12

Event-Related Potentials

An event-related potential (ERP) is a change in an EEG recording from the scalp that is related to the occurrence of an external or internal stimulus. The ERP is an "answer" from the brain that is "time-locked" to the stimulus or event—that is, the potential either coincides with or follows the stimulus after a brief delay. ERPs used to be called *evoked potentials*, but since they occur as a consequence of an event it is better to refer to them as "event-related." Furthermore, ERPs may occur in the absence of a stimulus, as when an expected event is omitted in a train of stimuli, or they may precede voluntary motor responses, and in these cases the potentials are not "evoked" by stimuli. ERPs are generated by the brain through extracellular potentials associated with the activity of groups of neurons firing in synchrony.

Psychophysiological research on ERPs is the fastest growing subfield of psychophysiology. Many different components of the ERP signal, and possible meanings of these components, have been identified over the last thirty years. ERPs are used not only in basic research on brain functions and cognitive processes, but also in clinical practice to identify disorders of cognitive and affective functioning. Some of the components of ERP recordings will be described in more detail below. Excellent reviews of the components and their psychological meanings are Näätänen (1992), Squires and Ollo (1986), Hillyard and Hansen (1986), and Donchin, Karis, Bashore, et al. (1986).

The ERP Signal

ERPs were first reported by Davis in 1939, who found that there was a relatively large negative response in the EEG about 100–200 msec after each presentation of an auditory stimulus. Although Davis could see the response by visual inspection, most ERPs are too small to be observed after a single-trial, although there are exceptions to this rule. For most recordings, the ERP signal must be averaged. The principle of *signal averaging* is illustrated in Figure 12.1.

When two sinusoidal signals that are completely out of phase with each other are added together, the result is a "zero signal," or a straight line. The summed average of sinusoidal signals that occur randomly with regard to each other tends to be just such a straight line. Signals that have an invariant time relationship to a repeated stimulus, however, tend to "sum," or build up, over time. In the case of ERPs, the time-invariant relationship of the response to the stimulus makes it possible to extract the response from the EEG background through signal averaging.

Signal averaging was pioneered by Dawson (1954), who superimposed EEG traces succeeding each stimulus presentation for a short period of time. Since the EEG amplitudes occur randomly in the traces, with signals out of phase with each other, and since the ERP is time-locked to the stimulus, only after averaging will the ERPs "stick out" from the background EEG, if enough trials are used. Signal averaging, in effect, is the enhancement of a portion of the EEG after each stimulus is presented. An example of signal averaging with sixteen stimulus presentations is shown in Figure 12.2. Although signal averaging is the rule in almost all ERP research, some components of the ERP complex are so large that they *can* be observed on a single trial. The first presentation of a completely unexpected auditory stimulus may produce quite large ERPs that can be identified by visual inspection.

Artifacts

Although signal averaging is rather straightforward, ERPs are subject to a range of artifacts that may confound or obscure the recordings. There are many sources of ERP artifacts, including the ECG, muscle tension, electrode sources, eye movements, and blinks probably pre-
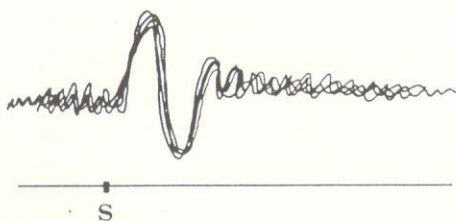
1)
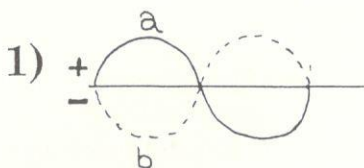
2) EEG
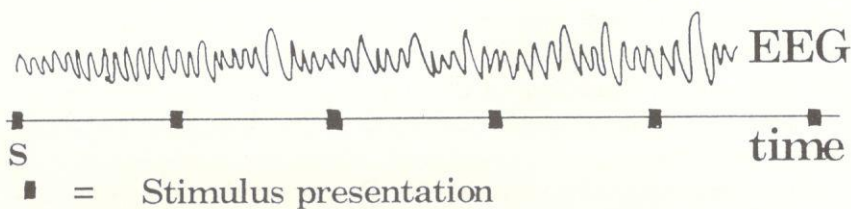
3) ERP   averaging

Figure 12.1. The principle of ERP averaging. If two sinusoidal waves (like EEG waves) that are out of phase with respect to their positive and negative amplitudes are superimposed *(1)* and the two signals (*a* and *b*) are summed, the result is a "zero-amplitude" signal. If an EEG signal is recorded after repeated stimulus presentations *(2)*, the EEG waves will be randomly out of phase with respect to each other and thus sum toward "zero" (as shown in *3*). The ERP will be nonrandom with respect to each stimulus presentation, however, and thus sum to a positive and negative deflection when the repeated EEG samples to the stimulus are "added" (averaged) on top of each other (also shown in *3*).
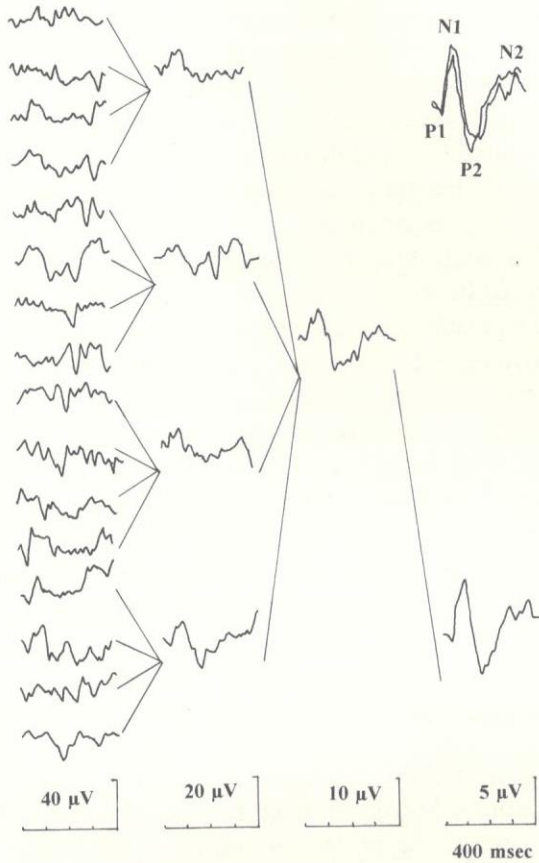
Figure 12.2. Successive ERP averaging to an auditory stimulus. (Note that negativity is recorded as the upward direction.) In the first column are the responses to a brief tone burst in 16 trials recorded at the vertex (C_z). In the second column, four groups of 4 responses have been averaged together to make a total of 4 responses from the original 16. The third column shows the average of all 16 responses. At the bottom of the fourth column is an average of 64 responses to the same tone burst, for comparison with the average to 16 responses in the third column. At the top of the fourth column are two averages of 32 responses, with ERP components indicated. (Adapted from Picton, 1980, with permission from Wiley and Sons and the author.)

sent the most interference. Eye movements and particularly blinks give rise to large potential shifts in the EEG, particularly at anterior and frontal electrode placements. There are basically two ways of handling eye-movement artifacts: rejection and correction. For example, all potential shifts in an EEG lead that exceed a preset value (e.g., 50 or 100 µV) might be automatically discarded from the ERP average. In some instances, however, as when only a few trials can be obtained, there may be too few trials left for an adequate average to be computed if trials are rejected because of interference from artifacts. In that case, mathematical algorithms are used to remove, or correct, the contribution of eye movements to the average (see Brunia, Moecks, Berg-Lenssen, et al., 1989). ERP recordings should therefore be complemented with simultaneous recordings of horizontal and vertical eye movements through, for example, electrooculography (see Chapter 14). It is recommended that horizontal and vertical eye movements be recorded on separate channels, but if this is not possible, a combined EOG measure may be derived by placing one electrode above the eye and the other electrode at the outer canthus of the eye.

Brain and Source Generators

Within certain limitations, ERPs may be considered brain correlates of mental operations. Moreover, from the distribution of ERP components over the scalp, the underlying regional brain activity may be inferred. This is, however, no easy task, since the same ERP deflections may be caused by almost any number of different source generators in the brain that act in linear fashion. This is called "the inverse problem" (Wood, McCarthy, Squires, et al., 1984), and there is no unique solution to it (see also the discussion of magnetoencephalography in Chapter 13). Part of the problem is that the inside of the skull is a volume-conducting space, conducting source-generator activity in many directions. ERPs represent electric fields that are generated by the flow of current when a large number of neurons are simultaneously activated. Electrical activity picked up by an electrode on the outside of the scalp, however, may not have its origin in the brain tissue directly underneath the electrode. If magnetoencephalography (MEG), which picks up the small magnetic fields generated by a dipole source in the brain (Hämäläinen, Hari, Ilmoniemi, 1993), is employed at the same

time as the ERPs are recorded, some of the problems inherent in localizing the source of the ERPs may be overcome.

BESA Analysis

In an attempt to decompose the recorded ERP waveform into its underlying multiple dipole source potentials, Scherg (e.g., 1989) have developed a method of analyzing multiple time-varying dipole sources localized within a spherical head model that are mapped onto a magnetic resonance image (MRI) of the brain. Their technique, *brain electric source analysis* (BESA), is a sophisticated mathematical method for linear summation of multiple dipolar fields generated by multiple restricted brain regions.

Advantages and Limitations

Despite the problems inherent in determining the source generator of an ERP in the brain, ERPs have several distinct advantages, the major one being the good temporal resolution. Measuring ERPs time-locked to a stimulus event make it possible to probe information-processing in the brain on a very minute time scale, in the range of milliseconds. In principle, it is possible to follow the time course of the processing of a stimulus in the brain, from the initial sensory registration to the preparation and execution of a motor response. ERPs are typically used to infer brain activity related to cognitive processing, including sensory memory (Näätänen, 1992), attention (Hillyard, 1993), and stimulus probability (Duncan-Johnson and Donchin, 1977).

ERP Components

The recording of ERPs requires the same equipment as recordings of EEG, with the important addition of a signal-averaging device or computer software for averaging. A simplified example of the different ERP components is given in Figure 12.3.

ERP components may be classified with respect to the *polarity* of the waveform, whether it is positive or negative. In Figure 12.3 positive waveforms have an upward deflection and negative waveforms have a downward deflection. It is customary in the ERP literature, however,
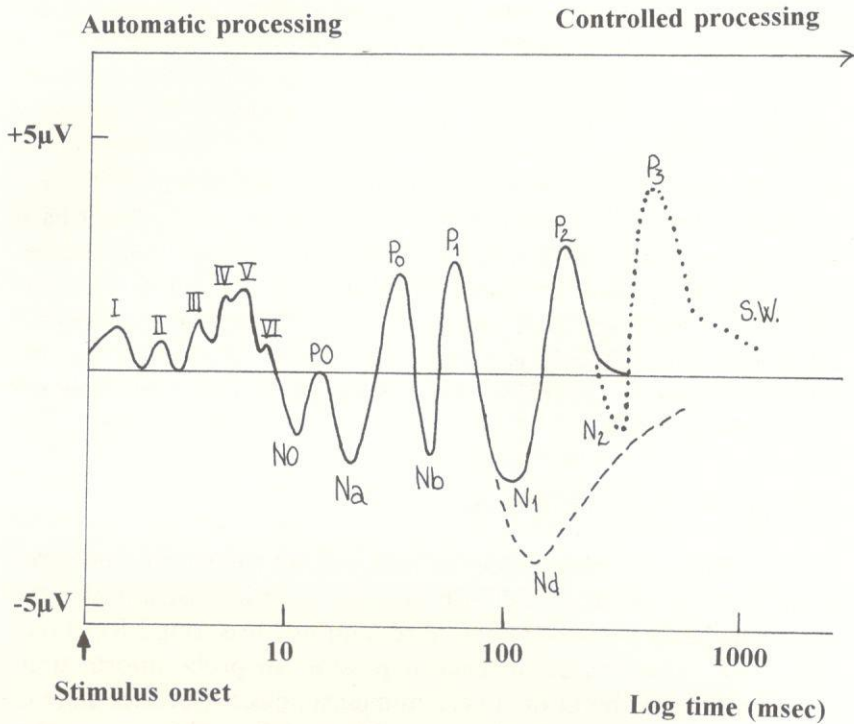
Figure 12.3. ERP components in the sampling interval (1,000 msec) after the presentation of a stimulus. This example is from an EEG recording of responses to an auditory stimulus of moderate intensity. Note the logarithmic x-axis. S.W. = slow wave activity. (Adapted from Hillyard and Kutas, 1983.)

to display negativity upwards, and positivity downwards, directly opposite to common conventions in mathematics. All figures, with one exception, in this chapter are drawn with positivity up. Figure 12.4 is a typical laboratory recording of ERP components occurring during 1,000 msec after the stimulus.

