Journal of Clinical Neurophysiology 2(4):327–354. Raven Press, New York © 1985 American Electroencephalographic Society

# Neuronal Generators and the Problem of Localization in Electroencephalography: Application of Volume Conductor Theory to Electroencephalography

### Pierre Gloor

# Montreal Neurological Institute and the Department of Neurology and Neurosurgery, McGill University, Montreal, Quebec, Canada

The principal tasks of the clinical electroencephalographer are to recognize particular waveforms of diagnostic significance, such as, for instance, spikes, sharp waves, delta waves, and to identify the likely location of their generators within the brain. The first of these, which is one of pattern recognition, is relatively easy to learn, but the second is difficult and requires an adequate understanding of some basic principles of physics and electrophysiology. Potential differences, in the brain as elsewhere, reflect the segregation of electrical charges at certain locations within a three-dimensional body. Although, generally speaking, the potential measured at some distance from an electrical charge decays with increasing distance according to a parabolic function, the situation is not as simple as one might infer from this. Thus, it is not necessarily true that the potential (or the potential difference between two electrodes) generated by a neuronal source is greater, the closer the measuring electrodes are to this source. The lack of a simple relationship between the size of a potential measured at a given point and the distance of this point from the generator derives from the fact that the generators of the EEG are not simple point-like charge accumulations, but have dipolar configurations (Bishop, 1949; Brazier, 1949; Li et al., 1956a, b; Spencer and Brookhart, 1961a, b; Creutzfeldt and Houchin, 1974; Kostopoulos et al., 1982; Gloor, 1983). More importantly, they are not even simple dipoles, but dipole layers that are convoluted (Bishop, 1949; Gloor et al., 1963; Calvet et al., 1964; Fourment et al., 1965; Vaughan, 1969, 1974, 1982; Gloor, 1975; Ball et al., 1977a, b; Klee and Rall, 1977). Their particular geometry and orientation with regard to the exploring electrodes are crucial determinants of the potential distribution within or at the surface of the three-dimensional body containing the generator (Gloor et al., 1963; Calvet et al., 1964; Jami et al., 1968; Vaughan, 1969, 1974; Gloor, 1975; Klee and Rall, 1977). In the daily practice of reading EEGs, often little attention is paid to these factors, and superficial conclusions

Address correspondence and reprint requests to Dr. Gloor at Montreal Neurological Institute, 3801 University Street, Montreal, Quebec, Canada H3A 2B4.

are frequently drawn from EEG records, based on the erroneous notion that the electrode or the pair of electrodes at which the largest potential is recorded is closest to the area of brain containing the generator of that potential. This concept is often uncritically and indiscriminately applied to the reading of both monopolar (referential) recordings in which there is some, but only partial, justification for this notion, and to bipolar recordings in which this concept is patently incorrect. In order to avoid such erroneous conclusions, the interpreter must possess some understanding of volume conductor principles. He must know how electrical fields on the scalp (or within the brain) result from cortical activity and how, starting from data provided by a traditional multichannel EEG recording, one may mentally construct an appropriate configuration and localization of the cerebral generator of the recorded potential.

There are a number of rigorous ways of treating the problem of volume conduction, and the mathematics involved can be quite difficult. A thorough review of this subject has recently been published by Nunez (1981) and is an excellent source of information for anyone who wishes to penetrate more deeply into the quantitative aspects of the biophysics of EEG. A briefer mathematical treatment is given by Lopes da Silva and van Rotterdam (1982). The approach used in this review is based on applying the solid angle theorem of volume conductor theory (Woodbury, 1960) to EEG, a concept that is implicitly present, although not explicitly stated, in the treatment given this subject by Nunez (1981). There are distinct advantages to applying the solid angle concept to cortical electrophysiology and EEG (Gloor et al., 1963; Calvet et al., 1964; Jami et al., 1968; Vaughan, 1974; Gloor, 1975), for it provides a conceptual framework that makes it possible to visualize cortical generators of EEG signals and the fields they produce three-dimensionally, without having to resort to complex mathematics.

The remainder of this review is divided into three main sections. Some readers may find it easier to initially skip the second selection entitled "The Solid Angle Concept Applied to Volume Conductor Theory" and read the third section first in which this concept is applied to clinical EEG. It is hoped that those who have elected to proceed in this fashion will be tempted to return to the second section, since it provides the neurophysiological and biophysical basis for the principles of localization in EEG presented in the third section.

#### THE GENERATORS OF THE EEG

#### The Cortical Pyramidal Neuron as the Principal Unitary Generator of EEG Waves

It is now generally accepted that the principal generators of the EEG are cortical neurons, more particularly pyramidal neurons (Bishop, 1949; Creutzfeldt and Houchin, 1974; Ball et al., 1977*a*,*b*; Gloor, 1983). A good starting point for gaining a better understanding of how these neuronal generators produce the signals recorded in the scalp EEG, therefore, is to determine the extracellular electrophysiological consequences of the synaptic excitation of a single cortical pyramidal neuron in response to an afferent (e.g., thalamocortical) volley that generates excitatory postsynaptic potentials (EPSPs) at multiple synaptic contacts located, e.g., on the apical dentritic tree of such a neuron (Fig. 1). The consequence of such an excitation is a depolarization of the apical den-

J. Clin. Neurophysiol., Vol. 2, No. 4, 1985



FIG. 1. Electrical field conforming to that of a dipole created by the synaptic excitation of a single cortical pyramidal neuron. It is assumed that the neuron has been excited by a set of excitatory synapses located on the apical dendrites. (Some thalamocortical afferents would produce such a response.) Because of the depolarization of the apical dendritic membrane, this segment of the neuron becomes extracellularly electronegative with respect to the soma and basal dendrites, which become electropositive. This causes current to flow through the extracellular medium as indicated by the solid lines with arrows. The potential distribution within the volume conductor corresponding to this current flow is portrayed by the isopotential surfaces represented as dashed lines. Each isopotential surface represents the geometric locus of all points that are at the same potential. The isopotential surfaces intersect the current paths at right angles (the drawing does not represent this in an entirely accurate way). The isopotential surfaces are drawn at levels separated from each other by potential differences of equal magnitude (arbitrarily assumed to be 100  $\mu$ V in the drawing). Note that the potential difference measured between points A and B, which are relatively remote from the excited cell, would measure 500  $\mu$ V, while no potential difference would be measured between D and C, even though they are much closer to the excited neuron.

dritic membrane, which becomes extracellularly electronegative with respect to the cell soma and the basal dendrites. This potential difference causes a current to flow through the volume conductor between a "source" represented by the nonexcited membrane of the soma and basal dendrites and the "sink" located at the level of the apical dendritic membrane sustaining the EPSPs. Some of this current takes the shortest route between the nonexcited and the excited segment of the membrane, but current also flows through more distant parts of the volume conductor, with current paths taking increasingly more remote, curving routes as shown in Fig. 1 by the solid lines with arrows. Even though current density rapidly drops off with increasing distance from its source, some current,

at least theoretically, flows even through the most distant part of the volume conductor. The electromotive force driving the current in the example pictured in Fig. 1 is the resting membrane potential of the unexcited segment of the neuron, i.e., the soma and basal dendrites. The extracellular current depicted in Fig. 1, however, is only part of the total current loop, which also has an intracellular component flowing along the long axis of the neuron, essentially within the dendritic trunk. This intracellular path carries the highest density current, since its magnitude is equal to the total, but much more dispersed extracellular current. The new technique of magnetoencephalography (MEG) (Cohen, 1972; Cuffin and Cohen, 1979; Barth et al., 1982; Cohen and Cuffin, 1983) makes use of the fact that intracellular currents are densest in these segments of cortical pyramidal neurons, which are orthogonally oriented to the cortical surface (Cuffin and Cohen, 1977).

If we make the assumption that the resistivity of cerebral tissue is homogeneous (which is not strictly true<sup>1</sup>), it is easy, from the pattern of extracellular current flow depicted in Fig. 1, to construct the corresponding pattern of potential distribution within the volume conductor. The lines of current flow are intersected at right angles by lines representing surfaces on which the potential is the same everywhere. These are called isopotential surfaces shown as dashed lines in Fig. 1. The convention, followed in this figure, is to draw lines representing isopotential surfaces at locations that are separated by distances corresponding to voltage differences of equal magnitude (100  $\mu$ V in Fig. 1). Thus, the electrical field around a single excited pyramidal neuron as portrayed in Fig. 1 assumes the well-known configuration of that of a dipole. The zero isopotential surface is located halfway between the positive and negative poles (represented in this instance by the accumulation of positive charges at the physiologically quiescent somatic and basal segment of the pyramidal neuronal membrane, and of negative charges at its excited apical dendritic segment). The zero-isopotential surface is the only one that is flat; all the others are curved and form a system of eccentric ellipsoid surfaces, each located within the space enclosed by the next lower isopotential surface. As is evident from Fig. 1, isopotential surfaces are much closer to each other across the shortest distance that separates the positive from the negative charges than in the regions beyond the two "ends" of the dipole. Between the two poles of the dipole the potential thus changes very rapidly with distance, whereas elsewhere in the volume conductor the potential gradient is much less steep.<sup>2</sup>

In speaking of an excited pyramidal neuron as a "dipole," one must bear in mind that this is a metaphor. The neurophysiologist's "dipole" is not identical with that of the physicist. A neuron is much too complex a structure, when one takes into consideration the distribution of electrical charges within and on the surface of the cell, that it could never be equated with the simple physical concept of a dipole. Even though the dipole model of cortical electrogenesis has been of enormous heuristic value in neurophysiol-

J. Clin. Neurophysiol., Vol. 2, No. 4, 1985

330

i

ŝ

1

i

1

É

7

£

i

ti

<sup>&</sup>lt;sup>1</sup>The cerebral cortex has a resistivity of less than half that of white matter (Nunez, 1981). Although this to some extent affects the configuration of the electrical fields within the brain, it has little effect on the extracranial EEG.

