REVIEW

The neurophysiological bases of EEG and EEG measurement: A review for the rest of us

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Abstract

A thorough understanding of the EEG signal and its measurement is necessary to produce high quality data and to draw accurate conclusions from those data. However, publications that discuss relevant topics are written for divergent audiences with specific levels of expertise: explanations are either at an abstract level that leaves readers with a fuzzy understanding of the electrophysiology involved, or are at a technical level that requires mastery of the relevant physics to understand. A clear, comprehensive review of the origin and measurement of EEG that bridges these high and low levels of explanation fills a critical gap in the literature and is necessary for promoting better research practices and peer review. The present paper addresses the neurophysiological source of EEG, propagation of the EEG signal, technical aspects of EEG measurement, and implications for interpretation of EEG data.

Descriptors: EEG/ERP, Methods, Signal propagation

Many valuable resources exist from which to learn the essentials of electroencephalography (EEG), ranging from deeply technical to more conceptual or operational. These resources cover topics such as EEG neurophysics (see Nunez & Srinivasan, 2006, for a detailed, technical discussion of the topics discussed in the present paper, and much more; also Buzsáki, Anastassiou, & Koch, 2012; Mulert & Lemieux, 2010; Speckmann, Elger, & Gorji, 2011), clinical perspectives (Schomer & Lopes da Silva, 2011; Smith, 2005), EEG analysis (Buzsáki, 2006), engineering perspectives (Litt & Cranstoun, 2003; Metting Van Rijn, Peper, & Grimbergen, 1990), event-related potentials (ERPs) (Fonaryova Key, Dove, & Maguire, 2005; Regan, 1989), higher-level discussions of the EEG research process from laboratory setup through statistical analysis (Luck, 2005), and study design and publication guidelines (Keil et al., 2014).

However, directing EEG researchers to many of these resources as explanatory or introductory material may do a disservice both to the researchers and to the resources. Lower-level explanations often require readers to make many inferences that readers without physics backgrounds find difficult. At the other end of the spectrum, higher-level explanations may gloss over underlying details that are necessary to achieve a thorough understanding of the neurophysics of the EEG signal and its measurement.

A thorough understanding of the source and measurement of EEG leads to better research habits. Researchers can avoid practices that lead to poor quality data during collection, such as inadvertently introducing noise sources to the recording room, and practices that lead to poor data analysis and interpretation, such as interpreting positive/negative waves to reflect activation/inhibition or equating EEG generator locations with measured EEG peaks at the scalp, to name a few. Errors such as these have been present in numerous manuscripts reviewed by the second author that were ultimately rejected due to these poorly drawn or overstated conclusions based on an inaccurate understanding of the underlying neurophysiology. As EEG/ERP research continues to pervade nontraditional and interdisciplinary neuroscience journals, the likelihood of these errors passing through the filter of peer review will only increase.

The goal of the present paper is to link more low-level, mechanistic explanations of EEG with more high-level, abstract explanations in a manner accessible to researchers who lack a strong background in physics and neurophysiology, enabling a thorough understanding of the EEG signal and its measurement. The present paper concludes with prescriptions of best practices regarding data collection and the conclusions that may be drawn from EEG data. The fundamentals discussed herein are applicable across fields that rely on EEG, from mental chronometry to generator analysis to clinical diagnosis, as greater care in data collection will yield better

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data quality and contribute to more appropriate interpretation of data irrespective of the specific nature of the research.

The general organization of this paper follows the EEG signal from its source in cortex to its measurement at the EEG amplifier. To begin, we consider a basic dipole model of neuron behavior, then we examine properties of neocortex that enable the signal to be measured. Next, we review how the signal travels and how it is measured by EEG equipment. In the final sections, we discuss how the principles of signal origin, signal propagation, and signal measurement relate to specific issues that are relevant for EEG researchers. Certain sections may appear redundant but are intended to address specific issues from different angles (e.g., "Why is electrode gel necessary?" and "Why do we aim for small resistance between electrode and scalp?"), which is intended to help practitioners account for these issues in their research.

The Neural Source of EEG

There is general agreement on the primary source of the EEG signal (see Avitan, Teicher, & Abeles, 2009 for a historical review): the EEG arises from synchronized synaptic activity in populations of cortical neurons (pyramidal cells organized along cortical columns) (see Holmes & Khazipov, 2007; Kandel, Schwartz, & Jessell, 2000; Lopes da Silva, 2010, for reviews). Excitation of the postsynaptic neurons creates an extracellular voltage near the neural dendrites that is more negative than elsewhere along the neuron. This situation is referred to as a *dipole*: a region of positive charge separated from a region of negative charge by some distance. The region of positive charge is referred to as a *source*, while the region of negative charge is referred to as a *sink*.

Electrodes detect the sum of positive and negative charges in their vicinity. In the case where an electrode is equidistant from both source and sink of a dipole, the electrode will measure a net neutral; so, an electrode can only detect dipoles when the electrode is closer to either the positive or negative end of the dipole. This means that two major types of dipoles are measurable in EEG: tangential dipoles (Figure 1a), which are oriented perpendicular to the surface, and radial dipoles (Figure 1b and 1c), which are oriented parallel to the scalp surface (Ahlfors, Han, Belliveau, & Hämäläinen, 2010; Whittingstall, Stroink, Gates, Connolly, & Finley, 2003). Dipoles have a positive and negative side, and therefore will produce both a positive deflection and a negative deflection at different regions of the scalp (Figure 1c).

