Chapter 2

Electrical Theory

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Abstract

The electrical properties of a cell are maintained by ions moving into and out of the cell. This ionic movement produces electrical potentials, which regulate cellular excitability. The purpose of electrophysiology is to measure cellular excitability by looking at ionic flow and potentials across the cell membrane. This chapter discusses the interpretation of electrophysiological measurements taking into account two forms of in vitro electrophysiology: current clamp and voltage clamp. The chapter begins by looking at field potentials, which are measured extracellularly in the current clamp configuration. Special attention should be paid to the direction of potentials (sinks and sources), which are dependent on positioning of the recording electrode as well as the type of ions moving into or out of a cell. We then discuss field potentials at an axon, a synapse, and the types of fields typically observed. We finish the chapter discussing interpretations of voltage clamp recordings in which currents can be measured.

Key words Nernst equation, Goldman-Hodgkin-Katz equation, Field potentials, Postsynaptic currents, Current rectification, Biological capacitors

1 Introduction

The electrical properties of a cell are maintained by ions moving into and out of the cell. This ionic movement produces electrical potentials, which regulate cellular excitability. The purpose of electrophysiology is to measure cellular excitability by looking at ionic flow and potentials across the cell membrane. This chapter discusses the interpretation of electrophysiological measurements taking into account two forms of in vitro electrophysiology: current clamp and voltage clamp. The chapter begins by looking at field potentials, which are measured extracellularly in the current clamp configuration. Special attention should be paid to the direction of potentials (sinks and sources), which are dependent on positioning of the recording electrode as well as the type of ions moving into or out of a cell. We then discuss field potentials at an axon, a synapse, and the types of fields typically observed. We finish the chapter discussing interpretations of voltage clamp recordings in which currents can be measured.

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2 Field Potentials (In Vitro)

The extracellular fluid consists of charged ions (e.g., Na^+, K^+, Ca^{2+}, Mg^{2+}, Cl^-, HCO^-) and is therefore a conductive medium. A conductive medium is any medium that can transmit electrical energy. In order to transmit electrical energy, a difference in electrical potential between adjoining regions is needed. The adjoining regions in this case are the extracellular and intracellular space, which are separated by a lipid membrane (Fig. 1a). Since neurons have a negative resting membrane potential (e.g., −70 mV; the intracellular side of the membrane is more negative than the extracellular side), negatively charged ions, like Cl^-, accumulate along the intracellular side of the membrane. Meanwhile, positively charged ions (e.g., Na^+, Ca^{2+}, K^+) accumulate along the lipid membrane on the extracellular side. What is produced is an electrical field across the lipid membrane. This field is created as positive ions tend to flow toward the negatively charged ions in the cytosol (with the electric field), while the negatively charged ions tend to flow toward the positively charged ions in the bath (against the electric field). This push or pull of a charge due to its interaction with another charge is known as force and this force is what a field potential measures. Therefore, a field potential is the force exerted on an ion in a conductive medium measured in the form of potential difference.

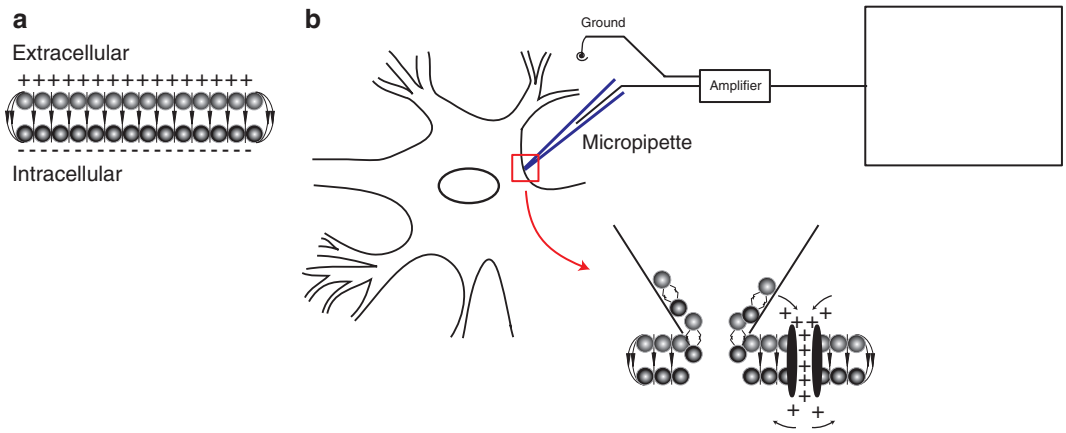

Fig. 1 (**a**) The separation of charge across the lipid membrane and the electric fields produced (*arrows*). The positively charged ions accumulate at the extracellular side of the membrane, while the negatively charged ions accumulate at the intracellular side. (**b**) A somatic whole cell recording showing positively charged ions passing through a transmembrane channel down the electrochemical gradient. This flow of ions is detected via a chloride silver wire connected to an amplifier, which transmits the signal to a digital output. The signal produced is the difference in potential between the recording electrode and the ground electrode, which is submerged in the bath solution