<sup>&</sup>lt;sup>2</sup>It is important to keep in mind that the field depicted in Fig. 1, as all other fields shown in subsequent fig-<sup>2</sup>It is important to keep in mind that the field depicted in Fig. 1, as all other fields shown in subsequent figures of this paper, portray the potential distribution prevailing *at an instant of time*: e.g., in the case of Fig. 1, this may be the moment when the potential resulting from the summed EPSPs generated on the apical dendritic tree of the pyramidal neuron reaches its peak, or, in the case of the fields illustrated in Figs. 5-11, the instant of time may be the peak of an EEG wave. In real time, such fields are continuously changing.

## APPLICATION OF VOLUME CONDUCTOR THEORY TO EEG 331

ogy, there are limits to its usefulness. The electrical field created by the excitation of a neuron structured like a pyramidal cell can easily be modeled to conform to that of a dipole, because one single long axis dominates the neuronal morphology, and synaptic contacts of different systems are segregated in such a manner that membrane potential changes tend to occur at or toward either end of this elongated neuronal element, depending on which class of synaptic inputs is being activated. The dipole concept, however, is not easily adaptable to multipolar neurons of the type found in the thalamus, the brainstem nuclei, and the anterior horn of the spinal cord (Lorente de Nó, 1947; Rall, 1962; Klee and Rall, 1977).

## Some Fundamental Principles of Volume Conductor Theory Derived from the Dipole Concept of Cortical Electrogenesis

Representing the dipole field of an excited single pyramidal neuron as shown in Fig. 1 is didactically useful, for it illuminates some fundamental principles of volume conductor theory. The first of these is that when a potential difference is set up within a volume conductor, currents flow throughout its entire extent. No part of it remains unaffected. Currents are thus not restricted to the immediate neighborhood of the generator, such as, for instance, the pyramidal neuron of Fig. 1, although they are densest there. This should come as no surprise to an electroencephalographer who has ever reflected on why an electrocardiogram "artifact" can appear in a scalp EEG recording. Obviously, currents generated by the cardiac dipole in the chest flow through the head at a considerable distance from the location of the generator and can set up measurable potential differences there.

Another principle is that a potential difference recorded between two electrodes within a volume conductor depends more on their orientation with regard to the configuration and orientation of the electrical field within it than on the proximity of the electrodes to the generator. Thus, a fairly large potential would be recorded between electrodes placed at points A and B in Fig. 1 (500  $\mu$ V in the hypothetical case depicted there), even though they are quite remote from the generator, whereas no potential would be recorded between electrodes located at C and D, even though these points are very close to the generator. This is because both C and D lie on the same isopotential surface, whereas A and B are located at isopotential surfaces that are 500  $\mu$ V "apart." Again, such a situation ought to be familiar to an electrodencephalographer: often in bipolar recordings an anterior temporal spike discharge, for example, may fail to appear in the electrode linkage F7-T3 of the 10-20 electrode system or may only be recorded there with a much smaller amplitude than in adjacent channels, even though these two scalp electrodes are closest to the generator of the spike, the anterior temporal cortex.

## THE SOLID ANGLE CONCEPT APPLIED TO VOLUME CONDUCTOR THEORY

#### **Basic Principles**

To understand how electrical potentials that are recordable on the scalp can be generated by populations of pyramidal neurons of the type depicted in Fig. 1, it is useful to introduce the solid angle concept of volume conductor theory. According to Woodbury





(1960), the potential P generated by a dipole layer in a volume conductor measured at any point within this conductor is proportional to the solid angle subtended by the dipole layer at the point of measurement (Fig. 2). This relationship can be expressed by the formula:

$$P = \frac{\pm e}{4\Pi} \Omega$$

where P is the potential measured at a given point in the volume conductor, e is the potential across the dipole layer, and,  $\Omega$  is the solid angle subtended by the dipole layer at point P. The relationship expressed in this formula applies to an ideal monopolar (referential) recording in which the reference electrode is unaffected by the potential across the dipole layer (for practical purposes a reference electrode at a large distance from that layer will sufficiently approximate this ideal situation). The solid angle concept is useful, because it is easily grasped intuitively. The visual angle under which we see objects is a familiar example of a solid angle. We are all aware that the apparent size of an object, e.g., that of a table top, depends both on the distance of the object and on the angle under which it is seen. The same applies to a potential generated by a dipole layer and measured by an exploring electrode. The measured potential is independent of the detailed geometric configuration of the dipole layer, but only depends on its "apparent size" when "seen" by an electrode from a particular vantage point. Figure 2 also shows that the electrical sign of the potential measured at any point around the dipole layer depends on the electrical sign at the surface of the dipole layer facing the measuring electrode. Thus, in Fig. 2, a negative potential  $(P^-)$  is measured on the negative, and a positive one  $(P^+)$  on the positive side of the dipole layer.

J. Clin. Neurophysiol., Vol. 2, No. 4, 1985

### Application of the Solid Angle Principle to a Single Excitable Cell

Let us now apply this principle to potentials generated by a single excitable cell, such as a neuron. We shall subsequently extend it to a neuronal population, such as the pyramidal cells of the cerebral cortex. It is a truism that no potential is measured around a quiescent excitable cell (neuron, nerve fiber, muscle fiber). A quiescent cell, however, has a membrane potential of about 60 to 80 mV, the interior side of the membrane being electronegative to its external surface. Such a charged membrane can be regarded as a dipole layer made up of an almost infinite number of virtual dipoles arranged in parallel alongside each other. This situation, in terms of the solid angle theorem, can formally be depicted as in Fig. 3A<sup>3</sup> taken from Woodbury (1960). Since the quiescent cell has a membrane potential that at rest is equal over its entire surface, the exploring electrode at P outside the cell effectively "looks" at two dipole layers of opposite spatial orientation. The one facing the electrode corresponding to the portion of the membrane proximal to the electrode presents its positive, the other on the reverse side of the cell presents its negative side to it [(a) in Fig. 3A]. The potential across these dipole layers is the membrane potential  $e_m$ . Since, as shown in (b) and (c) in Fig. 3A, the solid angles subtended by these two dipole layers are identical and their surfaces facing the exploring electrodes are of opposite electrical sign, the two solid angles cancel by algebraic summation:

$$P=\frac{+e_m}{4\Pi}\,\Omega^++\frac{-e_m}{4\Pi}\,\Omega^-,$$

since  $+e_m$  and  $-e_m$ , and  $\Omega^+$  and  $\Omega^-$ , respectively, are of equal magnitude in this case. [Intuitively, one can account for the absence of a measurable extracellular potential in the situation of a quiescent cell having a sizable membrane potential by imagining the currents that would be generated in a volume conductor by two oppositely oriented dipole layers represented by the proximal and the distal portions of the cell membranes depicted in Fig. 3A. Each of these, as shown schematically in (b) and (c) in Fig. 3A by the dashed lines with arrows, would induce currents of equal intensity to flow in opposite directions through the surrounding volume conductor. These currents would therefore cancel each other and thus there would be no measurable potential in the extracellular medium. It is also evident in (a) of Fig. 3A why, immediately upon penetration of a quiescent cell by a microelectrode, a very large potential is measured, since, once inside the cell, the electrode "sees" only the negative side of the dipole layer of the cell membrane. Since the latter surrounds the electrode on all sides, the solid angle reaches its maximum possible value analogous to  $360^{\circ}$  of a plane angle.]

Let us now follow Woodbury's (1960) reasoning and apply these principles to an excited cell (Fig. 3B). In such a cell, one segment of the membrane has undergone a potential change in the course of the generation of either a synaptic or an action potential. In the example shown here, it is assumed that the cell sustains an action potential. Since any action or synaptic potential never occupies at a given time the whole extent of

J. Clin. Neurophysiol., Vol. 2, No. 4, 1985

Server Barris

 $<sup>^{3}</sup>$ Note that in this and all subsequent figures solid angles are represented as plane angles in order to facilitate their diagrammatic representation.