Components may also be classified with respect to *latency*, that is, the latency in msec when a certain component deflection occurs in relation to a stimulus event. A third classification is the *ordinal number* of a component following a stimulus. Components are numbered in accordance with their appearance after the stimulus: for example, the first negative-going deflection after the brainstem potentials is called the N1 (or N100, because it typically appears with a latency of about 100 msec after the stimulus).
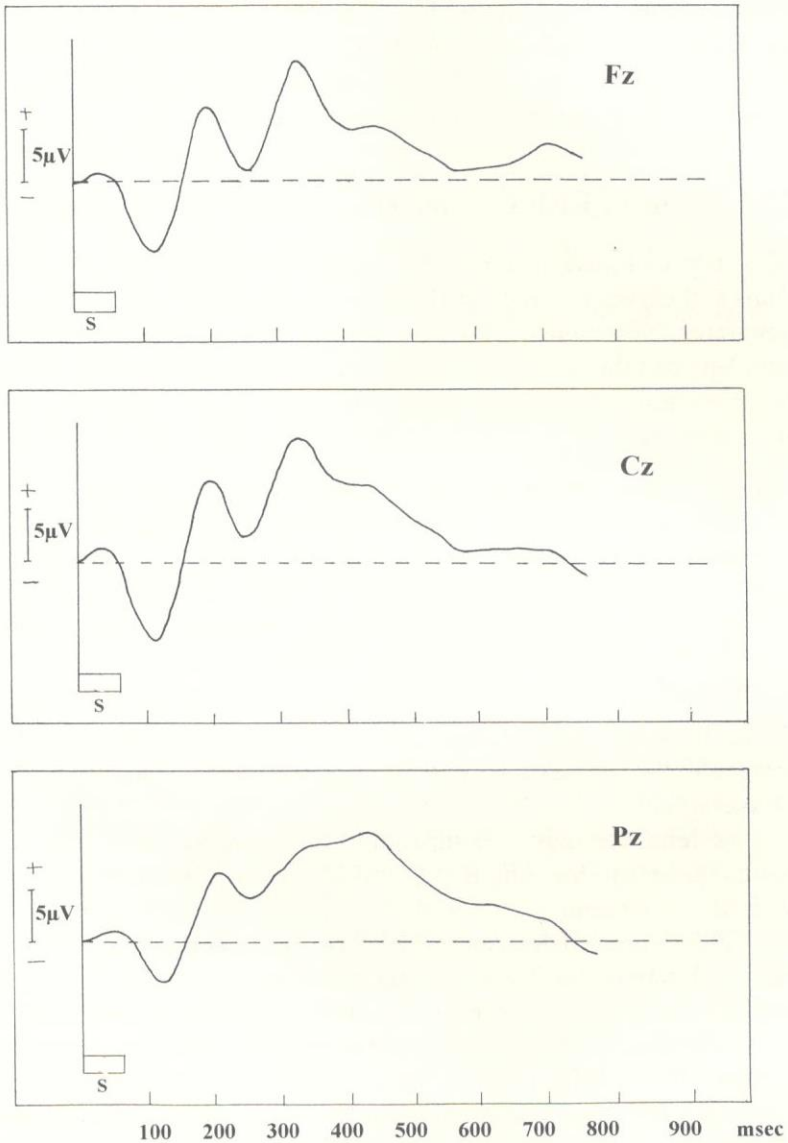
Figure 12.4. Laboratory recordings of the later components (N1, P2, and P3) recorded at three electrode leads (F_Z, C_Z, and P_Z). These components occur 100 msec and more after the stimulus has been presented. Each horizontal grid is 100 msec.

Components may, finally, be classified after their distribution on the scalp. For example, the typical P3, or P300 (Sutton, Braren, Zubin, and John, 1965; Sutton, 1979), has its maximum amplitude over the vertex (Cz) and parietal midline (Pz) of the scalp.

Definitions of ERP Components

Most textbooks use the term *ERP component* to denote both the deflections and curves recorded at the scalp site, and the underlying source generator. Näätänen and Picton (1987), however, have made a distinction between the recorded positive and negative peaks and the underlying cortical activity, calling only the latter an ERP component. In their own words:

> We define an EP "component" as the contribution to the recorded waveform of a particular generator process such as activation of a localized area of cerebral cortex by a specific pattern of input . . . Whereas the peaks and deflections of an EP can be directly measured from the average waveform, the components contributing to these peaks can usually be inferred only from the results of the experimental manipulation."'   (p. 376)

Thus, according to Näätänen and Picton (1987), the recorded ERP waves should not be called components but rather deflections, peaks, or averages.

This definition may be compared to the definition of an ERP component given by Donchin, Ritter, and McCallum (1978), who said that an ERP component was "a source of controlled, observable variability." This definition describes an ERP in terms of observable, recorded electrical activity, whereas Näätänen and Picton (1987) stressed the importance of linking the component with its localized physiological activity within the brain and with the generator process.

An ERP component is thus the contribution of this generator process to the observed, recorded waveform. Peaks, deflections, and averages do not represent any unitary brain events but instead, as discussed above, consist of the summed result of many different components whose electrical activity affects a single recording electrode. Different statistical methods, like principal-component analysis (PCA) or waveform subtraction, may be applied to disentangle the underlying components from the surface waveforms. For the sake of simplicity, and

to concur with common terminology in the ERP literature, in this book I will refer to both waveform deflections and true brain components as "components."

Prestimulus Potentials

Another way to classify ERP components is to separate those components that occur before a stimulus from those components that occur after the stimulus. Most of the discussion so far has been concerned with ERPs that follow a stimulus, but some components are characteristics of brain events that precede a stimulus.

Contingent Negative Variation

The contingent negative variation (CNV) (Walter, Cooper, Aldridge, et al., 1964) typically occurs in the waiting period between a warning stimulus and an imperative stimulus, when the subject is anticipating an event. Figure 12.5 shows the increase in cortical negativity that occurs just before the execution of a motor response; this increase is different from the large and narrow N1 response that occurs following the presentation of the "get-ready" stimulus. This is also called the *readiness potential* (Kornhuber and Deecke, 1965). If the interval between the warning and imperative stimulus is long enough, the CNV may be decomposed into two components: a sensory component (also called the "O wave"), reflecting the effect of the warning stimulus; and a motor or readiness component, reflecting the anticipation of the second, imperative stimulus (Loveless, 1983).

The CNV and movement-related potentials have been studied extensively by Brunia and his collaborators over the years (see, e.g., Brunia, Haag, and Scheirs, 1985). Brunia and co-workers usually employ a fixed foreperiod reaction-time paradigm, with a warning stimulus alerting the subject to get ready and an imperative stimulus requiring the subject to make the motor response, usually pressing a button held in the hand. By minute measurements of CNV and the readiness potential, Brunia has been able to trace the information processing and response preparation that goes on in the warning foreperiod. Specifically, Brunia and Vingerhoets (1980) recorded CNV simultaneously with bilateral electromyography (EMG) from the calf muscles preceding a plantar flexion of the right foot. The EMG over
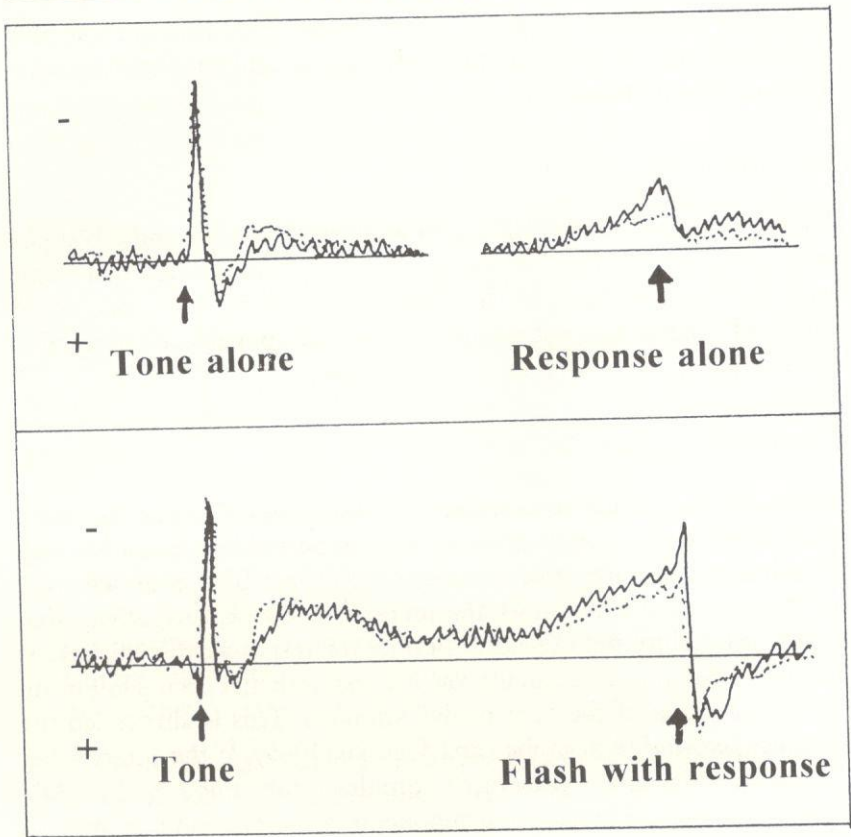
Figure 12.5.. Typical Contingent Negative Variation (CNV) recording in a two-stimulus paradigm. The first stimulus (tone) is a warning stimulus for the subject to get ready. The second stimulus (flash) is a signal to respond. C3 and C4 are two leads along the central midline of the scalp. (Note that negativity is up in this figure.) (Adapted from Rohrbaugh et al., 1976, with permission from the American Association for the Advancement of Science and the authors.)

the right side of the muscle increased systematically over time, the largest EMG values being observed when the motor-preparation wave of the CNV reached its maximum just before the release of the response.

Lateralized Readiness Potentials

More recently, Coles (e.g., 1989) has shown that the readiness potential, elicited when the subjects waits to respond after a warning stimulus, is lateralized over the motor cortex. Coles has shown that as the subject prepares to execute a motor response by squeezing a hand-held dynamometer, a negativity develops that is maximum at the scalp electrodes contralateral to the responding hand. Coles (1989) has suggested that this negative potential reflects response activation. An example of this kind of activation is shown in Figure 12.6, where the readiness potentials are recorded from the left (C3) and right (C4) central scalp locations. By subtracting the potentials recorded at the contralateral electrode from the potentials recorded at the ipsilateral electrode for right- versus left-hand responses, the lateralized readiness potential can be derived.

Slow Potential Shifts and Biofeedback

Birbaumer and his coworkers (e.g., Elbert, Birbaumer, Lutzenberger, and Rockstroh, 1979; Rockstroh, Elbert, Birbaumer, and Lutzenberger, 1982) have demonstrated that CNV-like potential shifts occur in a 6-second interval when subjects are instructed to enhance brain negativity or positivity voluntarily. The task is a biofeedback task in which the subject is provided with a visual display that conveys information about cortical potential shifts in the subject. By changing the information on the screen when the subject produces larger cortical negativitity, Birbaumer and his colleagues have shown how operant conditioning of CNV-like potentials is possible (see also Birbaumer, 1977).

