft. At 1 kHz this is 5.6 MΩ/ft, so that even a short length of cable can lead to signal attenuation if the electrode impedance does not remain small. If a shielded cable is necessary, it is generally helpful to provide some sort of negative capacitance compensation in the amplifier.

 R_m

The resistance of the metallic portion of the electrode is negligible. The appropriate formula is

$$R_m = \rho \, \frac{4L}{\pi d^2}$$

where L is the length in cm of that portion of the electrode where the diameter is d in cm. Since the electrode is tapered, the tip has the highest resistance, and this resistance may be estimated by assuming some mean value for d in this formula. For most metals the specific resistivity ρ is on the order of magnitude of $10^{-5} \Omega \cdot \text{cm}$. The resistance of a 1-mm

¹ Mininoise cable, model 250-3804, from Microdot Inc., S. Pasadena, Calif.

length of such a wire 10 μ in diameter is thus 1.3 Ω . Even if the wire is 1 μ in diameter, the resulting resistance of 130 Ω is still negligible.

 C_e

Whenever a metal electrode is immersed in an electrolyte, chemical reactions begin occurring at the interface. If the metal is partially soluble in the electrolyte, its own metallic ions are involved. If the metal is inert, such as platinum, it enters into the reactions by donating or receiving electrons. The ease with which electrons may be delivered or received by the metal is affected by such things as the work function of the metal, the hydration energy of ions, and the energies associated with participating chemical bonds. In isotonic saline, oxygen and hydrogen, through electrolysis, play dominant roles in the reactions. Those interested are referred to the very readable discussion by Davies^[6] and texts on electrochemistry, such as that by Butler. [7] It is not the purpose of this discussion to become involved in the complex and poorly understood electrochemistry of the situation; it is sufficient to note that as the reactions proceed, the passage of charges into or out of the metal rapidly produces an electric gradient at the interface which opposes further charge movement. In equilibrium, the metal becomes polarized with respect to the solution and although charge movements may continue in the form of exchange currents, the chemical and electrical gradients are equal and opposite, the net charge movement is zero, and the charges already transferred are trapped at the interface, forming what is called the electric double layer.

The electric double layer constitutes quite literally an electrolytic capacitor. Its value for bright platinum at 1 kHz is about 20 μ F/cm² or 0.2 pF/ μ ². This value has been measured at Johns Hopkins. Guld,[8] using the voltage step response of the tip impedance, reports a value of 1 pF/ μ^2 . Wyatt^[9] reports a value which, after an appropriate transformation to be discussed, amounts to 0.18 pF/ μ^2 . Butler^[7] reports a value of 20 μ F/cm². It does not, however, behave as a simple lumped capacitor of constant value. If one plots the real and imaginary parts of the electrode impedance Z_e over the frequency range of 100 Hz to 10 kHz, both C_e and R_e appear to vary with frequency. As Gesteland et al.[10] point out, the rate at which these parameters decrease with increasing frequency depends upon the presence of compounds adsorbable onto the metal, the diffusion rate of the ionic reactants such as oxygen in the vicinity of the tip, the rate constants of the reactions themselves, and the presence of polarizing currents from external direct-current sources. The most common testing solution for metal microelectrodes is physiological saline, and there it is found empirically that both R_e and C_e vary as $1/\sqrt{\omega}$ (Gesteland et al., [10] Schwan^[11]). In this case X_e also varies as $1/\sqrt{\omega}$, as does $|Z_e|$, while the phase angle, which is equal to $\tan^{-1} \omega C_e R_e$, remains close to 45°. This behavior indicates that the simple parallel resistor and capacitor shown in Fig. 1 is an inadequate model of the process. Since the liquid plate of the capacitor is a charge distribution in a conducting medium in which diffusion must play a role, the impedance would

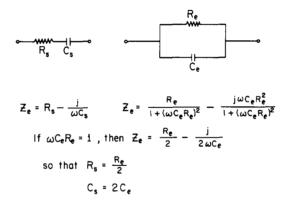


Fig. 3. The transformation between equivalent series and parallel circuits. For the empirically observed case when $\omega C_e R_e$ is unity over a wide frequency range, the transformation becomes particularly simple, as shown in the last line.