FIG. 3. Application of the solid angle principle to a single excitable cell. A: Axial section of a closed cylindrical cell. In (a), two oppositely polarized segments of the cell membrane with the same membrane potential  $e_m$  subtend the solid angle  $\Omega$  at an electrode located a point P. At this point, the potential contributed by the proximal membrane is  $(+e_{\pi}/4\Pi)\Omega^+$ , because this segment of the membrane faces P with its positive side (b), while the potential contributed by the distal membrane is  $(-e_m/4\Pi)\Omega^-$ , because this segment of the membrane faces P with its negative side (c). Since the membrane potential is the same for the proximal and the distal membranes, the resulting potential at P is zero  $[(+e_m/4\Pi)\Omega^+ + (-e_m/4\Pi)\Omega^- = 0]$ . The proximal and distal membranes, because they are electrically oriented in opposite directions, would produce currents of equal magnitude flowing in opposite directions through the extracellular medium and would therefore cancel (dashed circular lines with arrows). B: Potential measured at P when the cell shown in A is excited. The leftsided half of the cell is quiescent, and its right-sided half is excited and is assumed to sustain an action potential; hence, its membrane potential in that segment is reversed. The transition between the excited and quiescent portion of the cell is assumed to be abrupt and step-like. The total solid angle in B (a) is subdivided into three portions,  $\Omega_1$ ,  $\Omega_2$ , and  $\Omega_3$ , by the lines PA and PB. The potential at P contributed by the segment of the cell subtended at P by the solid angles  $\Omega_1$  and  $\Omega_3$  is zero, since the proximal and distal membrane segments "seen" under these angles are electrically oriented in opposite directions. However,  $\Omega_2$  subtends a small segment of the proximal active membrane portion as well as an equally small segment of the distal inactive membrane portion, both facing P with their negative sides (extracellular surface of the membrane of the active proximal and intracellular surface of the inactive distal portion of the membrane). The potential recorded at P is therefore negative and proportional to  $\Omega_2$ . This angle is also subtended by the cross-sectional area AB shown in (b), which represents the boundary between the active and inactive segments of the cell. (Reproduced with minor modifications from Woodbury, 1960.)

the membrane, we can distinguish between a quiescent segment of the cell membrane [left half of the cell in (a) of Fig. 3B] and an active segment, in which, in the case of excitation, the outside of the membrane has become electronegative [right half of the cell depicted in (a) of Fig. 3B]. We now make the simplifying assumption that the transition between the quiescent and the active part of the cell is abrupt, as show in Fig. 3B. This assumption, although incorrect, represents a permissible approximation of the real situation. As shown in (a) of Fig. 3B, an electrode at P "views" the excited cell under a solid angle that can be divided into three portions:  $\Omega_1$ ,  $\Omega_2$ , and  $\Omega_3$ . The angles  $\Omega_1$  and  $\Omega_3$  are facing exclusively the "inactive" or the "active" segment of the cell membrane, respectively. Both  $\Omega_1$  and  $\Omega_3$  are subtended simultaneously by a proximal and a distal segment of the cell membrane with opposite orientation of the dipole layer, and thus the negative and positive components of  $\Omega_1$  and  $\Omega_3$  cancel each other. Consequently,

J. Clin. Neurophysiol., Vol. 2. No. 4, 1985

# APPLICATION OF VOLUME CONDUCTOR THEORY TO EEG 335

these two segments of the membrane contribute nothing to the potential measured at P. Portion  $\Omega_2$ , however, is subtended by a segment of the active region of the proximal membrane and by a segment of the inactive region of the distal membrane. These two segments are dipole layers having the same spatial orientation: both face the exploring electrode at P with their negative side and subtend the angle  $\Omega_2$ . The potential at P will therefore be negative and proportional to  $\Omega_2$ . It is demonstrated in (a) of Fig. 3B that the straight line separating the inactive from the active region of the cell also subtends the same angle  $\Omega_2$  at P. Thus, if we picture the situation three-dimensionally as shown in (b) of Fig. 3B, the potential at P is proportional to the solid angle subtended by the cross-section of the cell at the level representing the boundary between its active and inactive regions.

If we now apply this concept to the cortical pyramidal neuron depicted in Fig. 1, we can, as shown in Fig. 4A, predict that any potential recorded at any point P in the volume conductor in which this neuron is embedded will be proportional to the solid angle  $\Delta\Omega$  subtended at P by the cross-sectional area of the pyramidal neuron that represents the boundary between the inactive and active segments of the cell (Gloor et al., 1963). Schematically, we can represent an excited pyramidal neuron of the type shown in Fig. 1 by the simple line diagram shown in Fig. 4B. We again make the assumption that the transition from the excited to the unexcited segment of the cell is sharp and step-like, as depicted in the diagram by the horizontal segment of the line, which at P subtends the plane angle  $\Delta\Omega'$ . The potential at P will be proportional to this angle.

# Application to Populations of Cortical Pyramidal Neurons

At this point, it becomes useful to consider some additional features of cortical microanatomy and electrophysiology. The first is that cortical pyramidal neurons are arranged in parallel alongside each other, each with their apical dendrites oriented at right angles to the cortical surface and their axonal poles facing toward the subcortical white matter. The second is synchronization of pyramidal cell activity. This is the inevitable consequence of the anatomical fact that each afferent fiber reaching the cortex, e.g., a single thalamocortical axon profusely ramifies as it enters the cortex and probably contacts several thousand cortical neurons (Sholl, 1956; Landry and Deschênes, 1981; Landry et al., 1982). Thus, even the discharge of a single action potential by a single thalamic neuron would simultaneously induce in all of the cortical cells receiving these terminals the same postsynaptic response consisting of EPSPs, which involve the same dendritic segment of each excited cortical neuron. Thus, a whole population of pyramidal neurons localized to a small circumscribed area of cerebral cortex would become excited simultaneously by a single action potential emitted by a single thalamic neuron, all of these neurons creating simultaneously virtually identical dipolar electric fields with the same orientation. In reality, this population of excited neurons is even larger, because many thalamic neurons within a thalamic nucleus projecting to a given area of cortex, discharge synchronously by virtue of an intrathalamic synchronizing mechanism, which is operative at least under some physiological conditions such as, for example, spindles, and by inference alpha rhythm (Andersen and Andersson, 1968). The consequence of this, therefore, is that in response to a single



FIG. 4. Application of the solid angle principle as diagrammed in Fig. 3 to a pyramidal neuron (A and B) and a population of cortical pyramidal neurons (C). A: Schematic drawing of a synaptically excited cortical pyramidal neuron of the type shown in Fig. 1. The potential at any point P in the surrounding volume conductor is proportional to the solid angle  $\Delta\Omega$  subtended by the cross-sectional area of the neuron separating the excited from the unexcited segment of the cell. As in Fig. 3B, the transition between these two segments is assumed to be abrupt and step-like. At all locations above the zero isopotential surface (dashed line 0) the potential is negative, below it positive. B: Diagrammatic representation of the situation depicted in A: the step-like solid line schematically diagrams the extracellular potential profile produced by the single excited pyramidal neuron shown in A. Negativity is plotted to the left and positivity to the right of the vertical dashed line 0. The horizontal segment of the solid line represents the cross-sectional area of the neuron at the transition between its excited and its unexcited segment. It is subtended at P by the angle  $\Delta\Omega'$ , which is the plane angle homologue of the solid angle  $\Delta\Omega$  shown in A. C: This diagram shows how the individual small solid angles of each excited cortical pyramidal neuron within a population of simultaneously excited neurons of this type stacked alongside each other within the cortex sum to form a much larger solid angle. Each individual pyramidal neuron is represented diagrammatically as in B. Potentials measured in the surrounding medium at  $P^-$  and  $P^+$  are proportional to the sum  $\Sigma \Delta \Omega^{\pm'}$  of all individual solid angles  $\Delta \Omega_{\pm}^{\pm'} + \Delta \Omega_{\pm}^{\pm'}$  $\Delta \Omega_3^{\pm \prime} + \dots \Delta \Omega_{\pi}^{\pm \prime}$  subtended by individual simultaneously excited pyramidal neurons of which four are represented in the figure. The polarity at P<sup>-</sup> is negative and at P<sup>+</sup> positive. (Based on Gloor et al., 1963.)

synchronized afferent thalamocortical volley thousands of pyramidal neurons stacked alongside each other within a given cortical area of macroscopic extent simultaneously go through a cycle of excitation during which all their apical dendrites simultaneously become electronegative with regard to their somata lying in deeper cortical layers.

