CHAPTER THREE

EVENT-RELATED BRAIN POTENTIALS

Methods, Theory, and Applications

MONICA FABIANI, GABRIELE GRATTON, & MICHAEL G. H. COLES

Introduction and Historical Context

Ever since Berger (1929) demonstrated that it is possible to record the electrical activity of the brain by placing electrodes on the surface of the scalp, there has been considerable interest in the relationship between these recordings and psychological processes. Whereas Berger and his followers focused their attention on spontaneous rhythmic oscillations in voltage (i.e., on the electroencephalogram or EEG), more recent research has concentrated on those aspects of the electrical potential that are specifically time-locked to events (i.e., on event-related brain potentials or ERPs). The ERPs are regarded as manifestations of brain activities that occur in preparation for, or in response to, discrete events, be they internal or external to the subject. Conceptually, ERPs are regarded as manifestations of specific psychological processes.

The history of ERP research is closely linked with the development of technologies that allow the extraction of event-related brain activity from the background EEG oscillations, which are usually much larger in amplitude and therefore tend to obscure it (for an extended review see Donchin 1979). The first of these techniques was based on the photographic superimposition of several time-locked EEG traces (Ciganek 1964; Dawson 1947). This method, however, was very cumbersome, and it was soon replaced by the development of several analog signal averagers (see Donchin 1979). However, it was not until the 1960s and the advent of digital computers (and thus of digital signal averaging) that ERP research really took flight.

The last three decades have seen several paradigmatic shifts in the focus of this research. In the 1970s and early 1980s, the analysis and interpretation of ERPs was informed by the computer analogy of the human information processing system: ERP components (i.e., peaks and troughs in the waveforms that tend to covary in response to experimental manipulations) could be viewed as subroutines within this system, each indexing some aspect of cognitive processing (Donchin 1979, 1981). Within this framework, the focus was mostly on the relationship between cognitive processes and ERP activity, without much reference to the possible underlying brain sources of the potentials. In the 1990s, however, the rapid expansion of noninvasive brain imaging methods (see e.g. Toga & Mazziotta 1996) and recent technological advances that allow simultaneous recordings from dense electrode arrays have brought forth two further changes (discussed more extensively in the next section): (i) several algorithms have been developed to derive the putative brain sources of surface-recorded electrical activity; and (ii) several attempts have been made at integrating the recording of ERPs with other brain imaging methods, such as positron emission tomography (PET), functional magnetic resonance imaging (fMRI), magneto-encephalography (MEG), and optical imaging (event-related optical signal, or EROS). At present, ERPs are one of the most established methods in cognitive neuroscience and are considered the "gold standard" in terms of temporal resolution among noninvasive imaging methods.

In the following section of this chapter we will review the procedures for ERP derivation, what is known about the underlying sources of ERPs and their relationship to physiological function, and the concept of component and some aspects of component quantification. Later in this chapter, we will focus on the relationship between ERPs and psychological function.

Physical Context

DERIVING EVENT-RELATED POTENTIALS

The procedures used to derive ERPs begin with the same amplifiers and filters used to obtain EEG (see Figure 1).

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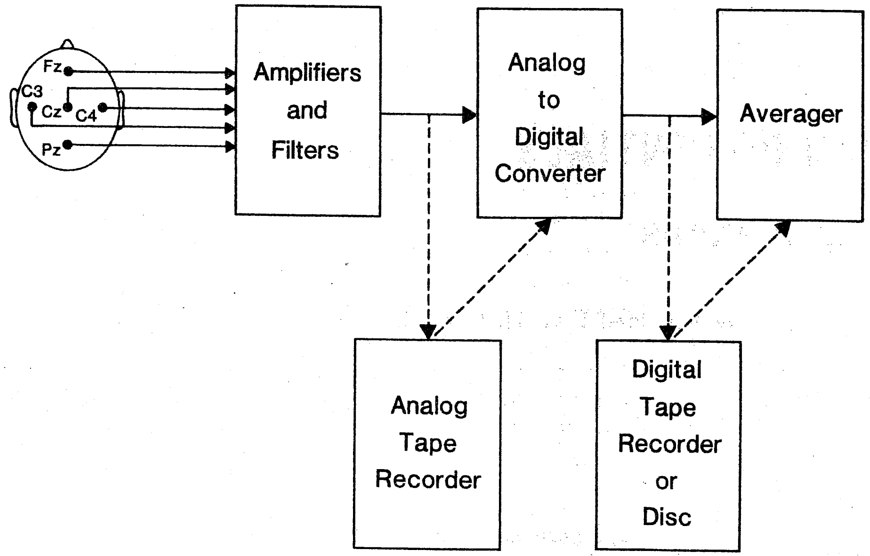


