

# 1 A Broad Overview of the Event-Related Potential Technique

## Overview, Goals, and Perspective of This Book

The event-related potential (ERP) technique provides a powerful method for exploring the human mind and brain, and the goal of this book is to describe practical methods and underlying concepts that will help you conduct great ERP research.

The first half of this book focuses on essential background information. This first chapter is an overview that is intended for people who are new to ERPs. The second chapter provides a closer look at ERPs, exploring issues that lurk below the surface of almost every ERP study. The third chapter is an overview of the most common and useful ERP components. The fourth chapter describes the design of ERP experiments; its goal is to help you design your own experiments and critically evaluate published research.

The second half of this book provides a detailed explanation of the main steps involved in actually conducting ERP experiments, including recording the electroencephalogram (EEG; chapter 5), rejecting and correcting artifacts (chapter 6), filtering the EEG and ERP waveforms (chapter 7), creating averaged ERPs and conducting time–frequency analyses (chapter 8), measuring amplitudes and latencies (chapter 9), and conducting statistical analyses (chapter 10). The goal is for you to understand how these steps really work so that you can make the best possible choices in how you conduct and analyze your own experiments.

To keep the length and price of this book reasonable, additional chapters and material are provided at a Web site (<http://mitpress.mit.edu/luck2e>), where they can be accessed by anyone at no cost. This Web site includes supplements to several of the chapters, which provide additional details or advanced materials. It also includes additional chapters on convolution (a simple mathematical procedure that is valuable in understanding ERPs); the relationship between the time and frequency domains; advanced statistical techniques; source localization; how to read, write, and review ERP papers; and how to set up and run an ERP lab.

You should feel free to skip around the book. If you are in the middle of running or analyzing your first ERP experiment, you may want to start with the chapters on recording data and performing basic data analysis steps. But be sure to come back to the first few chapters eventually, because they will help you avoid making common interpretive errors.

I have focused this book on mainstream techniques that are used in my own laboratory and in many other labs around the world. I learned many of these techniques as a graduate student in Steve Hillyard's laboratory at the University of California, San Diego (UCSD), and they reflect a long history of electrophysiological recordings dating back to Hallowell Davis's lab at Harvard in the 1930s. Davis was the mentor of Bob Galambos, who was in turn the mentor of Steve Hillyard. Galambos was actually a subject in the very first ERP experiment in the 1930s, and I got to spend quite a bit of time with him when I was in graduate school. Steve Hillyard inherited the Galambos lab when Bob retired, and he probably did more than any other early ERP researcher to show that ERPs could be used to answer important questions in cognitive neuroscience. Much of this book represents a distillation of 50-plus years' worth of ERP experience that was imparted to me in graduate school.

Although most of the basic ERP recording and analysis procedures described in this book are very conventional, some aspects of my approach to ERP research are different from those of other researchers, reflecting differences in general approaches to science. For example, I believe it is better to record very clean data from a relatively modest number of electrodes rather than to record noisier data from a large number of electrodes. Similarly, I believe that it is better to use a rigorous experimental design and relatively simple analyses rather than to rely on a long series of complex data processing procedures. As you will read in the following chapters, even the simplest processes (e.g., averaging, filtering, artifact rejection) can have unanticipated side effects. Consequently, the more processes that are applied to the data, the further you get from the signal that you actually recorded, and the more likely you are to have artificially induced an effect that does not accurately reflect real brain activity. Of course, some processing is necessary to separate the signal from the noise, but I believe the truth is usually clearest when the data speak for themselves and the experimenter has not tortured the data into confessing whatever he or she wants to hear (see box 1.1).

My views on dense-array recordings and sophisticated data processing techniques are heresy to some ERP researchers, but the vast majority of ERP studies that have had a significant impact on science (i.e., outside the fraternity of ERP researchers) have relied more on clever experimental design than on sophisticated data processing techniques. Even if your plans involve these techniques, this book will give you a very solid background for using them, and you will learn how to apply them wisely.

### Chapter Overview

This chapter provides a broad overview of the ERP technique. It is designed to give beginning ERP researchers the big picture of ERP research before we dive into the details. However, even advanced researchers are likely to find some useful information in this chapter.

The remainder of this chapter begins with a brief history of the ERP technique. Two examples of ERP research are then provided to make things more concrete. The next section briefly describes how ERPs are generated in the brain and propagated to the scalp. A more extended

**Box 1.1**

## Treatments and Side Effects

Data processing procedures that attempt to reveal a specific aspect of brain activity by suppressing “noise” in the data are analogous to treatments designed to suppress the symptoms of an underlying medical problem. As any physician can tell you, treatments always have side effects. For example, ibuprofen is a common and useful treatment for headaches and muscle soreness, but it can have negative side effects. According to *Wikipedia*, common adverse effects of ibuprofen include nausea, dyspepsia, gastrointestinal bleeding, raised liver enzymes, diarrhea, epistaxis, headache, dizziness, unexplained rash, salt and fluid retention, and hypertension. These are just the common side effects! Infrequent adverse effects of ibuprofen include esophageal ulceration, hyperkalemia, renal impairment, confusion, bronchospasm, and heart failure. Yes, heart failure!

ERP processing treatments such as filters can also have adverse side effects. According to *Luckipedia*, common adverse effects of filters include distortion of onset times, distortion of offset times, unexplained peaks, and slight dumbness of conclusions. Less frequent adverse effects of filters include artificial oscillations, wildly incorrect conclusions, public humiliation by reviewers, and grant failure.

This does not mean that you should completely avoid filters and other ERP processing procedures. Just as ibuprofen can be used effectively—in small doses—to treat headaches and muscle soreness, mild filtering can help you find real effects without producing major side effects. However, you need to know how to apply data processing techniques in a way that minimizes the side effects, and you need to know how to spot the side effects when they occur so that you do not experience public humiliation by reviewers and grant failure.

example of an ERP experiment is then provided to illustrate the basic steps in conducting and analyzing an ERP experiment. This example is followed by a discussion of two key concepts—oscillations and filtering—and then a more detailed description of the steps involved in collecting and processing ERP data. The final sections describe the advantages and disadvantages of the ERP technique and how it compares with other common techniques.

Note that some basic terminology is defined in the glossary. You should skim through it if you are not sure about the difference between an *evoked potential* and an *event-related potential*, if you don’t know how an *SOA* differs from an *ISI* or an *ITI*, or if you are not sure how a *local field potential* differs from a *single-unit recording*.

### A Bit of History

I think it’s a good idea to know a little bit about the history of a technique, so this section describes the discovery of ERPs in the 1930s and how the use of ERPs has progressed over the ensuing 80-plus years. However, you can skip this section if you don’t feel the need for a history lesson.

In 1929, Hans Berger reported a remarkable and controversial set of experiments in which he showed that the electrical activity of the human brain could be measured by placing an electrode

on the scalp, amplifying the signal, and plotting the changes in voltage over time (Berger, 1929). This electrical activity is called the electroencephalogram, or EEG. The neurophysiologists of the day were preoccupied with action potentials, and many of them initially believed that the relatively slow and rhythmic brain waves observed by Berger were some sort of artifact. For example, you can get similar-looking waveforms by putting electrodes in a pan of Jello and wiggling it. After a few years, however, human EEG activity was also observed by the respected physiologist Adrian (Adrian & Matthews, 1934), and the details of Berger's observations were confirmed by Jasper and Carmichael (1935) and Gibbs, Davis, and Lennox (1935). These findings led to the acceptance of the EEG as a real phenomenon.

Over the following decades, the EEG proved to be very useful in both scientific and clinical applications. However, the EEG is a very coarse measure of brain activity, and it cannot be used in its raw form to measure most of the highly specific neural processes that are the focus of cognitive neuroscience. This is partly because the EEG represents a mixed-up conglomeration of dozens of different neural sources of activity, making it difficult to isolate individual neurocognitive processes. Embedded within the EEG, however, are the neural responses associated with specific sensory, cognitive, and motor events, and it is possible to extract these responses from the overall EEG by means of a simple averaging technique (and more sophisticated techniques, such as time–frequency analyses). These specific responses are called *event-related potentials* to denote the fact that they are electrical *potentials* that are *related* to specific *events*.

As far as I can tell, the first unambiguous sensory ERP recordings from humans were performed in 1935–1936 by Pauline and Hallowell Davis and published a few years later (Davis, 1939; Davis, Davis, Loomis, Harvey, & Hobart, 1939). This was long before computers were available for recording the EEG, but the researchers were able to see clear ERPs on single trials during periods in which the EEG was quiescent (the first computer-averaged ERP waveforms were apparently published by Galambos & Sheatz, 1962). Not much ERP work was done in the 1940s due to World War II, but research picked up again in the 1950s. Most of this research focused on sensory issues, but some of it addressed the effects of top-down factors on sensory responses.

The modern era of ERP research began in 1964, when Grey Walter and his colleagues reported the first cognitive ERP component, which they called the *contingent negative variation*, or CNV (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). On each trial of this study, subjects were presented with a warning signal (e.g., a click) followed 500 or 1000 ms later by a target stimulus (e.g., a series of flashes). In the absence of a task, both the warning signal and the target elicited the sort of sensory ERP response that would be expected for these stimuli. However, if subjects were required to press a button upon detecting the target, a large negative voltage was observed at frontal electrode sites during the period that separated the warning signal and the target. This negative voltage—the CNV—was clearly not just a sensory response. Instead, it appeared to reflect the subject's preparation for the upcoming target. This exciting new finding led many researchers to begin exploring cognitive ERP components (for a review of more recent CNV research, see Brunia, van Boxtel, & Böcker, 2012).

The next major advance was the discovery of the P3 component by Sutton, Braren, Zubin, and John (1965). They created a situation in which the subject could not predict whether the next stimulus would be auditory or visual, and they found that the stimulus elicited a large positive component that peaked around 300 ms poststimulus. They called this the *P300* component (although it is now frequently called *P3*). This component was much smaller when the conditions were changed so that subjects could predict the modality of the stimulus. They described this difference in brain responses to unpredictable versus predictable stimuli in terms of information theory, which was then a very hot topic in cognitive psychology, and this paper generated a huge amount of interest. To get a sense of the impact of this study, I ran a quick Google Scholar search and found more than 27,000 articles that refer to “P3” or “P300” along with “event-related potential.” This is an impressive amount of P3-related research. In addition, the Sutton et al. (1965) paper has been cited more than 1150 times. There is no doubt that many millions of dollars have been spent on P3 studies (not to mention the many euros, pounds, yen, yuan, etc.).

During the 15 years after the publication of this paper, a great deal of research was conducted that focused on identifying various cognitive ERP components and developing methods for recording and analyzing ERPs in cognitive experiments. Because people were so excited about being able to record human brain activity related to cognition, ERP papers in this period were regularly published in *Science* and *Nature*. Most of this research was focused on discovering and understanding ERP components rather than using them to address questions of broad scientific interest. I like to call this sort of experimentation “ERPology” because it is simply the study of ERPs.

ERPology experiments do not directly tell us anything important about the mind or brain, but they can be very useful in providing important information that allows us to use ERPs to answer more broadly interesting questions. A great deal of ERPology continues today, resulting in a refinement of our understanding of the components discovered in previous decades and the discovery of new components. Emily Kappenman and I edited a book on ERP components a few years ago that summarizes all of this ERPology (Luck & Kappenman, 2012a).

However, so much of ERP research in the 1970s was focused on ERPology that the ERP technique began to have a bad reputation among many cognitive psychologists and neuroscientists in the late 1970s and early 1980s. As time progressed, however, an increasing proportion of ERP research was focused on answering questions of broad scientific interest, and the reputation of the ERP technique began to improve. ERP research started becoming even more popular in the mid 1980s, due in part to the introduction of inexpensive computers and in part to the general explosion of research in cognitive neuroscience. When positron emission tomography (PET) and then functional magnetic resonance imaging (fMRI) were developed, many ERP researchers thought that ERP research might die away, but exactly the opposite happened; most researchers understand that ERPs provide high-resolution temporal information about the mind and brain that cannot be obtained any other way, and ERP research has flourished rather than withered.

### Example 1: The Classic Oddball Paradigm

To introduce the ERP technique, I will begin by describing a simple experiment that was conducted in my laboratory several years ago using a version of the classic *oddball* paradigm (we never published this experiment, but it has been extremely useful over the years as an example). My goal here is to give you a general idea of how a simple ERP experiment works.