These are the features that make the application of the solid angle concept to volume conductor theory in EEG useful, for if a whole population of pyramidal neurons are simultaneously excited in the manner depicted in Fig. 1, then, by applying the model diagrammatically represented in Figs. 4A and B, the situation resulting from this can schematically be depicted as in Fig. 4C: the potential generated by such a synchronously active population of pyramidal neurons when recorded at point  $P^-$  in the surrounding volume conductor represents the sum  $\Sigma \Delta \Omega^{-r}$  of all the individual small solid

J. Clin. Neurophysiol., Vol. 2, No. 4, 1985

angles  $\Delta \Omega_1^{-'} + \Delta \Omega_2^{-'} + \Delta \Omega_3^{-'} + \dots \Delta \Omega_n^{-'}$  subtended at that point by each crosssectional area forming the boundaries between the active and inactive segments of each of the excited pyramidal neurons arranged in parallel to each other as diagrammatically represented in this figure (Gloor et al., 1963). The sum  $\Sigma \Delta \Omega^{-'}$  of all the individual small angles becomes a large angle subtended by a large cortical area that is likely to be of macroscopic extent and can be regarded as a macroscopic dipole layer. Near such an area of cortex (Fig. 4C), a negative potential will be recorded at P<sup>-</sup>, since this point faces the negative side of the cortical dipole layer, and a positive potential will be recorded at P<sup>+</sup>. From observations made by Abraham and Ajmone-Marsan (1958) and Cooper et al. (1962), it appears likely that synchronized activity of pyramidal neurons must involve areas of macroscopic extent in order to yield a potential that can be recorded in the scalp EEG. Cooper et al. (1965) estimated that such an area must at least measure 6 cm<sup>2</sup>.

#### Some Features of the EEG Explained by the Solid Angle Principle

From these considerations, a few at first glance paradoxical facts pertaining to EEG become easily explainable. First, there is the obvious paradox that the largest potentials generated by neurons, namely action potentials, which exceed synaptic potentials by almost one order of magnitude, are not recorded in the EEG, whereas the much smaller synaptic potentials summate to form EEG waves. The explanation for this paradox is quite simple. It is based on the fact that in order to summate to form a large solid angle, the individual solid angles contributed by individual neuronal elements must coexist in time. This imposes a stricter requirement for synchronization on short than on longer-lasting potentials. The duration of action potentials is very brief, on the order of about 1 ms, much briefer than that of synaptic potentials, which are at least 10 to 30 times longer in duration. An individual action potential is "viewed" by an electrode under a very small solid angle, the one subtended by the cross-section of an axon or of a neuronal soma. Obviously, only a microelectrode exceedingly close to the active neuron or fiber is able to "see" this cross-sectional area at a large enough solid angle to make the action potential recordable. But why do the individual small solid angles generated by synchronized action potentials generated, for example, by neighboring axons in a fiber tract not summate as do the synaptic potentials of pyramidal neurons as depicted in Fig. 4C? Surely, if the latter are the result of synchronized thalamocortical volleys, the action potentials constituting these volleys should be equally synchronized and hence should summate to form a large solid angle as they approach the cortex. This would indeed be the case, if these action potentials were perfectly synchronized down to a fraction of 1 ms and thus would coincide or largely overlap in time. Such a stringent requirement for near-perfect synchronization, however, does not apply to synaptic potentials that last for 10 to 30 ms or more. In their case, a lack of perfect synchronization of their generators in the millisecond range could still allow them to overlap in time for most of their duration, leading to a time-coherent potential change over an area large enough to be subtended by a large solid angle. Because of the very short duration of action potentials, however, even a slight asynchrony, e.g., a minimal difference in their timing in the millisecond range, would make it impossible for the individual solid angles of each action potential to coexist or significantly overlap in time. Hence, at no time

could there be an effective summation of the individual solid angles subtended by individual action potentials over a sufficiently large area to form a large macroscopic solid angle of the kind depicted in Fig. 4C, since the summation of  $\Delta\Omega_1 + \Delta\Omega_2 + \Delta\Omega_3 \dots + \Delta\Omega_n$  to form  $\Sigma\Delta\Omega$  depends on the simultaneity of  $\Delta\Omega_1 \longrightarrow \Delta\Omega_n$ .

The same general principle explains why in the EEG an inverse relationship generally exists between frequency and amplitude. The largest potentials recorded in the EEG are the slowest delta waves, whereas beta waves are always very small in amplitude, with alpha waves being of intermediate size. A delta wave may last for about ½ s (500 ms). Its neuronal generators most likely are also pyramidal neurons (Ball et al., 1977a). We may thus assume that when producing delta waves such neurons generate membrane potential changes of a duration of about 500 ms. Even if such individual neuronal delta wave generators within a relatively large cortical area were out of step with each other, even by as much as about, say 50 ms, there would still remain a period of 400 ms during which the membrane potential changes produced by the individual neuronal generators of delta waves within a relatively large area of cortex coincide in time. Thus, during this time span the individual microscopic solid angles contributed by each neuronal generator within this area could sum to produce a large. macroscopic solid angle. Hence, a large potential would be recorded in the EEG. By contrast, in the case of beta activity, if we assume that the same degree of asynchrony of 50 ms were to prevail among its individual generators distributed over a cortical area of similar size, the possibility of summation of the potential contributions of individual generators would be limited, since 50 ms is already within the range of the duration of individual beta waves. Since in general the degree of asynchrony should increase with increasing distance of individual generators from each other, and since long duration potentials will tolerate a larger degree of asynchrony before they cease to show a significant degree of overlap in time, the possibility of summation of time-coherent potential changes over a large area increases with decreasing frequency. Thus, the inverse relationship between frequency and amplitude of EEG waves becomes a predictable feature when the solid angle concept is applied to the biophysics of EEG.

Finally, the principles just enunciated also explain the lack of any clear-cut relationship between the amplitude of a signal in the cerebral cortex and the amplitude of the corresponding scalp EEG potential (Abraham and Ajmone-Marsan, 1958). Ratios of cortical versus scalp EEG amplitude of corresponding signals may vary between 58:1 and 2:1. Obviously, according to the solid angle principle, the larger the area of cortex sustaining synchronous activity, the smaller this ratio will be, thus making it possible for even relatively small-amplitude cortical potentials to appear in the scalp EEG.

#### APPLICATION OF THE SOLID ANGLE CONCEPT TO CLINICAL EEG

#### **General Principles**

The principles enunciated in the preceding section can be summarized as follows: The synchronous activity of a population of cortical pyramidal neurons creates conditions under which a cortical area of finite, but macroscopic, extent behaves like a dipole layer similar to that depicted in Fig. 2, where the upper (pial) surface at one instant in time is negative while the lower (white matter) surface is positive. According to the

J. Clin. Neurophysiol., Vol. 2, No. 4, 1985

-

solid angle principle, the potential measured in a monopolar recording by an electrode (e.g.,  $P^-$  or  $P^+$  in Fig. 2) at some distance from such a generator is not only proportional to the potential across the dipole layer, but more importantly, is also proportional to the solid angle  $\Omega$  subtended by this layer at the site of the electrode (for the mathematical expression of this relationship, see page 332). The visual angle being a familiar example of a solid angle, one may thus conceive of an electrode as "seeing" the dipole layer under a certain angle. It is therefore the apparent and not the real size of the cortical area acting as a dipole layer as "seen" by an electrode that determines the size of the negative side of such a dipole layer ( $P^-$  in Fig. 2) record negative potentials; those facing the positive side ( $P^+$  in Fig. 2) record positive potentials.

## Generator Consisting of Flat Area of Cortex Oriented in Parallel to the Scalp

The simplest situation that may be encountered in clinical EEG is that of a generator represented by a flat area of cortex oriented in parallel to the scalp surface as diagrammatically shown in Fig. 5<sup>4</sup>, which can be regarded as a view of the cross-section of the dipole layer shown in Fig. 2. If, in the space surrounding the excited cortical area, one plots the geometric location of all points at which this area of excited cortex is subtended by an angle of a given, constant size, all these points, according to the solid angle theorem, must be located on the same isoelectric surface of the electrical field. In Fig. 5, lines representing isoelectric surfaces were drawn, each representing the geometric locus of points at which the area of cortex is subtended by an angle that differs by 15° from that represented on the next line: such a 15° difference in angle was assumed to represent a potential difference of 10  $\mu$ V (for didactic purposes the solid angles are expressed here by plane angle homologues). It is evident from this figure that the electrical field created by such a dipole layer bears a striking similarity to that of a single dipole shown in Fig. 1. However, the larger the tangential extent of the dipole layer becomes, the more the shape of the dipole field becomes stretched out tangentially and thus increasingly appears as if flattened from both its positive and negative sides.

Figure 6 incorporates the upper part of Fig. 5 and shows the potential profile that would be measured by a string of electrodes arranged on the scalp along the straight line labeled S. The numbers along this line indicate the potentials that would be measured in an ideal monopolar (referential) recording at each point at which the corresponding isopotential surfaces intersect the line representing the scalp. By referring to Fig. 5 it becomes evident that a  $-80 \ \mu V$  signal would be recorded where the scalp is intersected by the isopotential surface representing the geometrical locus of all points at which the

<sup>&</sup>lt;sup>4</sup>In Fig. 5 and subsequent figures, the structure of the cerebral cortex has been simplified by assuming that it is constituted by only a single layer of pyramidal neurons. This is obviously a gross oversimplification. Such a scheme only applies to the archicortex of the hippocampus. However, since in the multilayered neocortex pyramidal neurons are all oriented in parallel, the fundamental principles that can be derived from a single-layered cortex such as the hippocampus (Gloor et al., 1963) still apply at least to the spatiotemporal average of cortical activity (Ball et al., 1977*a, b*), which resembles that produced by an idealized single-layered cortex of the type schematically depicted in Fig. 5. However, the details of the "internal fields" within the cortex are quite complex (Vaughan, 1974; Petsche et al., 1984), but these complexities are not much resembles that are the subject of this review.