A single neuron's dipole is too small to be measured as far away as the scalp. However, because electrodes detect the sum of charges in their vicinity, the dipoles from multiple neurons in a region will sum together. The sum of many individual dipoles in an area is measurable as a single dipole whose magnitude reflects the number of neurons whose dipoles are summing together (Dugdale, 1993; Kandel et al., 2000). However, because electrodes will measure the sum of both the positive and the negative ends of dipoles in the brain, in order to produce a measurable (nonzero) signal, neurons must be both (a) arranged in a parallel fashion, and (b) synchronously active (Figure 2). The parallel arrangement is necessary to produce a measurable dipole because, if the neurons are all arrayed in the same orientation, then their signals can sum to form a larger signal. In any other configuration, the individual dipoles' positive and negative ends will sum and cancel each other out. The synchronization of activity is necessary in order to yield (a) a net charge on the scalp-facing side of the dipole sheet, rather than charges cancelling each other out; and (b) a signal large enough to be measured.
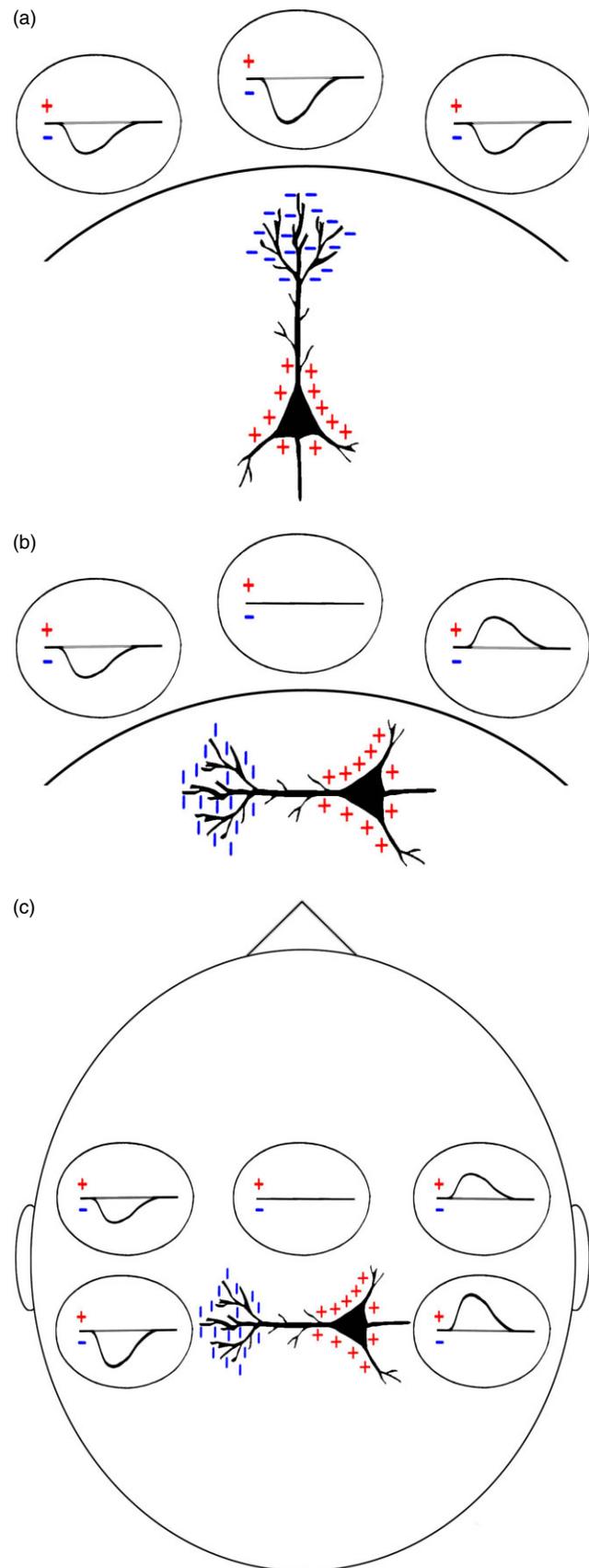

Figure 1. Radial and tangential dipole measurement. Radial dipoles (a) produce deflections in roughly one direction, while tangential dipoles (b and c) produce both directions of deflection.

The polarity of the signal measured at the scalp also depends on the particular orientation of the dipole (Figure 3). Consider the case of an excitatory postsynaptic potential (EPSP) at an apical dendrite. When an EPSP is triggered at a dendritic synapse, the local extracellular fluid becomes more negative with respect to the intracellular fluid as depolarizing current flows into the neuron. That current will flow out elsewhere along the neuron, which produces a local, albeit more distributed, extracellular positivity. In pyramidal neurons oriented perpendicular to the skull, the dendrites will be closer to the scalp and thus the local negativity of the extracellular fluid will be closer to the scalp, so an electrode on the scalp will measure the influence of the negativity and produce a negative deflection. The measured signal reflects the charge of the extracellular fluid rather than the charge of the intracellular fluid because volume conduction towards the skull (see next section) depends on the movement of ions and thus does not reflect the current within the neuron.
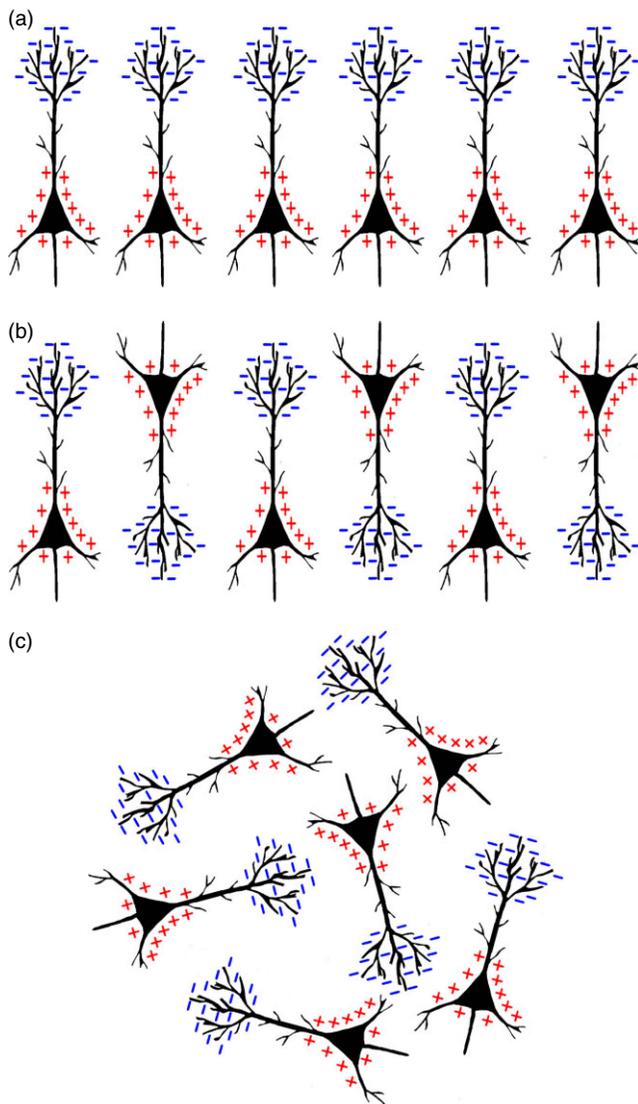