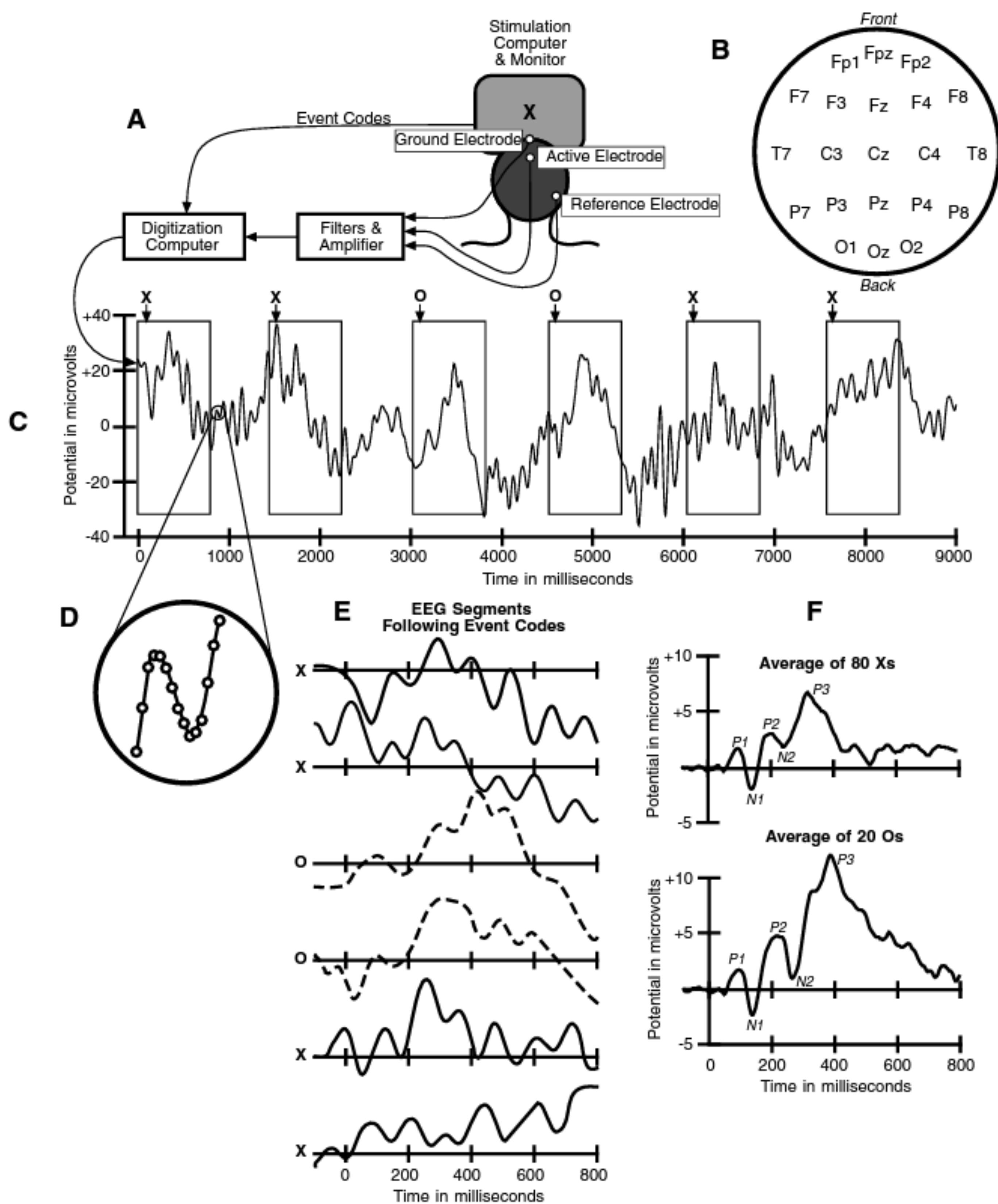
As illustrated in figure 1.1, subjects in this experiment viewed sequences consisting of 80% Xs and 20% Os, and they pressed one button for the Xs and another button for the Os. Each letter was presented on a computer monitor for 100 ms, followed by a 1400-ms blank interstimulus interval. While the subject performed this task, we recorded the EEG from several electrodes embedded in an electrode cap. As will be described in detail in chapter 5, EEG recordings typically require one or more *active* sites, along with a *ground* electrode and a *reference* electrode. The EEG from each site was amplified by a factor of 20,000 and then converted into digital form for storage on the *digitization computer*. Whenever a stimulus was presented, *event codes* (also known as *trigger codes*) were sent from the stimulation computer to the EEG digitization computer, where they were stored along with the EEG data (see figure 1.1A).

During each recording session, we viewed the EEG on the digitization computer, but the stimulus-elicited ERP responses were too small to discern within the much larger EEG. Figure 1.1C shows the EEG that was recorded at one electrode site from one of the subjects over a period of 9 s. The EEG waveform shown in the figure was recorded from the Pz electrode site (on the midline over the parietal lobes; see figure 1.1B), where the P3 wave is largest. If you look closely, you can see that there is some consistency in the EEG response to each stimulus, but it is difficult to see exactly what the responses look like. Figure 1.1D is a blowup of one small period of time, showing that the continuous voltage was converted into a discrete set of samples for storage on the computer.

The EEG was recorded concurrently from approximately 20 electrodes in this experiment, and the electrodes were placed according to the International 10/20 System (American Encephalographic Society, 1994a). As shown in figure 1.1B, this system names each electrode site using one or two letters to indicate the general brain region (e.g., Fp for frontal pole, F for frontal, C for central, P for parietal, O for occipital, T for temporal) and a number to indicate the

**Figure 1.1**

Example ERP experiment using the oddball paradigm. The subject viewed frequent Xs and infrequent Os presented on a computer monitor while the EEG was recorded from several active electrodes in conjunction with ground and reference electrodes (A). The electrodes were placed according to the International 10/20 System (B). Only a midline parietal electrode (Pz) is shown in panel A. The signals from the electrodes were filtered, amplified, and then sent to a digitization computer to be converted from a continuous analog signal into a discrete set of digital samples (D). Event codes were also sent from the stimulus presentation computer to the digitization computer, marking the onset time and identity of each stimulus and response. The raw EEG from the Pz electrode is shown over a period of 9 s (C). Each event code during this period is indicated by an arrow along with an X or an O, indicating the stimulus that was presented. Each rectangle shows a 900-ms epoch of EEG, beginning 100 ms prior to the onset of each stimulus. These epochs were extracted and then lined up with respect to stimulus onset (E), which is treated as 0 ms. Separate averages were then computed for the X and O epochs (F).



hemisphere (odd for left and even for right) and the distance from the midline (larger numbers mean larger distances). A lowercase *z* is used to represent the number zero, which indicates that the electrode is on the midline. Thus, F3 lies over frontal cortex to the left of the midline, Fz lies over frontal cortex on the midline, and F4 lies over frontal cortex to the right of the midline (for more details, see figure 5.4 in chapter 5).

At the end of each session, we performed a simple signal-averaging procedure to extract the ERP waveform elicited by the Xs and the ERP waveform elicited by the Os. The basic idea is that the recorded EEG contains the brain's response to the stimulus plus other activity that is unrelated to the stimulus, and we can extract this consistent response by averaging across many trials. To accomplish this, we extracted the segment of EEG surrounding each X and each O (indicated by the rectangles in figure 1.1C) and lined up these EEG segments with respect to the event codes that marked the onset of each stimulus (figure 1.1E). We then simply averaged together the single-trial EEG waveforms, creating one averaged ERP waveform for the Xs and another for the Os at each electrode site (figure 1.1F). For example, the voltage at 24 ms in the averaged X waveform was computed by taking the voltage that was measured 24 ms after each X stimulus and averaging all of these voltages together. Any brain activity that was consistently elicited by the stimulus at that time will remain in the average. However, any voltages that were unrelated to the stimulus will be negative on some trials and positive on other trials and will therefore cancel each other when averaged across many trials.

The resulting averaged ERP waveforms consist of a sequence of positive and negative voltage deflections, which are called *peaks*, *waves*, or *components*. In figure 1.1F, the peaks are labeled *P1*, *N1*, *P2*, *N2*, and *P3*. *P* and *N* are traditionally used to indicate positive-going and negative-going peaks, respectively, and the number indicates a peak's position within the waveform (e.g., P2 is the second major positive peak). Alternatively, the number may indicate the latency of the peak in milliseconds (e.g., N170 for a negative peak at 170 ms). If the number is greater than 5, you should assume it is referring to the peak's latency. Components may also be given paradigm- or function-based names, such as the *error-related negativity* (which is observed when the subject makes an error) or the *no-go N2* (which is observed on no-go trials in go/no-go experiments). The labeling conventions for ERP components can be frustrating to new researchers, but they become second nature over time, as discussed in box 1.2. Chapter 3 provides additional details about component naming conventions.

The sequence of ERP peaks reflects the flow of information through the brain, and the voltage at each time point in the ERP waveform reflects brain activity at that precise moment in time. Many of the highest impact ERP studies have made use of this fact to test hypotheses that could not be tested any other way (see chapter 4).

In the early days of ERP research, waveforms were plotted with negative upward and positive downward (largely due to historical accident; see box 1.3). The majority of cognitively oriented ERP researchers now use the traditional mathematical convention of plotting positive upward. However, many excellent researchers still plot negative upward, so it is important to check which

**Box 1.2**

## Component Naming Conventions

ERP component names can be very confusing, but so can words in natural languages (especially languages such as English that draw from many other languages). Just as the English word *head* can refer to a body part, a person who is the director of an organization, or a small room on a boat that has a toilet in it, the ERP term *N1* can refer to at least two different visual components and at least three different auditory components. And just as the English words *finger* and *digit* can refer to the same thing, the ERP terms *ERN* and *Ne* refer to the same ERP component. English words can often be confusing to people who are in the process of learning them, but fluent speakers can usually determine the meaning of a word from its context. Similarly, ERP component names can often be confusing to ERP novices, but expert ERPers can usually determine the meaning from its context.

One source of confusion is that the number following the P or N can either be the ordinal position of the peak in the waveform (e.g., N1 for the first negative peak) or the latency of the peak (e.g., N400 for a peak at 400 ms). I much prefer to use the ordinal position, because a component's latency may vary considerably across experiments, across conditions within an experiment, or even across electrode sites within a condition. This is particularly true of the P3 wave, which almost always peaks well after 300 ms (the P3 wave had a peak latency of around 300 ms in the very first P3 experiment, and the name *P300* has persisted despite the wide range of latencies). Moreover, in language experiments, the P3 wave generally follows the N400 wave, making the term *P300* especially problematic. Consequently, I prefer to use a component's ordinal position in the waveform rather than its latency when naming it. Fortunately, the latency in milliseconds is often approximately 100 times the ordinal position, so that P1 = P100, N2 = N200, and P3 = P300. The one obvious exception to this is the N400 component, which is often the second or third large negative component. For this reason, I can't seem to avoid using the time-based name *N400*.

convention is used in a given ERP waveform plot (and to include this information in your own plots). The waveforms in this book are all plotted with positive upward.

In the experiment shown in figure 1.1, the infrequent O stimuli elicited a much larger P3 wave than the frequent X stimuli. This is exactly what thousands of previous oddball experiments have found (see review by Polich, 2012). If you are just beginning to get involved in ERP research, I would recommend running an oddball experiment like this as your first experiment. It's simple to do, and you can compare your results with a huge number of published experiments.

The averaging process was conducted separately for each electrode site, yielding a separate average ERP waveform for each stimulus type at each electrode site. The P3 wave shown in figure 1.1F was largest at the Pz electrode but could be seen at all 20 electrodes. The P1 wave, in contrast, was largest at lateral occipital electrode sites and was absent at frontal sites. Each ERP component has a distinctive scalp distribution that reflects the location of the patch of cortex in which it was originally generated. As will be discussed in chapter 2 and the online chapter 14, however, it is difficult to determine the exact location of the neural generator source simply by examining the distribution of voltage over the scalp.

**Box 1.3**

## Which Way Is Up?

It is a common convention to plot ERP waveforms with negative voltages upward and positive voltages downward. I plotted negative upward in the first part of my career (including the first edition of this book) for the simple reason that this was how things were done when I joined Steve Hillyard's lab at UCSD. I once asked Steve Hillyard's mentor, Bob Galambos, how this convention came about. His answer was simply that this was how things were done when he joined Hal Davis's lab at Harvard in the 1930s (see, e.g., Davis, 1939; Davis et al., 1939). Apparently, this was a common convention among early physiologists. Manny Donchin told me that the early neurophysiologists plotted negative upward, possibly because this allows an action potential to be plotted as an upward-going spike, and this influenced manufacturers of early EEG equipment, such as Grass Instruments. Galambos also mentioned that an attempt was made in the early days of ERP research to get everyone to agree to a uniform positive-up convention, but the whole attempt failed (see Bach, 1998).