FIG. 5. Electrical field created in the surrounding volume conductor by a flat portion of cerebral cortex containing a population of synchronously active pyramidal neurons forming a dipole layer with the cortical surface being electronegative. The diagram can be considered to represent a tangential view of the cross-section of a disk of active cortex forming a dipole layer of the type shown in Fig. 2. The cortex is represented as if it were constituted by only one layer of pyramidal neurons. The solid lines represent isopotential levels. On each of these, any point subtends the cortical dipole layer with an angle of constant size. Each of these lines represents the geometric locus of points at which the area of active cortex is subtended by an angle that differs by 15° from that represented on the next line. This 15° difference is assumed to represent a potential difference of 10  $\mu$ V. The field created by such a dipole layer is similar to that of a single dipole, although it is stretched out in the tangential direction.

J. Clin. Neurophysiol., Vol. 2, No. 4, 1985



FIG. 6. Potential distribution along a line S on the scalp created by the portion at cortex shown in Fig. 5, which is assumed to be oriented in parallel to the surface of the scalp. The bell-shaped curve in the lower part of the figure plots the potential distribution along S. This distribution resembles that produced by a dipole oriented orthogonally with respect to the scalp surface: so-called "vertical dipole." (Note that this diagram does not take into account the distortion the field would normally undergo as a consequence of the electrical inhomogeneities of the tissues existing in the real situation; see pages 348–349 in the text.)

generator is subtended by an angle of 120°. A signal of  $-20 \ \mu$ V would be measured at points at which the scalp is intersected by the surface representing the 30° angles, and so on. The resulting potential profile along line S on the scalp plotted on the graph below the figure is a bell-shaped curve and shows that the largest potential would be recorded by an electrode facing the midportion of the flat cortical generator oriented in parallel to the scalp surface. However, the figure also shows that electrodes not directly overlying the generator still pick up smaller potentials, e.g.,  $-20 \ \mu$ V and  $-10 \ \mu$ v at the "30°" and "15°" isopotential-scalp intersections.



FIG. 7. Potential distribution along line S on the scalp created by the synchronous activation of a curved portion of cortex that occupies the crown of a gyrus and its two sides forming the proximal walls of the two adjacent sulci. At P1, the potential depends only on the solid angle  $\Omega_1^-$ , since at this point an electrode "sees" only a portion of the negative side of the dipole layer. At P2, an electrode "sees" the negative side of the portion of the dipole layer occupying the crown of the gyrus and the wall of the proximal sulcus under the angle  $\Omega_2$ ; however, it also "sees" under the smaller angle  $\Omega_2^+$  the positive side of the portion of the dipole layer located in the wall of the distal sulcus. The potential at P2 is therefore smaller than would be expected if only  $\Omega_{2}^{-}$ , were the angle determining the size of the potential at P2 and is proportional to the effective solid angle  $\Omega_{eff}$  which equals the difference between  $\Omega_2^-$  and  $\Omega_2^+$ , the polarity being negative, since  $\Omega_2^- > \Omega_2^+$ . As is the case for a flat area of cortex oriented in parallel to the scalp the potential profile is bell-shaped. (Taken in part from Gloor, 1975.)

#### **Convoluted Generators**

Fields created by flat cortical generators oriented in parallel to the surface of the scalp are probably the exception rather than the rule among those encountered in EEG. The cerebral cortex is a highly convoluted structure containing, strictly speaking, no flat surfaces at all. We therefore must consider how the convoluted pattern of the brain affects the electrical fields created on the scalp by generators occupying the curved surfaces of the gyri and sulci of the cerebral cortex. If a generator of synchronized activity occupies only the crown of a gyrus on the convexity of the brain, the field is essentially that shown in Fig. 6. Such a patch of cortex, for practical purposes, can be considered to be flat and oriented in parallel to the scalp surface.

If, however, the generator surface on the crown of such a gyrus extends into the proximal walls of the sulci flanking it on each side, the situation portrayed in Fig. 7 arises. On the scalp, at electrode P1 located over the crown of the gyrus, the solid angle  $\Omega_1^-$  subtended by the curved generator surface is relatively small in comparison to the total size of the generator surface, since the electrode only "sees" the negative side of the portion of the generator that occupies the crown of the gyrus. It does not "see" those portions of the generator that form the proximal walls of the two sulci flanking the gyrus, because it "looks" at them "edge-on," i.e., at P1 the walls of the sulci subtend a solid angle measuring for practical purposes zero. The potential at P1 is thus proportional to the size of  $\Omega_1^-$  and is negative in sign. The situation is different at electrode position P2. Here a larger portion of the negative surface of the curved dipolar layer is "visible." Both the crown of the gyrus and its adjacent portion, which forms the wall of the sulcus proximal to P2, are subtended at this point by the solid angle  $\Omega_2^-$ . However, the potential at P2 is not proportional to the size of  $\Omega_2^-$ , but considerably smaller. The reason for this is that

J. Clin. Neurophysiol., Vol. 2, No. 4, 1985

the electrode also "sees" the positive side of the segment of the curved dipole layer that lies in the wall of the sulcus distant to electrode P2. This segment is subtended at P2 by the solid angle  $\Omega_2^+$ . Since the two dipole layers subtended by the angle  $\Omega_2^-$  and  $\Omega_2^+$ present to electrode P2 surfaces of opposite electrical sign, the resultant effective angle at P2 is quite small and corresponds to the difference between these two angles ( $\Omega_{2eff}$ =  $\Omega_2^- = \Omega_2^+$ , i.e., the contributions of the potentials generated by the two walls flanking the gyrus to that measured at P2 partially cancel each other.<sup>5</sup> The potential at P2 is negative since  $\Omega_2^- > \Omega_2^+$ . For an electrode placed on the left-hand side of P1 in Fig. 7, the situation would be the same. Along a straight line S on the scalp, the potential profile would be a bell-shaped curve as depicted at the top of Fig. 7. This is a similar profile to that engendered by a flat cortical generator oriented in parallel to the scalp surface as shown in Fig. 6, although that produced by a curved area of cortex as in Fig. 7 is narrower at its "waist" than it would be if the generator did not extend into the neighboring sulci. The curvature of a generator surface can thus markedly influence the potential profile recorded on the scalp (Jami et al., 1968). If one were to increase the curvature of the gyrus depicted in Fig. 7 in such a way that the two sulci would curve further inward toward each other at their bottom, thus progressively narrowing the "stalk" of the gyrus, then even the potential recorded at P1 would become increasingly smaller, as the inner, positive sides of the sulci would also become "visible" from P1 and the angles under which they are seen would have to be subtracted from  $\Omega_{-}^{-}$ . In the extreme hypothetical case of total closure of the generator on itself, converting it from a "gyrus" to a "sphere," the surface monopolar potential anywhere outside this "sphere" would vanish, while a "transcortical" recording would still measure the potential across the dipole layer (Jami et al., 1968; Klee and Rall, 1977).

On the scalp along a line where the potential profile assumes the bell-shaped curve shown in Figs. 6 and 7, only the magnitude of the potential changes with distance, but not the electrical sign. Since the polarity anywhere on the scalp in such a situation is either negative or positive, such fields resemble those that would be generated by a single dipole oriented with its axis at a right angle to the scalp surface. Such fields are therefore often referred to as those of a "vertical dipole." This is a useful shorthand term, but it must be remembered that the dipole creating such a field is a fiction and that in reality the field is generated by a dipole layer, either of the type depicted in Fig. 6 or that shown in Fig. 7. The configuration of most potential fields encountered in clinical EEG conform to that of a "vertical dipole." Figure 8 shows how in a monopolar (referential) and in a bipolar recording taken on the scalp with equally spaced electrodes placed along line S of Fig. 6 or 7 the signals resulting from such a bell-shaped potential distribution would appear in an EEG record. In a monopolar (referential) recording,

and the second s

<sup>&</sup>lt;sup>5</sup>It is often not understood why only the solid angle subtended by the positive side of the distant wall of the sulcus must be subtracted from  $\Omega_2^-$  and not also that of the positive side of the proximal wall. This would obviously be inadmissible, since the potential at a particular site is a function of the distance and orientation of the dipole layer with regard to that site. A point on the negative side of a dipole layer can only be at a negative and not also simultaneously at a positive potential. One must also remember the principle depicted in (b) and (c) of Fig. 3A, that currents induced by a given dipole layer at a particular point in the volume conductor flow in one direction only. When two parallel dipole layers that are electrically polarized in opposite directions are present, as is the case for the quiescent neuron depicted in Fig. 3A and for the two walls of the sulci flanking a gyrus as shown in Fig. 7, the currents generated by the two oppositely polarized layers cancel, because each causes current to flow in a direction opposite to that induced by the other.