Figure 2. How parallel arrangement and synchronous activity allow signal to be measured at the scalp. a: The negative signals will sum to be measurable at the scalp. b: The positive and negative signals will "cancel each other out" at the scalp, and thus not be measurable. c: No clear dipole emerges from random arrangement of positive and negative charge pools, so no signal is measurable at the scalp.
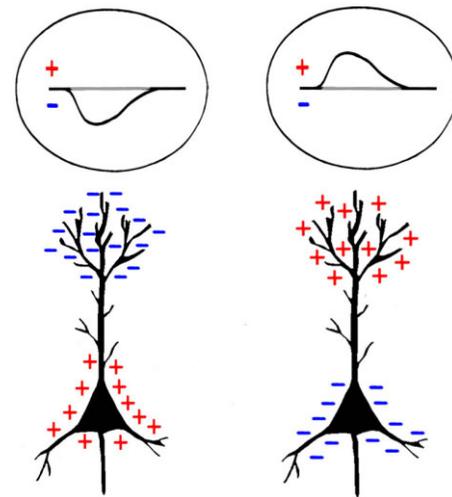

Figure 3. Measured EEG cannot determine if activity is excitatory or inhibitory. The neuron on the left is receiving either an IPSP (which produces an extracellular positivity) near the soma, or an EPSP (which produces an extracellular negativity) at the apical dendrites. Either of these signals will be measured as a negative deflection in the EEG. The neuron on the right is receiving either an EPSP near the soma or an IPSP at the apical dendrites. Either of these signals will be measured as a positive deflection in the EEG.

On the other hand, if an EPSP arrives at a synapse (in a pyramidal cortical neuron) that is closer to the cell body rather than in the dendritic arbor, then the positivity will be closer to the scalp and a scalp electrode will measure a positive deflection in voltage. Similarly, an inhibitory postsynaptic potential (IPSP), which would hyperpolarize the synaptic region, that is closer to the dendrite than the cell body will produce a positive voltage, while an IPSP closer to the cell body will produce a negative voltage. Thus, EPSPs and IPSPs can produce either a positive or negative deflection in the EEG signal, depending on whether the positivity is closer to the scalp than the negativity or vice versa.

A combination of thalamocortical and corticocortical connections are thought to drive the synchronous activity that gives rise to EEG (Buzsaki, 2006; Olejniczak, 2006; see Lopes da Silva, 2010, and Schaul, 1998, for discussion of specific rhythms). More specific discussions of neural sources of EEG (precise populations of neurons that contribute to the signal, etc.) tend to be based on a wide variety of reductionist assumptions, such as modeling highly ramified and complex dendritic arbors as tubes with simple spatial relationships to the neuron, or modeling the human skull as three or four concentric spheres. Experimental work intended to validate theoretical work has met with some degree of success, but with certain conflicts between data and theory thought to reflect violations of model assumptions (e.g., Rall's modeling of dendritic trees: see Nunez & Srinivasan, 2006, p. 178, for a discussion).

How EEG Travels From the Brain to the Recording Device

Within the Brain

Volume conduction is responsible for the propagation of the EEG signal within the brain. Consider the basics of electrical charge: opposite charges attract each other and like charges repel each other. Volume conduction is the process by which a pool of ions repels nearby ions of the same charge. Those repelled ions in turn

repel other ions of the same charge, resulting in a "wave" of charge that travels through the extracellular space. This same basic mechanism allows a signal to propagate through a wire, extracellular space, or other conductive volumes.

In the case of a homogenous volume, this wave of charged ions can propagate through the volume unimpeded. If currents were allowed to travel unimpeded through cortex, the result would be a cascade of firing action potentials with little specificity; in short, the brain would produce constant seizure events. However, the brain is not a homogenous volume. Ions cannot travel through myelin-coated nerve tracts or other physical barriers (Wolters et al., 2006). Different tissue densities may impede or permit ion flow, based on their inherent electrical properties as well as physical arrangement. Furthermore, dipoles are not all the same size: a signal from a large dipole may travel much further than a signal from a small dipole, much like a shout will travel further than a whisper.

From Brain to Electrode

In order to be measured with an electrode outside the head, the electrical signal created by neural firing must travel from the brain, through the dura layers, through the skull layers, through the scalp, and finally to the electrode. Once the volume-conducted signal reaches the edge of the volume it is traveling through, volume conduction can no longer occur, as ions cannot leave the volume. Between volumes, a form of capacitance becomes responsible for the signal's propagation (Figure 4).

A capacitor is, in its most general form, two pools of charges separated by an insulating layer (a *dielectric*). The insulating layer prevents ions from mingling; if no insulating layer were present, then the charges would freely mix, and the result would be a neutrally charged pool. But, if an insulating layer is present, then a charge difference may build up across the insulating layer, wherein negative ions push up against one side of the membrane and positive ions accumulate on the other side. How much charge builds up on the other side is determined by the properties of the insulating materials between the pools of charges, the size of the charged pool, and the distance between the pool of charge and the insulating layer. The sequence of layers from the brain to the dura layers, skull layers, scalp layers, electrode gel, and electrode thus forms a series of conductive volumes separated by insulating layers—akin to a stack of capacitors (Figure 4).

Consider an IPSP arriving at a synapse near a soma in cortical layer IV. The extracellular positivity will propagate via volume conduction to the near side of the closest insulating layer, at which point volume conduction cannot carry the signal further because the insulating layer is a physical barrier to ion flow. The positive ions accumulated at the near side of the insulating layer will repel positive charges on the other side of the insulating layer. The positive charges repelled and thus accumulated on the far side of the insulating layer will, in turn, push other positive charges away. This process will repeat through every capacitor in the stack until it reaches the electrode (Figure 4).

It is assumed that the majority of the EEG signal represents the capacitive arrangement described. However, electrons do flow between the gel and electrode (Usakli, 2010) creating half-cell (DC) potentials. This is why EEG system users are instructed to allow the electrodes to "settle" for a few minutes before beginning to record: the settling corresponds to the electrochemical interaction between the electrode and gel reaching a steady state, at which point the steady DC offset can be accounted for elsewhere in the system. For further information, see Geddes, Baker, & Moore (1969), Geddes & Roeder (2001), and Gencer (2005).