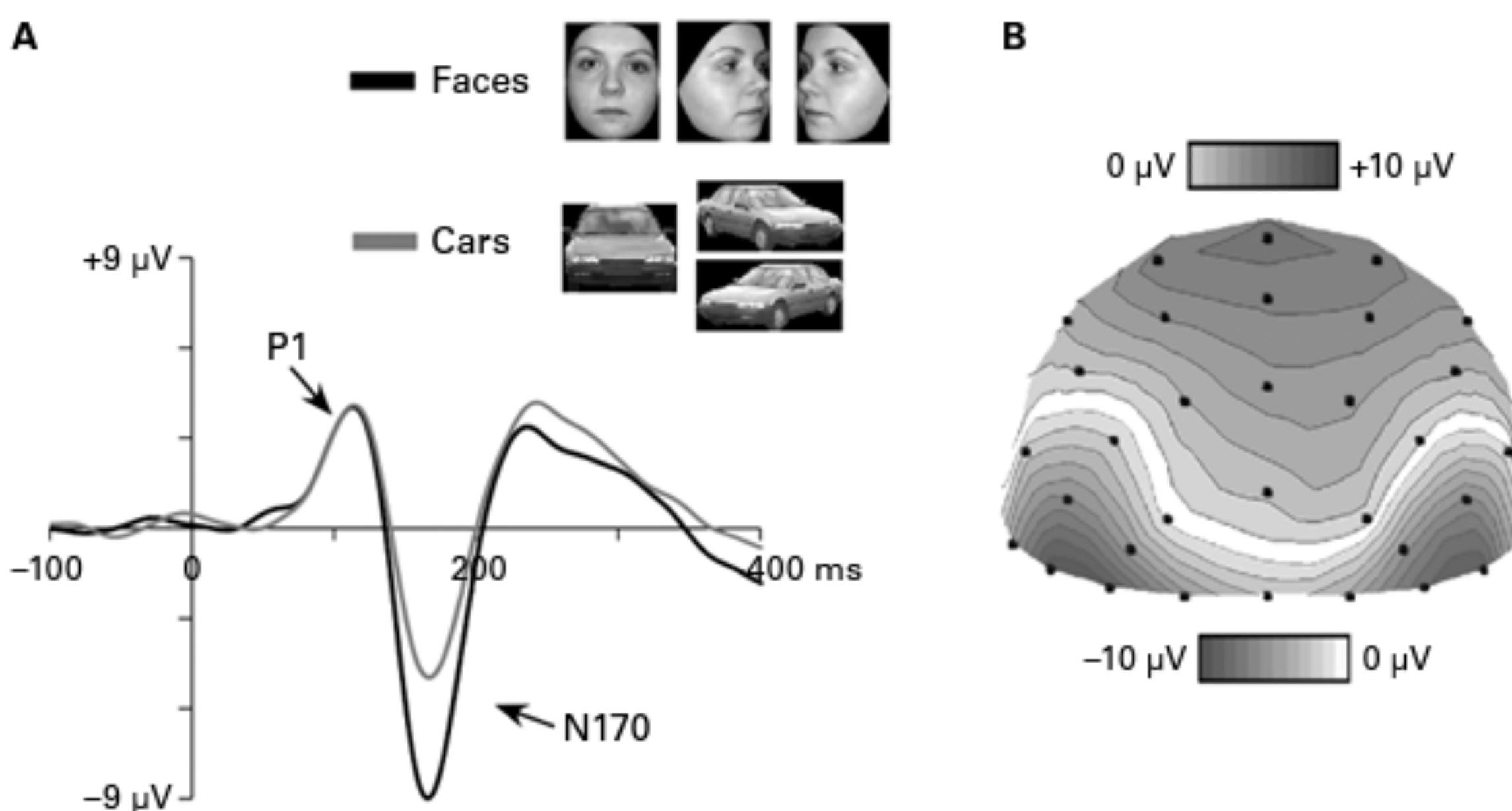
I eventually made the switch to positive-up because my primary goal in using ERPs is to make scientific contributions that influence a broad set of researchers (and because Emily Kappenman, then a graduate student, kept reminding me that it was the right thing to do). Almost all scientists outside the ERP world follow the centuries-old convention of the Cartesian coordinate system, in which positive is plotted upward. Plotting with negative upward makes ERP data less approachable for the broader scientific community, and there isn't a good scientific justification for it.

It was quite a bit of work for me to switch from negative-up to positive-up, because I had a huge library of figures and PowerPoint slides that had to be revised. Indeed, I ended up paying a talented undergraduate student, Candace Markley, to go through all my old files and switch the polarity. So I understand why many researchers are reluctant to switch. But it's worth the work in the long run, so I encourage everyone to plot with positive upward, just like the rest of the scientific world.

**Example 2: The N170 Component and Face Processing**

Now that I've explained a very simple ERP experiment, I'd like to describe a line of research that shows how ERPs can be applied to more interesting questions about the human mind. These experiments focused on the *N170* component, a face-related component that typically peaks around 170 ms after stimulus onset and is largest over ventral areas of visual cortex (figure 1.2). In a typical N170 paradigm, photographs of faces and various types of non-face objects are briefly flashed on a computer monitor, and subjects passively view the stimuli. In the ERP waveforms shown in figure 1.2A, the *X* axis represents time relative to stimulus onset (measured in milliseconds [ms]), and the *Y* axis represents the magnitude of the neural response (in microvolts [ $\mu$ V]). In the scalp map shown in figure 1.2B, the shading indicates the voltage measured at each electrode site during the time period of the N170 (with interpolated values between the individual electrode sites).

The N170 component is notable because it is larger when the eliciting stimulus is a face compared to when the stimulus is a non-face object, such as an automobile (see review by Rossion & Jacques, 2012). The difference between faces and non-face objects begins approxi-



**Figure 1.2**  
Example N170 experiment, including (A) ERP waveforms from an occipito-temporal electrode site (referenced to the average of all electrode sites) and (B) the scalp distribution of the voltage in the N170 latency range. Adapted with permission from Rossion and Jacques (2012). Copyright 2012 Oxford University Press.

mately 150 ms after the onset of the stimulus; this simple fact allows us to conclude that the human brain is able to distinguish between faces and other objects within 150 ms. The scalp distribution helps us to know that this is the same component that is observed in similar studies of the N170, and it suggests that the N170 generator lies in visual cortex (but note that conclusions about generators based on scalp distributions are not usually definitive).

Many researchers have used the N170 to address interesting questions about how faces are processed in the brain. For example, some studies have asked whether face processing is automatic by testing whether the face-elicited N170 is smaller when the faces are ignored. The results of these experiments indicate that face processing is at least partially automatic (Carmel & Bentin, 2002) but can be modulated by attention under some conditions (e.g., when the faces are somewhat difficult to perceive—Sreenivasan, Goldstein, Lustig, Rivas, & Jha, 2009). Other studies have used the N170 to ask whether faces are processed in a specialized face module or whether the same neural process is also used when people process other sorts of complex stimuli for which they have extensive expertise. Consistent with a key role for expertise, these studies have shown that bird experts exhibit an enhanced N170 in response to birds, dog experts exhibit an enhanced N170 in response to dogs, and fingerprint experts exhibit an enhanced N170 in response to fingerprints (Tanaka & Curran, 2001; Busey & Vanderkolk, 2005). Developmental studies have used the N170 to track the development of face processing, showing that face-specific processing is present early in infancy but becomes faster and more sophisticated over the course of development (Coch & Gullick, 2012). Studies of neurodevelopmental disorders

**Box 1.4**

## The Main Virtue of the ERP Technique

Virtually every textbook discussion of cognitive neuroscience techniques notes that the main advantage of the ERP technique is its high temporal resolution and the main disadvantage is its low spatial resolution. Given that this characterization of the ERP technique is so widely accepted, I am constantly amazed at how many studies try to use ERPs to answer questions that require high spatial resolution rather than high temporal resolution. I am also amazed at how many ERP studies use signal processing techniques (e.g., extreme filters) that reduce the temporal precision of the data. It should be obvious that ERPs are most appropriate for answering questions that require high temporal resolution, and I encourage you to think about using ERPs in this way. Some of the studies described in the online supplement to chapter 4 provide excellent examples of how to take advantage of this temporal resolution.

have shown that the N170 is abnormal in children with autism spectrum disorder (Dawson et al., 2002).

The N170 example illustrates the precise temporal resolution of the ERP technique, which is often touted as its main virtue (see box 1.4). ERPs reflect ongoing brain activity with no delay, and an ERP effect observed at 150 ms reflects neural processing that occurred at 150 ms. Consequently, ERPs are especially useful for answering questions about the timing of mental processes. Sometimes this timing information is used explicitly by asking whether two conditions or groups differ in the timing of a given neural response (just as one might ask whether reaction time differs across conditions or groups). In other cases, the timing information is used to determine whether a given experimental manipulation influences sensory activity that occurs shortly after stimulus onset or higher-level cognitive processes that occur hundreds of milliseconds later. For example, ERPs have been used to ask whether attentional manipulations influence early sensory processes or whether they instead influence postperceptual memory and decision processes (see, e.g., Luck & Hillyard, 2000).

**Brief Overview of the Neural Origins of ERPs**

In almost all cases, ERPs originate as postsynaptic potentials (PSPs), which occur when neurotransmitters bind to receptors, changing the flow of ions across the cell membrane (for more details, see chapter 2 and Buzsáki, Anastassiou, & Koch, 2012). Scalp ERPs are not typically produced by action potentials (except for auditory responses that occur within a few milliseconds of stimulus onset). When PSPs occur at the same time in large numbers of similarly oriented neurons, they summate and are conducted at nearly the speed of light through the brain, meninges, skull, and scalp. Thus, ERPs provide a direct, instantaneous, millisecond-resolution measure of neurotransmission-mediated neural activity. This contrasts with the blood oxygen level-dependent (BOLD) signal in fMRI, which reflects a delayed, secondary consequence of neural

activity. Moreover, the close link to neurotransmission makes ERPs potentially valuable as biomarkers in studies of pharmacological treatments.

When a PSP occurs within a single neuron, it creates a tiny electrical dipole (an oriented flow of current). Measurable ERPs can be recorded at the scalp only when the dipoles from many thousands of similarly oriented neurons sum together. If the orientations of the neurons in a given region are not similar to each other, the dipoles will cancel out and will be impossible to detect at a distant electrode. The main neurons that have this property are the pyramidal cells of the cerebral cortex (the primary input–output cells of the cortex). These cells are oriented perpendicular to the cortical surface, and their dipoles therefore add together rather than canceling out. Consequently, scalp-recorded ERPs almost always reflect neurotransmission that occurs in these cortical pyramidal cells. Nonlaminar structures such as the basal ganglia do not typically generate ERPs that can be recorded from the scalp, and interneurons within the cortex are thought to generate little or no scalp ERP activity. Thus, only a fraction of brain activity leads to detectable ERP activity on the scalp.

ERP components can be either positive or negative at a given electrode site. The polarity depends on a combination of several factors, and it is usually impossible to draw strong conclusions from the polarity of an ERP component (see box 2.1 in chapter 2).