3 Nernst Equation

The force exerted on an ion is subject to change when there is a change in the ionic equilibrium potential or the membrane potential. The ionic equilibrium potential can be calculated using the Nernst equation, which defines the equilibrium potential of an ion in terms of its intracellular and extracellular concentrations ([*C*]in and [*C*]out, respectively):

$$= \frac{RT}{zF} \ln \frac{[C]\text{out}}{[C]\text{in}}$$

where R is the gas constant (8.314 J/K mol), T is the temperature in Kelvin (K) (K = °C + 273.15), z is the ionic charge, and F is Faraday's constant (96,480 Coulombs/mol). At $T = 20$ °C and $z = +1$ the ionic equilibrium potential can be calculated using the following formula:

$$= 58\text{mV} \log \frac{[C]\text{out}}{[C]\text{in}}$$

For warm blooded animals when $T = 37$ °C and $z = +1$ the equation becomes to following:

$$= 62\ \text{mV} \log \frac{[C]\text{out}}{[C]\text{in}}$$

When z is negative as is the case for Cl^- and $T = 37$ °C the equation becomes

$$= -62\text{mV} \log \frac{[C]\text{out}}{[C]\text{in}}$$

or

$$= 62\text{mV} \log \frac{[C]\text{in}}{[C]\text{out}}$$

When z represents a divalent cation (i.e., Ca^{2+}) and $T = 37$ °C the equation then becomes

$$= 31\text{mV} \log \frac{[C]\text{out}}{[C]\text{in}}$$

Table 1 lists ionic concentrations and equilibrium potentials for K^+, Na^+, Ca^{2+}, and Cl^- [1]. Typically, the concentration distribution of these major ions follows these general rules: $[K^+]\text{in} > [K^+]\text{out}$, $[Na^+]\text{in} < [Na^+]\text{out}$, $[Ca^{2+}]\text{in} < [Ca^{2+}]\text{out}$, and $[Cl^-]\text{in} < [Cl^-]\text{out}$ [1].

Table 1
Ionic concentrations and equilibrium potentials

Mammalian cell	Inside (mM)	Outside (mM)	Equilibrium potential $= \frac{RT}{zF} \ln \frac{[C]out}{[C]in}$ $T = 37$ °C
K^+	140	5	−89.7 mV
Na^+	5–15	145	+61.1 mV to +90.7 mV
Ca^{2+}	1–2	2.2–5	+136 to +145 mV
Cl^-	4	110	−89 mV

The equilibrium potential values discussed indicate that if the membrane potential is equal to a particular ion's equilibrium potential, the ionic movement will remain stagnant. However, as the membrane potential moves further away from the ionic equilibrium potential, the driving force for that ion to flow down its electrochemical gradient increases (Fig. 13.1A).

4 Goldman–Hodgkin–Katz Equation

The Nernst equation discussed above can be used to calculate the equilibrium potential of a single ionic species. The membrane potential equals the equilibrium potential of that ion if it is the only ion present in solution. However, if two or more ions coexist than the membrane potential (V_m) can be calculated using a simple linear equation:

$$= \left[\frac{g1}{g1 + g2 + \cdots} \right] E_{m1} + \left[\frac{g2}{g1 + g2 + \cdots} \right] E_{m2} + \cdots$$

where g refers to the conductance and Em refers to the equilibrium potential of each ionic species. Using this equation is convenient and is theoretically solid approach. However, this equation does not apply to ions with low concentrations. When the concentrations of ions become important, the Goldman–Hodgkin–Katz equation can be used:

$$= \frac{RT}{F} \ln \left\{ \frac{px[C]out}{px[C]in} + \frac{px[C]out}{px[C]in} + \frac{px[C]in}{px[C]out} + \cdots \right.$$

where p is the membrane permeability for a given ion (x). Note that in the third additive group of the equation the intracellular concentration moves to the numerator and the extracellular concentration moves to the denominator. This occurs when anions are included in the equation (e.g., Cl^-).

5 Ionic Gradients Maintained

The potential difference can only be measured when there is a flow of ions between the intracellular and extracellular space. The ionic flow is made possible by transmembrane channel activation. Once the activated channels open, ions flow down their electrochemical gradient, creating an electrical potential difference between the recording and ground electrodes (Fig. 1b).

Generally, there are three types of receptors/channels that are responsible for creating electrical potential differences. They are excitatory receptors, inhibitory receptors, and voltage-gated channels. As ions flow into or out of these receptors/channels, a current is generated, thus creating a potential change of the membrane (Voltage (V) = current (I) × resistance (R)). Depending on the position of the recording electrode, it detects an active current sink, an active current source, a passive current source, or a passive current sink (Fig. 2a).

When excitatory receptors become activated at synapses, Na^+ or Ca^{2+} flows from the extracellular space into the intracellular compartment. This flow of ions produces a potential known as an excitatory postsynaptic potential (EPSP). At the site where positive ions enter the neuron an active current sink is formed. This occurs as the positively charged ions rush intracellularly leaving behind a net negative charge (Fig. 2a). As positive ions flow inside the cell, there must be an equivalent flow of positively charged ions flowing outside the cell, known as a passive current source. The passive current source is generated at a distance away from the active current sink. As positively charged ions rush into the cell at the active current sink, a flow of positive charged ions flows out of the cell creating the passive current source.