Measurement Issues

Signal Summation and Smearing

An electrode's output is a single voltage per measurement typically taken every 1–2 ms (or 1–0.5 kHz). This measured voltage reflects the sum of all charged ions that are, through the capacitive stack discussed above, pushing or pulling on the electrons in the electrode at the time that the measurement is taken. A measurement of voltage at any position on the scalp will consist of the sum of influences from many sources of electric fields because the brain is full of dipoles. Each dipole exerts influence in nearly all directions, so a dipole will influence the charge in a range of scalp locations, not just on the scalp immediately above the dipole. This is referred to as *spatial smearing* of the signal and is a byproduct of volume conduction and the "sandwich" of capacitors between the brain and the electrode (e.g., Freeman, 1980).

Due to cycles in neural activity, the voltage measured at the scalp cycles between positive and negative; the rate of this cycling is the signal's frequency. The frequency bands of typical EEG span from 0.1 Hz to around 30 Hz. Higher frequencies (gamma, 30–80 Hz, and higher) are more difficult to study, as these frequencies are heavily attenuated by the skull and scalp layers, and may be overshadowed by muscular and ocular artifacts (Freeman, 1980; Srinivasan, Nunez, & Silberstein, 1998). However, electrocorticogram (ECoG; EEG measured on the surface of the brain, rather than the surface of the scalp) recordings indicate that these higher frequencies do modulate concurrent with cognitive activity (e.g., Crone, Sinai, & Korzeniewska, 2006), and certain methods of analyzing standard EEG data have been successful in finding
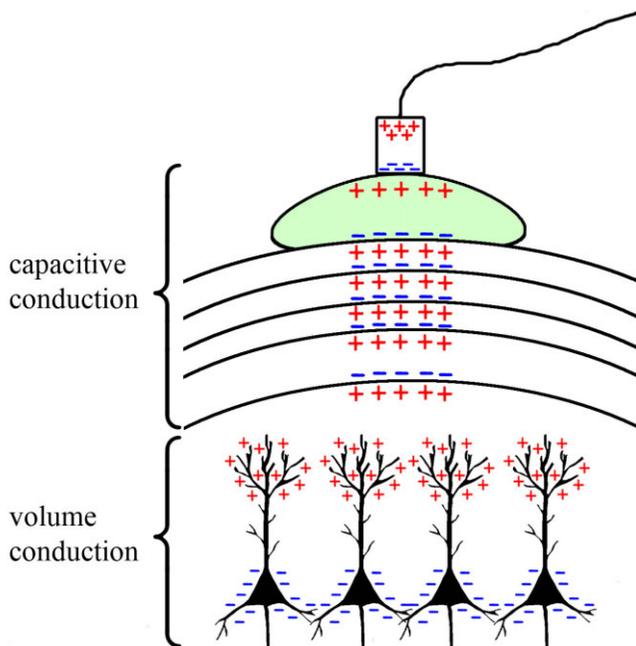

Figure 4. The capacitor stack with electrode gel, showing the neural signal propagating through layers of brain, dura, skull, and electrode gel to reach the electrode. Because the gel is a conductor, the signal reaches the electrode with less attenuation than if the gel were not present.

cognitive effects in high-frequency bands as well (Onton & Makeig, 2009; for reviews, see Kaiser & Lutzenberger, 2005; Pantev, 1995; but see Yuval-Greenberg & Deouell, 2011, for a discussion of oculomotor artifacts, and Hipp & Siegel, 2013, for a discussion on circumventing such artifacts).

Can EEG Detect Dipoles Anywhere in Cortex?

Research indicates differential sensitivities of magnetoencephalography (MEG) and EEG (e.g., Ahlfors et al., 2010). MEG can only measure magnetic fields that leave the skull, so MEG cannot detect dipoles oriented perpendicular to the scalp (radial dipoles). In contrast, EEG can measure any dipole whose source and sink are not equidistant to the electrode, so it may be sensitive to both tangential and radial dipoles (Ahlfors et al., 2010). To examine how this may be the case, consider the model laid out in Figure 1: dipoles parallel to the surface of the scalp cannot be measured immediately above the center of the dipole, because both positive and negative ends of the dipole would be measured equally, resulting in a net neutral. However, dipoles parallel to the scalp may be measured at electrodes that are not directly above them, as these dipoles will be nonparallel to other skull regions that are not immediately above. Thus, the signal measured in EEG may originate from both cortical sulci, which would produce radial dipoles, and cortical gyri, which would produce tangential dipoles, as long as those dipoles are large enough or near enough to the skull to be measurable.

Thus, the limitation on the EEG signal appears to be not the alignment of dipoles, as in MEG, but rather if the size of the electric field produced by a set of neurons is large enough to be measurable at the surface. The larger the pool of neurons involved in synchronous activity, the stronger the electric field they produce (Nunez & Srinivasan, 2006), and thus the further away they can be measured. A large dipole deep in the brain may still be measurable at the electrode, although it may contribute a smaller signal than the surface sources will because the strength of the electric field produced by a dipole drops off very rapidly.[1] Simulated EEG dipoles indicate that deep sources may be more prone to noise contamination, though it is unclear if this is simply due to the greater distance traveled by the signal from a deep source or due to passage through more potential sources of noise (Whittingstall et al., 2003). It is unclear the extent to which signals from deep sources may interfere or interact with shallower sources (e.g., Anastassiou, Perin, Markram, & Koch, 2011).

Which Electrical Sources in the Brain Will be Measured at the Scalp?

A common goal in EEG research is to interpret changes in EEG as reflecting changes in activation in certain brain regions. Identifying those brain regions is a major challenge, as a measurement at the surface of the scalp may reflect the sum of signals that have traveled from many disparate brain regions. There are two major methods of understanding the signal propagation from brain sources to scalp electrodes: computer simulations and experiments on patients who undergo surgery to control epilepsy. The methods are largely complementary in their strengths and weaknesses;

simulations are much more flexible, but are simplified models of the brain, while surgical patients are fully realistic brains, but are studied using activity that may be less externally valid (discussed below).

Most, if not all, simulation work is conducted in extremely simplified head models consisting of only three volumes, each homogenous: scalp, skull, and brain. In certain cases (e.g., Leahy, Mosher, Spencer, Huang, & Lewine, 1998; Whittingstall et al., 2003), the overall shape of each volume is based on structural MRI or X-ray, and so the volumes do reflect reality more closely than do perfectly spherical volume models. However, collapsing the structural complexity of the brain into a single homogenous volume with a single conductivity ignores many factors that are thought to influence signal conduction, such as inhomogeneity of conductivity and interactions among different electrical elements (e.g., Van den Broek, Reinders, Donderwinkel, & Peters, 1998). Even the skull is inhomogeneous—it consists of at least three sublayers, each with different conductivities to different frequencies (Akhtari et al., 2002). Furthermore, skin conductivity varies as a function of dead skin cells, oil content, water content, sweat, etc., so simplifying each of these factors to single conductivity values may miss important variability (e.g., Leahy et al., 1998; Ollikainen, Vauhkonen, Karjalainen, & Kaipio, 1999).