seem to be more adequately described by a distributed rather than a lumped parameter network. Indeed, a transmission line with a high series resistance and large shunt capacitance per unit length is one such distributed model. Its input impedance varies as $1/\sqrt{\omega}$ and, since the system is linear and Bode's phase-attenuation theorems hold, its gain variation of -10 dB/dec demands a constant phase angle of 45°. There is, however, little to be gained by seeking a more exact equivalent circuit. In practice, the recording of extracellular spike activity is done over the bandwidth of 100 Hz to 10 kHz, and the impedance measured at the commonly accepted mean frequency of 1 kHz is quite adequate to specify tip properties. There is one further point concerning an equivalent circuit for Z_{e} that is made in Fig. 3. Many investigators describe the tip impedance by an equivalent series combination of a resistor R_s and capacitor C_s . The equivalence between the series and parallel representations is given in Fig. 3 for any specific frequency ω , but for the special case where C_e and R_e vary as $1/\sqrt{\omega}$ so that $\omega C_e R_e$ = 1, the two circuits become equivalent at all frequencies; that is, they become truly indistinguishable, and the conversion from one circuit to the other is a simple factor of two. As ω approaches zero in the real case, the condition $\omega C_e R_e = 1$ breaks down, and at dc, since the tip resistance is finite, the parallel circuit is more appropriate than the series; but over the frequency range of interest here, the series and parallel circuits may be considered interchangeable.

At 1 kHz, $0.2 \text{ pF}/\mu^2$ becomes 785 M $\Omega \cdot \mu^2$ of capacitive reactance X_e . Since the phase angle is 45°, R_e is also 785 M $\Omega \cdot \mu^2$, and $|Z_e|$ is thus 557 M $\Omega \cdot \mu^2$. It is worthwhile to examine this component for the two common tip shapes shown in Fig. 4. That shown in Fig. 4(a) is typical of the tip produced with indium-filled pipettes, [41] and that in Fig. 4(b) is typical of the more common electrode that is made with lead solder glass [31] or Insl-X. [51] The cone height h in Fig. 4(b) runs from 5 to 25 μ , depending on the experimenter, the dipping or glassing technique, and the structure being recorded from; the value of 12 μ is chosen as typical. The two tips shown have impedances (at 1 kHz) of 88.7 and 9.8 M Ω . These tips would be extremely noisy (e.g., in excess of 30 μ V rms for a 10-kHz bandwidth), very susceptible to at-

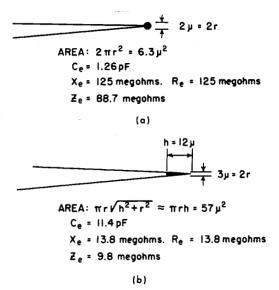


Fig. 4. The shape and surface area of two electrode tips in common use. C_e is the unplatinized tip capacitance, X_e is the capacitive reactance at 1 kHz, and R_e and Z_e are the unplatinized shunt resistances and tip impedances, respectively.

tenuation by shunt capacitance C_s , and represent no advantage at high frequencies over glass pipettes except perhaps in mechanical strength. Fortunately platinizing will reduce these impedances by two orders of magnitude, that is, to around 1.0 and 0.10 M Ω , respectively. Thus platinizing, which increases the effective surface area by a spongy deposit of platinum black, is the mechanism by which metal microelectrodes achieve their superiority over glass pipettes for extracellular recording.

However, it is not uncommon for investigators to use nonplatinized metal tips. The varnish-coated, sharpened steel insect pin deserves an honorable place in the history of single-unit recording, and it and unplatinized tungsten electrodes are still very much in use. Such tips generally have an impedance of about 5 M Ω . This means that 557/5 = 111 μ^2 of metal must be exposed. If the tip is cone-shaped, as in Fig. 4(b), and the cone base is 5 μ , then the cone height h must be about 14 μ . Some investigators feel that such a tip is very large although it has been used in many laboratories to isolate successfully both cell bodies and fibers. These investigators feel that better isolation can be achieved by smaller tips (a notion supported empirically rather than by theory), in which case platinizing becomes a mandatory step.