# Exogenous versus Endogenous Components

A distinction is usually made between "exogenous" and "endogenous" components (Donchin, Ritter, and McCallum, 1978). Exogenous

components usually occur within the first 100–200 msec after the stimulus; endogenous components occur later, from 100–200 msec and up to 500–1000 msec.

Exogenous components reflect the first neural processing of the physical characteristics of a stimulus. Moreover, they are obligatory responses to the stimulus, and the magnitude of the response is not dependent on the cognitive processing of the stimulus. These responses are called "exogenous" for just this reason—they are derived from "outside" the subject. Subjects in an experiment designed to tap exogenous components are typically asked to remain passive while stimuli are presented over and over again. Common experimental situations designed to elicit the early exogenous components are "photic driving" and "checkerboard reversals." Examples of exogenous components are the so-called brainstem potentials (see below).

Endogenous components, on the other hand, are elicited in complex experimental situations and often require active participation from the subject. They involve higher cognitive processes like attention or memory. Typical examples of endogenous components are the P3 component and the just-described CNV. Endogenous components are so named because they are driven from "inside" the subject—they are not obligatory to the physical characteristics of the stimulus. Their elicitation will depend on the nature of the information-processing requirements in the stimulus task. For example, the endogenous components occurring in the time interval between a warning stimulus and an imperative stimulus in a reaction-time experiment is dependent on

Figure 12.6. Examples of lateralized readiness potentials. Shown at top are idealized scalp-recorded brain potentials from the left (C3) and right (C4) scalp sites in a warned reaction-time task when subjects know in advance of the imperative stimulus the hand to be used to execute a correct response. WS = warning stimulus, IS = imperative stimulus. As subjects prepare to execute a movement, a negativity develops that is maximum at scalp sites contralateral to the responding hand. The asymmetry in these potentials is illustrated by subtracting the potential recorded at the scalp site ipsilateral to the movement (middle). Then, the difference potentials for left- and right-hand movements are averaged to yield lateralized readiness potentials (second from bottom). The lowermost panel shows the response activation phenomenon that Coles (1989) has suggested is reflected in the lateralized readiness potential. (Adapted from Coles, 1989, with permission from the Society for Psychophysiological Research and the author.)

Left Hand

Right Hand

Average

Lateralized
Readiness
Potential
(LRP)

Response
Activation

Correct

Incorrect
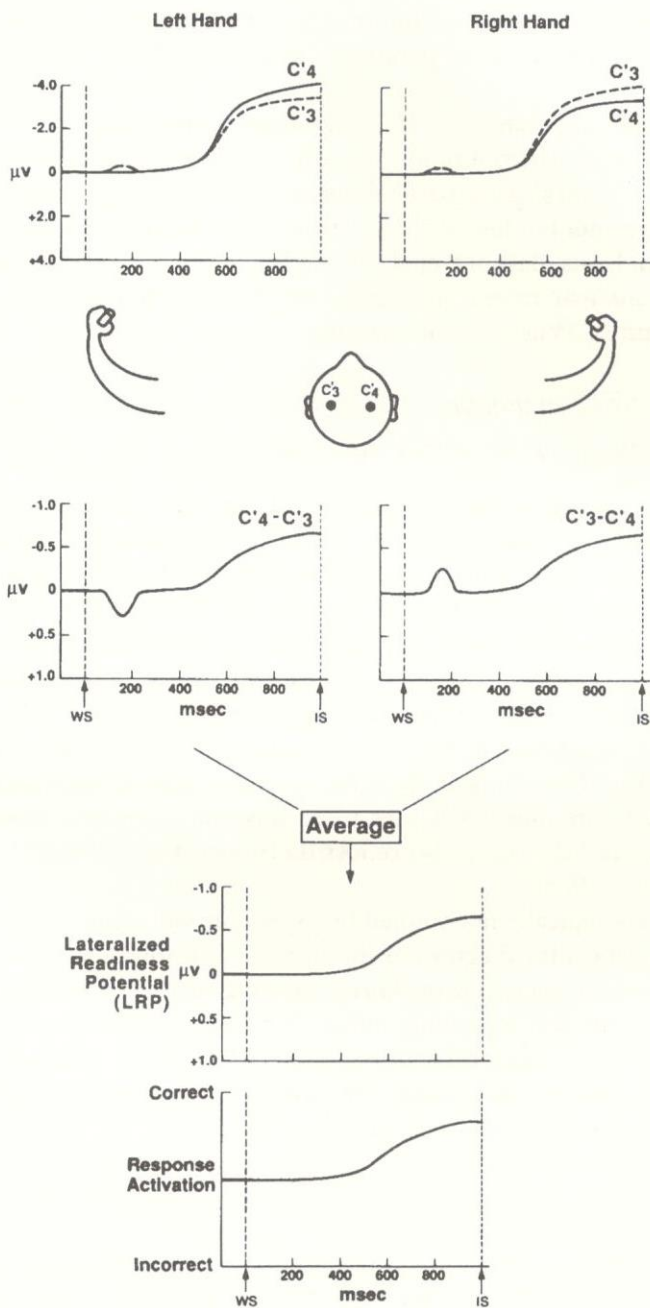
the subject's processing of the warning stimulus and anticipation of and preparation for the imperative stimulus, as reflected in the typical CNV.

Although endogenous ERP components have their distinct topographical scalp distributions—usually the larger responses are recorded at central and parietal leads—their corresponding dipole sources may not be close to the electrode with the maximum amplitude (Donchin, Karis, Bashore, et al., 1986). Some evidence exists that these components may have a subcortical origin in the hippocampus (Halgren, Squires, Wilson, et al., 1980).

Exogenous Components
The Auditory Brainstem Potentials

The auditory brainstem potentials (ABR) are seven deflections in the ERP signal occurring in the first 10 or 12 msec after the delivery of a click to the ear (Picton, Stapells, and Campbell, 1981). The seven waveforms are numbered I–VII (see Figures 12.3 and 12.7). The first deflection (wave I) reflects activity in the eighth cranial nerve, which is the hearing nerve. Wave II reflects activity in the cochlear nucleus, although this is not unambiguously agreed upon. Waves III–V reflect activity in the pons, the lateral lemniscus, and the inferior colliculus. Waves VI–VII involve activity in the medial geniculate body, although it has been questioned whether these waveforms are true brainstem responses, and that they also reflect thalamocortical activity (Vaughn and Arezzo, 1988).

ABRs are typically not studied by psychophysiologists, but they are important tools for diagnosing the source of various hearing deficits. ABRs are easily elicited with short auditory clicks. In neurology, ABRs are frequently used to identify tumors localized at the brainstem level. The ABR is also abnormal in patients with multiple sclerosis (MS), and several studies have shown how ABRs may be used in the diagnosis of MS (reviewed in Squires and Ollo, 1986).

Middle-Latency Components

After 10–12 msec, ABRs are replaced by the so-called middle-latency components (N0, P0, Na, Pa, Nb). These waveforms, which include both positive and negative deflections, are the first signs of activity in
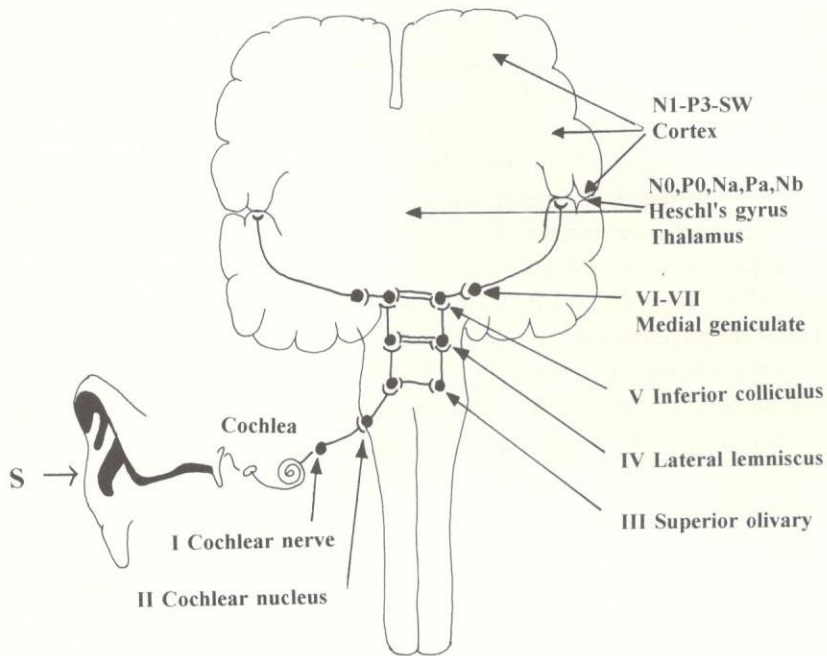
Figure 12.7. Suggested anatomical locations of different ERPs and other brain potentials recorded in response to an auditory stimulus. The components I to IV have a brainstem localization and a latency of 1–12 msec. The components N0 to Nb have their focus at the thalamic/auditory cortex level and a latency of 12–50 msec. The late components N1-P3-SW have their origin in the cortex and a latency of 100–1,000 msec. SW = slow wave activity.

the auditory cortex involving the Heschl's gyrus. The middle-latency waves are also related to thalamic activity.

Long-Latency Exogenous Components (N1 and P2)

From 100 msec and up to 200–300 milliseconds after the auditory stimulus, long-latency exogenous components, notably the N1 and the P2, are detected. These components are called *transient* since they share characteristics with endogenous components. In the auditory modality, the N1 usually peaks at about 100 msec, and it is therefore also called the N100. This is a relatively large waveform that is almost

invariantly elicited to repeated presentations of auditory stimuli. The P2 has its peak around 180–200 msec after the stimulus and is therefore also designated the P200.

The N1 may be preceded by a small deflection, the P1 component, with a peak at about 50 msec. The P1, N1, and P2 components have somewhat longer latencies in the visual modality, but their interrelationships remain constant. The auditory N1 is most likely generated in the primary auditory cortex in the temporal lobe (Vaughn and Ritter, 1970). The N1 and P2 components share a great deal of overlap in how they are elicited by external stimulus conditions, although their scalp distribution is somewhat different. Thus, both the N1 and P2 may be considered to reflect neuronal activity generated in the superior temporal lobe involving the auditory cortex.

The N1 Attention Effect

The N1 component is related to selective attention, so, in a more restricted sense, it is not exclusively an exogenous component. It shares features with the later endogenous components. The N1 is related to processing negativity, an additional endogenous component (see below).

In a now classical study, Hillyard, Hink, Schwent, and Picton (1973) asked subjects to ignore tones presented to one ear while they were attending to tones of a different frequency presented to the other ear. The N1 component recorded by the vertex (Cz) electrode was enhanced for stimuli presented to the attended ear. This study solved a problem for early ERP studies, pointed out by Näätänen (1967): since stimulus sequences were presented in a predictable and fixed sequence, it was possible for the subject to prepare for the presentation of a stimulus.

The N1 effect observed by Hillyard et al. (1973) had an early latency of about 50 msec in some instances and was thought to reflect an early selection process in selective attention. It is generally believed to index Broadbent's (1971) concept of the stimulus-set mode of attention. Broadbent suggested that attention is related to a process that passively admits sensory input from a maintained set over the attended channel rather than to a process that requires active discrimination of each individual stimulus (Loveless, 1983).

The N1 component elicited in response to a brief auditory stimulus

is one of the best-known ERP components. Näätänen, Alho, and Sams (1985) suggested that the N1 actually consists of two components, one emanating from the auditory cortex, the other perhaps not specific to any modality, since it may also be elicited by visual stimuli. Later it was suggested that it actually consists of three subcomponents. The amplitude of the N1 increases with increases in the interstimulus interval (ISI), up to about 10 sec. Its peak latency is also affected by the length of the ISI. The typical N1 effect observed by Hillyard et al. (1973) is illlustrated in Figure 12.8.