To help grasp this concept, picture a cylinder lying horizontal with holes located equidistant apart on the top surface. Now picture the cylinder completely filled with water. As additional water is poured through one hole (active current sink), excess water inside the cylinder flows out (passive current source) from the adjacent holes. This flow of water out of the cylinder decreases as the distance increases from the active current sink. This example is similar to how current flows into and out of the neuron. See the electric field in Fig. 2b. The arrows indicate the direction that the positive ions flow (positive charge always flows with the electric field), meaning that negative ions must flow opposite (negative charge always flows against the electric field). The force is strongest at the site of receptor activation. Therefore, the electric field is the strongest and is illustrated by small distance between lines. The force decreases as the distance increases from the active current sink. This is illustrated by the increase in the distance between electric field lines further from the active current sink.

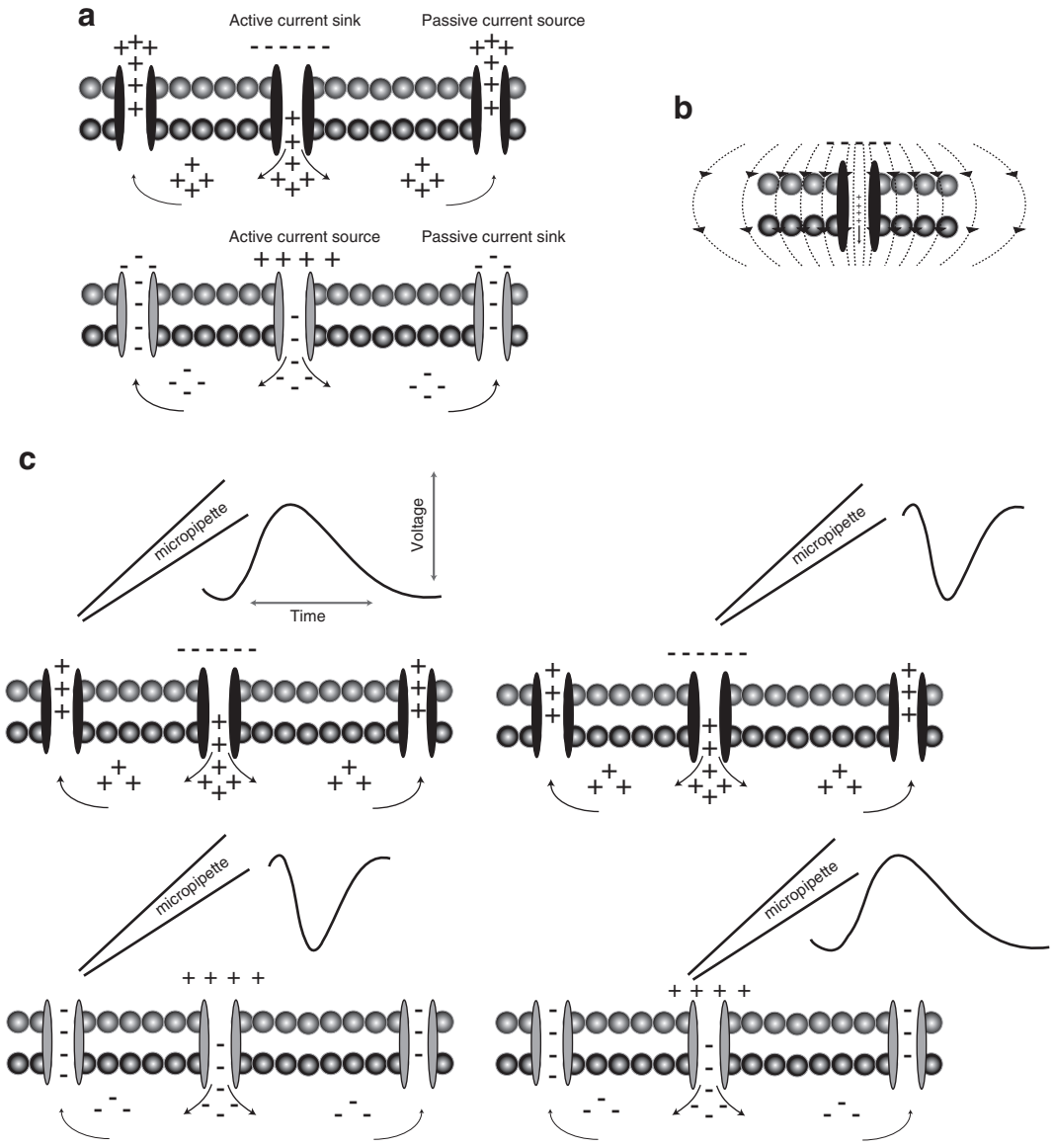

Fig. 2 (**a**) (*Top*) The flow of positively charged ions down the electrical gradient following cationic channel activation. As positively charged ions move through the channel intracellularly, a net negative charge is left extracellularly (active current sink). As positively charged ions move from the extracellular compartment to the cytosol, an equivalent flow of positively charged ions moves in the opposite direction creating a passive current source adjacent to the active current sink. (*Bottom*) The flow of negatively charged ions against the electrical gradient following anionic channel activation. As negatively charged ions move through the channel intracellularly, a net positive charge is left extracellularly (active current source). As negatively charged ions move from the extracellular compartment to the cytosol, an equivalent flow of negatively charged ions moves in the opposite direction creating a passive current sink adjacent to the active current source. (**b**) An electric field generated following activation of a cationic channel and subsequent ionic movement. The *arrows* indicate the flow of positively charged ions flowing with the electric field. The force is the strongest at the site of receptor activation and decreases as the distance from the active current sink increases. (**c**) The potentials that are generated in the signal detected are dependent upon the position of the micropipette in relation to the sinks and sources. (*Top*) Shows a positive potential detected at the passive current source (*left*), while a negative potential is measured at the active current sink (right). (*Bottom*) As anions move from the extracellular space into the cytosol, a negative potential is measured at the passive current sink (*left*), while a positive potential is measured at the active current source (*right*)