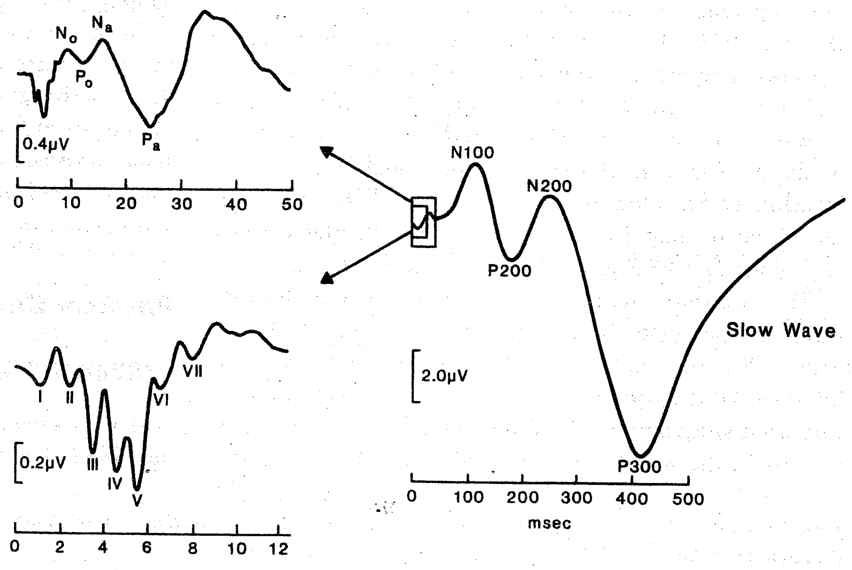
Figure 1. Schematic representation of the operations involved in the recording of event-related brain potentials. From left to right: (a) Top view of the head, indicating the placements of five electrodes (Fz, C3, Cz, C4, and Pz) from which EEG is recorded – note that other locations are also frequently used. (b) The EEG signal is then transferred to an amplifying and filtering system. (c) The amplified and filtered signal may be stored temporarily on an analog magnetic tape. (d) The analog signal is then converted into a digital signal by sampling the potential at a high frequency (usually at least 100 Hz) by an analog-to-digital converter. (e) The digitally transformed signal may be stored on a digital storage device (magnetic tape or disk). (f) Finally, ERPs are extracted from the digitized EEG signal via point-by-point averaging across a large sample of trials (more than 20).

Electrodes are attached to the scalp at various locations and connected to amplifiers. The recording locations are usually chosen according to the International 10–20 system (Jasper 1958) or expanded versions of this system (e.g. Nuwer 1987), so that between-laboratory and between-experiment comparisons are possible. The outputs of the amplifiers are converted to numbers by a device for measuring electrical potentials, an analog–digital converter. The potentials are sampled at a frequency ranging from 100 to 10,000 Hz (cycles per second) and are usually stored for subsequent analysis.