The N1 Neural Substrates

The neural substrates, including the dipolar magnetic field, of the N1 (N100) component of the ERP and the typical "N1 effect" observed by Hillyard and his co-workers (see Woldorff et al., 1993) have been identified through the use of magnetoencephalography techniques (see Figure 12.9). These "maps" locate the principal source generator for the N1 attention effect over the temporal cortex involving the primary auditory cortex.

The N2 Component

Negative deflections that occur around 200 msec after the presentation of a deviant stimulus in a train of stimuli are labeled "N2." As will be discussed in more detail below, the earlier deflection (N2a) share common features with the so-called mismatch negativity (MMN) deflection. A later deflection (N2b) is one of the endogenous components discussed in a later section of this chapter. The N2b is triggered by an auditory change in a train of stimuli, and particularly when the subject is attending to the deviant stimulus. The distribution of the N2b over the scalp is broad, resembling the distribution of the modality-nonspecific N1 component (Nätäänen, 1992).

The P2 Component

Closely related to the N1 is the P2 component, or deflection. Although they typically occur together in the auditory modality, the two components can be dissociated from each other. Furthermore, their scalp
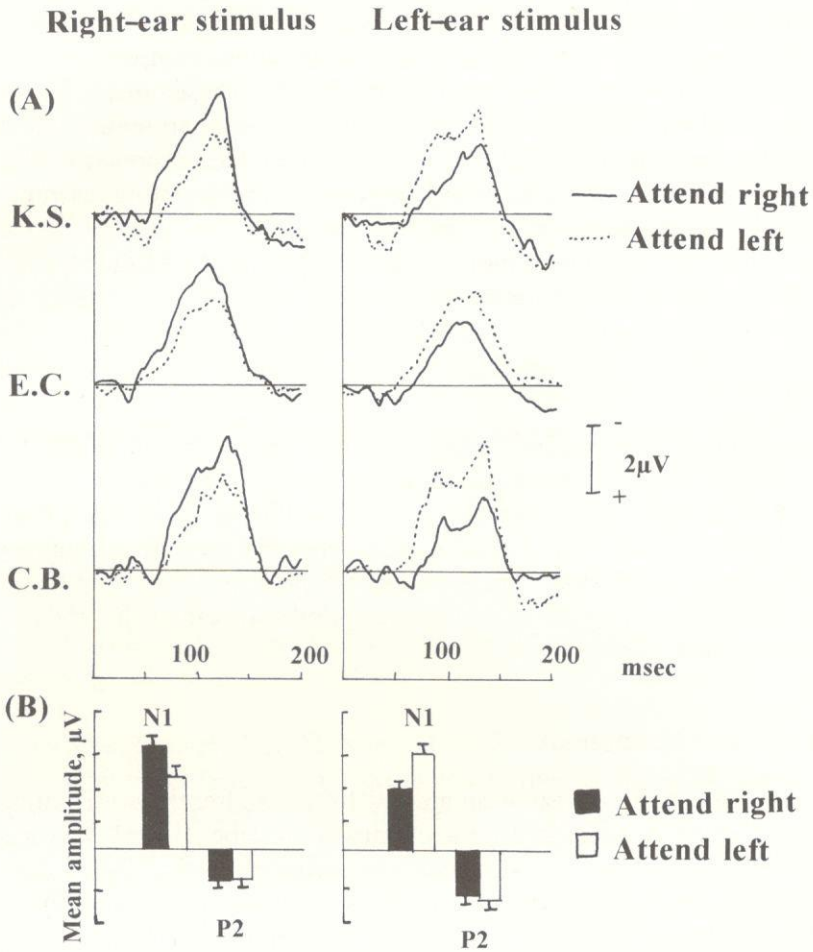
Figure 12.8.   ERPs from three subjects (K.S., E.C., C.B.). Each tracing is an average of 1,024 stimulus presentations to each ear under attend-right *(solid line)* and attend left *(dashed line)* conditions. The bar graphs show the mean and standard error for group data (10 subjects). Note that negativity is up. (From Hillyard et al., 1973, with permission from the American Association for the Advancement of Science and the authors.)
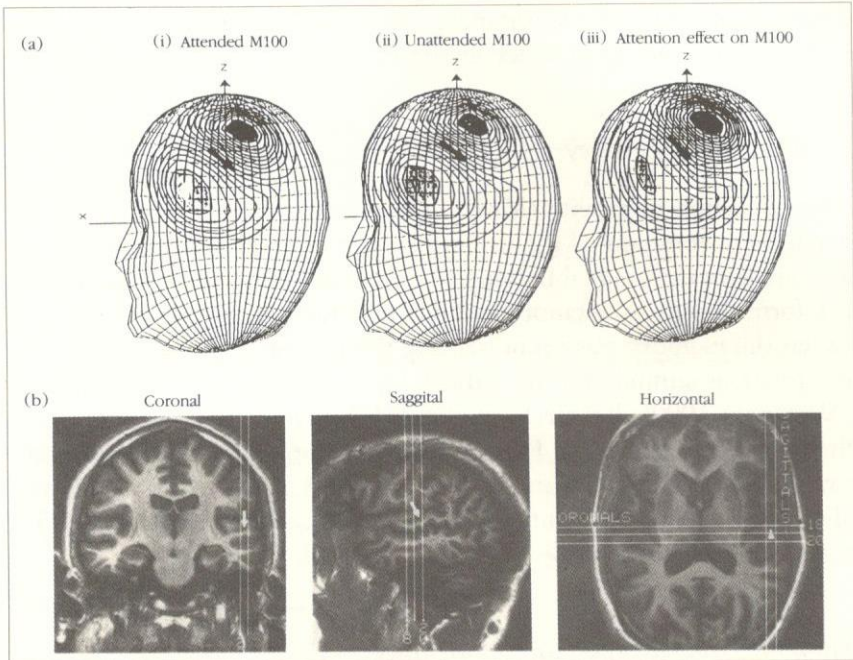
Figure 12.9. Magnetic-field distributions *(a)* for the M100 component (same as N100m in Figure 13.7) elicited by right-ear tones in a dichotic listening experiment. Separate mappings are shown for the M100 elicited by attended tones, unattended tones, and the "attention effect," which is the subtracted differential between the attended and unattended responses. These mappings show a dipolar field with magnetic field lines emerging from the head superiorly and entering inferiorly. The arrows indicate the direction and schematic positioning of the single equivalent dipole sources that were calculated to best fit these surface ERF distributions. Below, MRI scans indicate the calculated location of the best-fit dipole sources for the subject shown in *(a)*. The dipoles for the attended M100, the unattended M100, and the differential M100 attention effect were all situated within millimeters of one another in the auditory cortex of the supratemporal plane (location of the arrow). (From Hillyard, 1991, reprinted with permission from the author.)

distributions also differ (Näätänen, 1992): the N1 is maximal over the vertex (Cz) of the scalp, whereas the P2 is not so focally localized.

Mismatch Negativity

The mismatch negativity (MMN) deflection can be thought of as a cortical concomitant of the orienting response (OR) to change, as it also involves the gradual buildup of a memory template. Thus, MMN is a form of sensory memory and it is generated by a discrepancy between the memory trace representing the precise physical features of the previous stimuli and the sensory input from the deviant stimulus (Näätänen, 1990). Research on the MMN component is intimately linked to the work of the Finnish psychophysiologist Risto Näätänen (see Näätänen, 1992, for an excellent summary), although others have also made substantial contributions (see, e.g., Hillyard et al., 1973, regarding the N1 effect).

Stimulus Deviance and Passive Attention

Mismatch negativity may involve a passive attentional shift that occurs when there is a mismatch between what is currently represented in short-term memory and the properties of a presented stimulus. Thus, in contrast to the N1-P2 complex, the MMN wave is considered a response to stimulus deviance, in terms of physical characteristics. The scalp distribution of the MMN is modality-specific, particularly for the auditory modality. The MMN occurs around 100–250 msec after the presentation of a deviant stimulus against a background of more frequent stimuli, while the subject either ignores the stimuli or perform some task related to them.

The MMN is a negative waveform that occurs in response to deviant stimuli imbedded in trains of more frequent stimuli. The task of the subject is typically not to attend to the stimuli but to engage in some other, distracting activity. For example, as in the experiment whose results are shown in Figure 12.10, the subjects might be presented with blocks of auditory stimuli consisting of a standard stimulus of 1,000 Hz on 80 percent of the trials and a deviant stimulus of a slightly higher frequency (between 1,004 to 1,032 Hz) on 20 percent of the trials. In this experiment, the interstimulus interval was kept at 1 sec,
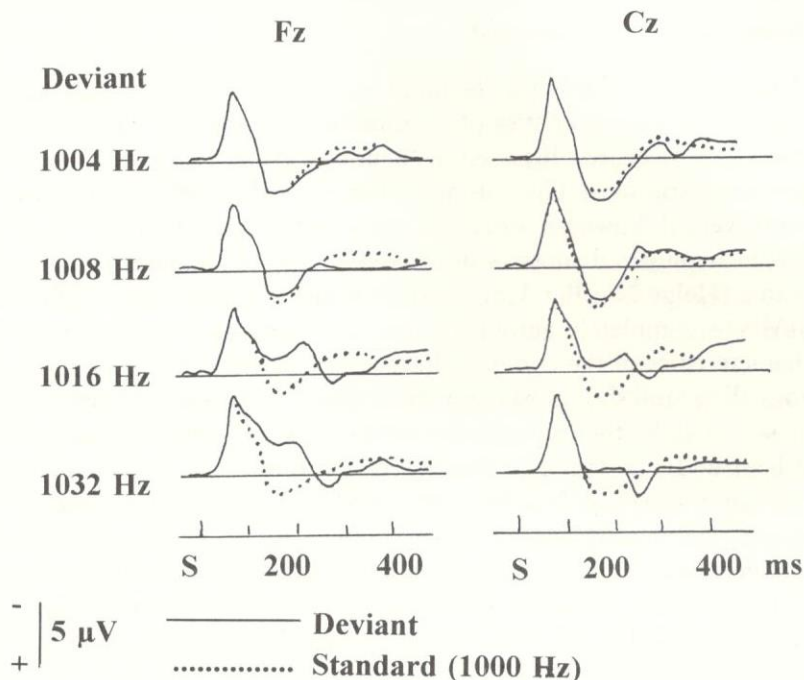
Figure 12.10. The grand average ERPs to standard stimuli of 1,000 Hz *(dotted line)* and deviant stimuli *(solid line)* of 1,004, 1,008, 1,016, and 1,032 Hz. Eighty percent of the stimuli were standard stimuli and 20 percent were deviant stimuli. (Data from Sams et al., 1985, reprinted with permission from Elsevier Science Publishers and the authors.)

and the subjects were distracted from the stimuli by reading a book (Sams, Paavilainen, Alho, and Näätänen, 1985).

The MMN response to the deviant stimulus is usually derived from a difference-waveform. A *difference-waveform* is obtained by subtracting the ERP waveform in the infrequent, deviant condition from the corresponding waveform in the frequent, standard condition. See Figures 12.13 and 12.14 for examples of difference-waveforms. The MMN thus appears as a negative deflection that typically starts at about 100 msec after stimulus delivery and lasts until 200–250 msec after the stimulus. The largest MMNs were elicited to the 1,032 Hz deviant stimulus, which suggests that the magnitude of the MMN is related to the degree of physical deviance between the standard and deviant stimuli.