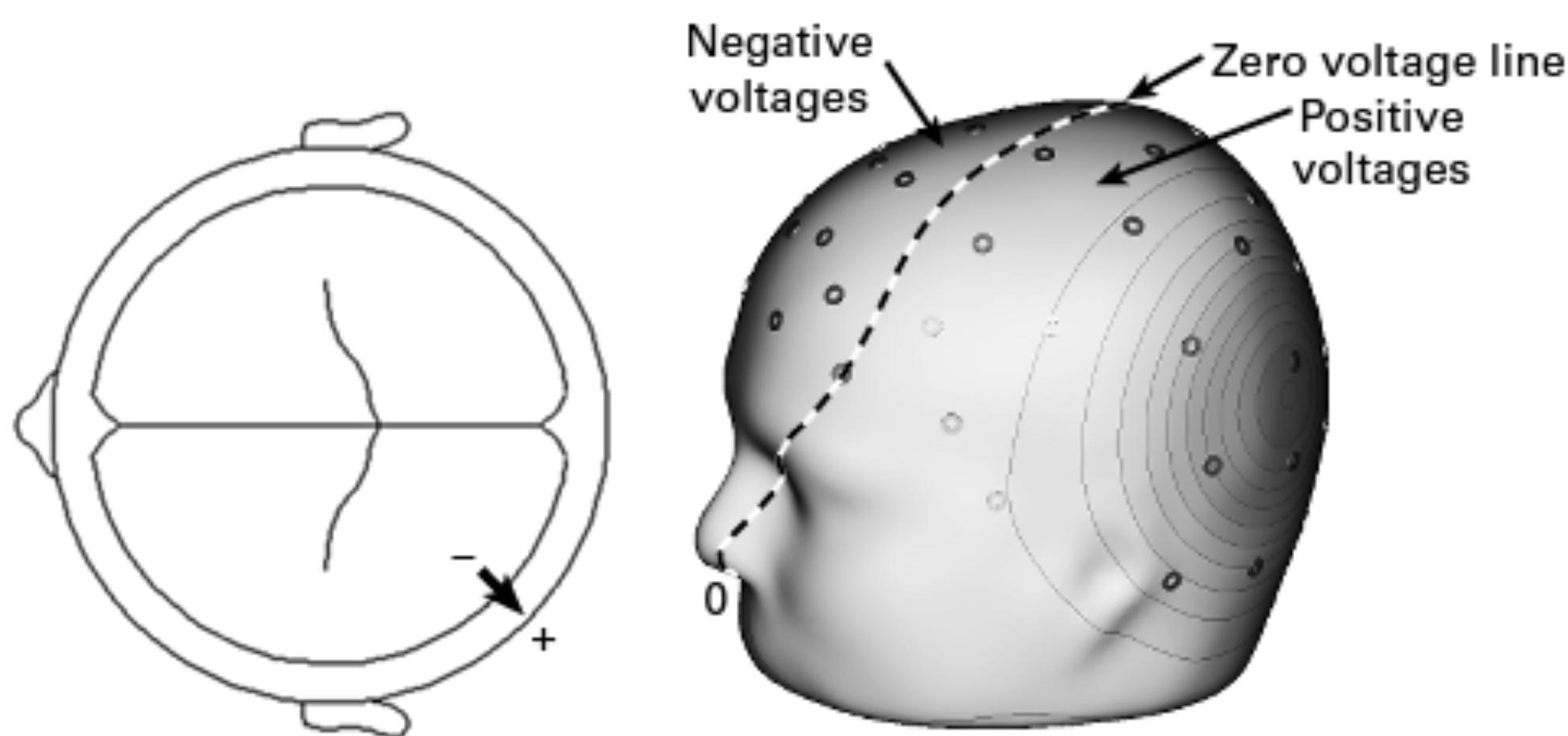
When the dipoles from many individual neurons sum together, they can be represented quite accurately with a single *equivalent current dipole* that is the vector sum of the individual dipoles. For the rest of this chapter, the term *dipole* will refer to these aggregates that represent the dipoles from many individual neurons.

The voltage recorded on the surface of the scalp will be positive on one side of the dipole and negative on the other, with a single line of zero voltage separating the positive and negative sides (figure 1.3). The voltage field spreads out through the conductive medium of the brain, and the high resistance of the skull and the low resistance of the overlying scalp lead to further spatial blurring. Thus, the voltage for a single dipole will be fairly broadly distributed over the surface of the scalp, especially for ERPs that are generated in relatively deep cortical structures.

Electrical dipoles are always accompanied by magnetic fields, but the skull is transparent to magnetism, leading to less blurring of the magnetic fields. Consequently, it is sometimes advantageous to record the magnetic signal (the magnetoencephalogram, or MEG) rather than—or in addition to—the electrical signal (the EEG). However, MEG recordings require very expensive equipment and are much less common than EEG recordings.

### Example 3: Impaired Cognition in Schizophrenia

This section will provide a more detailed discussion of a specific experiment, in which ERPs were used to study impaired cognition in schizophrenia (Luck et al., 2009). This will serve both to show how ERPs can be used to isolate specific cognitive processes and to provide a concrete example of the steps involved in conducting an ERP experiment.



**Figure 1.3**

Distribution of voltage over the scalp (right) resulting from a single dipole in the brain (left). The dipole is shown in an axial section through a schematic brain, and the positive and negative ends of the dipole are indicated by plus (+) and minus (-) signs, respectively. The scalp distribution shows a strong area of positive voltage right over the positive end of the dipole. This positive voltage gradually declines until it reaches a line of zero voltage, and then weak negative voltages are present on the other side of the head. Images courtesy of J. Bengson.

The goal of this experiment was to ask why behavioral reaction times (RTs) are typically slowed in schizophrenia patients when they perform simple sensorimotor tasks. That is, are RTs slowed in patients because of an impairment in perceptual processes, an impairment in decision processes, or an impairment in response processes? ERPs are ideally suited for answering this question because they provide a direct means of measuring the timing of the processes that occur between a stimulus and a response. On the basis of prior research, we hypothesized that the slowing of RTs in schizophrenia in simple tasks does not result from slowed perception or decision, but instead results from an impairment in the process of determining which response is appropriate once the stimulus has been perceived and categorized (which is called the *response selection* process).

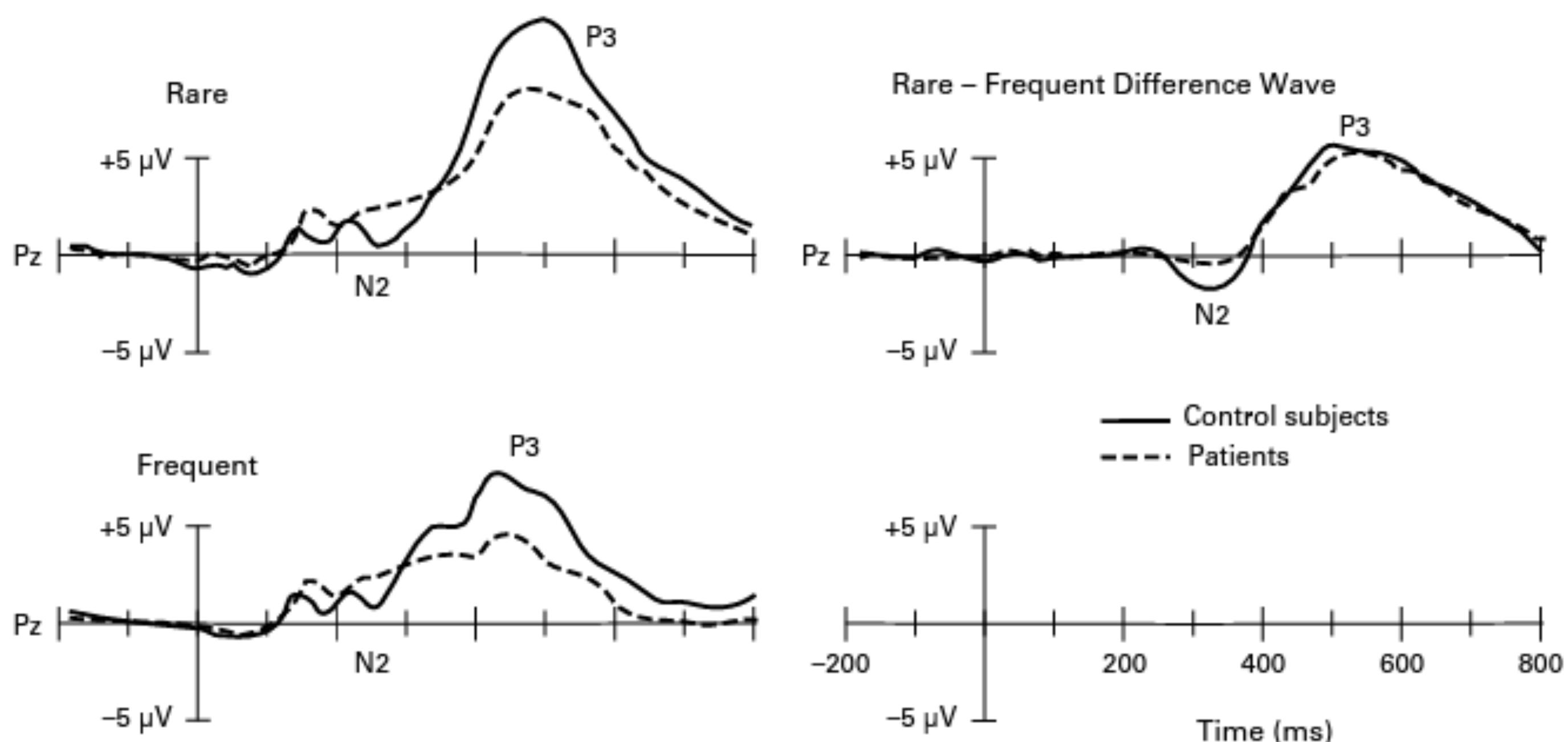
To test this hypothesis, we recorded ERPs from 20 individuals with schizophrenia and 20 healthy control subjects in a modified oddball task. In each 5-min block of trials, we presented a sequence of letters and digits at fixation. Each stimulus was presented for a duration of 200 ms, with a stimulus appearing every 1300–1500 ms (the reason for this particular timing is described near the end of chapter 4). Subjects made a button-press response for each stimulus, pressing with one hand for letters and with the other hand for digits. One of these two categories was rare (20%) and the other was frequent (80%) in any given trial block. Both the category probabilities and the assignment of hands to categories were counterbalanced across trial blocks.

This design allowed us to isolate specific ERP components by means of *difference waves*, in which the ERP waveform elicited by one trial type was subtracted from the ERP waveform elicited by another trial type (much like difference images in fMRI studies). Difference waves are extremely useful in ERP research because they isolate neural processes that are differentially active for two trial types, eliminating the many concurrently active brain processes that do not

differ between these trial types. This is important because the different ERP components are ordinarily mixed together, making it difficult to determine exactly which component—and which psychological or neural process—differs across conditions or groups. Difference waves can pull out a subset of the components, making it possible to draw more specific conclusions.

In the current study, rare-minus-frequent difference waves were constructed to isolate the P3 wave, which tells us about the time course of stimulus categorization (i.e., the process of determining whether the stimulus falls into the rare or frequent category). A separate set of difference waves was constructed to isolate the *lateralized readiness potential* (LRP), which reflects the time course of response selection after stimulus categorization (e.g., determining whether the left button or right button is the appropriate response for the current stimulus). The LRP is isolated by subtracting the voltages over the ipsilateral hemisphere (relative to the responding hand) from the voltages over the contralateral hemisphere. We found that RTs were slowed by approximately 60 ms in patients compared to control subjects, and the question was whether this reflected a slowing of perception and categorization (which would produce a delay in the P3 difference wave) or whether it reflected a slowing of postcategorization response selection processes (which would produce a delay in the LRP difference wave). Chapter 3 provides extended discussions of these components and how they can be used to isolate these different processes.

Figure 1.4 shows the ERPs elicited by the rare category, the ERPs elicited by the frequent category, and the rare-minus-frequent difference waves. These are *grand average* waveforms,



**Figure 1.4**

Grand average ERP waveforms recorded from schizophrenia patients and healthy control subjects at the Pz electrode site (Luck et al., 2009). ERPs are shown for the rare stimulus category, for the frequent stimulus category, and for the difference between the rare and frequent stimuli.

meaning that average waveforms were first computed across trials for each subject at each electrode site, and then the waveforms at each electrode were averaged across subjects. These grand averages simply make it easier to look at the data (just like graphs of the mean RT across subjects in behavioral experiments).

As in many previous studies, the voltage during the period of the P3 wave (approximately 300–800 ms) was reduced in the schizophrenia group relative to the control group. However, the voltage during this period is the sum of many different components, not just the P3 wave. The rare-minus-frequent difference wave allows us to better isolate the P3 wave and to focus on brain activity that reflects the classification of the stimulus as belonging to the rare or frequent category. Notably, patients exhibited no reduction in the amplitude of the P3 wave in the difference waves (although the preceding N2 was diminished—for similar results, see Potts, O'Donnell, Hirayasu, & McCarley, 2002). The most important finding was that the timing of the P3 was virtually identical in patients and controls, which indicates that patients were able to perceive and categorize these simple stimuli just as fast as controls, even though patient RTs were delayed by 60 ms.

This implies that the slowing of RT reflects an impairment in processes that follow stimulus categorization. Indeed, the LRP—an index of response preparation—was delayed by 75 ms in onset time and diminished by 50% in amplitude for patients compared to controls. Moreover, the degree of amplitude reduction across patients was significantly correlated with the degree of RT slowing. Thus, for a relatively simple perceptual task, the slowed RTs exhibited by the schizophrenia patients appear to result primarily from a slowing of response selection (as evidenced by the later and smaller LRP) rather than a slowing of perception or categorization (as evidenced by no slowing or reduction of the P3).