Where the recording electrode is placed dictates the field potential direction (positive or negative) as well as the field potential magnitude. If the recording electrode is positioned at the active current sink, a negative potential is recorded. However, if the electrode is located at the passive current source, a positive potential is recorded (Fig. 2c). The magnitude of the field potential is dependent on the distance from the recording electrode (i.e., the field potential decays as the square of the distance).

In addition to active current sinks and passive current sources, there are active current sources and passive current sinks. When inhibitory receptors at synapses become activated there is an influx of negatively charged ions (Cl^- or HCO_3^-) into the neuron. This flow of ions is known as an inhibitory postsynaptic potential (IPSP). As negatively charged ions flow intracellularly, there is a net positive potential extracellularly at this site (active current source). Since negatively charged ions are flowing into the cell, they also must be flowing out of the cell adjacent to the active current source (passive current sink) (Fig. 2c). If the recording electrode is positioned at the active current source, a positive potential is recorded. However, if the electrode is located at the passive current sink, a negative potential is recorded (Fig. 2c).

IPSPs are also detected when K^+ channels open causing K^+ to flow from inside the cell to outside. When K^+ channels open, an active current source is detected nearby the activated K^+ channel site while a passive current sink is located adjacent to this site.

Finally, there is an important point to discuss. Conductance (the ability to conduct electrical charge) is dependent upon temperature. Increasing temperature always increases the solution's conductivity by 1.5–5 % per degree Celsius. Therefore, when performing an in vitro field potential experiment, it is wise to keep your recordings at a consistent temperature. Otherwise, discrepancies in your results can mount.

6 Field Potentials Along an Axon

When an action potential is generated in the soma and moves along the axon, sodium channels open. Subsequently, an influx of positively charged ions enters the cell leaving behind an excess negative charge (active current sink). The current that is produced flows into the intracellular fluid and exits the membrane at more distal locations (passive current source) (Fig. 3a). As the action potential propagates down the axon towards the dendrites, the sinks and sources move to accompany the current flow. So if an action potential was elicited at point A and the recording electrode was positioned at point B, a positive potential would be detected since the electrode would be located at the passive current source. If the action potential moves right below the recording electrode, the