Automatic Deviance Detection

Originally, the MMN was believed to indicate automatic analysis of the physical characteristics of a stimulus and to be elicited whenever there is a mismatch between a "neuronal memory model" and the presented stimulus. The automatic nature of the MMN is somewhat controversial, however, since the deflection is smaller when it is elicited in hypnotized subjects instructed to ignore all tones being presented (Helge Nordby, University of Bergen, unpublished results). If MMN is completely automatic and dependent only on the physical characteristics of the stimulus, instructing subjects in hypnosis to ignore all stimuli should have no effect on the MMN's amplitude. One must conclude, therefore, that the MMN is influenced by attention, at least under certain experimental conditions.

In another study, Nordby, Roth, and Pfefferbaum (1988) demonstrated that the MMN could be elicited also to temporal stimulus changes: for example, having the standard and the deviant tones similar except that the deviant is shorter in duration. Nordby et al. (1988) found that MMN was also elicited by stimulus-repetition effects.

MMN and Memory

MMN is a rather robust empirical phenomenon, and it has been related to a variety of stimulus situations and experimental conditions: the spatial origin of a stimulus, memory, phonetic change, partial omission, sleep effects, and drug effects. Näätänen (1992) suggested that MMN is generated by a memory process that registers the stimulus change, which would indicate a kind of memory representation of the standard stimulus (Näätänen, Paavilainen, and Reinikainen, 1989). An alternative explanation is that the MMN is a response to a difference between sequentially presented stimuli and is generated by activation of new afferent neuronal elements corresponding to the frequency of the deviant stimuli. These neuronal afferents will remain responsive over the course of an experiment because the interstimulus interval between the deviant and the standard stimuli is long in comparison with the interval between the consecutive standard stimuli (Näätänen, 1992).

Visual ERPs

Visual ERPs (VERPs) differ from auditory potentials in that they consist of fewer waves. Visual ERPs are typically elicited in response to light flashes, as in "photic driving" experiments, or to patterned stimuli, as in the "checkerboard reversal" paradigm. This paradigm is the presentation of white and black squares that reverse in position every second or half-second. The VERPs are recorded at each reversal of the checkerboard; that is, whenever the squares change position, there is a trigger pulse to the EEG recording channel instructing the computer "to start sampling" for the VERP.

The most prominent VERP is a large positive potential that occurs at approximately 100 msec after the squares change position. The visual P1 (P100) is usually largest over the occipital cortex, although the distribution varies with stimulus conditions, including the luminance, contrast, and spatial frequency of the visual stimuli used. Typical VERPs elicited in response to the checkerboard paradigm are seen in Figure 12.11.

The latency of the visual P1 is typically prolonged in patients with multiple sclerosis (Halliday, McDonald, and Mushin, 1973), and this fact is often used in neurological practice to diagnose the disease. P1 latency prolongation occurs also in other neurodegenerative diseases, like Parkinson's disease and Huntington's chorea (see Squires and Ollo, 1986, for an overview).

Visual Attention and the Cuing Paradigm

In a recent series of studies, Mangun, Hansen, and Hillyard (1987) and Mangun, Hillyard, and Luck (1993) have shown facilitation of the early P1 component in studies of selective attention to spatial localizations. These studies are based on the so-called attention-cuing paradigm in selective attention (e.g., Posner and Driver, 1992). The standard Posner paradigm is illustrated in Figure 12.12.

A trial usually begins with the presentation of two rectangles on the computer screen while the subject is fixating the center cross. One of the rectangles suddenly becomes brighter (represented in Figure 12.12 as a double line). On half of the trials the left rectangle becomes brighter, on the other half of the trials it is the right rectangle. The
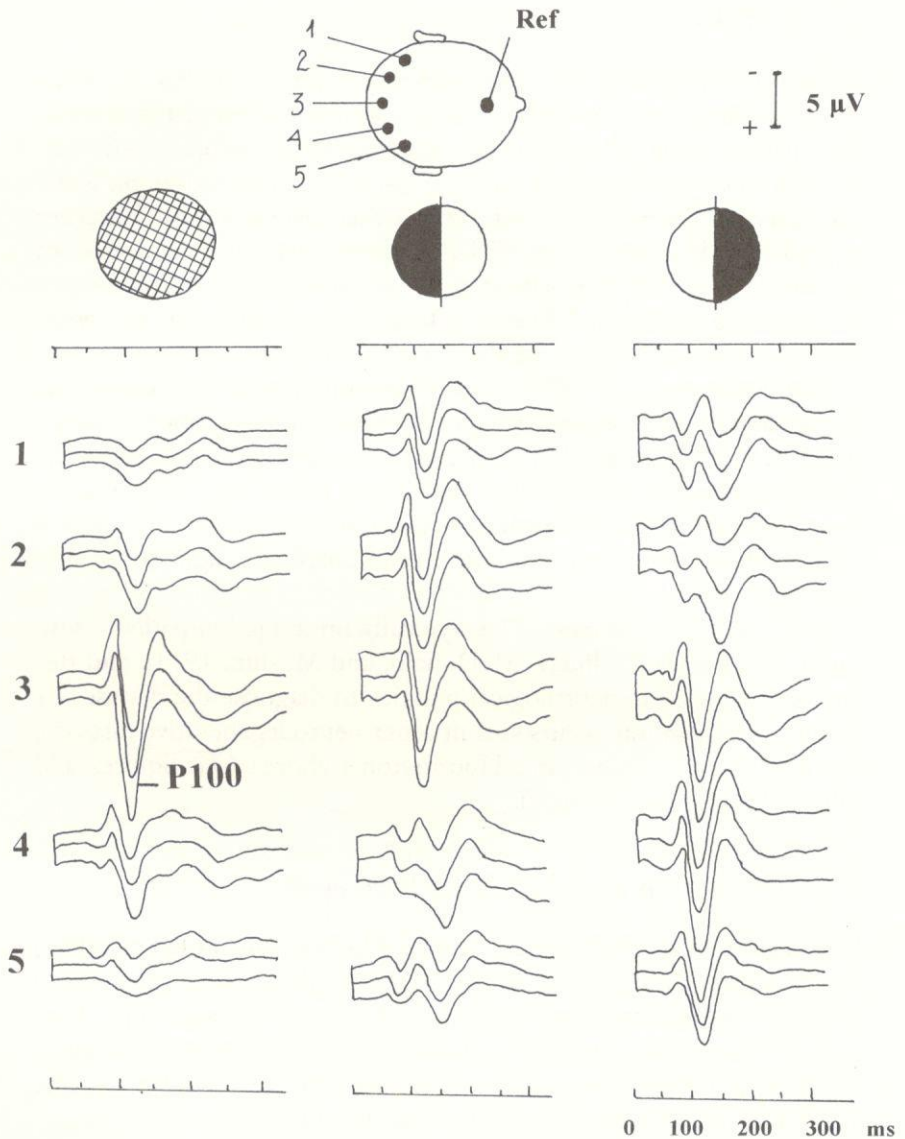
Figure 12.11. Examples of visual ERPs to three different black-and-white stimuli, recorded from 5 different electrode locations (indicated at top). Note the large visual P100 component at about 100 msec after stimulus presentation. (Adapted from Squires and Ollo, 1986, with permission from Oxford University Press, Inc., and the authors; originally adapted from the work of McCarthy and Wood.)
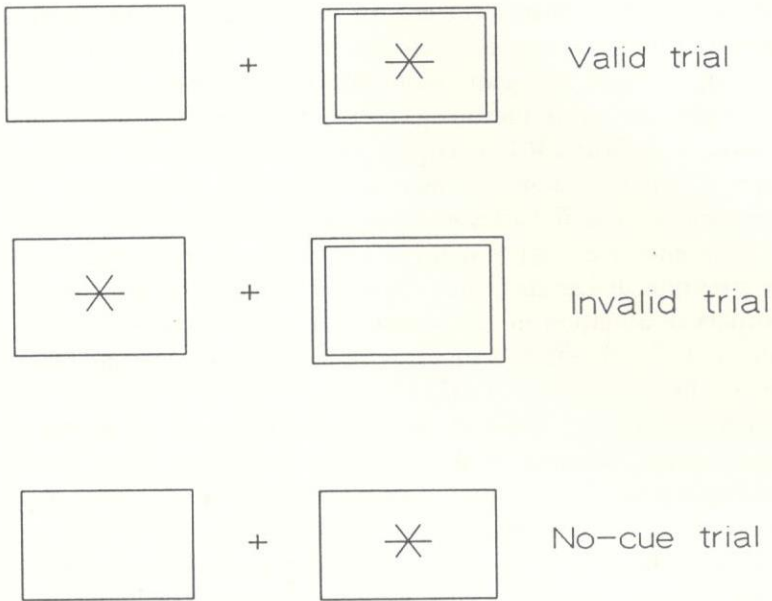
Figure 12.12. The visual attention cuing paradigm developed by Michael Posner employs the presentation of different display for valid, invalid, and no-cue trials. Typically, reaction times are prolonged on invalid trials.

brighter rectangle acts as a cue to attract the subject's attention to its spatial location without moving the eyes. This is called *explicit cuing.* After a short delay of a few hundred milliseconds, an asterisk appears in either the illuminated or the other rectangle. The task of the subject is typically to press a button as fast as possible when the asterisk appears. The asterisk is thus a target stimulus that follows the cue stimulus in this reaction-time (RT) task.

Those trials in which the asterisk appears inside the illuminated rectangle are the valid trials, the others invalid trials. In addition, control trials in which no cue is given are interspersed among valid and invalid trials. Valid trials are more frequent than invalid trials.

The typical behavioral finding is that RTs are faster on valid trials and slower on invalid trials, in comparison with the no-cue control trials. Posner (e.g., Posner and Petersen, 1990) has suggested a series of elementary mental operations in order to explain the orientation of attention to the cued target. When the target occurs in a spatial loca-

tion different from that of the cue, shifting attention to the target involves interrupting ongoing activity, moving attention to the new location, and re-engaging attention at the target's spatial location. Usually, there is a behavioral advantage for the cued location over the uncued location, with shorter RTs to targets presented at the cued location and longer RTs to targets at the noncued location. These effects are called *attention facilitation* and *attention inhibition*, respectively.

The attention-cuing paradigm is frequently used in studies of selective attention. It has also been employed in clinical settings to study disorders of attention in schizophrenic subjects (Posner, Early, Reiman, et al., 1988) and in patients with parietal-lobe damage (Posner, Walker, Friedrich, et al., 1987).

There are several different variants of the Posner paradigm. In a variant used by Mangun et al. (1987), for example, a centrally placed arrow pointing either to the left or right visual half-field was used as the cue. This is called *implicit cuing*. The target to which the subject pressed a button was a vertical bar flashed inside a rectangle or square display. A valid trial was defined as a trial in which the light flash appeared inside the rectangle at the location to which the arrow pointed, invalid trials as those in which the light flash appeared at the opposite side of the location to which the arrow pointed.

The RTs showed the typical Posner effect, but there were also significant effects for the early N1 and P1 waves of the ERP, occurring at 170 and 110 msec, respectively. These effects are illustrated in Figure 12.13, for left-field target presentations. The P110 and N170 components shown in the figure were larger in the valid condition than in the invalid condition. Increased amplitudes during invalid trials were seen for the P3 component at about 350 msec, a finding that has later been replicated by Hugdahl and Nordby (1994).