FIG. 8. Monopolar (referential) and bipolar recordings obtained by five electrodes arranged in a straight line on the scalp along which the potential profile is bell-shaped as in Figs. 6 and 7. If the reference electrode (REF) is at "zero," the amplitude of the EEG signal in a monopolar recording (lefthand column) at each electrode is proportional to the ordinate at points 1 to 5 corresponding to these electrode positions. In a bipolar recording (right-hand column), the EEG signals at each pair of electrodes are proportional to the difference between the two ordinate values at the points of the curve corresponding to the two electrodes forming the bipolar pair. In an unbroken chain of bipolar recordings extending from electrode 1 to electrode 5, a phase reversal appears between the two channels sharing as the common electrode the one located closest to the apex of the bell-shaped curve (electrode 3 in the present example).

the signals are all of the same polarity, and the amplitude of the signal at each electrode is proportional to the height of the curve at each electrode position provided the reference potential is zero. If the electrodes are linked in a straight, unbroken bipolar chain, the amplitude of the signal in each channel connected to a pair of neighboring electrodes is proportional to the differences between the potentials appearing in a monopolar recording at each of the electrodes of the bilpolar pair as shown in Fig. 8. (This value is proportional to the difference between the two solid angles subtended by the cortical generator surface at the two electrodes of the bipolar chain.) Furthermore, a phase reversal appears between the two channels sharing as the common electrode that located closest to the position corresponding to the peak of the bell-shaped curve (electrode 3 in Fig. 8).

#### Generator Occupying the Wall of a Sulcus

The situation is different from that depicted above if the cortical generator occupies one wall of a sulcus oriented orthogonally to the scalp surface. The potential field distribution on the scalp created by such a generator is as portrayed in Fig. 9. Electrodes

J. Clin. Neurophysiol., Vol. 2, No. 4, 1985

344

3

# APPLICATION OF VOLUME CONDUCTOR THEORY TO EEG 345

P1 and P2 face the negative side of the generator surface that is oriented at a right angle to the scalp surface. The negative surface of the generator is subtended by the solid angles  $\Omega_1^-$  and  $\Omega_2^-$  at P1 and P2, respectively, and the signals there are proportional to the sizes of these angles and of negative polarity. Conversely, electrodes at P4 and P5 "see" the positive side of the generator, the corresponding solid angles being  $\Omega_4^+$  and  $\Omega_5^+$ . Potentials of positive sign and of a magnitude proportional to the sizes of these angles will thus be recorded at these two electrode positions. Electrode P3 "looks" at the vertically oriented generator surface "edge-on." Its positive as well as its negative sides subtend a solid angle that is virtually zero ( $\Omega^{\pm} = O$ ) and thus no potential is recorded at P3, in spite of the fact that this is the electrode closest to the generator.

The potential distribution on the scalp resulting from the situation shown in Fig. 9 resembles that which would be generated by a dipole with its axis oriented in parallel to the scalp surface. Such a field is therefore often referred to as that of a "horizontal dipole." Again, the fictional aspect of this terminology must be kept in mind. Along a straight line on the scalp, such a "horizontal dipole" creates a potential profile as presented by the curve at the top of Fig. 9. It has two peaks, one negative, the other positive. Fields generated by "horizontal dipoles" are less common in scalp EEG than those generated by "vertical dipoles." However, this may be in part more apparent than real, for frequently the "horizontal dipolar" configuration of a field is overlooked by the interpreter. If one were to record in a monopolar fashion from the electrodes P1 to P5 in Fig. 9, the signals at P1 and P2 would be phase-reversed with respect to those appearing at P4 and P5, while no signal would be recorded at P3 (Fig. 9, lower part). In an unbroken chain of bipolar recordings linking all electrodes between P1 and P5, twophase reversals of opposite orientation would appear, one at P2 and the other at P4, whereas the largest signal would be recorded in the two channels linking electrode P2-P3 and P3-P4, respectively (Fig. 9, lower part). Thus, the appearance of a single phase reversal in a monopolar scalp EEG recording and of two phase reversals of opposite electrical sign in a straight-lined unbroken bipolar scalp EEG recording are indicative of a generator behaving as a "horizontal dipole," which presumably is located within one wall of a cortical sulcus. If a careful analysis of such a field configuration is not made, the record may erroneously be interpreted as indicating the presence of two separate generators, and the inferred localization of these generators would be incorrect, especially since the locations of the positive and negative maxima may be far apart from each other and the amplitude in monopolar recordings will be lowest at the electrode closest to the generator. In recordings along a straight line, the field configuration of a "horizontal dipole" indicates that, in a bipolar recording, the generator is located halfway between the two phase reversals or halfway between the two electrodes of a monopolar (referential) chain between which the phase reversal occurs. That such a generator most likely occupies the wall of a sulcus is demonstrated by the example taken from an electrocorticogram shown in Fig. 10. In this bipolar recording, epileptiform spikes display two phase reversals of opposite electrical sign at electrodes B and C, and indeed a sulcus was found to run transversely across the first temporal convolution between these two electrodes. It was assumed that the spikes were generated by cortex forming one of the walls of this sulcus. Figure 11 shows an example of a "horizontal dipole" field observed in a scalp EEG. The monopolar recording on the left shows a phase reversal occurring between electrodes C3 and P3 (and also in the contralateral chain

J. Clin. Neurophysiol., Vol. 2, No. 4, 1985

一、"我有"我们一下有一些是有一些我们有一些我们们有一些人们有一个的事情。"他们有这些有些我们的是我有些"你的是我们"



FIG. 9. Potential distribution along a line on the scalp created by the synchronous activation of an area of cortex occupying one wall of a sulcus. Electrodes placed at points P1 and P2 "see" only the negative side of the dipole layer corresponding to the pial surface of the cortex of the wall of the sulcus that has been activated. The potentials measured at P1 and P2 are negative and proportional to  $\Omega_1^-$  and  $\Omega_2^-$ . Electrodes at P4 and P5 "see" only the positive side of the dipole layer corresponding to the white matter surface of the sulcal cortex. The potentials at P4 and P5 are positive and proportional to  $\Omega_4^+$  and  $\Omega_5^-$ . An electrode strategically placed at P3 would record no potential, since it "looks" at the dipole layer "edge on." the solid angle subtended at this point being zero. As shown on the top of the figure, the potential distribution along a straight line on the scalp would rise to a negative peak on its right side. As shown in the two columns in the lower part of the figure, the potentials in a monopolar recording (left column) would be phase reversed between the left and the right of P3, while two phase reversals of opposite electrical sign would appear in a bipolar recording consisting of an unbroken chain of electrodes from P1 to P5 (right column), with a "negative" phase reversal appearing at P2 and a "positive" one at P4. The field distribution on the scalp in this situation resembles that produced by a single dipole oriented in parallel to the scalp surface: so-called "horizontal dipole."

between C4 and P4). Maximum negativity was recorded at P3 and T5 and maximum positivity at F3. In the bipolar recording over the left hemisphere, there are two phase reversals of opposite electrical sign: that of positive polarity at F3 and that of negative polarity at P3. The profiles of the potential along the chain of electrodes from Fp1 to O1 computed from the monopolar and bipolar recordings are quite similar, considering the fact that the two recordings were not obtained simultaneously. This potential profile is



FIG. 10. Bipolar electrocorticogram recording taken from the temporal lobe in an epileptic patient shows spike discharges with a surface distribution characteristic of a "horizontal dipole" (double phase reversals of opposite electrical sign). The potential profile plotted at the bottom of the figure suggests that the spikes are generated by discharge originating in the wall of a sulcus located between electrodes B and C. On inspection of the brain, a sulcus was found to run transversely across the first temporal convolution at the expected location as shown in the brain diagram at the top.

very similar to that of Fig. 9 and conforms to that of a "horizontal dipole." The configuration of the field on the scalp shown in this figure suggests the presence of a vertically oriented generator located in the cortex of the central fissure. Whether it occupies the anterior or posterior wall of this fissure is impossible to deduce from this field configuration. However, since surface-negative signals are more common in EEG than surface-positive ones, one may conjecture that the generator is located on the anterior wall of the central fissure.

If a generator were to occupy both walls of a sulcus, no signal would be recorded on the scalp, because all electrodes on either side of the sulcus would simultaneously see



FIG. 11. Samples from a scalp EEG show sharp waves (indicated by an arrow) with a potential distribution characteristic of a "horizontal dipole." A sample of monopolar recording using a cervical reference electrode is shown on the left, and a sample of an anteroposterior bipolar recording is shown on the right. Phase reversals are indicated by black circles. In the lower part of the figure the potential profiles along the left superior longitudinal electrode row as derived from the monopolar (solid line) and from the bipolar (dashed line) recordings shown in this figure are plotted. They show maximum positivity at F3 and maximum negativity at P3. The two potential profiles were not obtained concurrently. The electrical field on the scalp representing this sharp wave is shown at the top center of the figure. It conforms to that of a "horizontal dipole" and suggests that the sharp wave was generated by cortex occupying one of the walls (probably the anterior one) of the central fissure.

under an approximately identical solid angle the positive side of the dipole layer forming one wall of the sulcus and the negative side of the dipole layer forming the other wall. At an electrode immediately above the sulcus, the generator surface would subtend a solid angle close to zero (Gloor, 1975; see Fig. 1C).