Nonsimulated dipoles (e.g., Smith, Sidman, Flanigin, Henke, & Labiner, 1985) generally involve current injection into patients undergoing surgery for epileptic seizures. While these data benefit from being measured from a real brain, they often use single-point sources of current injection rather than a more realistic distributed set of activations. While the signal may propagate more realistically, the signal source itself is less realistic, so it is unclear how well these results may be generalized. Furthermore, the brains in question are selected because they're undergoing surgery to correct abnormalities that produce epileptic activity, so it may be the case that results are systematically biased due to the specially selected population.

Why is Electrode Gel Necessary?

The EEG signal within the brain is carried via volume conduction, but once the signal reaches the skull, it can no longer be carried by ions because ions cannot pass through the skull. While cerebral spinal fluid and various ion-filled substances in the brain are very good conductors (e.g., Baumann, Wozny, Kelly, & Meno, 1997), they are separated from the electrode by several layers of poor conductors, including the skull, dead skin cells, hair, and air in the interstices of hair (Figure 5). Ideally, the highly conductive electrode gel will saturate the space beneath an electrode, filling in the air pockets between hairs and thus providing a conductive path from scalp to electrode. This makes another capacitor on top of the previously discussed stack (Usakli, 2010; see Figure 4). A variety of "dry" electrodes, used without application of gel, are being developed for use in EEG research (e.g., Gargiulo et al., 2010), but the technology that allows for dry recording is beyond the scope of this paper (see Chi, Jung, & Cauwenberghs, 2010, for a review).

If Measuring a Clear Signal is So Difficult That it Requires Specialized Gel, Why is it So Easy for Noise to Contaminate the Signal?

What is signal? What is noise? An EEG recording system measures electrical activity. However, it will measure electrical activity

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1. As described by Coulomb's law at a rate of $1/distance^2$, or at a rate of $1/distance^3$ because the source is a dipole (Hopkins, 1999); both estimates assume spherical propagation.
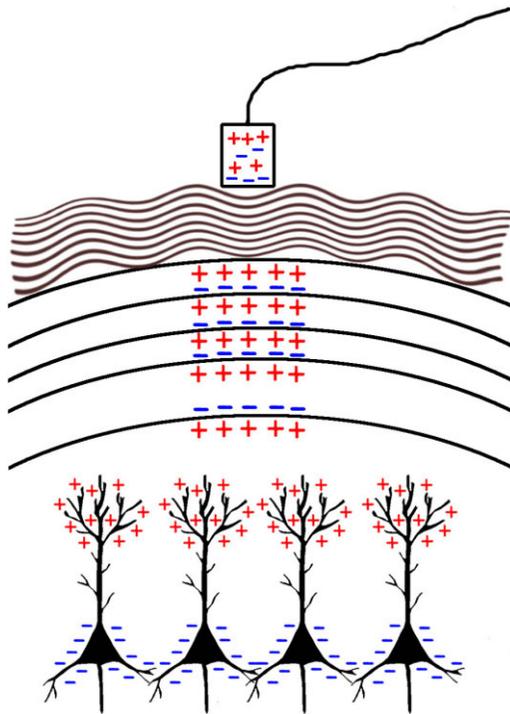
Figure 5. The capacitor stack with no electrode gel. Note that the layer composed of hair and air is an insulator rather than a conductor, so the signal is attenuated when measured at the electrode.

that arises from the brain as well as electrical activity that arises from other sources. In this case, signal refers to the portion of measured voltage that reflects the brain, and noise refers to the portion of the voltage that reflects other sources. The signal-to-noise ratio (SNR) is a measure of how much signal the system measures compared to how much noise, so a higher SNR reflects a better-quality signal that is contaminated by less noise. Accordingly, successful measurement of a signal like EEG depends in part on minimizing sources of noise that would otherwise overwhelm the EEG signal.

It is worth noting that, depending on the research question at hand, elements of the EEG itself may be considered noise. For example, background EEG at particular frequencies may make it more difficult to measure certain ERPs (Gruber, Klimesch, Sauseng, & Doppelmayr, 2005; Klimesch et al., 2004). Particular ERP components such as the N1 and P1 are proposed to emerge or at least are determined by the superposition of underlying oscillations at several frequency bands (Gruber et al., 2005). For more in-depth discussion considering neural sources of signal and noise, see Barry, de Pascalis, Hodder, Clarke, and Johnstone (2003). External and internal sources of noise are discussed below, followed by a discussion of the amplifier and its role in EEG measurement.

External noise. Compared to the brain signal, the amplitudes of noise sources are gigantic. The electrical power supply in buildings is often the loudest source of noise (Metting van Rijn et al., 1990) at 120 volts in the United States, which is several orders of magnitude larger than the microvolt sources measured at the scalp. Electric field strength decreases exponentially with the distance from the source to the measurement, so the relatively large electric

fields produced by current-carrying wires in the walls, ceiling, floor, lights, computer monitor, and video equipment will influence measured noise proportional to their distance from the electrodes and electrode leads. See Ferree, Luu, Russell, and Tucker (2001) for an excellent discussion of modernizing computational approaches to noise sources.

EEG systems may solve the problem of external noise through two general means: passive shielding and active electrodes. Either rooms or electrode cables (or both) may be shielded. A passive shield is essentially a piece of conductive metal (a Faraday cage) that surrounds the region to be shielded and cancels out or shunts away electromagnetic radiation (Dugdale, 1993). This cancelling out occurs when electrons within the conducting material are "pushed" by external electrical activity, producing a net neutral electrical charge from the point of view of anything within the cage. An unshielded electrode lead acts as an antenna that will detect electrical noise that isn't eliminated by the room's shielding, but shielded electrode leads are more expensive, more delicate, and heavier than unshielded cables. Active electrode systems bypass the issue by placing an amplifier as close to the electrode as possible. Amplifying the signal before passing it along an unshielded wire means that, even if noise is introduced during the signal's journey to the main amplifier, the SNR is still quite large (e.g., Metting Van Rijn, Kuipers, Dankers, & Grimbergen, 1996).