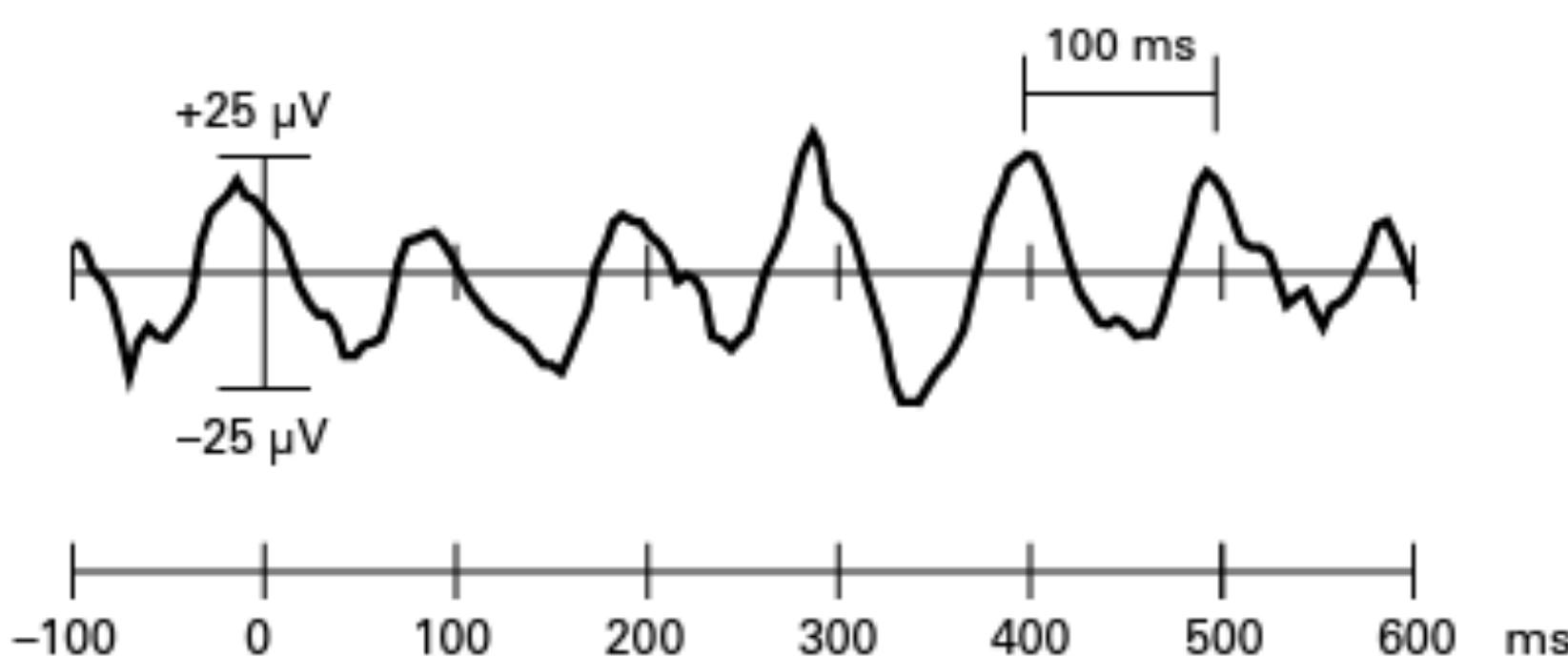
This example makes two key points. First, it shows how difference waves can be used to isolate specific ERP components that reflect specific processes. Second, it shows how ERPs can be used to precisely assess the timing of specific processes that occur between a stimulus and a response.

## Oscillations and Filtering

### EEG Oscillations

The brain is constantly active, whether you are awake or asleep and whether or not any distinct stimuli are present. All of this brain activity leads to constant variations in the pattern of PSPs across the billions of neurons in your brain, and this leads to a constantly varying EEG on the scalp. These many different types of brain activity get combined together at the individual scalp electrodes, creating a complicated mixture. One portion of this mixture consists of brief, transient brain responses to internal and external events (i.e., ERPs). Another portion consists of ongoing activity that is not driven by discrete events. Much of this non-event-driven activity is oscillatory in nature, reflecting feedback loops in the brain.

The most prominent such oscillation is the alpha wave, a voltage that goes up and down approximately 10 times per second. This is illustrated in figure 1.5, which shows a 700-ms

**Figure 1.5**

Single-trial EEG from an occipital electrode site with large alpha activity. Note that each peak of the alpha oscillation is separated by approximately 100 ms, which tells you that it is occurring at 10 Hz and is therefore an alpha oscillation.

segment of EEG recorded at an occipital scalp site (from 100 ms prior to a stimulus until 600 ms after the stimulus). You can see that the EEG is going up and down repetitively, and you can figure out that the frequency is approximately 10 cycles per second by noting that each cycle lasts approximately 100 ms. Alpha oscillations are usually most prominent over the back of the head and tend to be large when the subject is drowsy or when the subject's eyes are closed. These alpha waves can be either a large signal or a large source of noise, depending on whether you are interested in the processes reflected by the alpha or in some small, transient, stimulus-elicited ERP component that is present at the same scalp sites and is obscured by the alpha waves (see the glossary if you are not sure what I mean by *noise* here).

If you present stimuli at irregular intervals (e.g., every 900–1100 ms), the stimulus will occur at a different point in the alpha cycle (a different *phase*) on each trial, and the alpha oscillations will ordinarily average to nearly zero if you average together a large number of trials (because the voltage at a given poststimulus time point will be positive on some trials and negative on others). However, a stimulus may reset the alpha phase so that the phase after stimulus onset is similar across trials. In this case, considerable alpha may remain in the poststimulus alpha. Some researchers have proposed that ERP components mainly consist of this kind of *phase resetting* of ongoing EEG oscillations (e.g., Makeig et al., 2002). It turns out to be quite difficult to rigorously test this possibility (see review by Bastiaansen, Mazaheri, & Jensen, 2012), but my guess is that only a small proportion of stimulus-locked ERP activity consists of these kinds of oscillations.

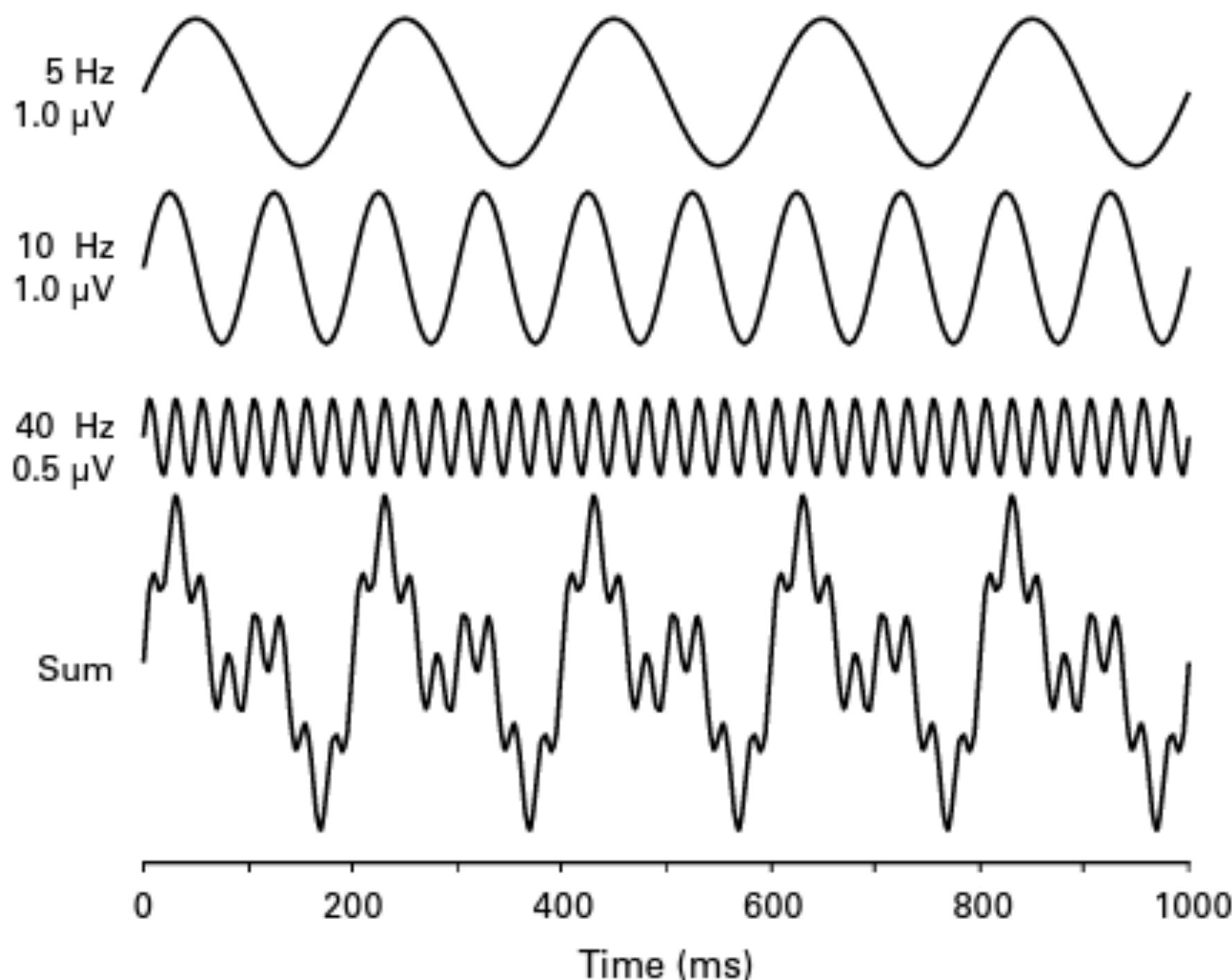
A stimulus may also lead to the initiation of a new oscillation, but with a phase that varies from trial to trial. These oscillations will ordinarily cancel out when you create an averaged ERP waveform (because the voltage at a given poststimulus time point will be positive on some trials and negative on others). However, it is possible to perform a *time-frequency* analysis, which extracts the amplitude at a given frequency independent of its phase prior to averaging. This makes it possible to see the time course of stimulus-elicited oscillations (see chapter 8 and the online chapter 12 for details).

EEG oscillations are mainly classified according to frequency bands. In addition to the alpha band (8–13 Hz), there are also delta (<4 Hz), theta (4–8 Hz), beta (13–30 Hz), and gamma (>30 Hz) bands. It is tempting to think that a given frequency band reflects a specific process, but that is not generally true. For example, 8- to 13-Hz oscillations over motor cortex (often called *mu* oscillations) are clearly different from the 8- to 13-Hz alpha oscillations observed over visual cortex.

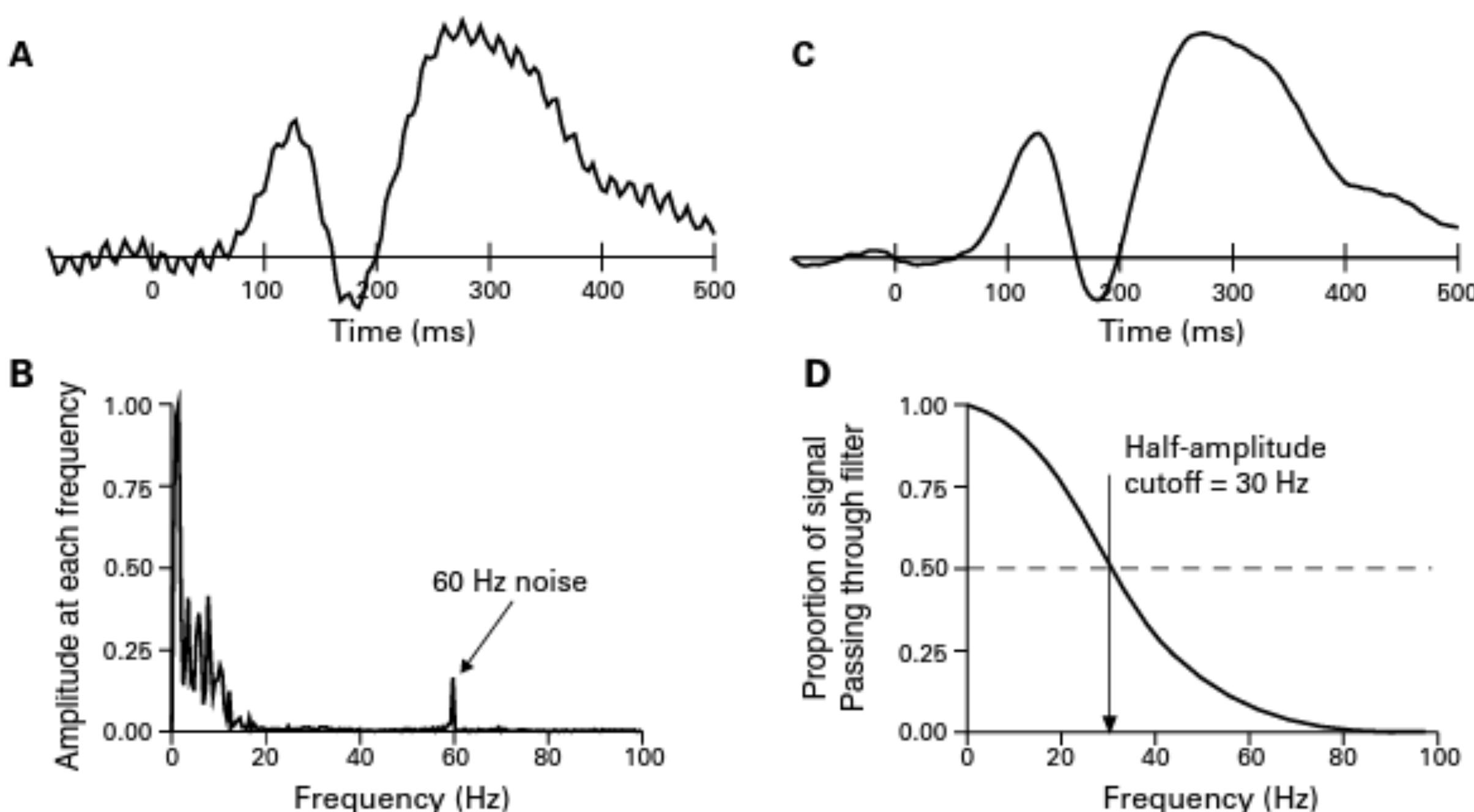
### Fourier Analysis

The EEG typically contains a mixture of multiple simultaneous oscillations at different frequencies. To show you what this mixture looks like in a very simple situation, figure 1.6 shows three individual sine waves and their sum. Although these sine waves are mixed together in the recording, it is possible to determine the amplitudes and frequencies of the individual sine waves. This is achieved by means of *Fourier analysis*, a mathematical process that can compute the amplitudes, frequencies, and phases of the sine waves that sum together to equal the observed waveform (if you need a reminder about what these terms mean, see the *sine wave* entry in the glossary).