The ERP is small (a few microvolts) in comparison to the EEG (about 50 μV). Thus, the analysis generally begins with a procedure to increase the discrimination of the "signal" (the ERP) from the "noise" (background EEG). The most common procedure involves *averaging* samples of the EEG that are time-locked to repeated occurrences of a particular event. The number of samples used in the average is related to the signal-to-noise ratio. However, in all cases, the samples are selected so as to bear a constant temporal relationship to an event. Because all those aspects of the EEG that are not time-locked to the event are assumed to vary randomly from sample to sample, the averaging procedure should result in a reduction of these potentials, leaving the event-related potentials visible.[1] The resulting voltage × time function (see Figure 2) contains a number of positive and negative peaks, which are then subjected to a variety of measurement operations (see Chapters 32 and 33 of this volume).

Because ERP measures are always taken as differences in potential between two recording locations, they will vary as a function of (a) the electrode site at which they are recorded and (b) the reference electrode used. Spatial (topographic) distribution is regarded as an important discriminative characteristic of the ERP (Donchin 1978; Sutton & Ruchkin 1984). Therefore, positive and negative peaks in the ERP are generally described in terms of their characteristic scalp distribution, their polarity, and their latency.

Figure 2. A schematic representation of ERP components elicited by auditory, infrequent target stimuli. The three panels represent three different voltage × time functions: the left bottom panel shows the very early sensory components (with a latency of less than 10 msec); the left top panel shows the middle latency sensory components (with a latency of between 10 and 50 msec); and the right panel shows late components (latency exceeding 50 msec). Note the different voltage and time scales used in the three panels, as well as the different nomenclatures used to label the peaks (components). Adapted from Donchin (1979) with permission from the author and Plenum Publishing.



The labels given to the peaks of an ERP waveform usually include descriptors of polarity and latency. According to this logic, P300 refers to a positive peak with a modal latency of 300 msec. A similar labeling system involves a descriptor of polarity (P or N) followed by a number designating the ordinal latency of the component. Within this system, "P3" refers to the third positive peak in the waveform. Other descriptors that can be used in labeling peaks make reference to the scalp locations at which the potential is maximal (e.g., frontal P300), or to the psychological or experimental conditions that control the potential (e.g., novelty P3, readiness potential, mismatch negativity or MMN).

THE EXOGENOUS VERSUS ENDOGENOUS DISTINCTION

From a psychological point of view, it is convenient to distinguish between different types of ERPs. First we can identify those ERPs whose characteristics are mostly controlled by the physical properties of an external eliciting event. Such evoked potentials are considered to be obligatory and are referred to as "sensory" or "exogenous." Second, we can identify ERPs whose characteristics are determined more by the nature of the interaction between the subject and the event. For example, some ERPs vary as a function of the information processing activities required of the subject; others can be elicited in the absence of an external eliciting event. These potentials are referred to as "endogenous." (For a discussion of the distinction between exogenous and endogenous potentials, see Donchin, Ritter, & McCallum 1978.)

Although the exogenous–endogenous distinction is a useful method for classifying many ERP components, some potentials possess characteristics that are intermediate between these two groups and are therefore called "mesogenous." The N100 is such an example, for it is sensitive to both the physical properties of the stimulus as well as to the nature of the interaction between the subject and the event (e.g., whether the event is to be attended).

FROM THE BRAIN TO THE SCALP: THE GENERATION AND PHYSIOLOGICAL BASIS OF ERPs

In this section, we review evidence that relates the scalp-recorded electrical activity to its underlying anatomical and physiological basis (see also Allison, Wood, & McCarthy 1986; Nunez 1981). It is generally assumed that ERPs are distant manifestations of the activity of populations of neurons within the brain. This activity can be recorded on the surface of the scalp because the tissue that lies between the source and the scalp acts as a volume conductor. Because the electrical activity associated with any particular neuron is small, at the scalp it is only possible to record the integrated activity of a large number of neurons. Two requirements must be met for this integration to occur: (i) the neurons must be active synchronously, and (ii) the electric fields generated by each particular neuron must be oriented in such a way that their effects at the scalp cumulate. As a consequence, only a subset of the entire brain electrical activity can be recorded from scalp electrodes.