 R_e

When equilibrium is reached between a metal electrode and an electrolyte, the net flow of electrons (or ions) into or out of the metal is zero. This does not mean that all chemical exchanges have ceased but merely that rates in each direction are equal; that is, the electron efflux from the metal due to the electrical gradient (if the electrode polarization is negative) is equal and opposite to the electron influx from the chemical gradient (in which an anion is neutralized by the metal). This equilibrium current i_0 can be unbalanced by the application of an external voltage source that shifts

the metal from its equilibrium potential by ΔV . If, for example, ΔV is positive (metal to electrolyte) in the foregoing example, the electrical gradient is weakened and the chemical gradient dominates so that there is a net influx of electrons to the metal. Following Davies' [6] analysis for the oxygen electrode, the net current may be expressed as the difference in the influx and efflux currents which are predicted by classical kinetic theory from the rates at which an ion will pass over an energy barrier at temperature T by thermal agitation:

$$i = i_0 e^{F\Delta V/2RT} - i_0 e^{-F\Delta V/2RT}.$$

For voltage changes of less than a few millivolts this expression may be replaced by the linearization

$$i=i_0\frac{F}{RT}\Delta V.$$

Since RT/F is about 60 mV at room temperature, the resistance of the electrode may be expressed as

$$R_e = \frac{\Delta V}{i} = \frac{0.06}{i_0}.$$

From Davies^[6] one may take i_0 as 4.5×10^{-6} A/cm², whence R_e is $1.33 \times 10^4 \ \Omega \cdot \text{cm}^2$ or $1.33 \times 10^6 \ \text{M}\Omega \cdot \mu^2$. This is an extremely high resistance. The resistance of the tip shown in Fig. 4(b) would be $1.33 \times 10^6/57$ or 23 300 M Ω . If one tries to measure the dc resistance of an electrode in saline, one finds the value to be so high that the measurement is usually compromised by the input resistance of the amplifier. As already mentioned, R_e is frequency dependent, varying as $1/\sqrt{\omega}$ in the region around 1 kHz where its value is much less than this calculated dc value. Thus, the tip of a microelectrode is primarily an electrolytic capacitor whose leakage resistance R_e , while not negligible, does not make an important contribution to the total impedance. Two cautionary conclusions may be drawn from this. The dc resistance of an electrode tip measured with impressed voltages on the order of 1 mV will result in extremely high values which have little relevance to the impedance at 1 kHz. The dc resistance measured by impressing 10 volts across an electrode (in saline) in series with a 1-M Ω resistor (such as might occur with a volt-ohmmeter) will result in a very low value of resistance which has even less to do with the tip impedance. The decomposition voltage of hydrogen at a platinum cathode is around 1.3 volts (e.g., Moore^[12]). Beyond this, bubbles rapidly form and the tip acts like a diode. The current that would flow is, in this example, 10 volts less 1.3 volts divided by 1 M Ω or 8.7 μ A. The "electrode resistance" would appear as 1.3 V/8.7 μ A or 150 k Ω , an equally meaningless number. Consequently, the dc resistance of a microelectrode, no matter how it is measured, is an irrelevant parameter in microelectrode performance.

Platinizing: The deposition of platinum black onto microelectrode tips is the only method so far devised to bring the impedance of the tip down to useful values while at the same time keeping the exposed metallic area very small. Platinizing is done by passing a dc current through the tip while it is immersed in Kohlrausch's solution (3-percent $PtCl_2$, 0.025 N HCl, and 0.025-percent lead acetate, commercially available²) with the tip cathodal to an indifferent platinum electrode. Some investigators use 3-percent chloroplatinic acid (without the lead acetate) with success, and those investigators using lead solder glass cut the solution to 0.05 percent since this glass is readily attacked by acids. (Even in saline this glass dissolves at a rate of 0.1 μ /h.) The decrease in tip impedance, due to the deposition of a spongy colloidal layer of platinum, is a function of the plating current density and the amount deposited.