The amazing thing about Fourier analysis is that any waveform, no matter how complex, can be reconstructed by summing together a set of sine waves. For example, figure 1.7 shows how



**Figure 1.6**  
Example of the summation of oscillations at different frequencies. Three different sine waves are shown here, along with their sum. The EEG often looks like the sum of several sine waves. The goal of the Fourier transform is to determine the amplitudes, phases, and frequencies of the sine waves that sum together to form a complex waveform.

**Figure 1.7**

(A) ERP waveform containing substantial noise at 60 Hz (which you can determine by counting six peaks in every 100-ms period). (B) Fourier transform of the waveform in panel A, showing the amplitude at each frequency (note that the phase of each frequency is not shown here). (C) Filtered version of the waveform in panel A. (D) Frequency response function of the filter that was used to create the waveform in panel C from the waveform in panel A.

Fourier analysis can be applied to an averaged ERP waveform. Figure 1.7A shows an ERP waveform that contains a lot of “noise” at 60 Hz (artifactual electrical activity picked up from the recording environment that looks like a ripple superimposed on the ERP waveform). Figure 1.7B shows the Fourier transform of this waveform. The *X* axis of the transformed data is frequency instead of time, and the graph indicates the amplitude at each frequency. Note that most of the amplitude is at frequencies of less than 20 Hz, but there is a fairly substantial amplitude at 60 Hz; this represents the 60-Hz noise oscillation that you can see in the ERP waveform. We could reconstruct the original ERP waveform by taking a sine wave of each frequency and each amplitude shown in figure 1.7B and summing them together (we would also need to know the phase of each frequency, which is not shown here).

Fourier analysis has a fundamental limitation that is not always realized by people who use it: The presence of an amplitude at a given frequency in a Fourier transform does not mean that the original waveform actually *contained* an oscillation at that frequency. It just means that if we wanted to re-create the original waveform by summing together a set of sine waves, we would need to include an oscillating sine wave at that frequency. In some cases, the original waveform really does contain sine waves, such as the 60-Hz noise oscillation shown in the ERP waveform in figure 1.7A. However, the Fourier transform shown in figure 1.7B also shows a lot of activity at 13 Hz, and there is no reason to believe that the brain was actually oscillating at

13 Hz when it generated the ERP waveform shown in figure 1.7A. The activity at 13 Hz in figure 1.7B just means that we would need to use a 13-Hz sine wave of a particular amplitude if we wanted to reconstruct the ERP waveform by adding sine waves together. Chapter 7 will discuss this issue in much greater detail.

### Filtering

Filtering is an essential concept in ERP research, and it will arise again and again in the upcoming chapters. Chapter 7 describes filters in detail, but I want to make sure you understand the basics now so that you can understand everything in chapters 2–6. Fortunately, now that you know the basics of the Fourier transform, it's easy for me to explain filtering.

In EEG and ERP research, filters are used to suppress noise that contaminates the data, making it difficult to see the signal of interest. For example, the 60-Hz noise in figure 1.7A would hamper our ability to accurately measure the amplitude and latency of the different components in the waveform. Figure 1.7C shows what the waveform looks like after the high frequencies have been filtered out. The filtered version looks much nicer, doesn't it?

The term *filter* has a general meaning outside of signal processing (e.g., you can have a coffee filter, an air filter, an oil filter, etc.). Filters can be described in terms of what they block and what they do not block. An air filter, for example, may trap particles that are larger than 0.01 mm and allow air and smaller particles to pass through. The filters that are typically applied to EEG and ERP data are usually described in terms of the frequencies that pass through the filter (i.e., the frequencies that are not blocked by the filter and therefore appear in the filter's output). The filter used in figure 1.7 is a *low-pass* filter, which means that it passes low frequencies and attenuates (blocks) high frequencies. It is also possible to use a *high-pass* filter, which attenuates low frequencies and lets higher frequencies pass through. If you apply both a low-pass filter and a high-pass filter at the same time, you will have a *band-pass* filter (i.e., a filter that blocks low and high frequencies, allowing the intermediate frequencies to pass). It's also possible to have a *notch* filter, which filters out one narrow frequency band and passes everything else.

Personally, I find it confusing to describe filters in terms of the frequencies that they pass rather than the frequencies that they block. For example, it's confusing to use the term *low pass* for a filter that blocks high frequencies. However, that's the standard terminology, and we're stuck with it.

For most filters, there is a range of frequencies that "passes through" the filter almost completely (and is therefore present in the filter's output), a range of frequencies that is attenuated almost completely, and a range of frequencies in the middle that is partially attenuated. This is quantified by a filter's *frequency response function*. Figure 1.7D shows the frequency response function for the filter that was used to create the waveform in figure 1.7C. At each frequency, this function tells you the proportion of the signal that will pass through the filter (which is the complement of the proportion that is attenuated by the filter). For example, the frequency response function shown in figure 1.7C has a value of 0.80 at 20 Hz, which means that 80% of the 20-Hz activity will pass through the filter and the remaining 20% will be blocked by the

filter. A filter's frequency response function is often summarized by a single number called the *cutoff frequency*. This number typically represents the frequency at which 50% of the signal passes through the filter and 50% is suppressed, and it is therefore called the *half-amplitude cutoff* (see chapter 7 for some important details about cutoff frequencies). The filter shown here has a half-amplitude cutoff at 30 Hz, and it passes less than 10% of the signal at 60 Hz (which is why the 60-Hz noise has been almost completely removed in the filtered waveform). You might find it strange that there is a broad range of frequencies that are partially passed and partially blocked by this filter; the reasons for this will be discussed in chapter 7.

### Overview of Basic Steps in an ERP Experiment

This section will provide an overview of the basic steps involved in conducting an ERP experiment, beginning with recording the EEG and finishing with statistical analyses. Each of these topics is covered in more detail in the subsequent chapters, and the goal of this section is to provide a big-picture overview.

#### Recording the Electroencephalogram (Chapter 5)

Figure 1.1A shows the basic setup of an ERP experiment. The EEG is recorded from electrodes on the scalp, with a conductive gel or liquid between each electrode and the skin to make a stable electrical connection. The electrical potential (voltage) can then be recorded from each electrode, resulting in a separate waveform for each electrode site. This waveform will be a mixture of actual brain activity, biological electrical potentials produced outside of the brain (by the skin, the eyes, the muscles, etc.), and induced electrical activity from external electrical devices that is picked up by the head, the electrodes, or the electrode wires. If precautions are taken to minimize the non-neural potentials, the voltages produced by the brain (the EEG) will be relatively large compared to the non-neural voltages.

The EEG is quite small (usually under 100 microvolts,  $\mu\text{V}$ ), so the signal from each electrode is usually amplified by a factor of 1,000–100,000. This amplification factor is called the *gain* of the amplifier. A gain of 20,000 was used in the experiment shown in figure 1.1, and a gain of 5000 was used in the experiment shown in figure 1.4. The continuous voltage signal is then turned into a series of discrete digital values for storage on a computer. In most experiments, the voltage is sampled from each channel at a rate of between 200 and 1000 evenly spaced samples per second (i.e., 200–1000 Hz). In the experiment shown in figure 1.1, the EEG was sampled at 250 Hz (one sample every 4 ms).

The EEG is typically recorded from multiple electrodes distributed across the scalp. Different studies use very different numbers of electrodes. For some studies, all of the relevant information can be obtained from five to six electrodes; for others, as many as 256 electrodes are needed. You might think that it's best to record from as many channels as possible, but it becomes more difficult to ensure the quality of the data when you record from a lot of channels (see the online supplement to chapter 5).

### Artifact Rejection and Correction (Chapter 6)

There are several common artifacts that are picked up by EEG recordings and require special treatment. The most common of these arise from the eyes. When the eyes blink, a large voltage deflection is observed over much of the head, and this artifact is usually much larger than the ERP signals. Moreover, eyeblinks are sometimes systematically triggered by tasks and may vary across groups or conditions, yielding a systematic distortion of the data. Large potentials are also produced by eye movements, and these potentials can confound experiments that use lateralized stimuli or focus on lateralized ERP responses. Thus, trials containing blinks, eye movements, or other artifacts are typically excluded from the averaged ERP waveforms. In the study shown in figure 1.4, for example, three patients and two controls were excluded from the final analysis because more than 50% of trials were rejected (mainly due to blinks). In the remaining subjects, 23% of trials were rejected on average.

This approach has two shortcomings. First, a fairly large number of trials may need to be rejected, thus reducing the number of trials contributing to the average ERP waveforms. Second, the mental effort involved in suppressing eyeblinks may impair task performance (Ochoa & Polich, 2000). These problems are especially acute in individuals with neurological or psychiatric disorders, who may blink on almost every trial or may perform the task poorly because of the effort devoted to blink suppression. Fortunately, methods have been developed to estimate the artifactual activity and subtract it out, leaving artifact-free EEG data that can be included in the averaged ERP waveforms. Some of these artifact correction techniques are known to make systematic errors in estimating and removing the artifactual activity, but many of these techniques work quite well for blinks and certain other artifacts.

### Filtering (Chapter 7)

Filters are usually used to remove very slow voltage changes (<0.01–0.1 Hz) and very fast voltage changes (>15–100 Hz) because scalp-recorded voltages in these frequency ranges are likely to be noise from non-neural sources. Frequencies below 0.1 Hz and above 18.5 Hz were filtered from the waveforms shown in figure 1.4. Filters can dramatically distort the time course of an ERP waveform and can induce artifactual oscillations when the low cutoff is greater than approximately 0.5 Hz or when the high cutoff is less than approximately 10 Hz, so caution is necessary when extreme filters are used. Filters can be applied to the EEG, to the averaged ERPs, or both. The appendix of this book describes the effects of changing the order in which operations such as filtering and averaging are applied to the data.

### Computing Average ERP Waveforms (Chapter 8)

ERPs are typically small in comparison with the rest of the EEG activity, and ERPs are usually isolated from the ongoing EEG by a simple averaging procedure. To make this possible, it is necessary to include *event codes* in the EEG recordings that mark the events that happened at specific times, such as the onset of each stimulus (figure 1.1A). These event codes are then used as a time-locking point to extract segments of the EEG surrounding each event (figure 1.1E).

Recall that figure 1.1 shows the EEG recorded over a 9-s period in an oddball task with frequent X stimuli (80%) and infrequent O stimuli (20%). Each rectangle highlights a 900-ms segment of EEG that begins 100 ms before an event code and extends until 800 ms after the event code. The 100-ms period before the event code is used to provide a prestimulus baseline period.