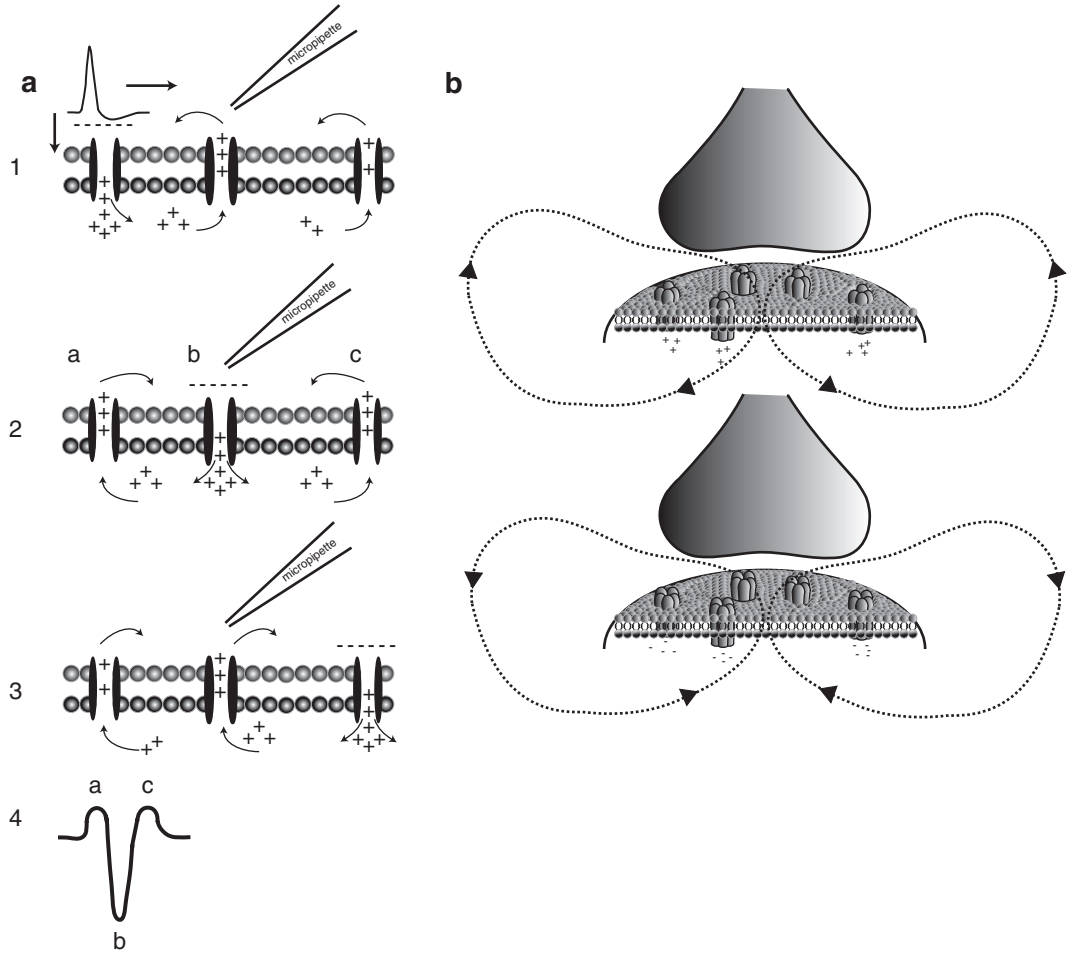

Fig. 3 (**a**) An action potential is generated and propagates along an axon while extracellular potentials are measured by a micropipette. The micropipette is stationary and detects potential differences (relative to ground) as the action potential moves along the axon. (*1*) An action potential elicits sodium channel activation upstream of the micropipette creating a passive current source at the recording site. (*2*) The action potential propagates down the axon opening sodium channels adjacent to the recording site creating an active current sink. (*3*) The action potential continues to propagate down the axon creating a passive current source at the recording site. This sequence of events creates a positive–negative–positive detected signal *n*. The negative potential produces the largest amplitude because the electrical gradient is strongest at the site of the active current sink. Where the passive current sources are measured a weaker electrical gradient exists. (**b**) *Top*. Positive ions flow intracellularly through activated excitatory receptors creating an active current sink at the synapse and passive current sources at adjacent regions. *Bottom*. Negative ions flow toward the cytosol through activated inhibitory receptors creating an active current source at the synapse and passive current sinks at adjacent regions. *Lines* represent the electrical field generated at each synapse

recording electrode would detect a negative potential (active current sink). Finally, the recording electrode would detect a positive potential as the action potential moves further along the axon past the recording electrode (passive current source). The result is a positive–negative–positive potential. The generation and propagation

of action potentials produces a field potential known as a population spike. A population spike refers to the summed synchronous action potentials of a pool of neurons. The relevance of population spikes is discussed in the analysis section below.

7 Field Potentials at Synapses

Synaptic potentials are generated as postsynaptic receptors become activated by presynaptic neurotransmitter release. As receptors are opened, current can flow into the neuron creating a potential. At excitatory synapses an EPSP appears when positive ions flow intracellularly (active current sink) and exit the membrane at more distal locations (passive current source) (Fig. 3b). At inhibitory synapses, an IPSP appears when negative ions flow intracellularly (active current source) and exit the membrane at more distal locations (passive current sink) (Fig. 3b). The representative traces recorded for EPSPs and IPSPs at active and passive current sinks and sources are illustrated in Fig. 3b.

8 Types of Fields

The central nervous system generates at least three distinct field potential patterns. The field patterns are open fields, closed fields, and open-closed fields [1, 2].

Open fields are generated in neurons that have a long apical dendrite, which extends away from the soma. The neurons with this phenotype are arranged side-by-side in a columnar fashion (Fig. 4a). This neuronal arrangement is seen in the hippocampus, cerebellum, and cerebral cortex. When measuring field potentials in an open field, a negative extracellular potential is measured at an active or passive current sink. In contrast, positive extracellular potentials are measured at an active or passive current source. For example, if a backpropagating action potential is generated at the soma, the soma has a negative extracellular field potential. The dendrites, on the other hand, have a positive extracellular field potential. This generates a dipole (equal and oppositely charged poles separated by a distance) (Fig. 4a). Between the charged poles is a zero potential line (a region in space where there is no potential generated) that extends ad infinitum horizontally (Fig. 4a). However, the amplitude of field potentials decays as the square of the distance [2, 3]. Because of this, the zero potential as well as the negative and positive isopotentials (a region in space where every point is at the same potential) can only be detected if they are nearby the potential difference created by the current flow.