Sensory Gating

The increased amplitudes of the long-latency exogenous P1 and N1 components suggest a gating of early sensory-evoked activity in the visual pathways. The findings by, for example, Mangun et al. (1987) thus support Posner's suggestion that providing the subject with information of the probable spatial location of a target stimulus will result in selective facilitation of sensory processing. In addition, Hugdahl and Nordby (1994) suggested that the enhanced P3 amplitude they
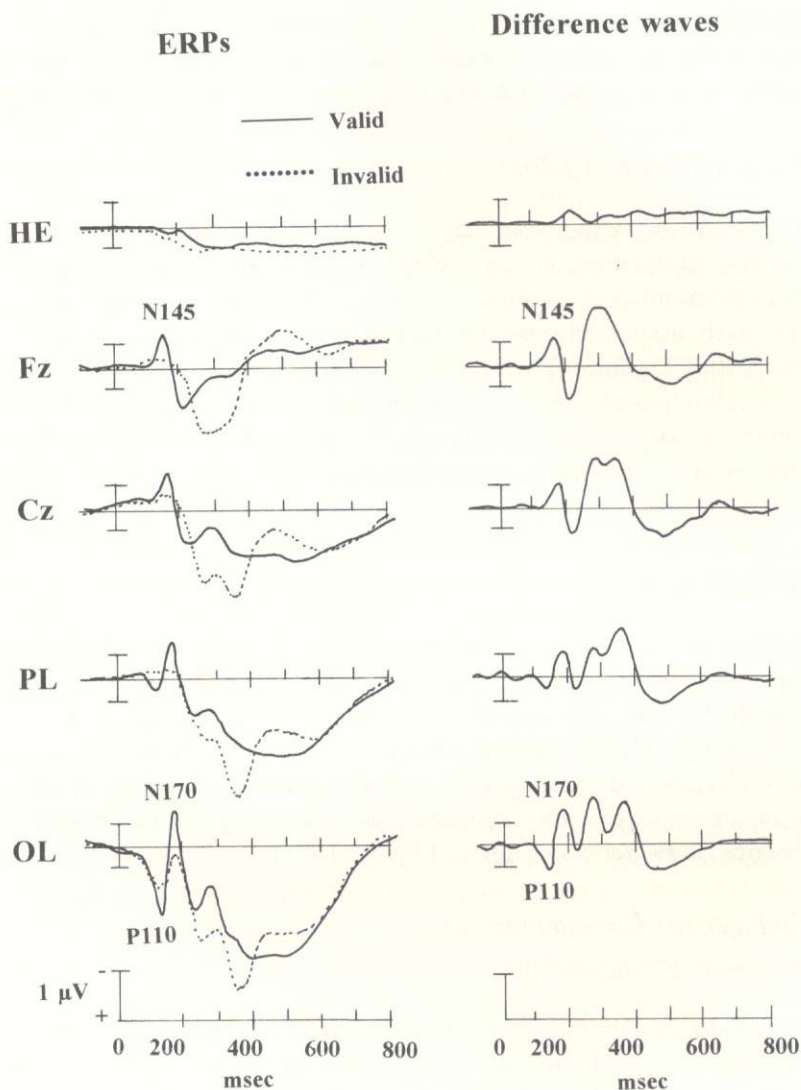
Figure 12.13. ERPs *(left)* recorded from five different electrode locations during responses to invalid and valid left visual field cue trials in the Posner attention cue-target paradigm (the cue was an arrow pointing to either the left or right side). Difference waveforms *(right)* are produced by subtracting the invalid from the valid ERP waves. Note the early components around 100–200 msec for recordings made under the valid condition, indicating attentional facilitation. (Data from Mangun et al., 1987, reprinted with permission from Elsevier Science Publishers and the authors.)

recorded after presentation of invalidly cued targets, and the distribution of the P3 mainly over central and frontal areas, may reflect the interrupt/disengage processing in the frontal cortex on invalid trials.

Somatosensory ERPs

Somatosensory exogenous ERPs are typically recorded as responses to nerve stimulation. For example, an experiment might require a brief electric stimulation to the median nerve of the arm. A whole range of very early waves can typically be seen after nerve stimulation, such as the N10, P15, and N20/P30 waves (which occur from 10 to 30 msec after stimulation). These waves probably reflect transmission in the somatosensory system from the brachial plexus nerve at the spinal cord level, over the thalamus, to the somatosensory cortex posterior to the central sulcus.

40 Hz ERPs

Patients who have received anesthetic drugs, such as benzodiazepine, sometimes show a 40 Hz component ERP to auditory stimulation. The 40 Hz ERP consists of two to four periodic occurrences in the 40 Hz range (Galambos, Makeig, and Talmachoff (1991). It disappears during states of deep anesthesia, including unconsciousness, and it has been suggested that this component is an indicator of the presence or absence of awareness (Kulli and Koch, 1991).

Endogenous Components
Processing Negativity

Processing negativity (PN) is considered an endogenous component (Näätänen et al., 1978) generated by a cerebral process that is different from the process that generates the exogenous N1 component. A typical experimental setup for the study of PN presents subjects with four types of tone stimuli that differ along two dimensions (e.g., pitch and location), each having two levels (e.g., left- vs. right-ear presentation, or high vs. low pitch). The subject may be instructed to try to detect the high-pitch tones presented in the left ear. Thus, the subject is instructed to actively attend to some features of the stimuli. The result is larger negativity in the response to the attended tones in the left

pected stimulus that merely "confirms" what was expected or known. Information delivery is thus inversely related to *stimulus probability*, in the sense that the less probable an event is, the larger is the information delivery.

In later research, stimulus probability became the major variable for eliciting the P3 wave. The most typical experimental paradigm is the *oddball paradigm*, a presentation of two tones that differ in pitch and probability. One of the tones, often referred to as the "frequent" or the "standard" tone, has a probability of occurring during each trial of 80–90 percent, while the other tone, as the "infrequent" or "target" tone, occurs with only 10–20 percent probability and is randomly interspersed among the more frequent standard tones.

The P3 is observed as a large positive deflection following presentation of the target stimulus (see Figure 12.14). The deflection is particularly apparent when the subject is actively attending to the infrequent tones, as one might be if instructed to count the "odd" stimuli. Note also that the classic P3 elicited in the oddball paradigm is maximal at parietal lead over the cortex.

The optimal condition to elicit a large P3 is 10–20 percent probability of stimulus occurrence. Duncan-Johnson and Donchin (1977) recorded ERPs in an experiment employing a typical oddball paradigm that varied both which stimulus was the target and the probability of occurrence. The critical feature in this experiment (see Figure 12.15) was stimulus probability, irrespective of whether the tone was the standard or the target. However, Polich (1990) demonstrated that the length of the interstimulus interval (ISI) affects the P3 independently of stimulus probability. By gradually increasing the ISI from 2 to 10 sec, Polich (1990) demonstrated that the P3 amplitude in response to the infrequent stimulus was larger only for the shorter ISIs.

Context Updating and the OR

The brain generators of the P3 are not completely identified, but at least some aspects of the P3 seem to be generated in the hippocampal region (although some would disagree). In a general sense, since the hippocampus is closely related to memory and memory processes, some authors have claimed that the P3 is also associated with memory and learning, particularly context updating (Donchin, 1981).

The dependence of the P3 on stimulus probability, with larger P3 amplitudes elicited by improbable events, links the P3 to the orienting
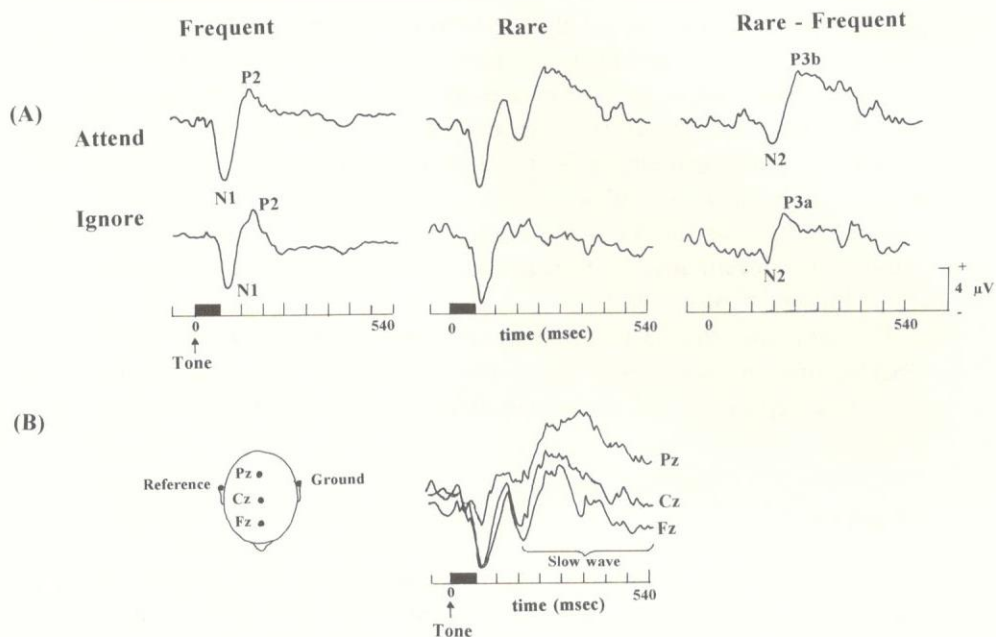
Figure 12.14. P300 (P3) components recorded in an experiment employing the typical oddball paradigm, with frequent and rare tones. At right are the difference waveforms, for which the ERPs to the rare tone are subtracted from the ERPs to the frequent tone. The upper waveforms were recorded while the subject is instructed to attend to the rare tone, the lower ones while the subject is instructed to ignore the rare tone. (Data from Squires and Ollo, 1986, reprinted with permission from Oxford University Press and the authors.)

response (OR) and the neuronal model (see Chapter 7). An OR interpretation of the P3 requires that P3 be elicited to novel, surprising stimuli and that it decline in amplitude over a number of trials (habituation). The first requirement, elicitation by unexpected events, is a typical feature of the P3. Regarding the second requirement, however, common folklore in ERP research has it that P3s can be elicited repeatedly over numerous trials with no obvious habituation. It is therefore interesting to contrast this common belief with a recent study by Polich (1990), who found a decline in P3 amplitude when comparing early with later trial blocks. Moreover, Donchin, Heffley, Hillyard, et al. (1984) argued that when the subject receives the stimulus passively the P3 also habituates over trials.

Donchin (1981) suggested that the P3 reflects the updating of work-

ing memory and named this change to the memory *context updating*. Subjects are presumed always to have a subjective expectancy, or "schema," that guides their responses to future stimuli. When an unexpected stimulus upsets this expectancy in subjective context, the schema in working memory is updated to enable the subject to act appropriately on the stimulus. In other words, the P3 is elicited whenever the subjective model of the environment has to be changed because new relevant information is being delivered with the stimulus (Donchin and Coles, 1988).

The view that the P3 component is related to context updating in working memory is not exclusive of an OR explanation, since it is possible to interpret the OR within the theoretical perspective of context updating.