## Influence of Electrical Inhomogeneities

Up to now we have assumed that the generators of EEG signals were located in an electrically homogeneous medium of infinite extent. This is obviously incorrect. There are a number of electrical inhomogeneities interposed between the cortical generators and the electrodes on the scalp that affect the potential distribution on the scalp generated by intracranial sources (Rush and Driscoll, 1968; Vaughan, 1974; Nunez, 1981; Lopes da Silva and van Rotterdam, 1982). The most obvious inhomogeneity is that represented by the boundary between the scalp and the surrounding air, which is an almost perfect dielectric. Obviously, currents generated by an intracranial source cannot pass through the surrounding air and are therefore deflected from what their course in a conducting medium would normally be. They are increasingly more deflected the

# APPLICATION OF VOLUME CONDUCTOR THEORY TO EEG 349

closer they approach the boundary between scalp and air, and thus the current density near this boundary line increases considerably. This leads to a distortion of the electrical field, which theoretically has the effect of increasing the potential differences measured on the scalp over what they would be if air were a conducting medium and thus would steepen the slope of the bell-shaped curve shown in Figs. 6 and 7. The scalp-air interface, however, is not the only boundary between media of different electrical properties. Others are the cerebrospinal fluid (CSF) covering the cortex with a conductivity about four times that of underlying brain tissue, followed by the skull with a conductivity of about 1/80th that of brain, assuming a thickness of 0.75 cm, and finally the scalp and subcutaneous tissues with a conductivity roughly comparable to that of brain (Nunez, 1981). Surrounding a sphere containing a dipole with a shell of either higher (e.g., CSF) or of lower (e.g., skull) conductivity reduces the potential recorded from the outer surface (scalp) (Geisler and Gerstein, 1961). The major inhomogeneity among the tissues surrounding the brain is the skull. Because of its poor conductivity, it inhibits current flow to the scalp. For a single vertically oriented dipole (not a dipole layer) close to the scalp surface, it has been estimated that the potential at the scalp right "above" the dipole would be reduced to one-seventh to one-eighth of the value to be expected in a homogeneous medium, but, as one moves laterally from this position on the scalp, the potential becomes larger than would be expected (Nunez, 1981). The bell-shaped curve on the scalp would thus be flattened in its midportion and broadened on its sides, the so-called "smearing" effect of skull and scalp (Geisler and Gerstein, 1961; Henderson et al., 1975; Nunez, 1981). It is much more difficult to make simple predictions regarding the distortions of the field in the case of dipole layers as opposed to single dipoles. Much depends on their size, configuration (degree of convolution), distance from the scalp, and orientation. It can be assumed, however, that the "smearing effect" of skull and scalp would be reduced for generators of the kind portrayed in Fig. 7, in which the generator surface extends from the crown of the gyrus into the proximal walls of the adjacent sulci. The distortions introduced by these inhomogeneities can be likened to the effect produced by curved mirrors: they do affect some quantitative aspects but do not fundamentally alter the qualitative aspects of the picture. In any rigorous quantitative study, these distortions, however, must be taken into account. A detailed quantitative treatment of this problem is presented in Nunez' monograph (1981).

#### DISCUSSION

The approach to the analysis of volume conductor principles in EEG based on the solid angle concept as presented in this review is a useful tool for weaning the electroencephalographer from simplistic views of cortical electrogenesis that sometimes ignore even the simplest fundamental principles of volume conductor theory. It allows one to visualize the generators of EEG waves as dipole layers corresponding to segments of the cerebral cortex that can be viewed quite realistically as conforming to the major and familiar features of macroscopic brain anatomy. Modeling the sources of EEG potentials as single point-like dipoles does not lead to such realistic concepts. The reason why, in spite of this, the single dipole model has remained attractive is that, based on first principles of electrical field theory, it allows one to compute from the field configuration

on the scalp the location of a hypothetical virtual single dipole in the brain that could account for the recorded scalp potential (Brazier, 1949; Geisler and Gerstein, 1961; Schneider, 1972; Smith et al., 1973; Henderson et al., 1975; Nunez, 1981). Such computations, however, are bound to yield anatomically and physiologically erroneous results (Geisler and Gerstein, 1961; Jami et al., 1968; Henderson et al., 1975; Kell and Rall, 1977). In one instance, for example, such computations derived from epileptic discharges recorded in a scalp EEG have led to a presumptive localization of a single dipole source in the region of the centrum semiovale (Schneider, 1972), which physiologically makes no sense. Generally, one can say that the larger the cortical generator, the more the hypothetical current dipole assumed to be responsible for the field on the scalp is displaced deep into the brain (Magnus, 1961; Schneider and Gerin, 1970; Schneider, 1972; Henderson et al., 1975). The reason for this is that fields created by dipole layers produce a tangential profile on the scalp, which resembles that created by a hypothetical single dipole located deep within the brain substance (Brazier, 1949; Geisler and Gerstein, 1961; Vaughan, 1974). The caveat against modeling EEG generators as single dipoles applies not only to the traditional EEG but also to evoked potentials (Vaughan, 1969) and to the MEG. Modeling the magnetic field based on the assumption that the field corresponding to an identifiable signal recorded in the MEG can be reduced to one generated by a single point-like current dipole is fraught with difficulties similar to those inherent in modeling electrical fields based on this assumption. The two methods, however, may be complementary in some respects, since MEG is particularly adept at identifying "horizontal dipoles," while EEG is better at detecting "vertical dipoles" (Cohen and Cuffin, 1983).

The solid angle concept applied to EEG makes it virtually certain that all signals recorded in the standard scalp EEG are generated in the cerebral cortex. Only this structure has the anatomical and physiological organization capable of producing large dipole layers, a prerequisite for making potentials recordable in a standard scalp EEG. To produce a recordable EEG potential on the scalp, a dipole layer in the depth of the brain, say, for example, in the thalamus, would have to occupy an enormously large surface oriented in parallel to the scalp, which is obviously anatomically impossible, or it would have to produce an enormously large potential across the dipole layer [about 10,000  $\mu$ V, according to Nunez (1981)], which is physiologically impossible. The fact that thalamic neurons are not structured and arrayed like pyramidal neurons of the cerebral cortex, but are multipolar, makes it a priori unlikely that thalamic activity, even when synchronized, could produce "open fields" similar to the type encountered in the cortex (Lorente de Nó, 1947; Rall, 1962; Vaughan, 1969, 1982; Klee and Rall, 1977). Any signals reflecting small "open field" components of thalamic generators, if at all present, would be so small that they would be masked by the much larger-amplitude signals of cortical origin.

Computer averaging, however, can improve the signal-to-noise ratio sufficiently to render signals recordable that normally are submerged in the ongoing EEG activity. The widely used technique of sensory evoked potential recording is based on this principle. The fact that a signal can only be extracted from the EEG by averaging indicates that either the solid angle subtended by its generator at the site of recording is very small or that the potential across a hypothetical large dipole layer acting as its generator is very low. In the situation commonly encountered in evoked potential studies, it is the first of these factors that usually prevents the recording of the signal in the surface scalp EEG. The solid angle in these cases is small, either because the generator in the cortical sensory area occupies only a small area of cortex or because the generator is very remote from the surface of the scalp (e.g., in the case of brainstem auditory or short latency somatosensory evoked potentials). Such potentials not appearing in the unaveraged EEG can more successfully be modeled by assuming that they are produced by a single dipole than signals recorded in the standard EEG, because in this special case a single dipole represents a reasonably accurate approximation of the real situation, owing to the smallness of the generator surface.

Some of the conditions encountered in intracerebral depth electrode recordings are also better understood when viewed in the light of the solid angle concept (Gloor, 1984). In contrast to recording conditions on the scalp, intracerebral electrodes can be in direct contact with or in very close proximity to some generators, while remaining just as remote as scalp electrodes are from others. An intracerebral electrode in direct contact with even a very small generator, especially if its surface is curved and presents its concave side to the electrode, will "see" this surface under a very large solid angle, much larger than any that can be subtended on the scalp by any generator in the brain. More distant generators that, however, are not necessarily very remote from the electrode are subtended by solid angles of similar size to those encountered on the scalp. They thus yield a much smaller potential that may be missed in intracerebral depth electrode recordings, because the gains have to be considerably reduced to make it possible to record in an undistorted fashion the activity of generators that, owing to their close proximity to some electrodes, produce very large potentials. It is not within the scope of this review to go into this problem in more detail (see Gloor, 1984), but it is useful to remind oneself that intracerebral recordings with depth electrodes suffer from some degree of tunnel vision, although what they see through the tunnel is very distinct and precise.