Two considerations further restrict the likely sources of the ERP. First, because the ERP represents the synchronous activity of a large number of neurons, it is probably not due to the summation of presynaptic potentials (spikes), since these potentials have a very high frequency and short duration. On the other hand, postsynaptic potentials, which have a relatively slower time course, are more likely to be synchronous and hence to summate and so produce scalp potentials. Thus, it is commonly believed that most scalp ERPs are the summation of the postsynaptic potentials of a large number of neurons that are activated (or inhibited) synchronously (Allison et al. 1986).

A second consideration concerns the orientation of neuronal fields. Because the electric fields associated with the activity of each individual neuron involved must be oriented in such a way as to cumulate at the scalp, only neural structures with a specific spatial organization may generate scalp ERPs. Lorente de Nò (1947) specified the spatial organizations that are required for the distant recording of the electrical activity of a neural structure. He distinguished between two types, "open fields" and "closed fields." A structure having an open-field organization is characterized by neurons that are ordered so that their dendritic trees are all oriented on one side of the structure while their axons all depart from the other side. In this case, the electric fields generated by the activity of each neuron will all be oriented in the same direction and summate. Only structures with some degree of open-field organization generate potentials that can be recorded at the scalp. Open fields are obtained whenever neurons are organized in layers – as in most of the cortex, parts of the thalamus, the cerebellum, and other structures.

A structure with a closed-field organization is characterized by neurons that are concentrically or randomly organized. In both cases, the electric fields generated by each neuron will be oriented in very different (sometimes opposite) directions and thus will cancel each other out. Examples of closed-field organization are given by some midbrain nuclei.

From this analysis it is clear that ERPs represent just a sample of the brain electrical activity associated with a given event. Thus, it is entirely possible that a sizeable portion of the information processing transactions that occur after (or before) the anchor event are silent as far as ERPs are concerned. For this reason, some caution should be used in the interpretation of ERP data. For instance, if an experimental manipulation has no effect on the ERP, we cannot conclude that it does not influence brain processes. By the same token, if two experimental manipulations have the same effect on the ERP, it cannot be concluded that they necessarily influence identical processes.

FROM THE SCALP TO THE BRAIN: INFERRING THE SOURCES OF ERPs

So far we have examined how particular properties of neuronal phenomena may determine whether they will be recorded at the scalp. We have approached the problem of ERP generation in a direct fashion, from properties of the generators to predictable scalp observations. In most cases, however, we have only limited information about the neural structure(s) responsible for a specific aspect of the ERP. Our database consists of observations of voltage differences between scalp electrodes or between scalp electrodes and a reference electrode. To determine which neural structures are responsible for the scalp potential (i.e., to identify the neural generators of ERPs), we must solve the "inverse problem"; that is, we have to infer the *unique* combination of neural generators whose activity results in the potential observed at the scalp.

In solving this problem, we are confronted with an indefinite number of unknown parameters. In fact, an indefinite number of neural generators may be active simultaneously, and each of them may vary in amplitude, orientation of the electric field, and location inside the head. Because a limited number of observations (the voltage values recorded at different scalp electrodes) is used to estimate an indefinite number of parameters, it is clear that the inverse problem does not have a unique solution (i.e., an infinite number of different combinations of neuronal generators could produce the same scalp distribution). A further complication is that the head is not a homogeneous medium. Therefore, the electric field generated by the activity of a given structure is difficult to compute. A particularly important distortion of the electric fields is caused by the skull – a very low-conductance medium that reduces and smears electric fields. For all these reasons, we cannot unequivocally determine which structures are responsible for the ERP observed at any given moment when the only information available is provided by the potentials recorded at scalp electrodes.