Internal noise. Participants produce a number of internal sources of noise that are particularly insidious because they can't realistically be excluded while collecting data (Luck, 2005). These sources of noise may influence the signal more predictably (the ~1 Hz oscillation of the electrocardiogram, the periodic rib cage expansions and contractions of breathing) or less predictably (DC potentials over time, muscle tension, blinking), but because all arise from within the body, they can't be eliminated during the process of data collection. These noise sources can be minimized to some degree by controlling environmental factors and participant behavior, but, generally, internal sources of noise must be dealt with through various methods of filtering and artifact detection in postprocessing, which are beyond the scope of this paper.

Why is the Amplifier Necessary, and What Does it Do?

The purposes of an amplifier in an EEG system are to (a) maximize the SNR of the measured voltage, and (b) increase the size of a signal above the size of noise that may be introduced in later elements of the circuit (T. Freeman, personal communication, January-February, 2011). For example, a signal may be measured at the scalp and then travel through a long wire before reaching the acquisition computer, and noise may be introduced as the signal is traveling along the wire. If the signal was not amplified before the noise was introduced, then the SNR will be reduced even more from the point of measurement; if the signal was amplified before the noise was introduced, then the impact of the noise on the SNR will be smaller.

One particular characteristic of amplifier design, the input impedance of the amplifier, is vital to EEG collection. Input impedance determines how well the amplifier can tolerate a poor connection to the scalp (or, roughly, how well the amplifier can tolerate a weaker signal; Ferree et al., 2001; Gargiulo et al., 2010). The input impedance of an amplifier is a fixed value determined by the amplifier's design (Self, 2009).

Why is the Amplifier Input Impedance Important?

Understanding impedance and voltage.[2] Impedance is very similar to resistance, but is present in AC circuits rather than DC circuits. Because the currents measured from the brain are alternating (the voltages switch between positive and negative), most of the elements of the EEG circuit are discussed in terms of impedance. For the purposes of this paper, we will discuss resistance, because resistance is generally more familiar than impedance; the two phenomena behave similarly enough for present purposes that the differences don't impact this explanation.

Resistance (R, measured in ohms), current (I, measured in amperes or amps), and voltage (V, measured in volts) are all inter-related properties of electricity. Current is the amount of electrical charge that moves from one place to another in a given period of time. Voltage is a measure of how much charge is present at one location relative to how much charge is present at another location. Because voltage is a relative measure, it must be measured as a difference of two points. When there is a difference in charge between two locations (in other words, a voltage is present), charge will tend to move from one location to the other to equalize the net charge. In other words, the presence of a voltage will lead to a flow of charge (a current). The rate of that flow of charge will be determined by the resistance of the substance that separates the two locations. Ohm's law states that the voltage measured across two points of a circuit is equal to the current in the circuit multiplied by the resistance between those two points (voltage equals current times resistance, or V = IR). Because the current in an EEG measurement is determined by the size of the brain's electric field acting on the electrode, the current cannot be changed through external means; so, for our purposes, we assume current to be constant at any given moment.

Voltage is defined as the difference in charge between two locations; if a voltage is measured between a location immediately before a source of resistance in a circuit and immediately after that source of resistance, it is said to be measured *across* the resistance. If a voltage is measured across a resistance, the voltage will be lower after the resistance relative to before the resistance. This is referred to as a *voltage drop*, or how much the voltage decreases across a given resistance (for an example, see Figure 6). This

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2. The electrical terms introduced here are discussed in a simplified manner for ease of understanding. For a more thorough treatment, see Dugdale (1993) or any convenient introductory physics textbook.
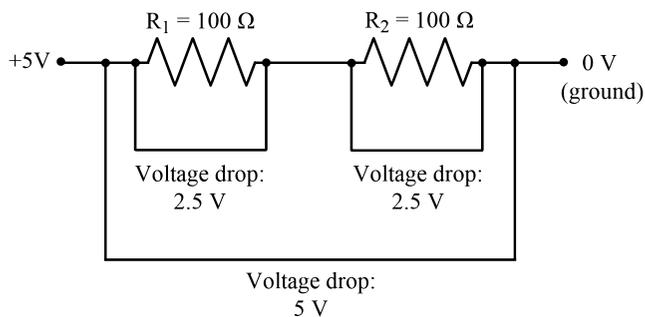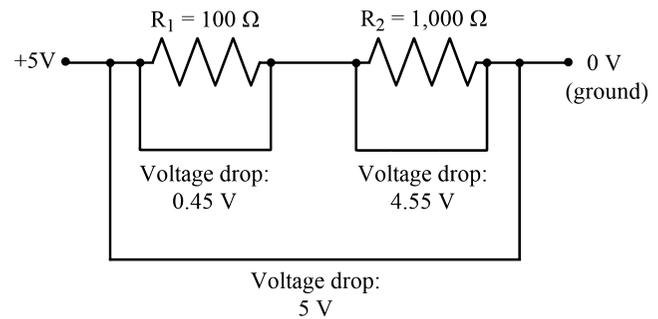
Figure 6. Voltage drop across resistance. Each resistor in the circuit will produce a voltage drop proportional to the total resistance. Here, if both resistors are 100 ohms, then each resistor represents half of the total resistance, so each resistor would drop half of the voltage.

$$\text{R1 Voltage drop} = 5V * \frac{100}{100 + 1{,}000} = 0.45V$$

$$\text{R2 Voltage drop} = 5V * \frac{1{,}000}{100 + 1{,}000} = 4.55V$$

Figure 7. Calculating voltage drops across resistance. Each resistor in the circuit will produce a voltage drop proportional to the total resistance. If one of the resistors here has a resistance of 100 ohms and the other has a resistance of 1,000 ohms, then the former is 100/1,100 of the total resistance, and so drops 100/1,100 of the total voltage (see calculations beneath the figure).

voltage drop is how a voltage can be measured. Every resistive component in a circuit will cause a drop in voltage as measured from before the component to after the component.

The sum of the voltage drops across the entire circuit—from the electrical source (the positive side) to the electrical sink (the negative side)—will equal the voltage of the source. For example, if a circuit in an alarm clock is powered by a 9-volt battery, then the sum of all the voltage drops in the alarm clock's circuitry will equal 9 volts. However, the size of the voltage drop across a specific resistor is determined by the proportion of the resistor's resistance to the total resistance in the circuit. Consider the example in Figure 7.