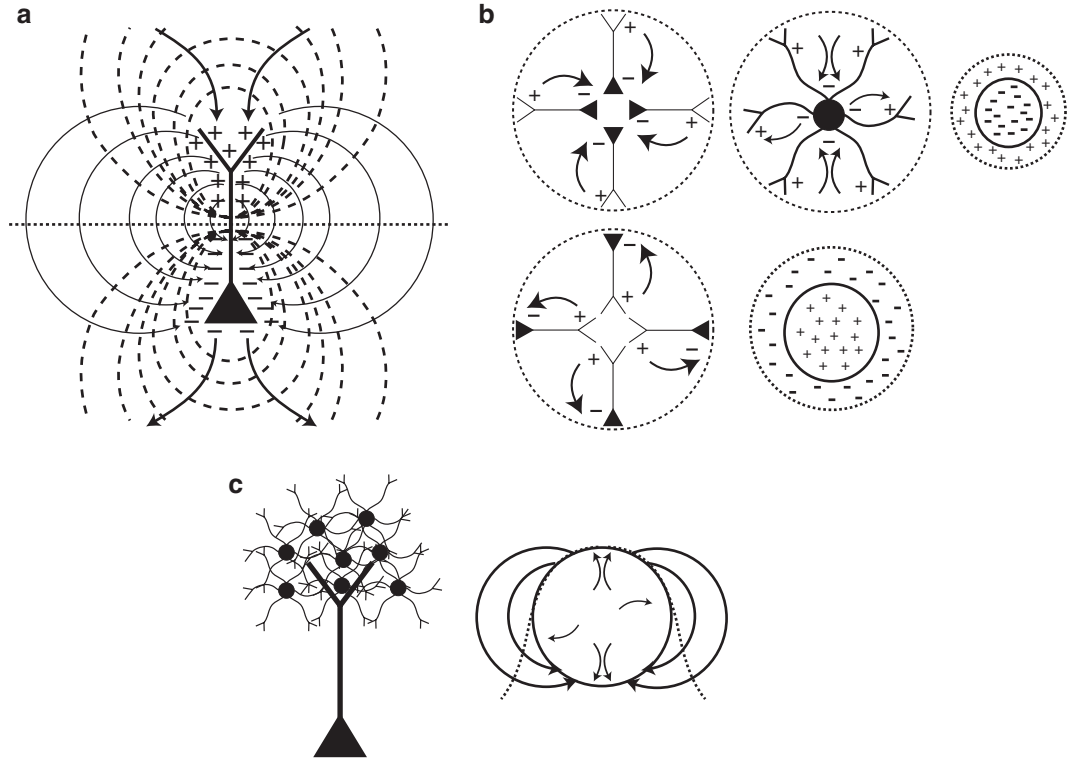

Fig. 4 Types of field potentials. (**a**) An open field generated from a neuron with an apical dendrite extending vertically away from the soma. The illustration shows a backpropagating action potential initiated at the soma with the corresponding extracellular potentials produced. Above the zero potential line (*dotted horizontal line*), positive isopotentials are generated at the passive current source (*curved dashed lines*), while below the zero potential line, negative isopotentials are generated at the active current sink. *Arrows* indicate the direction of the electric field produced by the backpropagating action potential. The separation of charges in an open field produces extracellular dipole currents (*solid curved lines*) flowing from the source to the sink. (**b**) (*Top*) A closed field generated by (1) a group of neurons situated with centralized somas and dendrites positioned radially (*left*) or (2) a single neuron with a central soma and radially extending dendrites (*middle*). Figure shows a backpropagating action potential with an active current sink at the soma and a passive current source at the dendrites producing closed potentials (*right*) and a zero potential line (*dotted line*). (*Below*) A closed field produced backpropagating action potentials in a group of neurons with somas positioned peripherally with dendrites extending centrally (*left*) generating closed field potentials (*right*). In all examples of a closed field, the extracellular currents flow radially from sources to sinks. (**c**) An open-closed field generated by an apical dendrite extending vertically away from the soma into a group of neurons situated with centralized somas and dendrites positioned radially. The isopotential line is illustrated as the *dashed black line*

Closed fields are generated from neurons that extend dendrites radially from a central soma (i.e., stellate-shaped spinal motor neurons). They are also generated from neurons that extend dendrites centrally from somas positioned peripherally (Fig. 4b). The isopotential is spherical with a diameter dependent upon dendritic electrical excitability (Fig. 4b). Recording field potentials from neurons arranged as shown in Fig. 4b results in active or passive current sinks where a negative potential is generated and

active or passive current sources generated where a positive potential exists. Unlike open fields, where potentials extend ad infinitum horizontally, closed fields produce potentials that extend spherically in a closed circle. In a closed field, where the dendrites extend radially from the central soma, action potential generation results in negative–positive spikes at all distances from the soma [4].

Open-closed fields are the third type of field potential. They are generated when both radial dendrites and columnar dendrites coexist in a neuron pool. As seen from Fig. 4c, positive potentials can be recorded above the isopotential line and negative potentials can be recorded from below the isopotential line.