Notwithstanding these problems, investigators have tried to identify the neural sources of the scalp ERP using a variety of approaches, involving both noninvasive and invasive techniques. Noninvasive techniques include scalp recordings from dense electrode arrays combined with interpolated mapping and source analysis algorithms (which involve complex mathematical procedures and are based on a number of assumptions) as well as the combination of ERPs with other imaging methods that possess higher spatial resolution (e.g., PET, fMRI, MEG, EROS). Invasive techniques include recordings from indwelling macroelectrodes (in humans or in animals) and lesion data (also in humans or animals).

Dense Electrode Arrays and Source Modeling

During the last few years, several companies have marketed data acquisition systems for electrophysiology designed to record from a large number of channels (up to 256; see e.g. Tucker 1993). These systems allow investigators to derive detailed maps of brain electrical activity, which can (in principle) reveal differences that are of interest for the study of various experimental conditions and/or subject populations. Yet because the skull operates as a low-pass spatial filter, the question has arisen of what is the effective optimal spatial sampling for ERP recording. For instance, Srinivasan and colleagues (1996; see also Tucker 1993) have recently shown that 256 locations may accurately reproduce the most significant local variations in scalp electrical activity.

The increase in the number of recording locations has facilitated the study of the distribution of ERP activity across the scalp and, in particular, the construction of accurate maps of surface activity, which are usually based on interpolation procedures (Perrin et al. 1987). Another advantage of dense-array recording is the possibility of generating models of the three-dimensional locations of the brain generators involved in producing the surface ERP activity (i.e., equivalent dipole analysis). Computational approaches to dipole analysis involve generating several alternative hypotheses about the neural structures that may be active at a given moment and that may be responsible for an observed scalp ERP. The distribution of potentials across the scalp that would be generated by each of these structures can then be computed using a direct approach. Finally, the structure whose activity best accounts for the observed scalp distribution can be identified (Scherg, Vajsar, & Picton 1989; Scherg & Von Cramon 1986; see also Chapter 33).

ERPs and Other Imaging Methods

These computational approaches make a number of assumptions that cannot always be verified, and they also require the availability of specific neurophysiological knowledge about candidate underlying structures. In some cases, this knowledge can be based on data obtained with other imaging methods, such as the use of magnetic field recordings (MEG). Magnetic fields generated by brain activity are extremely small in relation to magnetic fields generated by environmental and other bodily sources. Therefore, their measurement is both difficult and expensive. The advantage of measuring the magnetic field is that it is practically insensitive to variations of the conductive media (such as those due to the presence of the skull). It is therefore easier to compute the source of a particular field. An in-depth discussion of the problems and characteristics of MEG is beyond the scope of this chapter and can be found elsewhere (Beatty et al. 1986). We will only note here that using MEG to determine the source of neural components still requires assumptions about the number of neural structures active at a particular moment in time.

In other cases, knowledge about candidate ERP sources can be based on the integration of data from a variety of different imaging methods applied to the same subjects in the same experimental conditions. In this way, one can exploit the differential spatial and temporal resolutions of the different methods. Some issues related to this approach are discussed by Gratton in Chapter 33 of this volume.

Invasive Methods

Invasive techniques can also be used for the identification of the sources of ERP components. One such technique involves implanting electrodes within the brain of humans or animals. Research on humans has been made possible by the need for recording EEG activity in deep regions of the brain for diagnostic purposes (Halgren et al. 1980; Wood et al. 1984). A problem with human research is that the indwelling electrodes are located according to clinical rather than scientific criteria and may therefore fail to map the regions involved in the generation of scalp ERPs. This issue may be partially addressed by research on animals (e.g., Buchwald & Squires 1983; Csepe, Karmos, & Molnar 1987; Javitt et al. 1992; Starr & Farley 1983). However, a problem with animal research is the difficulty of determining whether the ERP observed in animals corresponds to that observed in humans, since there are fundamental differences in the anatomy and physiology of animal and human brains. Finally, a general problem with depth recording is that it is difficult to know the extent to which the scalp-recorded ERP is due to the activity of the structures that have been identified by the indwelling electrodes. This problem can be addressed, at least in part, by lesion studies with animals and humans showing that lesions in the structure identified as the candidate generator result in the elimination of the scalp potential. Examples of animal lesion studies have been reported by Paller et al. (1988b) and by Javitt et al. (1992); studies of lesioned human patients have been made by Alho et al. (1994), Johnson (1988, 1989, 1993), and Knight (1984, 1997; see also Knight et al. 1981).