This property can be used to measure the voltage in a circuit. A voltmeter measures the voltage in a circuit (say, across the poles of a battery) by inserting a very, very large resistor in the path of the circuit. This resistor is so much larger than every other source of resistance in the circuit that it represents almost all of the resistance, and so almost all of the voltage drops across it. Thus, a voltmeter can measure how much voltage is present in a circuit.

An amplifier uses input impedance in a similar way. The amplifier measures the voltage in a circuit (in this case, the EEG signal) by inserting a very, very large resistor (the input impedance) into the circuit. The input impedance is so much larger than every other source of resistance in the circuit that it represents almost all of the resistance, and so almost all of the voltage drops across it. This is important for two reasons: first, that the EEG signal is very small, so it is important to measure as much of the signal as possible; and second, that the impact of electrical noise is minimized. The relationship between electrical noise and the amplifier is discussed in the next section.

Electrical noise and the importance of high input impedance.[3] Consider a simplified EEG system consisting of electrodes on the scalp, an amplifier, and wires connecting the electrodes to

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3. This section draws on several technical manuals and textbooks, but mostly on interviews with an electrical engineer (T. Freeman, personal communication, January–February, 2011).
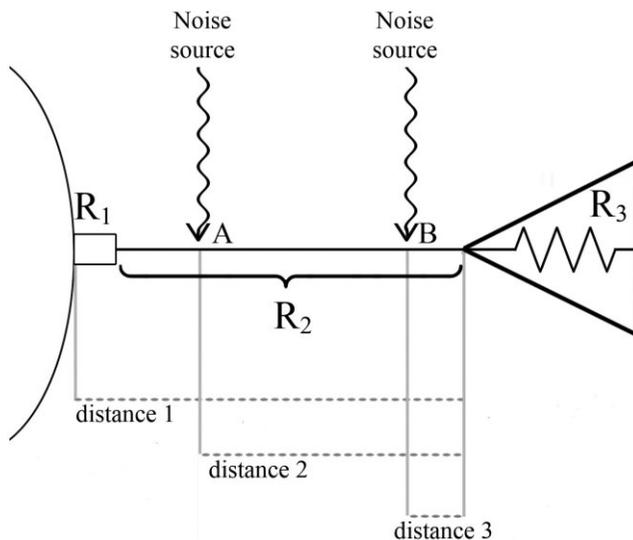
Figure 8. Noise entering the EEG measurement system.

the amplifier. There are three major sources of resistance in this circuit: the resistance between the scalp and the electrode, the input impedance of the amplifier, and the wire between the electrode and the amplifier. Wires produce resistance, the magnitude of which is determined by the material and the size of the wire. This resistance is additive: if a particular material produces 1 ohm of resistance per centimeter of wire, then 2 cm will produce 2 ohms of resistance, 6 cm will produce 6 ohms of resistance, and so on.

"Noise" here refers to any voltage that is measured at the amplifier that is not what the system is intending to measure, which means any voltage that isn't representing brain activity. This noise can arise from common ambient electrical activity (wall mains, computer monitors, cell phones). We will consider noise entering the system at the wire between electrode and amplifier (Figure 8). Noise can enter the system at any point in the wire: just after the electrode, partway to the amplifier, or just before the amplifier. This means that the noise will physically travel along the wire for either the same distance that the EEG signal travels, or a shorter distance.

Because the resistance of a wire is determined by both its material and its length, the longer a signal travels along the wire, the more resistance it encounters. The resistance encountered by a signal will influence how much of that signal is measured by the amplifier. Consider that, when a noise source enters the wire part way between the electrode and the amplifier, it will travel a shorter distance along the wire than the EEG signal will, and thus it will experience less resistance. For example, assume that the wire from the electrode to the amplifier has a resistance of 1 ohm per centimeter. If the wire is 1 m long, then the EEG signal will travel through 100 ohms of resistance (1 ohm/cm * 100 cm). Any sources of electrical noise will enter the wire at the electrode or later than the electrode, so a noise source will travel 1 m or less to reach the amplifier. If the noise enters the wire at 5 cm from the amplifier, then it will travel through 5 ohms of resistance (1 ohm/cm * 5 cm) before it reaches the amplifier.

The input impedance of the amplifier is determined by its design and does not change (Self, 2009). Thus, the input impedance of the amplifier will be the same value for both signal and noise. However, because the signal and noise experience a different amount of resistance in the rest of the circuit, the amplifier's input impedance

will make up a different proportion of the total resistance for signal and noise. The noise will always experience less resistance, because it travels along less of the wire before it reaches the amplifier. In our example, say the input impedance is 100 ohms:

Signal: 100 ohms of resistance from the wire, 100 ohms from the amplifier. The ratio of amplifier resistance to total resistance is $100/100 + 100 = .5$. This results in a voltage drop across the input impedance of the amplifier that is 50% of the signal's voltage.

Noise: 5 ohms of resistance from the wire, 100 ohms from the amplifier. Ratio of amplifier resistance to total resistance is $100/100 + 5 = .9524$. This results in a voltage drop across the input impedance of the amplifier that is 95.24% of the noise's voltage.

As discussed above, the voltage drop across a specific resistance depends on the ratio between that specific resistance and the total resistance. In this case, half of the signal's voltage would drop across the wire's resistance, and half would drop across the amplifier's input resistance. However, only 1/20th of the noise's voltage would drop across the wire, and 19/20ths would drop across the amplifier's input resistance. Accordingly, the signal is attenuated much more than the noise, so the noise contributes much more (proportionally) to the total voltage measured at the amplifier. This does not fulfill the amplifier's primary goal of maximizing the SNR of the EEG.

The previous example discussed an amplifier with an input impedance not much larger than the wire's impedance. If, on the other hand, the amplifier's input impedance is enormous, then the ratio of signal resistance to total resistance and the ratio of noise resistance to total resistance are much closer together. If the input resistance of the amp is 1 million ohms, then:

Signal: 100 ohms of resistance from the wire, 1,000,000 ohms of resistance from the amplifier. Ratio of amplifier resistance to total resistance is 1,000,000/1,000,100. This results in a voltage drop across the input impedance of the amplifier that is 99.990% of the signal's voltage.

Noise: 50 ohms of resistance from the wire, 1,000,000 ohms of resistance from the amp. Ratio of amplifier resistance to total resistance is 1,000,000/1,000,050. This results in a voltage drop across the input impedance of the amplifier that is 99.995% of the noise's voltage.