A final important comment should be made. Modeling EEG generators as curved dipole layers corresponding to segments of the convoluted cerebral cortex, while conceptually attractive, highlights a major difficulty inherent in identifying the true location and extent of neuronal generators of given EEG signals. By proceeding, as in this review, namely by starting from an assumed anatomical generator, it is easy to predict what configuration a field created by such a generator would have on the scalp and hence to deduce theoretically how the corresponding electrical signal would appear in either a monopolar (referential) or bipolar scalp EEG recording. As electroencephalographers, however, we are called upon to perform the reverse task: starting from a given scalp configuration, we are to infer the location and orientation of the cortical generator. For theoretical reasons, this inverse problem is only soluble for single-current dipoles and not for distributed sources, such as dipole layers (Gabor and Nelson, 1954; Schneider, 1972; Vaughan, 1969, 1974, 1982; Klee and Rall, 1977; Nunez, 1981). A given distribution of potential on the scalp can thus be engendered by more than one hypothetical source. The number of alternatives, however, is not unlimited, and if one takes into consideration some constraints imposed by brain anatomy and physiology, some theoretically possible solutions can be eliminated as being incompatible with anatomical and physiological facts even though some uncertainties may still remain. Vaughan (1969, 1974) has shown that such an approach is very successful

Ĵ

when applied to identifying the neuronal sources of evoked potentials. The main advantage of the solid angle approach to volume conductor theory in EEG, however, is that it provides a sufficiently realistic concept of cerebral electrogenesis, which makes it possible to take into account physiological and anatomical realities pertaining to the brain, as well as the everyday realities encountered by the clinical electroencephalographer in his reading of EEG records. EEG waves, when viewed in this perspective, no longer remain somewhat disembodied signals about which only crudely empirical conclusions can be reached concerning their relationship to brain structure and function.

#### **CONCLUSIONS**

The main generators of the potential changes constituting the EEG are cortical pyramidal neurons. When activated synchronously within a cortical area of finite and macroscopic extent they create dipole layers that are coextensive with the area of cortex containing the synchronously active population of pyramidal neurons. By applying the solid angle theorem of volume conductor theory, it can be shown how the dipole fields of individual single pyramidal neurons within such a synchronously active population summate to create the large macroscopic fields on the scalp, which can be detected by standard EEG recording techniques.

These large fields can be regarded as cortical dipole layers that, because of the convolutional pattern of the brain, may assume a variety of complex shapes. At each point of measurement, the potential is proportional to the solid angle subtended by the cortical dipole layer as "seen" from an electrode at that point. This helps to understand how the often intricate geometry of cortical dipole layers translates itself into patterns of potential distributions on the scalp surface.

Examples are presented of fields created on the scalp by cortical generators encompassing the crown of a gyrus, an entire gyrus including in addition to its crown the proximal walls of the two adjacent sulci, or one wall of a sulcus oriented orthogonally to the scalp surface. The way such fields express themselves in monopolar (referential) and bipolar scalp EEG recordings are illustrated.

The solid angle principle makes it possible to go beyond pure empiricism in EEG localization and to relate with a fair approximation the pattern of distribution of electrical signals recorded on the scalp to well-known underlying macroscopic anatomical features of the brain. It therefore provides a rational basis for principles of localization in clinical EEG.

Acknowledgment: The author gratefully acknowledges his indebtedness to Gregory Popow, who drew the diagrams illustrating this paper, Giséle Robillard for typing the manuscript, and Drs. Massimo Avoli, Jean Gotman, Terence Peters, and Felipe Quesney for their helpful suggestions.

#### REFERENCES

Abraham K, Ajmone-Marsan C. Patterns of cortical discharge and their relation to routine scalp electroencephalography. *Electroencephalogr Clin Neurophysiol* 1958;10:447-61.

Andersen P, Andersson SA. Physiological basis of the alpha rhythm. New York: Appleton-Century-Crofts, 1968:1-235.

Ball GJ, Gloor P, Schaul N. The cortical electromicrophysiology of pathological delta waves in the electroencephalogram of cats. *Electroencephalogr Clin Neurophysiol* 1977a;43:346-61.

Ball GJ, Gloor P, Thompson CJ. Computed unit-EEG correlations and laminar profiles of spindle waves in the electroencephalogram of cats. *Electroencephalogr Clin Neurophysiol* 1977b;43:330-45.

Barth DS, Sutherling W, Engel J Jr, Beatty J. Neuromagnetic localization of epileptiform spike activity in the human brain. Science 1982;218:891-4.

Bishop GH. Potential phenomena in thalamus and cortex. *Electroencephalogr Clin Neurophysiol* 1949; 1:421-36.

Brazier MAB. A study of the electrical fields at the surface of the head. *Electroencephalogr Clin Neurophy*siol 1949; Suppl 2:38-52.

Calvet J, Calvet MC, Scherrer J. Etude stratigraphique corticale de l'activité EEG spontanée. Electroencephalogr Clin Neurophysiol 1964;17:109-25.

Cohen D. Magnetoencephalography: detection of the brain's electrical activity with a superconducting magnetometer. Science 1972;175:664-6.

Cohen D, Cuffin BN. Demonstration of useful differences between magnetoencephalogram and electroencephalogram. *Electroencephalogr Clin Neurophysiol* 1983;56:38-51.

Cooper R, Winter AL, Crow HJ, Walter WG. Comparison of subcortical, cortical and scalp activity using chronically indwelling electrodes in man. *Electroencephalogr Clin Neurophysiol* 1965;18:217-28.

Creutzfeldt O, Houchin J. Neuronal basis of EEG-waves. In: Rémond A, ed. Handbook of electroencephalography and clinical neurophysiology. Amsterdam: Elsevier Scientific Publishing Co., 1974:2C5-2C54 (Creutzfeldt O, ed; vol 2, part C).

Cuffin BN, Cohen D. Magnetic fields of a dipole in special volume conductor shapes. IEEE Trans Biomed Eng 1977;BME-24:372-81.

Cuffin BN, Cohen D. Comparison of the magnetoencephalogram and electroencephalogram. Electroencephalogr Clin Neurophysiol 1979;47:132-46.

Fourment A. Jami L. Calvet J. Scherrer J. Comparaison de l'EEG sur le scalp avec l'activité élémentaire des dipôles corticaux radiaires. *Electroencephalogr Clin Neurophysiol* 1965:19:217-29.

Gabor D, Nelson CV. Determination of the dipole of the heart from measurements on the body surface. J Appl Phys 1954;25:413-6.

Geisler CD, Gerstein GL. The surface EEG in relation to its sources. Electroencephalogr Clin Neurophysiol 1961;13:927-34.

Gloor P. Contributions of electroencephalography and electrocorticography to the neurosurgical treatment of the epilepsies. In: Purpura DP, Penry JK, Walter RD, eds. Neurosurgical management of the epilepsies. New York: Raven Press, 1975:59-105 (Advances in neurology; vol 8).

Gloor P. Certains aspects de la physiologie et de la pathophysiologie des fuseaux ches le chat. Rev EEG Neurophysiol 1983;13:3-19.

Gloor P. Electroencephalography and the role of intracerebral depth electrode recordings in the selection of patients for surgical treatment of epilepsy. In: Porter RJ, Mattson RH, Ward AA, Dam M, eds. Advances in neurology, vol 15. New York: Raven Press, 1984:433-7.

Gloor P, Vera CL, Sperti L. Electrophysiological studies of hippocampal neurons. I. Configuration and laminar analysis of the "resting" potential gradient, of the main transient response to perforant path, fimbrial and mossy fiber volleys and of "spontaneous" activity. *Electroencephalogr Clin Neurophysiol* 1963:15:353-78.

Henderson CJ, Butler SR, Glass A. The localization of equivalent dipoles of EEG sources by the application of electrical field theory. *Electroencephalogr Clin Neurophysiol* 1975:39:117-30.

Jami L. Fourment A. Calvet J. Thieffry M. Etude sur modèle des méthodes de détection EEG. Electroencephalogr Clin Neurophysiol 1968;24:130-45.

Klee M, Rall W. Computed potentials of cortically arranged populations of neurons. J Neurophysiol 1977; 40:647-66.

Kostopoulos G, Avoli M, Pellegrini A, Gloor P. Laminar analysis of spindles and of spikes of the spike and wave discharge of feline generalized penicillin epilepsy. *Electroencephalogr Clin Neurophysiol* 1982; 53:1-13.

Landry P, Deschênes M. Intracortical arborizations and receptive fields of identified ventrobasal thalamocortical afferents to the primary somatic sensory cortex in the cat. J Comp Neurol 1981;199:345-71.

Landry P. Villemure J, Deschênes M. Geometry and orientation of thalamocortical arborizations in the cat somatosensory cortex as revealed by computer reconstruction. *Brain Res* 1982:237:222-6.

Li CL, Cullen C, Jasper H. Laminar microelectrode analysis of cortical unspecific recruiting responses and spontaneous rhythms. J Neurophysiol 1956a:19:131-43.

Li CL, Cullen C, Jasper H. Laminar microelectrode studies of specific somatosensory cortical potentials. J Neurophysiol 1956b;19:111-30.

Lopes da Silva F, van Rotterdam A. Biophysical aspects of EEG and MEG generation. In: Niedermeyer E. Lopes da Silva F, eds. *Electroencephalography: basic principles, clinical application and related fields.* Baltimore: Urban & Schwarzenberg, 1982:15-26.