In summary, although solving the inverse problem does present difficulties, several techniques have been developed for identifying the source of ERP components. Although no single method may be able to give definitive answers in all cases, the convergence of several techniques may provide useful information about the neural structures whose activity is manifested at the scalp by the ERP.

THE CONCEPT OF COMPONENT AND ITS ALTERNATIVES

As we have noted, the ERP can be described as a voltage × time × location function. We assume that the various voltage fluctuations represented by this function reflect the summed activity of neuronal populations. This neurophysiological activity, in turn, is assumed to correspond to some psychological process. One concept that has evolved in the area of ERP research is that of *component,* which is commonly taken to reflect the tendency of segments of the ERP waveforms to covary in response to specific experimental manipulations. According to this logic, the total ERP is assumed to be an aggregate of a number of ERP components. Components can be defined in three different ways (Fabiani et al. 1987; Näätänen & Picton 1987). First, components can be defined in terms of the positive and negative peaks (maxima and minima) that are observed in the ERP waveform. Second, components can be defined as aspects of the ERP waveform that are functionally associated – in other words, that covary across subjects, conditions, and/or locations on the scalp. Third, components can be defined in terms of those neural structures that generate them. These definitions may converge in some circumstances. However, as Näätänen and Picton (1987) indicated, a peak in the ERP waveform (e.g., the N1) may represent the summation of several functionally and structurally distinct components. It can also be assumed that the same brain structure may contribute to more than one component and that different brain structures may produce activity that is functionally equivalent (e.g., homologous structures in the left and right hemispheres, such as the primary sensory and motor cortices). Thus, the adoption of one or another of these definitions will have important consequences for the interpretation of the component structure of the ERP waveform. A corollary of this is that different measurement procedures will be required depending on the type of component definition adopted. These procedures will be reviewed in subsequent sections after a brief discussion of general measurement issues.

Recently, other approaches to the interpretation of the ERP have been developed in which the "classic" concept of component is not required. For instance, investigators have used subtraction methods to isolate effects that may be riding over several different components. These include, among others, the repetition effect (i.e., the differential response observed for items that have been previously seen with respect to new items) and the attention effect (i.e., the differential response to items that are attended with respect to those that are not). Note that, by using this approach, the focus is shifted from an interest in describing the functional significance of the ERP component per se to an interest in what the observed ERP can tell us about the way stimuli are processed.

QUANTIFICATION OF ERP COMPONENTS

In this section, we describe some general measurement issues pertaining to the ERP as well as procedures that have been used to quantify ERP activity. As mentioned earlier, the precise choice of measurement operations will depend, at least in part, on the way in which ERP activity is interpreted. For further information about ERP measurement issues, see Chapter 33.

Artifacts

The potential recorded at the scalp can be influenced by sources of electrical activity that do not arise from the brain. Examples of these sources of artifact include the movement of eyeballs and eyelids, tension of the muscles in the head and neck, and the electrical activity generated by the heart. These artifacts can be dealt with in the following ways. First, one can set up the recording situation so that artifacts are minimized. This can be accomplished by suitable choice of electrode locations and of the subject's environment and task. Second, one can simply discard records that contain artifacts. Unfortunately, this procedure may lead to a bias in the selection of the observations and/or subjects. Third, one can use filters to attenuate artifactual activity. This procedure is useful when the frequency of the artifactual activity is outside the frequency range of the ERP signal of interest. For example, the frequency of electromyographic (EMG) activity is higher than that of most endogenous ERP components. Fourth, one can attempt to measure the extent of the artifact and then remove it from the data. This procedure has been used most frequently in the case of ocular artifacts, and a number of correction algorithms have been developed (for reviews see Brunia et al. 1989; Gratton 1998). The use of correction procedures is particularly useful whenever the number of trials that can be collected is limited or when participants have difficulty controlling their eye movements (e.g., children or patient populations).