P3-latency

The latency of the P3—that is, the time to its peak amplitude from the presentation of a stimulus—is not determined by the same parameters that determine P3 amplitude. Donchin and Coles (1988) suggest that P3 latency reflects the duration of stimulus evaluation: the longer it takes for a subject to evaluate the novelty or significance of a stimulus, the longer the latency. P3 latency is typically prolonged in certain neurodegenerative disorders, as Alzheimer's disease (see Squires and Ollo, 1986).
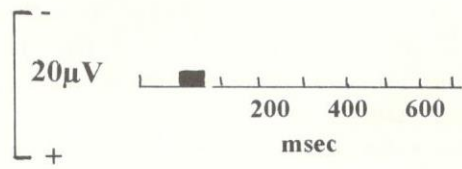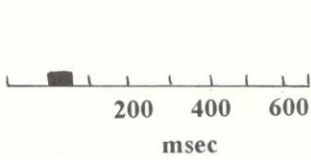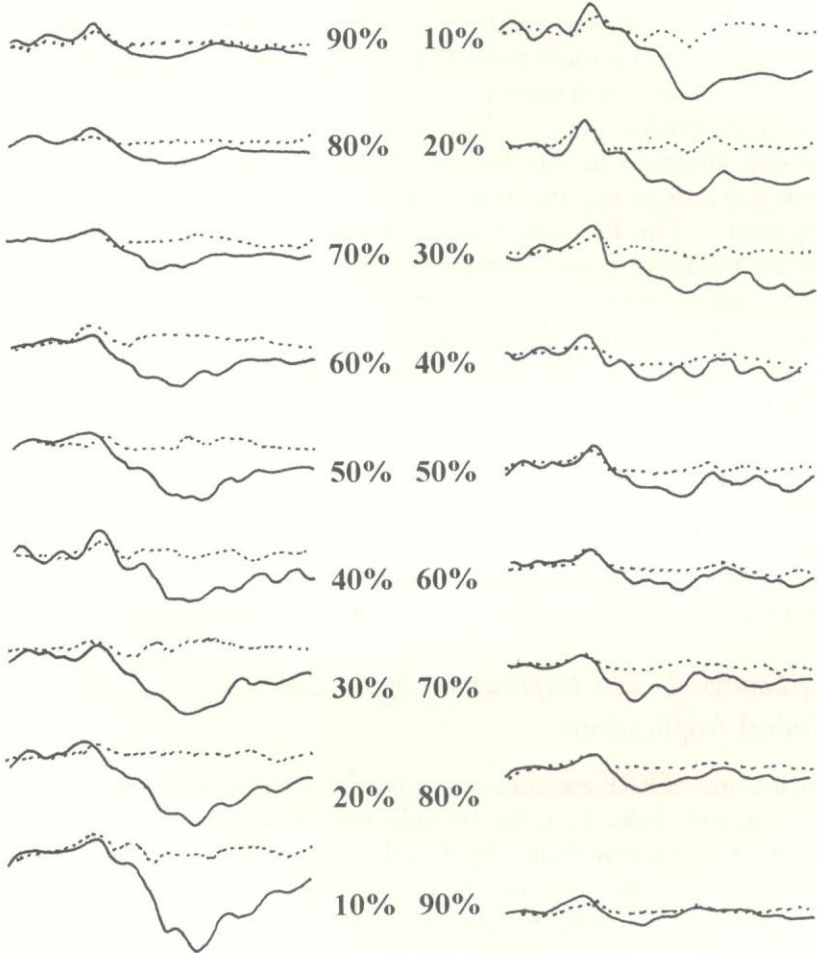
P3a and P3b

The P3 may in most cases be regarded as a single, unitary waveform elicited in response to improbable events, in particular when the sub-

Figure 12.15. Effects of varying the stimulus probability in the oddball paradigm with two auditory stimuli. The task of the subject was to count the number of the high-frequency tone in a session. ERPs were recorded from Pz. Note that the P300 component is largest when the subjects are asked to attend to (count) the stimuli and when there is a fairly large discrepancy between the probabilities for the attended and ignored stimuli. (Data from Duncan-Johnson and Donchin, 1977, reprinted with permission from the Society for Psychophysiological Research and the authors.)

Count High
Ignore

High tone   Low tone

90% 10%
80% 20%
70% 30%
60% 40%
50% 50%
40% 60%
30% 70%
20% 80%
10% 90%

200 400 600
msec

20μV

200 400 600
msec

ject has to pay close attention to the occurrence of the less frequent events. However, Squires, Squires, and Hillyard (1975) observed that the P3 actually consists of two distinct waveforms, P3a (with a latency around 250 msec) and P3b (with a peak latency around 300 msec).

The P3a has a more frontal scalp distribution, whereas the "classic P3b" distribution is more parietal. It has been suggested that the P3a "registers" a mismatch between the current memory template and the incoming stimulus—that is, the P3a would act as an attention switch, focusing attention to the deviant stimulus—while the P3b reflects more elaborate processing, involving active discrimination and action preparation. The P3a and P3b waveforms often overlap in subjects actively attending to stimuli during an oddball task, making it difficult to distinguish between them. P3a shares features with the MMN (see above) in that both are related to deviations in the physical characteristics of the stimulus (Näätänen, 1992). They differ, however, in the sense that MMN also may be elicited without subjective awareness of the stimulus deviation. The P3a is therefore a more genuine endogenous component than the MMN.

Figure 12.16 gives schematic representations of the P3a and P3b waveforms. Note the difference in scalp distribution between the two waveforms, with the P3a being maximal over the central and frontal areas while the P3b has a more posterior scalp distribution.

Psychophysiological Implications of the ERP
Clinical Applications

The features of ERP waveforms may be affected by various psychological disorders. Table 12.1, for example, lists the amplitudes and latencies of P3 waveforms elicited by the oddball paradigm in subjects with different clinical disorders (see Squires and Ollo, 1986, for further details). As a general rule, P3 latency is prolonged in individuals with disorders related to the aging process, particularly various forms of dementia, such as Alzheimer's disease, and degenerative disorders, such as Parkinson's disease. Note also that the latency is prolonged in elderly individuals not affected by such disorders.

P3 amplitudes are reduced in patients in whom various psychopathologies, such as schizophrenia and depression, or alcoholism have been diagnosed. It is, however, unclear whether these reductions reflect a direct cortical correlate of psychopathology, or whether they
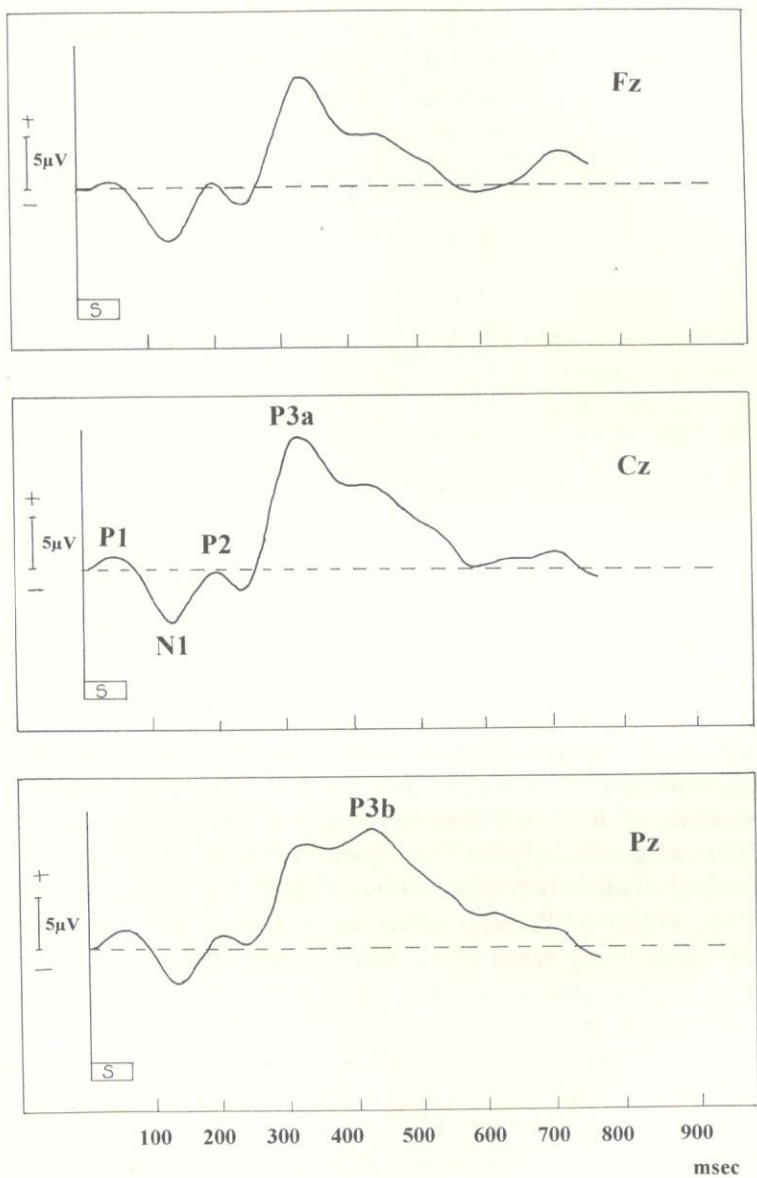
Figure 12.16. Development of the P3b component over the parietal lead, with P3a over the central lead. The distinction between P3a and P3b is difficult to make for recordings from frontal leads.

Table 12.1. P3 latency prolongation and P3 amplitude reduction in clinical groups with diminished mental function.

Effect on P3 wave	Clinical Diagnosis	References
Latency prolongation	Normal aging	Pfefferbaum et al. (1980b)
	Dementia	Syndulko et al. (1982) K. Squires et al. (1980)
	Head trauma	Syndulko et al. (1982) K. Squires et al. (1980)
	Retardation	N. Squires et al. (1979)
	Alcoholism	Pfefferbaum et al. (1979) Skerchock and Cohen (1981)
Amplitude reduction	Alcoholism	Begleiter et al. (1980) Porjesz et al. (1980)
	Schizophrenia	Verleger and Cohen (1978) Roth et al. (1980b)
	Depression	Goodin et al. (1978b) Litzelman et al. (1980)

Source: Adapted from Squires and Ollo (1987), with permission from Oxford University Press and the authors.

are secondary phenomena due to reduced activation and motivational drive in schizophrenic and depressive patients. P3 amplitude reduction is also observed to some extent in persons affected by dementia.

ERPs, and particularly the P3 amplitude, have been linked to claims of a biological mediation of alcoholism (Elmasian, Neville, Woods, et al., 1982; Begleiter, Porjesz, Bihari, et al., 1984). Both these papers reported that young males with a family history of alcoholism showed attenuated P3 amplitudes to both auditory and visual stimuli. Thus, P3 amplitude seemed to be a "marker" of risk for alcoholism in sons of fathers who were alcoholics. Both studies noted a significant reduction of the P3 amplitude between subjects with a family history of alcoholism and the controls (subjects with no family history of alcoholism). After the initial reports of a link between P3 amplitude and alcoholism, several investigators tried to replicate the original findings but with varying success. For example, Polich and Bloom (1988) found no systematic relationship between P3 amplitude and family history of alcoholism. In a recent literature survey and meta-analysis, however, Polich, Pollock, and Bloom (1994) concluded from the studies re-

viewed that individuals with a family history of alcoholism demonstrated smaller P3 amplitudes than individuals without a family history of alcoholism. Moreover, a possible reason for the failure of some investigators to replicate these findings may be what the authors called "moderator variables"—that is, differences in age, task difficulty, and stimulus modality across studies.

Language Processing

Although deviant, unexpected events are associated with mismatch negativity (MMN) and the P3 amplitude, some unexpected events, such as the presentation of incongruent semantic information, elicit late negative potentials around 400 msec, the N400 wave (Kutas and Hillyard, 1980). The N400 is lateralized to the right hemisphere and is maximal over the centroparietal scalp regions.

The typical paradigm used to elicit the N400 waveform is a reading task: the subject is asked to read a sentence whose last word is semantically incongruent with the rest of the sentence, thus creating a "surprise" effect. The words are presented serially on a screen, and the subject must read the words one by one at a fixed rate. An incongruent sentence, for example, may read: "The pizza was too hot to cry." The N400 amplitude is related to the degree of incongruity, possibly reflecting the existence of a specific cortical processor of semantics.

Related to the studies on N400 by Marta Kutas is ERP research on linguistic processing in congenitally deaf subjects (Neville, Kutas, and Schmidt, 1982). This research has determined that the late negative wave is not asymmetrically distributed in deaf adults, which may indicate a difference in cortical organization of language function in deaf and hearing subjects.

Word Repetition and Recognition Memory

In a conceptually similar study to that of Kutas and Hillyard (1980), Rugg (1985) also found a negativity around 400 msec after the presentation of words that had been primed by previous presentation or through semantic association. Rugg (1985) recorded ERPs when subjects performed a lexical decision task (deciding whether a string of letters briefly flashed on a screen is a word or not), in which a proportion of the words were either semantic associates or repetitions of the

preceding word. RTs were faster to the second item of pairs that were associated, as well as to repeated words that had been primed by the preceding word. The ERPs to the semantic primes were larger than those to targets, with a maximal negative peak amplitude around 400–450 msec after the stimulus was presented.