Although the methods and results of platinizing large electrodes (1 mm²) do not carry over directly to small microelectrode tips, these protocols at least form a useful background against which the variations found for small tips may be better appreciated. These data, shown in Fig. 5. are rescaled from Schwan^[11] and originally described observations on the equivalent series capacitance of a pair of identical gross electrodes at 20 Hz. The rescaling in Fig. 5 is done by dividing the capacitance by two to convert from a series capacitance to an equivalent parallel capacitance and then multiplying by two to convert from a pair of electrodes to a single electrode. The remaining conversion is the scaling of C_e by the square root of the frequency ratio, namely $\sqrt{20/1000}$ or 0.14, to make the measurements relevant to 1 kHz. This converted value for C_e is shown on the ordinate in Fig. 5 in pF/ μ^2 . The first abscissa shows the amount deposited in C/cm². Immediately below this axis the amount deposited is expressed in the more meaningful units of $\mu A \cdot s/\mu^2$. At any given plating current density, the abscissa in C/cm² may be converted directly to time by dividing by the current density which may be expressed in C/s · cm². This has been done in the third scale for a current density of 10 mA/cm² with time expressed in minutes. Platinum has an atomic weight of 195.2 g, a density of 21.4 g/cm³, and, in chloroplatinic acid, a valence of 4. Consequently, one coulomb of platinum occupies 2.36×10^{-5} cm³ and the abscissa in C/cm² may be expressed in the thickness of the deposited layer in microns (fourth scale). Inspection of Fig. 5 shows that the best plating current is 100 pA/ μ^2 and that the greatest increase in effective area occurs after 40 minutes of plating with a consequent buildup of 6 μ . Since the calculation for buildup was based on metallic platinum rather than the spongy form actually deposited, this figure is an underestimate of the actual thickness. The result of this platinizing is to increase the surface capacitance C_e from 0.2 pF/ μ^2 to 60 pF/ μ^2 (a ratio of 300 to 1) or decrease the impedance at 1 kHz from 557 $M\Omega \cdot \mu^2$ to 1.86 M $\Omega \cdot \mu^2$.

As mentioned, these calculations, which apply to gross electrodes, cannot be applied directly to microelectrode tips. For example, for the tip shown in Fig. 4(a), a plating current density of 10 mA/cm^2 (0.0001 $\mu\text{A}/\mu^2$) would mean a current of 0.00063 μA . In fact, such a tip will not plate at all with such a current, and platinum will not begin to deposit

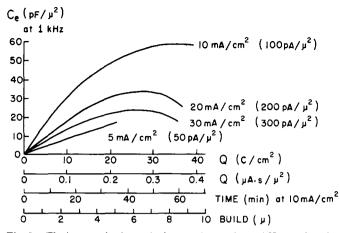


Fig. 5. The increase in electrode tip capacitance C_e at 1 kHz as a function of amount deposited and plating current density. Redrawn and rescaled from Schwan.^[11] The platinum surface was roughened with emery cloth for the upper curve.

until 0.02 μ A, which is a current density of 318 mA/cm². This phenomenon is not understood but may be associated with the inability to maintain concentration gradients in the neighborhood of so small a tip due to the rapid diffusion times. As a rule of thumb, it is necessary to use current densities about 10 times those used for gross electrodes.

The second problem peculiar to microelectrode tips concerns the amount of platinum one can afford to deposit on so small a tip. Clearly the $6-\mu$ buildup in the example given is out of the question. Thus microelectrode tips are plated for much shorter periods of time than indicated in Fig. 5. In spite of all these differences, it is still possible to reduce the tip impedance by about two orders of magnitude. In this laboratory a current of 0.02 µA for about 10 seconds gives satisfactory results. The tip impedance is measured during plating so that plating may be stopped whenever the impedance has fallen to about 0.5 M Ω . This usually occurs after 5 to 15 seconds. Plating is done by means of a 0- to 35-volt power supply in series with a 1000-M Ω resistor. Some investigators platinize with much higher currents, such as 5 μ A or about 50 A/cm². This also produces tips of low impedance, but the platinum black has a tendency to be very spiny and delicate and is easily scraped off.

Several miscellaneous remarks should be made about platinizing. Platinum black will not adhere to tungsten and is easily scraped off in brain tissue, especially by the pia. An intermediate plating of gold³ seems to solve this problem. Immediately after platinizing the impedance will start to rise, rapidly at first, then more slowly. Typically, an electrode plated to 0.2 M Ω will rise to 0.35 M Ω in the first few minutes, to 0.5 M Ω after a few hours, and to 0.8 M Ω by the next day. For this reason many investigators prefer to platinize (or replatinize) just prior to use. Fig. 6 shows the circuit used to measure electrode impedances. The oscillator, through a 1000-M Ω resistor, pumps an ac current of 100 pA through the tip impedance. The voltage developed across

³ Code 3020-30 (Alkaline) gold-plating solution, Sifco Metachemical, ladelphia, Pa. Inc., Cleveland, Ohio.