9 Postsynaptic Currents

So far we have discussed electrical potential differences between the recording electrode and the reference electrode. Now we are going to discuss current measurements, which directly measure the amount of ions moving through a channel. Current is measured in ampere (amp) and 1 amp equals 1 coulomb (unit of electrical charge)/second. Therefore, when we measure currents, we are measuring how many ions pass through a given point/second. The major advantage is that electrophysiologists are able to measure how many ions flow through a specific channel.

10 Inward vs. Outward Current (Whole-Cell Configuration)

Inward current describes any flow of ions that makes the cell more depolarized (Fig. 5a). For example, positive ions flowing into the cell depolarizes the cell causing an inward current (Fig. 5a). Similarly, negative ions flowing out of the cell also depolarize the cell causing an inward current (Fig. 5a).

Outward current describes any flow of ions that makes the cell more hyperpolarized. This occurs if positive ions flow out of the cell (typical of K+ channels, although there are some exceptions—inward rectifier K+ channels) or if negative ions flow into the cell (typical of GABAR and glycine receptors which are permeable to Cl–).

Electrophysiologists should be aware that the flow of ions depends on the ionic concentrations of the internal and external environment. Physiologically, Cl– flows into the cell meaning an outward current. However, many publications show a Cl– channel with inward current [5]. In these experimental settings, Cl– flows out of the cell since the internal solution contains a high Cl– concentration, shifting the physiological Cl– reversal potential from –70 mV to ~0 mV (Fig. 5a). The reason this is done experimentally is because the neuron can be voltage clamped at a more physiologically relevant potential (i.e., –70 mV) while recording Cl– currents.

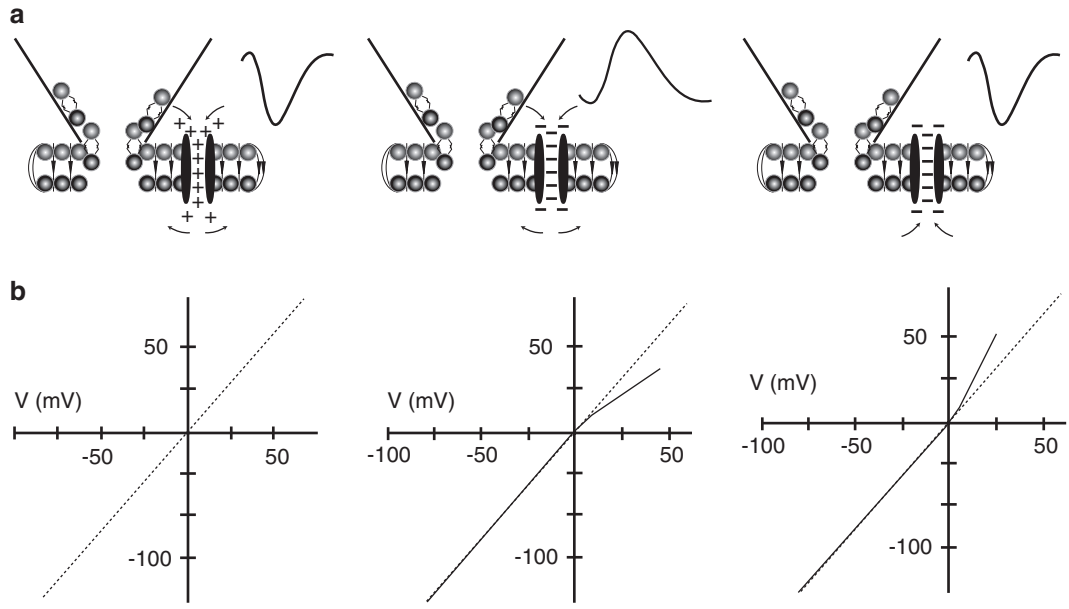

Fig. 5 Inward vs. outward current and current rectification. (**a**) Inward currents recorded in the whole cell configuration following the flow of positive ions from the extracellular to the intracellular side of the membrane (*left*). Outward currents recorded in the whole cell configuration following the flow of negative ions from the extracellular to the intracellular side of the membrane (*middle*). Inward currents recorded in the whole cell configuration following the flow of negative ions from the intracellular to the extracellular side of the membrane (*right*). (**b**) Illustration of the characteristic rectified currents seen in neurobiology including no rectification (*left*), inward rectification (*middle*), and outward rectification (*right*)

11 Current Rectification

Rectification describes voltage-dependent changes in channel conductance. Electrophysiologists have investigated both inward and outward rectifier channels. Inward rectifier channels pass more inward current than outward current, which is characteristic of calcium permeable AMPA receptors (GluR2-lacking) or inward-rectifier potassium channels. Calcium permeable AMPARs are inward rectifiers because at membrane potentials >0 mV the channel pore is blocked by polyamines, thus minimizing the flow of outward current (Fig. 5b). Similarly, inward-rectifying potassium channels are blocked by polyamines at depolarizing membrane potentials (Fig. 5b). Conventionally, K^+ flows out of the neuron, but inward-rectifier K^+ channels are open at hyperpolarizing potentials more negative than potassium's reversal potential. Therefore, K^+ flows into the cell to bring the cell back to its resting potential. However, as stated before, at more positive potentials inward-rectifier K^+ channels are inhibited by polyamines, reducing the flow of K^+ out of the cell.