In several more recent studies (e.g., Rugg and Nagy, 1987, 1989; Friedman, 1990), it has been shown that repetition of a word in a string of words yields larger negative N300 and positive P300 responses after the first presentation of a word than after the repetition of the word. The "old versus new" effect could be either an enhancement of the P3 following the new item or a reduction in negativity in the response to the recognized items in the word string. Some authors have argued that the sustained positive wave during repetition priming to the second presentation of a word is different from a late P3; this sustained wave is labeled P600 since it occurs around 600 msec after the repeated word is presented.

A typical recognition-memory experiment (e.g., Friedman, 1990) involves presentations of blocks of around fifty words for about 300 msec on a screen at intervals of 2 sec. A certain number of nonrepeated words are presented between the first and second presentation of the repeated word. Subjects are instructed to respond "old" or "new" for each word seen on the screen by pressing one of two buttons as quickly as possible. ERPs to the new and old items are then separately averaged. Interestingly, the old-new effect in the ERPs was independent of whether the subject correctly identified a previously presented item as "old" or not. Thus, there is a dissociation between subjective awareness memory and cortical processes involved in this kind of recognition memory. In a recent paper, Dool, Stelmack, and Rourke (1993) reviewed the N400 literature with specific reference to dyslexia and dyslexic children. In general, dyslexic children have smaller N400 amplitudes than control children. This difference may indicate difficulties in semantic processing of words and problems in accessing words.

ERPs, Sleep, and Hypnosis

ERPs generated during sleep and during various sleep stages have been extensively studied (see Chapter 11 for a description of sleep stages). Summarizing the findings in the literature, Shagass (1972) concluded that the latency of the ERP becomes longer as an individual progresses

into deeper sleep stages, with the exception that ERPs during REM sleep are similar to those during the waking state. Overall, the data suggest that ERPs do occur during sleep, indicating a specific response from the brain to an external stimulus that the subject is not consciously experiencing.

Since then, other studies have shown that the auditory ERPs during REM differ from the corresponding potentials recorded during the waking state. A recent study from our laboratory (Nordby, Hugdahl, Stickgold, Brønnick, and Hobson, unpublished) showed that negative slow-wave shifts to the infrequent stimulus presented in the oddball paradigm (passive condition) during REM sleep differed from the potentials recorded during both non-REM sleep and the waking state. Frequent and infrequent stimuli were presented to the subject before going to sleep, during non-REM periods, during REM periods, and after awakening in the morning. Stimuli were 75 dB tones that differed in frequency and that were presented with 80 and 20 percent probabilities for the frequent and rare tones, respectively.

In this experiment REM versus non-REM periods were identified through recordings obtained by the Nightcap procedure developed by Allan Hobson and colleagues (Mamelak and Hobson, 1989). This procedure utilizes a piezoelectric sensor attached to the eyelid to detect eye movements while the subject sleeps. The main results (see Figure 12.17) were larger P2 responses to the infrequent stimulus during sleep than during waking, and particularly during REM sleep. Moreover, there was a profound negative slow-wave shift at about 500–700 msec after the deviant stimulus in REM sleep.

The question of whether instructions to a subject in a hypnotic state either to block or to enhance perceptual sensations also alter brain potentials has received mixed empirical support. Early studies (Shagass and Schwartz, 1964) found that hypnotic suggestions had no effect on responses to somatosensory stimuli, nor did instructions to "dim" or "make brighter" a visual stimulus have any effect (Beck, 1963). However, more recent studies have shown significant reduction of the P3 amplitude elicited in responses to visual stimuli when subjects in hypnosis were instructed to imagine a cardboard box blocking their view of the monitor presenting the stimulus (Spiegel, Cutcomb, Ren, et al., 1985; see also Spiegel, 1991).

Interestingly, the P3 attenuation that followed hallucinatory blocking of the visual field was more pronounced over the right hemi-

Wake

Pre-sleep

Post-sleep
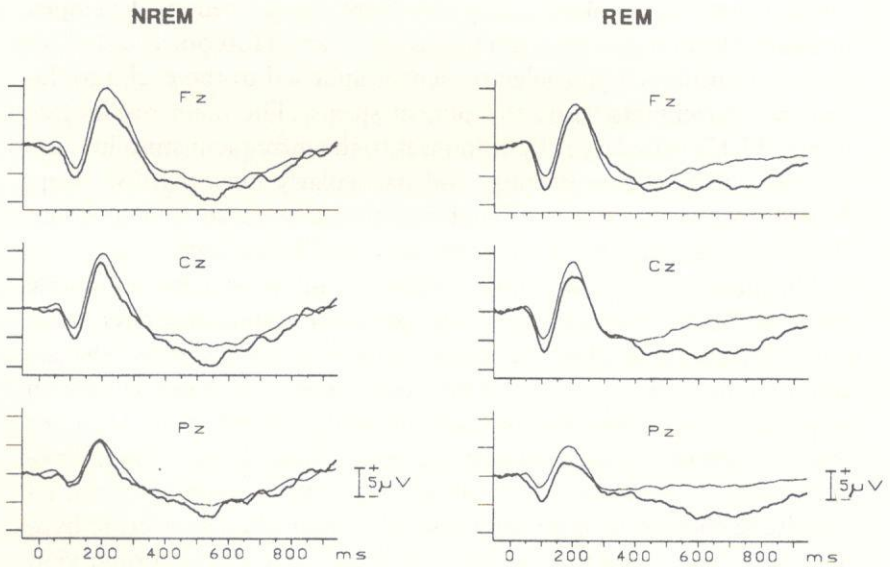
Sleep

NREM

REM
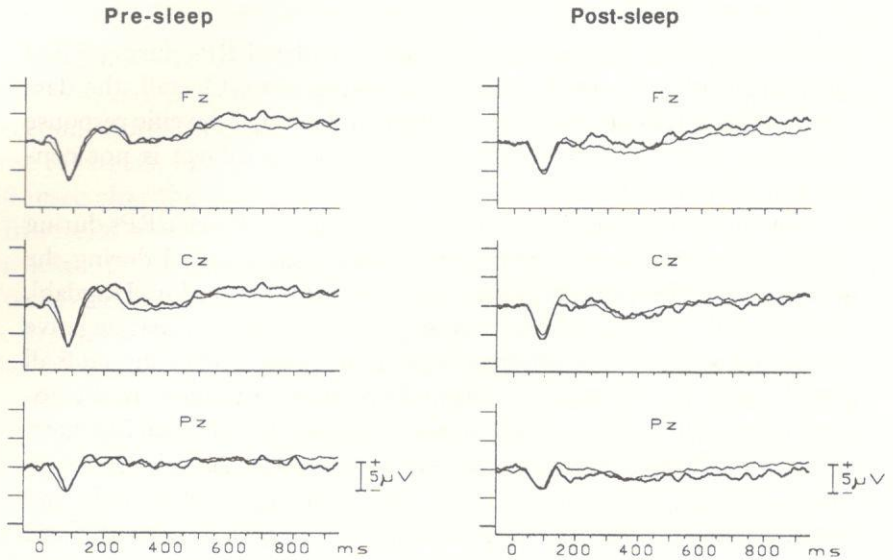
Figure 12.17. ERP responses to tones in an experiment using a passive oddball paradigm during wake and REM and NREM sleep. Note the profound N1-P2 complex and the slow-wave negativity during sleep, and particularly during REM sleep, indicating a kind of hypervigilance during REM sleep.)

sphere, possibly indicating a right-hemisphere activation shift in hypnosis. No blocking effect was observed in nonhypnotizable subjects. Spiegel (1991) also reported similar P3 reduction in responses to somatosensory stimuli when the subjects in hypnosis imagined that their hand was becoming cool and numb. In addition to the P3 reduction, there was also reduction of the early P1 component, suggesting an early filtering, or gating, mechanism in the sensory modality.

Summary

Figure 12.18 presents a highly schematized and simplified view of some of the later exogenous and endogenous components of event-related potentials (ERPs) that traditionally have attracted the interest of psychophysiologists. Early components of the ERP (those to the left on the horizontal axis, which represents time) probably reflect automatic, nonvolitional kinds of processing. The later components reflect active, controlled engagement on behalf of the subject and attention switching as the "gatekeeper" into a controlled mode of processing. The cognitive processes listed under the different ERP waveforms represent a continuum of more automatic processes, from the comparison of the physical features of stimuli involved in mismatch negativity (MMN) to higher-level cognitive processing, such as the detection of semantic incongruities reflected in the N400 component. ERPs have good temporal resolution—changes that occur in just milliseconds can be detected—although their spatial resolution—the exact localization of the source generator in the underlying brain tissue—is poorer. A major challenge to future research in ERP psychophysiology is to identify and localize the source dipoles that give rise to the various scalp-recorded ERP waveforms.

ERPs are a noninvasive measure of localized cortical activity in response to external (or internal) triggering events. An example used often in this chapter is the presentation of an unexpected auditory stimulus against a background of recognized, familiar tones. ERPs provide important information about central nervous system (CNS) activity in conjunction with psychological events. In this respect ERPs complement other psychophysiological measures that are focused on the activity of the automatic nervous system (ANS), like electrodermal or cardiovascular measures. ERPs and autonomic measures typically
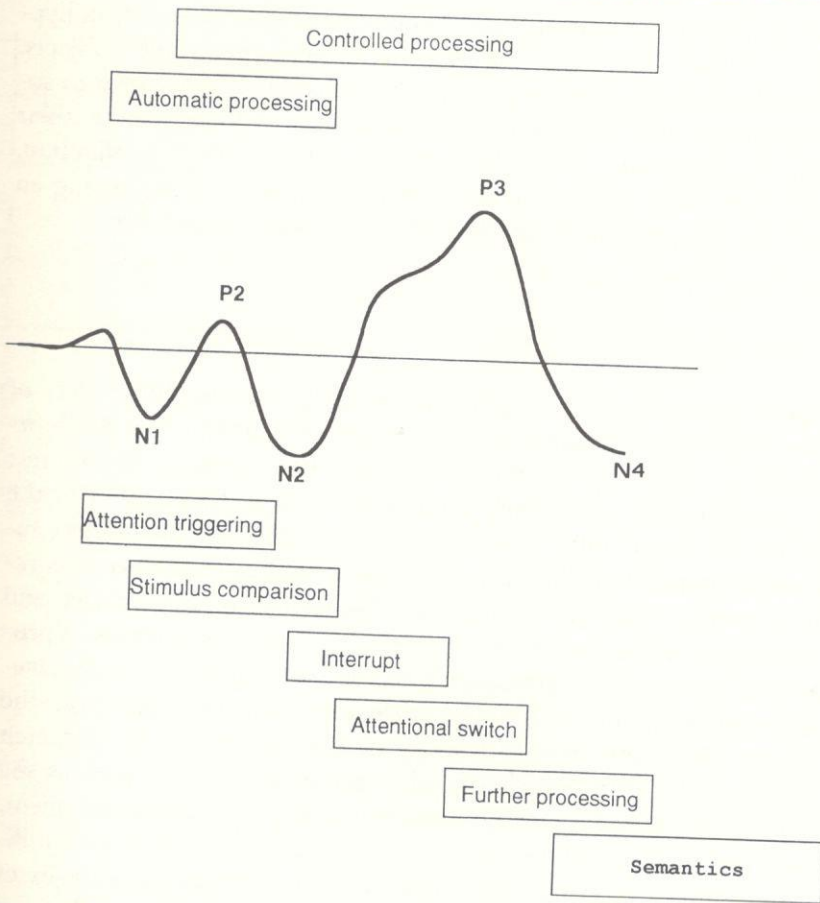
Figure 12.18. Summary of ERP components and cognitive processes, illustrated on a continuum from automatic to controlled processing. (Courtesy of Helge Nordby, University of Bergen.)

operate on different time scales (see also Chapter 1), however, with ERPs operating in the range of milliseconds and electrodermal responses operating in the range of seconds. It is sometimes difficult, therefore, to obtain simultaneous CNS and ANS measures within the same experimental setting. This integration of CNS and ANS measures is, however, important for the future development of psychophysiological knowledge.