In this way, the amplifier maximizes the SNR: instead of measuring a voltage that is composed of a small amount of the signal and a large amount of the noise, it measures nearly the entire signal and nearly all of the noise. Modern EEG amplifiers typically have very high input impedances compared to older amplifiers, and thus can tolerate much more electrically noisy conditions (nonabraded scalp, recording outside a specially shielded room, etc.; Ferree et al., 2001). However, high-impedance amplifiers can only mitigate some noisy conditions, while other conditions require different accommodations in order to collect clean data (see Kappenman & Luck, 2010, for a comprehensive discussion of electrode impedance).

Connection Between the Electrode and the Scalp

Why is it important to minimize resistance between electrode and scalp? Of all the connections in an EEG system, the connection between electrode and scalp is the most relevant for day-to-day usage. Older systems require extensive preparation (skin abrasion, etc.) to reduce the resistance of the electrode-scalp connection as much as possible, while newer systems are more tolerant of connections with higher resistance due largely to high input

impedances. In both cases, a smaller resistance between scalp and electrode is preferred.

At first it may seem odd that this resistance should be small, given the preceding discussion on the merits of an amplifier with very large input resistance. The reason for this difference is that we have different goals for the signal at the scalp versus the amplifier: signal is passed along at the scalp, but measured at the amplifier. A smaller resistance allows more signal to pass through, because it drops less voltage, leaving more voltage to continue through the circuit. A very large resistance is what allows the voltage to be measured, because it drops as much voltage as possible, and that voltage drop is what is measured.

How does the amplifier's input impedance allow it to tolerate a poorer connection to the scalp? As noted above, an EEG system should minimize the resistance across the scalp-electrode interface in order to minimize the voltage drop at that interface, so as much voltage as possible remains to be measured at the amplifier. If the amplifier's input impedance is low, then (a) the scalp-electrode impedance will make up a larger proportion of the total impedance, and so the voltage drop across the scalp-electrode resistance will be greater; and (b) the signal will be dominated by noise as discussed in previous sections. If, on the other hand, the amplifier's input impedance is much larger than the scalp-electrode resistance, then even a fairly high scalp-electrode resistance will still represent a very small portion of the total resistance. Thus, the higher the input impedance, the larger the electrode impedance that can be tolerated without losing signal quality.

Concluding Principles

The previous sections discussed the neurophysiological source of EEG, propagation of the EEG signal, and measurement of the EEG signal by the amplifier. Here, the final section will conclude with a small set of principles regarding collection and interpretation of data based on the previously discussed neurophysiological bases of EEG.

First Principle: Care in Collection

Improvements in technology allow greater leeway in collection parameters—poorer connections to the scalp, higher ambient noise, and so on—than in past EEG collection systems. However, the basic principle remains that it is preferable to expend a little extra effort at the outset to collect clean data than to collect noisy data and try to correct for it in postprocessing. Our discussion on electrodes leads directly to a practical principle governing expenditure of a little bit of time to achieve cleaner recordings: letting electrodes settle, or allowing the half-cell potential of each electrode to reach a steady state before collecting data. Letting electrodes reach this steady state eliminates certain slow voltage changes that would otherwise be measured. The process doesn't even necessitate major changes to an experimental protocol: allowing electrodes to reach steady half-cell potentials requires only a few minutes of waiting, during which participants can receive instructions, fill out paperwork, or complete other small tasks.

Second Principle: Care in Localization

As discussed throughout the previous sections, signal propagation is complex but is typically modeled with a host of simplifying assumptions. Sources all over the brain may contribute to a meas-

ured signal at the scalp; however, an infinite number of configurations of these sources may generate a particular pattern of voltage measured at the scalp. This task of knowing only the final surface voltage pattern and working backwards to determine which sources within the brain produced that voltage pattern is referred to as *the inverse problem*. There is no absolute answer to the inverse problem, but there are methods of approximation, many of which have met with success based on certain assumptions (correlation of sources, etc.). A discussion of particular source analysis techniques is beyond the scope of this paper; see Pascual-Marqui (1999) and Grech et al. (2008) for reviews and comparisons of methods, and Grave de Peralta Menendez, Murray, Michel, Martuzzi, and Andino (2003) and Phillips, Rugg, and Friston (2002) for discussion of neuroimaging and biophysical constraints that can be applied to the problem.

Our discussion on signal propagation and measurement leads to practical principles of using source localization analysis. Firstly, particularly if you are applying source localization as it is offered in a software package (e.g., BESA; www.besa.de), be aware of the assumptions that each method relies on and be certain that your data are compatible with these assumptions. Secondly, in light of EEG's spatial limitations, it is ideal to apply source localization methods in conjunction with information from additional methods that are more optimized for providing spatial information (fMRI, MEG) in order to constrain solutions to the inverse problem.

Third Principle: Care in Interpretation

We discussed the generators of the EEG signal, and noted that the positive or negative direction of an EEG deflection is not dependent on positive or negative ions alone, but can be inverted dependent on the location of the input and orientation of dendritic arbors. Additionally, the dipoles measured by EEG consist of both positive and negative sides, so a positive EEG deflection measured at a particular location will be balanced by a negative deflection elsewhere on the scalp. Thus, based only on the deflection of an EEG signal, an observer cannot infer that a generator involved excitatory or inhibitory current. Accordingly, several interpretations downstream of this inference are also inappropriate to draw from EEG data alone, such as inferring effort or efficiency from a positive or negative deflection.

This is not to say that direction of an EEG or ERP waveform cannot be used as evidence in support of some phenomenon, only that interpreting deflections of EEG data is most valid when it is used as one of multiple forms of converging evidence. For example, if a paradigm elicits certain changes in cerebral blood flow as measured by fMRI or NIRS, or changes in glucose metabolism as measured by positron emission tomography, an EEG deflection may support a conclusion of efficiency. Another approach might be to interpret the direction of a deflection relative to some other condition, taking care to design studies such that comparing a waveform in condition A to a waveform in condition B is as meaningful and useful as possible in addressing experimental hypotheses.

Concluding Remark

All told, it is beneficial to EEG researchers to be aware of the physical processes that underlie the EEG signal and the means by which that signal is measured. Understanding these processes enables greater awareness of the assumptions and the reasoning behind various aspects of EEG methodology, which in turn may improve experimental design and interpretation of EEG data.

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