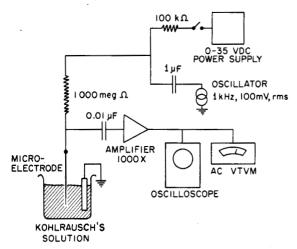


Fig. 6. A simplified schematic for measuring the impedance of a microelectrode tip while simultaneously platinizing it.

this impedance is directly proportional to the electrode impedance. It is amplified and then displayed on an oscilloscope or read directly on an ac vacuum tube voltmeter calibrated in megohms. If, for example, the tip impedance is 1 M Ω , the voltage across it will be 100 μ V. This is amplified by 1000 to 100 mV, and the meter is adjusted to read 100 mV (or 1 M Ω) full scale. In this way the tip impedance is measured at signal levels comparable to those which it will record and well below the nonlinear range. The impedance measured in Kohlrausch's solution (0.05 percent) is a little higher than in isotonic saline, but not significantly. Plating is done by mixing the dc current directly with the ac current in the 1000-M Ω resistor.

R

The spreading resistance of the saline bath is easily found. Imagine a spherical tip of radius r_e . The resistance of a thin spherical shell of saline at radius r of thickness dr of specific resistivity ρ is

$$dR_s = \rho \, \frac{dr}{4\pi r^2}.$$

Integrating from r_e to infinity yields

$$R_s = \int_{r_e}^{\infty} dR_s = \frac{\rho}{4\pi r_e} = \frac{\rho}{2\pi d}$$

where d is the tip diameter. Using 72.5 Ω cm for ρ , one can find that for a 1- μ tip R_s is 115 k Ω , for a 2- μ tip, it is 57 k Ω , and for a 5- μ tip, 23 k Ω . For tips of other than spherical shapes the above formula is not exact, but clearly this resistance is generally negligible when compared to Z_e . For example, the 2- μ tip of Fig. 4(a) has an unplantinized impedance of 89 M Ω . Platinizing will lower this to 1.0 M Ω against which the value of 0.057 M Ω is small enough to be neglected. Thus, regardless of tip shape, R_s is much less than Z_e (this is certainly true of unplatinized tips) and consequently can be neglected.

The values calculated for R_s assume an open (homogeneous) solution and are pertinent in isotonic saline. In the brain, however, the tip is not in an open solution but is

surrounded by glial cells which are separated from neurons and each other by narrow clefts on the order of 150 Å wide. Consequently, an important question is whether, in central nervous tissue, currents at 1 kHz flow through or around glial and nerve cells. To obtain a rough answer to this question, imagine a wall built of cubic glial cells 10 μ on an edge laid together with 150-Å spaces between them. Assume a membrane capacitance of 1 μ F/cm² (0.01 pF/ μ ²) and resistance of 1000 $\Omega \cdot \text{cm}^2$ (100 000 $M\Omega \cdot \mu^2$).^[13] Since the front surface of each cell is $100 \mu^2$ in area, its capacitance is 1 pF, its capacitive reactance is 157 $M\Omega$, and its resistance is 1000 M Ω . Combining front and back walls (ignoring the cytoplasm), the transglial impedance is 314 M Ω capacitive reactance shunted by 2000 M Ω resistance. The resistance of a single intercellular cleft 10 μ wide by 0.015 μ thick by 10 μ long is 48.3 M Ω . Since each repeating unit in the wall contains two such clefts, the extracellular resistance across the wall is 24 megohms per cell. Since 24 megohms is considerably smaller than 314 megohms, most of the current (92 percent) flows between the cells, not through them, at 1 kHz. As a result R_s should be much higher in tissue than in saline, but in practice the electrode tip probably ruptures cell membranes at or near the tip, causing it to be surrounded by a pool or wick of mixed intra- and extracellular fluid which serves to keep R_s near the low value it would have in saline. Even if R_s should increase by ten times it would still only be comparable to or smaller than Z_e . One can in fact observe increases in R_e in certain positions along a track in brain tissue, at which point further advancement of the electrode often results in a sudden large-voltage baseline transient and an immediate drop in tip impedance to its normal value. Such behavior is compatible with the notion that the tip becomes enfolded with membranes which cause the total tip impedance to rise through a rise in R_s and that the tip suddenly ruptures the membranes, whereupon the impedance drops. It should be noted in the foregoing calculation that the assumed value of glial membrane resistance could be reduced by two orders of magnitude (to $10 \Omega \cdot \text{cm}^2$) before the conclusion would be seriously altered. Electrical continuity between glial cells through tight junctions would affect the argument to some extent, but if the current sources and sinks lie outside such a glial electrical syncytium, the current must first get into it before being conducted by it. This argument suggests that paths around the glial cells would still have a lower impedance at 1 kHz than paths through them.