Figure 1.1E shows these same segments of EEG, lined up in time. Stimulus onset is time zero. There is quite a bit of variability in the EEG waveforms from trial to trial, and this variability largely reflects the fact that the EEG is the sum of many different sources of electrical activity in the brain, many of which are not involved in processing the stimulus. To extract the activity that is related to stimulus processing from the unrelated EEG, the EEG segments following each X are averaged together into one waveform, and the EEG segments following each O are averaged together into a different waveform (figure 1.1F). Any brain activity that is not time-locked to the stimulus will be positive at a given latency on some trials and negative at that latency on other trials, and if many trials are averaged together, these voltages will cancel each other out and approach zero. However, any brain activity that is consistently elicited by the stimulus—with approximately the same voltage at a given latency from trial to trial—will remain in the average. Thus, by averaging together many trials of the same type, the brain activity that is consistently time-locked to the stimulus across trials can be extracted from other sources of voltage (including EEG activity that is unrelated to the stimulus and non-neural sources of electrical noise). Other types of events can be used as the time-locking point in the averaging process (e.g., button-press responses, vocalizations, saccadic eye movements, electromyographic activity).

You are probably wondering how many trials must be averaged together for each averaged ERP waveform. This depends on several factors, including the size of the ERP effect being examined, the amplitude of the unrelated EEG activity, and the amplitude of non-neural activity. For large components, such as the P3 wave, very clear results can usually be obtained by averaging together 10–50 trials. For smaller components, such as the P1 wave, it is usually necessary to average together 100–500 trials for each trial type to see reliable differences between groups or conditions. Of course, the number of trials that is required to observe a significant difference will also depend on the number of subjects, the variance across subjects, and the size of the effect. In the experiment shown in figure 1.4, each subject received 256 oddball stimuli and 1024 standard stimuli. This is more trials than would be typical for a P3 study, but it was appropriate given that we were also looking at the much smaller LRP and that we anticipated rejecting a large percentage of trials due to eyeblinks.

### Quantification of Amplitudes and Latencies (Chapter 9)

The most common way to quantify the magnitude and timing of a given ERP component is to measure the amplitude and latency of the peak voltage within some time window. For example, to measure the peak of the P3 wave in the data shown in figure 1.4, you might define a measurement window (e.g., 400–700 ms) and find the most positive point in that window. Peak

amplitude would be defined as the voltage at this point, and peak latency would be defined as the time of this point. Of course, it is also possible to search for negative peaks, such as the N1 wave.

Finding peaks was the simplest approach to measuring ERPs prior to the advent of inexpensive computers, when a ruler was the only available means of quantifying the waveform (Donchin & Heffley, 1978). This approach is still widely used, but it has several drawbacks, and better methods for quantifying ERP amplitudes and latencies have been developed. For example, the magnitude of a component can be quantified by measuring the mean voltage over a given time window. As discussed in chapter 9, mean amplitude is usually superior to peak amplitude as a measure of a component's magnitude.

A related measure can be used to quantify component latency. Specifically, it is possible to define the midpoint of a component as the point that divides the region under the waveform into two equal-area subregions. This is called the 50% area latency measure, and it was used to quantify the timing of the P3 wave in the data shown in figure 1.4.

### Statistical Analysis (Chapter 10)

In most ERP experiments, an averaged ERP waveform is constructed at each electrode site for each subject in each condition. The amplitude or latency of a component of interest is then measured in each one of these waveforms, and these measured values are then entered into a statistical analysis just like any other variable. Thus, the statistical analysis of ERP data is often quite similar to the analysis of traditional behavioral measures.

However, ERP experiments provide extremely rich data sets, usually consisting of several gigabytes of data. This can lead to both the implicit and explicit use of many statistical comparisons in a single study, which can dramatically increase the probability of a Type I error (i.e., concluding that a difference is real when it was actually a result of random variation). The explicit use of multiple comparisons arises when, for example, separate statistical analyses are conducted for each of several different components. The implicit use of multiple comparisons occurs when researchers first look at the waveforms and then decide on the time windows and electrode sites to be used for quantifying component amplitudes and latencies. If a time window is chosen because the difference between conditions is greatest in that time window, then this biases the results in favor of statistical significance, even if the difference was caused by noise. A similar problem arises if the researcher finds the electrode sites with the largest differences between conditions and then uses only those sites for the statistical analyses. With enough electrode sites, it is almost always possible to find a statistically significant difference between two groups or two conditions at a few electrode sites due simply to random noise. When reading papers that describe ERP studies, you should be suspicious if unusual, idiosyncratic, and unjustified electrode sites or measurement windows are selected for the statistical analyses. Fortunately, new statistical methods have been developed that can minimize or eliminate this problem (see online chapter 13).

### What Are ERPs Good For?

The ERP technique is the best available technique for answering many important scientific questions, but it is a terrible technique for answering others. To do high-impact ERP research, you need to understand the kinds of questions that ERPs can readily answer. The following paragraphs describe several ways in which ERPs have been successfully used in prior research (for a more extensive discussion, see Kappenman & Luck, 2012). There are certainly other useful ways to apply the ERP technique, but these will provide a good starting point.

#### Assessing the Time Course of Processing

The most commonly cited virtue of the ERP technique is its temporal resolution (see box 1.4). But this is not merely a matter of being able to reliably measure values of 358 ms versus 359 ms, which can easily be accomplished with reaction time measures, eye tracking measures, cardiac measures, and so forth. The key is that ERPs provide a *continuous* measure of processing, beginning prior to the stimulus and extending past the response. In a behavioral experiment, we get no data during the period between the stimulus and the response, but this is the period when most of the “action” is happening. ERPs give us a measure of the moment-by-moment activity during this period. That is, ERPs show us the “action.” ERPs (and other EEG signals) also give us information about the state of the brain prior to the onset of the stimulus, which has an enormous impact on the way that the stimulus is processed (Worden, Foxe, Wang, & Simpson, 2000; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Vanrullen, Busch, Drewes, & Dubois, 2011). ERPs also provide information about brain activity that occurs after a response has occurred or after a feedback stimulus has been presented, reflecting executive processes that determine how the brain will operate on subsequent trials (Holroyd & Coles, 2002; Gehring, Liu, Orr, & Carp, 2012).

#### Determining Which Process Is Influenced by an Experimental Manipulation

What can we do with this wonderful continuous temporal information? A common use is to determine which processes are influenced by a given experimental manipulation. As an example, consider the Stroop paradigm, where subjects must name the color of the ink in which a word is drawn. Subjects are slower when the word is incompatible with the ink color than when the ink color and word are the same (e.g., subjects are slower to say “green” when presented with the word “red” drawn in green ink than when presented with the word “green” drawn in green ink). Do these slowed responses reflect a slowing of perceptual processes or a slowing of response processes? It is difficult to answer this question simply by looking at the behavioral responses, but studies of the P3 wave have been very useful in addressing this issue. Specifically, it has been well documented that the latency of the P3 wave becomes longer when perceptual processes are delayed, but several studies have shown that P3 latency is not delayed on incompatible trials in the Stroop paradigm, indicating that the delays in RT reflect delays in some

**Box 1.5**

## A Neuroimaging Technique?

Many people include ERPs in the category of neuroimaging techniques, but this doesn't seem right to me. Unambiguous neuroimaging techniques such as fMRI provide an image of the brain, but ERPs do not directly give us an image of the brain. As discussed in online chapter 14, ERPs can be used to create *models* of the distribution of activity over the cortical surface, but the actual image of the brain typically comes from MRI data. It is, of course, possible to plot the distribution of voltage over the scalp, but this makes ERPs a *scalpoimaging* technique rather than a *neuroimaging* technique. ERP waveforms are also images, but they are not neuroimages in any particularly meaningful sense. To avoid overpromising and underdelivering, I prefer to leave the term *neuroimaging* to research that more directly provides an image of the brain.

postperceptual stage (see, e.g., Duncan-Johnson & Kopell, 1981). Thus, ERPs are very useful for determining which stage or stages of processing are influenced (or not influenced) by a given experimental manipulation. Several specific examples are described in the online supplement to chapter 4. I have used ERPs for this purpose in many of my own studies (see especially Vogel, Luck, & Shapiro, 1998).

I would like to stress that the information provided by ERPs is different from, and complementary to, the information provided by neuroimaging techniques (see box 1.5 for a discussion of whether ERPs are a neuroimaging technique). Neuroimaging techniques can isolate different processes to the extent that the different processes are anatomically distinct. It has become very clear, however, that each area of cortex is involved in a great many processes. Thus, finding an effect of an experimental manipulation in primary visual cortex does not guarantee that this effect reflects a modulation of sensory processing; it could instead reflect a working memory representation that was generated 200 ms after stimulus onset and stored in primary visual cortex (Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009). In this situation, the timing of the effect could tell us whether the effect happened during the initial sensory processing period or at a later point in time.

**Identifying Multiple Neurocognitive Processes**

In behavioral experiments, it is often parsimonious to invoke a single underlying process to explain changes in behavior that are produced by many different manipulations. However, ERP recordings provide a much richer data set, often making it clear that a given experimental manipulation actually influences several different processes (i.e., several different ERP components) and that a given pattern of behavior might be caused by different mechanisms in different experiments. For example, behavioral studies often treat selective attention as a single mechanism, but different manipulations of attention influence different ERP components (Luck & Hillyard, 2000; Luck & Vecera, 2002). Similarly, different ERP components appear to reflect different mechanisms of memory retrieval (Wilding & Ranganath, 2012).

### Covert Measurement of Processing

An important advantage of ERPs over behavioral measures is that ERPs can be used to provide an online measure of processing when a behavioral response is impossible or problematic. This is called the *covert measurement of processing*. In some cases, covert measurement is necessary because the subject is incapable of making a response. For example, ERPs can be recorded from infants who are too young to be instructed to make a response (see review by Coch & Gullick, 2012). ERPs are also used for covert monitoring in people with neurological disorders who are unable to make behavioral responses (Fischer, Luaute, Adeleine, & Morlet, 2004).

Covert monitoring is also useful when normal processing would be distorted by using a task that requires a behavioral response. In attention research, for example, it can be difficult to design a task in which behavioral responses can be obtained for both attended and unattended stimuli—a stimulus isn't really “unattended” if the subject is instructed to respond to it. In contrast, ERPs can easily be used to compare the processing of attended and unattended stimuli without requiring a response to the unattended stimuli. Consequently, ERPs have been used extensively in attention research (see review by Luck & Kappenman, 2012b). In studies of language comprehension, ERPs can be used to assess the processing of a word embedded in the middle of a sentence—at the time the word is presented—rather than relying on a response made at the end of the sentence (see review by Swaab, Ledoux, Camblin, & Boudewyn, 2012).

The ability to measure processing covertly and continuously over the entire course of a task with millisecond-level temporal resolution makes the ERP technique the best available technique for answering many important questions about the human mind. Much of perception, cognition, and emotion unfolds on a timescale of tens or hundreds of milliseconds, and ERPs are particularly valuable for tracking such rapid sequences of mental operations.

### A Link to the Brain?

In most cases, ERPs are more valuable for answering questions about the mind than for answering questions about the brain (to the extent that these can really be dissociated). That is, although ERPs are a measure of brain activity, they are usually too coarse to permit specific and definitive conclusions to be drawn about brain circuitry. As an analogy, imagine that you were trying to understand how your computer works by measuring the temperature from sensors placed at a variety of locations on the computer’s case. You could learn quite a bit about the general principles by which the computer operated, and you would be able to draw conclusions about some of the major components of the computer’s hardware (e.g., the power supply and the hard drive). However, you would never unravel the circuitry of the computer’s central processing unit, and you would never decode the computer’s program. Similarly, ERPs can occasionally be used to draw strong conclusions about some coarsely defined components of the brain, and they can be used to draw weak conclusions about others. But as discussed in the previous paragraphs, the main advantage of the ERP component is its ability to track the time course of processing, not to measure the operation of specific neural systems.

**Box 1.6**

## ERPs, Desperation, and the Blues

Over the years, I have encountered many cases of people who have tried to use ERPs to answer questions that just can't be answered with this technique. These people desperately want ERPs to be able to answer questions that are better answered with fMRI or single-unit recordings, and this desperation leads them to cast aside their usual critical abilities.

As an analogy, consider this story about the American blues musician Sonny Boy Williamson. In the early 1960s, many young musicians in England were fascinated with American blues music, and they desperately wanted to be able to play it. Sonny Boy Williamson went on a tour of England during this time, and he spent some time jamming with these English musicians, but he was not impressed. According to legend, when he returned to the United States he remarked, "Those English boys want to play the blues so bad—and they DO play it so bad." Whenever I see ERP researchers who try to answer questions about the brain that go beyond the limits of the technique, I always think, "Those ERPers want to study the brain so bad—and they DO study it so bad."

It should be noted that many of these English musicians who played the blues "so bad" became famous rock musicians (e.g., Eric Clapton, Jimmy Page, Jeff Beck). That is, they turned their weakness into a strength by playing a related but distinctly different style of music. By analogy, ERPers should stop trying to be neuroimaging researchers and do their own style of science.