Outward rectifier channels on the other hand pass more outward than inward current, which is characteristic of TREK-1 K^+ channels (Fig. 5b) Therefore, upon the same driving force, the outward flow of K+ is greater than the inward flow with the opposite direction (Fig. 5b).

12 Biological Capacitors

Capacitors have the ability to store charges (Q) when a voltage, ΔV, is applied (Fig. 6a). The ability for a capacitor to store charge is measured as capacitance (C; measured in farads, F) so that:

$$C = Q / DV$$

In electrophysiology, capacitance can be introduced by the electrode (immersed part), the biological membrane, and the stray capacitance (from the recording electrode to grounded surfaces or from the recording electrode holder).

The electrode's capacitance is formed across the glass walls. Therefore, the glass used to construct recording electrodes can greatly affect the capacitance (see Chap. 4). However, typically when immersed in the bath the capacitance of the recording electrode is 1 pF/mm of immersion depth [6].

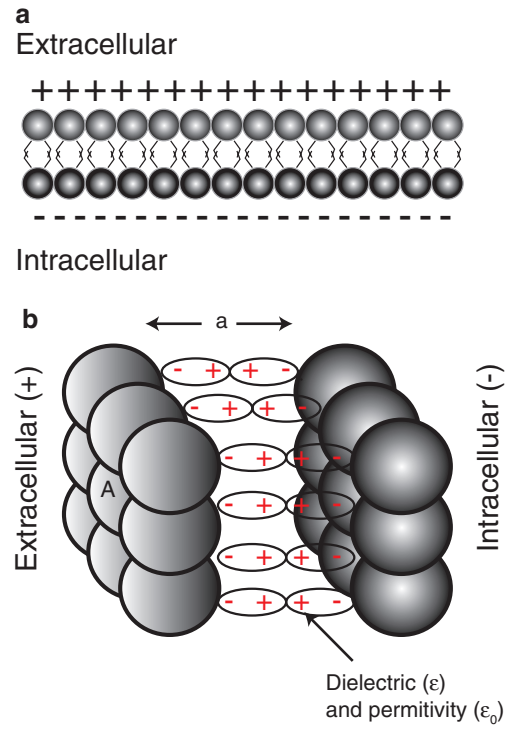

Fig. 6 Biological membranes as capacitors. (**a**) The properties of a lipid membrane enable charges to be separated along the extracellular and intracellular surface. Positive charges accumulate extracellularly, while negative charges accumulate at the intracellular surface. (**b**) The capacitive properties of the lipid membrane are illustrated. Contributing to the capacitance is the distance separating the extracellular and intracellular lipids (*a*), the surface area (*A*), and the dielectric and permittivity constants (ε and ε_0, respectively). The dielectrics are created as polar molecules situated in the lipid bilayer are oriented according to the extracellular and intracellular charges

Biological membranes are analogous to parallel-plate capacitors due to similar geometry (Fig. 2b). Their capacitance is directly proportional to their surface area (A) (the larger the cell, the greater the capacitance), to the dielectric constant of the medium separating the membrane (ε) (figure showing this), to the permittivity constant (ε_0) (referring to the ability of a substance to store electrical energy in an electric field), and it is inversely proportional to the distance (a) separating the plates.

$$C = A\varepsilon\varepsilon_0 \,/\, a$$

Biological membranes are typically less than 10 nm thick with an approximate capacitance of 1 μF/cm^2.

Stray capacitance is the capacitance that exists between conductive elements in a circuit. Typically, this capacitance is very low (a few picofarads) [6]. However, when stray capacitance couples to high impedance points, such as the micropipette input, circuit operation can be severely affected.

13 Electrophysiology Clamping Techniques

Current clamp: Current clamp maintains or clamps the current such that no net current flows through the membrane. This is accomplished by passing a time-varying or known constant current and measuring the changes in membrane potential.

Voltage clamp: In voltage clamp mode, the cell's potential is maintained at a command voltage by passing positive or negative current from the recording electrode into the cell. This way the membrane potential can be maintained at a consistent voltage throughout the entire experiment. In voltage clamp, the experimenter is essentially measuring the current that is needed to maintain the command voltage.

Dynamic clamp: Dynamic clamp refers to injecting conductance into a recorded cell in order to reproduce electrical effects of ion channels when they become activated [7].

14 Summary

Field potentials are maintained by ionic movement between intracellular and extracellular compartments. Depending on the movements of cations and anions, and the location of recording pipettes (e.g., axon, synapse, and soma), field potential sinks and sources can be measured. These potentials depend upon the driving force pushing ions down the electrochemical gradients, which can be calculated via the Nernst equation listed above. In addition to measuring cellular potentials, currents produced by ionic flow can

also be measured. Much like field potentials, cation or anion movement dictates the direction of the current trace measured during experimentation. Since electrophysiological measurements take into account electrical activity, biological as well as experimenter factors, such as capacitance, can be introduced affecting the electrical circuit. Attention must be paid to neutralizing capacitance if possible in order to prevent unwanted artifacts from being introduced into the electrophysiological measurements.

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