DISCUSSION

The foregoing description of the elements of microelectrode recording makes it possible to understand, however crudely and approximately, which elements are important, which are unimportant, and how the size of the exposed metal at the tip and the action of platinizing result in the tip impedances found in practice. Unfortunately, knowledge of these qualities does not permit one to tell how a given electrode will perform in brain tissue. Consider a hypothetical metal tip that has been introduced into gray matter 20μ from a neuron without in any way traumatizing the tissue around it. When the dendritic tree of this neuron discharges into its soma at the peak of an action potential, the extracellular fluid around the soma becomes negative. Theoretical studies such as those of Rall^[14] suggest that if the cell is about 20 μ in diameter, the tip should be located on an isopotential line of about 200 µV at the peak of the action potential. Clearly, if the tip size could be changed from 1-\mu diameter up to 5-\mu diameter or from a spherical shape to a conical shape, it would still record a spike 200 μV high. The potential gradient at this point is about 5 $\mu V/\mu$ and, therefore, the potential difference between two points separated by 10 μ is about 50 μ V. Thus, the presence of an electrode with a tip diameter of 10 μ will begin to distort the current flow pattern. Nevertheless, the tip, whose surface itself constitutes an isopotential line, will still come to some mean value between the front and back isopotential lines that would exist if the tip were not there, and so it should still record a potential of about 175 μ V. Thus the potential that the tip would record is almost independent of the tip size over the range of 1 to 10 μ . On the other hand, there is considerable difference in the amount of tissue trauma created by the insertion of a 1- or $10-\mu$ tip to a point close to a neuron, and for this reason the smaller tip would record better from the cell than the $10-\mu$ tip which would have destroyed it before reaching it. This is a good example of how the electrical properties are to some extent irrelevant in recording from neurons where shape per se is much more important.

Isolation is another example. Again from the studies of Rall, [14] a 20- μ cell body should create a 100- μ V spike at a distance of 50 u from the center of the cell. Putting it the other way, the neurons within a 100-µ-diameter sphere around an electrode tip should generate at that tip spike potentials of 100 μ V or greater. The volume of this sphere is $5.25 \times 10^5 \ \mu^3$. There is of course an enormous range of cell sizes and densities in the central nervous system, but for a rough calculation assume all cells to be 20 μ in diameter. If they are spaced about 60 μ apart (cubic array, 60 μ center to center), which is typical of motor neurons in the monkey oculomotor nucleus, the cell density is $1/60^3$ or 4.6×10^{-6} $cells/\mu^3$. In the cortex the cells may be crowded closer together, say, 40 μ apart. This is a cell density of 1.56×10^{-5} cells/ μ^3 . In the 100- μ -diameter sphere around the electrode tip, one should predict from these two cell densities that 2 and 8 cells, respectively, should generate 100 μ V or more at the tip. Looked at another way, in a 2-mm electrode track the tip should record from 70 to 234 cells, depending on cell density. In actual practice, in gray matter, one sees only a tiny fraction of these cells, and why this is so is a very disturbing question to users of microelectrodes. Since the spectrum of extracellular spikes lies in the neighborhood of 1 kHz, when the dendritic tree discharges into the de-

polarized soma, the currents, as we have suggested, flow principally in the extracellular clefts between the glial cells. This means that the currents flow through very tortuous channels on their way to the soma. If the electrode tip is in such a channel it may record well, but if it is in a nearby glial cell it will record almost nothing even though that glial cell is adjacent to a large neuron. If the tip has compressed the tissue around itself, it may not only render nearby nerve cells inexcitable but may also compress the extracellular spaces locally so as to divert action potential currents away from the tip. Thus it may be merely a fortuitous set of circumstances based on local geometry and good luck that enables the tip to record an action potential at all. and it is the low probability of occurrence of these circumstances that accounts for the low incidence of cell recordings actually encountered.

All this is, at the moment, speculation. The main point is that the factors which govern the behavior of a metal microelectrode in nervous tissue are not as yet known. The problem is most complex, and not until one has much more control over the size and shape of the exposed metallic tip will it be possible to make much experimental progress. Nevertheless, a low electrode impedance, while not sufficient for good recording ability, is at least necessary, and it has been the aim of this discussion to describe, if only in a crude and simple way, those factors governing the electrical properties of metal microelectrodes.

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