This does not mean that ERPs can never be used to answer questions about the brain. In some cases, the temporal information provided by ERPs can provide at least a coarse answer to such questions. In other cases, we have multiple converging sources of evidence about the neural generator of a given ERP component and can therefore use this component to assess activity in a specific region of cortex (see, e.g., the discussion of the C1 component in chapter 3). Answering questions about the brain with ERPs is therefore possible, but it takes a lot of hard work, cleverness, and careful thought (see box 1.6 for a lighthearted analogy).

People often think it should be possible to combine ERPs with fMRI and thereby obtain both high temporal and high spatial resolution. Although this has sometimes been done, it is much more difficult than most people imagine. The fundamental difficulty is that ERPs and the BOLD signal reflect different aspects of brain activity, and it is quite likely that an experimental manipulation would impact one of these measures without impacting the other. It is even possible to imagine scenarios in which the ERP and fMRI effects would go in opposite directions (Luck, 1999). Consequently, although it may someday be possible, it is not currently possible to directly combine ERP and fMRI data without unjustifiable assumptions.

**Biomarkers**

ERPs have the potential to be used as biomarkers in medical applications. That is, ERPs can be used to measure aspects of brain function that are impaired in neurological and psychiatric diseases, providing more specific information about an individual patient's brain function than could be obtained from traditional clinical measures (for a detailed discussion, see Luck et al.,

2011). This information could be used to determine whether a new treatment has an impact on the specific brain system that is being targeted. This information could also be used in the clinic to determine which medications are most likely to be effective for a given individual. For example, there is some evidence that the mismatch negativity (MMN) component is a relatively specific measure of PSPs produced by the binding of glutamate to *N*-methyl-D-aspartate (NMDA) receptors (Javitt, Steinschneider, Schroeder, & Arezzo, 1996; Kreitschmann-Andermahr et al., 2001; Ehrlichman, Maxwell, Majumdar, & Siegel, 2008; Heekeren et al., 2008). The MMN could therefore be used as a biomarker to test whether a new treatment influences NMDA responsiveness or whether a particular patient would benefit from such a treatment.

ERPs have several desirable properties for use as biomarkers: (a) they are directly related to neurotransmission; (b) they are relatively inexpensive and can be recorded relatively easily in clinical settings; (c) they can easily be recorded in animal models (Woodman, 2012); (d) in some cases, they have been shown to be reliable and sensitive measures of individual differences (Mathalon, Ford, & Pfefferbaum, 2000); and (e) they are practical for large ( $N > 500$ ) multisite studies (Hesselbrock, Begleiter, Porjesz, O'Connor, & Bauer, 2001). However, there are also several hurdles that must be overcome for ERPs to be widely used as biomarkers. For example, it is not trivial to develop experimental paradigms that isolate a specific ERP component while also having good measurement reliability. In addition, differences between individuals can reflect “nuisance factors” such as differences in skull thickness and cortical folding patterns, which may make it difficult to use ERPs in clinical settings. Moreover, we do not yet have widely accepted quality assurance metrics that make it possible to demonstrate that valid, low-noise data have been obtained for a given individual. However, these problems are presumably solvable, so ERPs have considerable promise for use as biomarkers in the near future.

### What Are ERPs Bad For?

In addition to understanding situations in which ERPs are particularly useful, it is worth considering the shortcomings of the ERP technique and the kinds of questions that cannot be easily answered with ERPs. I have tried to make the limitations as well as the strengths of the ERP technique clear throughout this book, because you need to know the limitations in order to do top-quality research (box 1.7).

The most challenging aspect of ERP research is that the waveforms recorded on the scalp represent the sum of many underlying components, and it is difficult to decompose this mixture into the individual underlying components. This is called the *superposition problem*, because multiple components are superimposed onto the same waveform (see chapter 2 for details). Similarly, it is difficult to determine the neural generator locations of the underlying components. These two problems are the most common impediments to the successful application of the ERP technique. There are many solutions to these two problems, but different solutions are needed in different types of experiments, so it is difficult to provide a simple one-sentence description of when these problems will arise and when they will be solvable. Chapters 2 and 4 and online

**Box 1.7**

## Ugly Little Secrets

I teach two to four ERP Boot Camps each year, including a 10-day boot camp at the University of California, Davis, each summer and a few mini boot camps at universities, industry sites, and conferences. I like to tell boot camp participants that I am going to tell them all of the ugly little secrets involved in ERP research, because they need to know the plain truth if they are going to do ERP research themselves. I say this in a conspiratorial voice, suggesting that they should keep the ugly little secrets to themselves. We don't want fMRI researchers to know our secrets! But we should speak the truth freely among ourselves, so this book presents an unvarnished view of ERPs.

I also tell ERP Boot Camp participants that they will sometimes get depressed when they hear about the limitations of the ERP technique and the problems with some of the analytical approaches that they'd like to use. But there are many strategies that can be used to overcome or sidestep almost every limitation. The key is to fully understand the underlying nature of ERPs and the analytical techniques that are used in ERP research, such as filtering, source localization, and time–frequency analysis. So, if you find yourself getting a little depressed, just keep reading and you will eventually learn how to avoid the limitations of ERPs and run amazing experiments that will bring you fame and fortune.

chapter 14 will describe these problems and the various solutions in more detail. The best solution is often to figure out a clever experimental design in which isolating and localizing a given ERP component is not necessary to distinguish between competing hypotheses (see the discussion of *component-independent experimental designs* in chapter 4).

Another key limitation of the ERP technique is that a given mental or neural process may have no ERP *signature* (i.e., no clear contribution to the scalp-recorded voltage). As will be discussed in chapter 2, scalp ERPs are recordable only when a particular set of biophysical conditions are met, and only a fraction of brain activity meets these conditions. Although there are dozens of distinct ERP components, there are surely hundreds or thousands of distinct brain processes that have no distinct ERP component.

Another limitation arises from the fact that ERPs are small relative to the noise level, and many trials are usually required to accurately measure a given ERP effect. Although some components are large enough to be reliably measured on single trials (mainly the P3 component), it is usually necessary to average between 10 and 500 trials per condition in each subject to achieve sufficient statistical power. This makes it difficult to conduct experiments with very long intervals between stimuli and experiments that require surprising the subjects. In principle, one could increase the number of subjects to make up for a small number of trials per subject, but the time required to prepare the subject usually makes it unrealistic to test more than 50 subjects in a given experiment (and sample sizes of 10–20 are typical). I have frequently started designing an ERP experiment and then given up when I realized that the experiment would require either 10 hours of data collection per subject or 300 subjects.

To use the ERP technique, it is also necessary to have measurable events that can be used as time-locking points. Some imprecision in the timing of the events can be tolerated in many cases (perhaps  $\pm 10$  ms in a typical cognitive or affective experiment), but ERPs cannot usually be used if the presence or timing of the events is difficult to determine (e.g., when the onset of a stimulus is very gradual).

ERPs are also difficult to use for measuring brain activity that extends beyond a few seconds (e.g., long-term memory consolidation). The main reason for this is that large, slow voltage drifts are present on the scalp due to non-neural factors (e.g., skin potentials), and these drifts add more and more variance to the waveform as time passes after the time-locking point (see figure 8.2D in chapter 8). These slow drifts are ordinarily removed with filters, but this would also remove slow neural effects.

Clean ERPs are difficult to record when subjects make frequent head, mouth, or eye movements. Head movements often cause slight shifts in electrode position, which in turn create large voltage artifacts. Consequently, subjects remain seated in a chair in almost all ERP studies. Mouth movements also create artifacts, especially when the tongue (which contains a powerful dipole) makes contact with the top portion of the mouth. Studies involving speech typically examine the ERPs leading up to the onset of speech, excluding the time period in which the subjects are actually speaking. Like the mouth, the eyes contain a strong dipole, and eye movements lead to large voltage changes on the scalp. Almost all ERP studies therefore require subjects to maintain constant fixation.

The preceding paragraphs describe several of the most common conditions in which ERPs are problematic. This does not mean that ERPs can never be used in these situations; it just means that the challenges will be significant. If you are new to the ERP technique, it is better to avoid these situations. Once you have some experience, you may develop clever ways around these problems, leading to important new discoveries.

### Comparison with Other Physiological Measures

Table 1.1 compares the ERP technique with several other physiological recording techniques along four major dimensions: invasiveness, spatial resolution, temporal resolution, and cost. The other classes of techniques that are considered are microelectrode measures (single-unit, multi-unit, and local field potential recordings) and hemodynamic measures (PET and fMRI). ERPs are grouped with event-related magnetic fields (ERMFs), which are the magnetic counterpart of ERPs and are extracted from the MEG (see chapter 2).

#### Invasiveness

Microelectrode measures (single-unit recordings, multi-unit recordings, and local field potentials) require insertion of an electrode into the brain and are therefore limited to non-human species or human neurosurgery patients. The obvious disadvantage of primate recordings is that

**Table 1.1**

Comparison of invasiveness, spatial resolution, temporal resolution, and cost for microelectrode measures (single-unit and local field potential recordings), hemodynamic measures (PET and fMRI), and electromagnetic measures (ERPs and ERMFs)

Parameter	Microelectrode Measures	Hemodynamic Measures	Electromagnetic Measures
Invasiveness	Poor	Good (PET) Excellent (fMRI)	Excellent
Spatial resolution	Excellent	Good	Undefined/poor (ERPs) Undefined/better (ERMFs)
Temporal resolution	Excellent	Poor	Excellent
Cost	Fairly expensive	Expensive (PET) Expensive (fMRI)	Inexpensive (ERPs) Expensive (ERMFs)

human brains are different from primate brains. The less obvious disadvantage is that a monkey typically requires months of training to be able to perform a task that a human can learn in 5 min, and once a monkey is trained, it usually spends months performing the tasks while recordings are made. Thus, monkeys are often highly overtrained and probably perform tasks in a manner different than that of an experimentally naïve human subject. This can make it difficult to relate monkey results to the large corpus of human cognitive experiments. Intracranial recordings from human subjects are becoming increasingly valuable, but they are of course limited to a relatively small number of subjects who are having electrodes implanted for medical reasons. PET experiments are also somewhat problematic in terms of invasiveness: to avoid exposing subjects to excessive levels of radiation, a small number of conditions can be tested for each subject. In contrast, there is no significant safety-related restriction on the amount of ERP or fMRI data that can be collected from a single subject.

### Spatial and Temporal Resolution

Electromagnetic measures and hemodynamic measures have complementary patterns of spatial and temporal resolution, with high temporal resolution and poor spatial resolution for electromagnetic measures and poor temporal resolution and high spatial resolution for hemodynamic measures. ERPs have a temporal resolution of 1 ms or better under optimal conditions, whereas hemodynamic measures are limited to a resolution of (at best) several hundred milliseconds by the sluggish nature of the hemodynamic response. This is a huge difference, and it means that ERPs can easily address some questions that PET and fMRI cannot hope to address. However, hemodynamic measures have a spatial resolution in the millimeter range, and this cannot be matched by scalp electrical recordings (except under certain unusual conditions). In fact, as will be discussed in greater detail later in chapter 2 and online chapter 14, the spatial resolution of the ERP technique is fundamentally undefined because there are infinitely many internal ERP generator configurations that can explain a given pattern of ERP data. Unlike PET and fMRI, it is not typically possible to specify a principled margin of error for an ERP localization claim (especially when multiple sources are simultaneously active). That is, with

current techniques, it is impossible to know whether a given localization estimate is within some specific number of millimeters from the actual generator source. It may someday be possible to localize ERPs definitively, but at present the spatial resolution of the ERP technique is simply undefined.

### Cost

The ERP technique is much less expensive than the other techniques listed in table 1.1. It is possible to equip a good ERP lab for less than \$50,000, and the disposable supplies required to test a single subject are very inexpensive (\$1–3). The actual recordings can easily be carried out by a graduate student or an advanced undergraduate, and the costs related to storing and analyzing the data are minimal. These costs have dropped a great deal over the past 20 years, largely due to the decreased cost of computing equipment. fMRI is fairly expensive (typically \$500/hour), and PET is exorbitantly expensive, primarily due to the need for radioactive isotopes with short half-lives and medical personnel. Microelectrode recordings in non-human primates are also fairly expensive due to the per diem costs of maintaining the monkeys, the cost of the surgical and animal care facilities, and the high level of expertise required to record electrophysiological data from awake, behaving monkeys. Intracranial recordings in humans are not extraordinarily expensive, given that they are “piggybacked” onto clinical procedures, but it is very difficult to get access to the patients.

### Suggestions for Further Reading

#### Top Ten Papers Every New ERP Researcher Should Read

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### Broad Reviews of the ERP Technique

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### Books on ERPs and Related Topics

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