Signal-to-Noise Ratio

Several procedures have been advocated to increase the signal-to-noise ratio, including filtering, averaging, and pattern recognition (Coles et al. 1986; see also Chapter 33). Filtering involves the attenuation of noise whose frequency differs from that of the signal. For example, most endogenous components have frequencies of between 0.5 Hz and 20 Hz. Thus, at the time of recording (or later, at the time of analysis), analog or digital filters can be used to attenuate activity outside this frequency range. Great care should be taken in the selection of filters. The amplitude and latency of an ERP component (as well as the general ERP waveform) will be distorted if the bandpass of the filter excludes frequencies of interest (see Figure 3).

Averaging involves the summation of a series of EEG epochs (or trials), each of which is time-locked to the event of interest. These EEG epochs are assumed to be the product of two sources: (i) the ERP, and (ii) other voltage fluctuations that are not time-locked to the event. Because, by definition, these other fluctuations are random with respect to the event, they should average to zero and so leave the time-locked ERP both visible and measurable. If (a) the ERP signals are constant over trials, (b) the noise is random across trials, and (c) the ERP signals are independent of the background noise, then the signal-to-noise ratio will be increased by the square root of the number of trials included in the average.

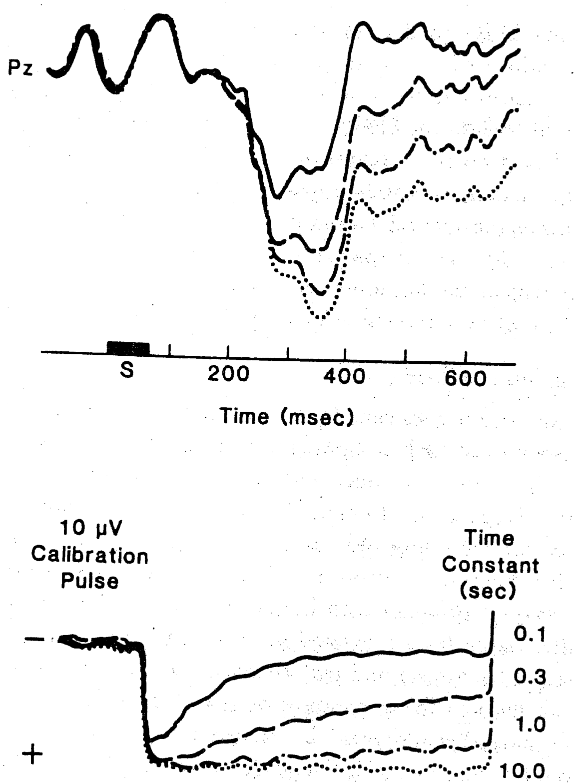


Figure 3. ERPs elicited by counted, rare tones (upper panel). The data recorded with four different high-pass filter settings ("time constant") are superimposed. Stimulus occurrence is indicated by an S on the time scale. Calibration pulses (lower panel) are plotted on the same voltage × time scale as the ERPs. Note the reduction in amplitude and deformation of the ERP waveshape produced by progressively shorter time constants, which reduce low-frequency activity. Reprinted from Duncan-Johnson & Donchin (1979) with permission from the authors and The Society for Psychophysiological Research.

One of the problems with the averaging procedure is that the three assumptions described in the previous paragraph are typically not always satisfied. In particular, if the latency of the ERP varies from trial to trial (latency jitter), then the average ERP waveform will not be representative of the actual ERP of any individual trial. A related issue is that investigators may be interested in measures of the ERP on individual trials. Thus, a major thrust in ERP methodology has been to derive procedures for single-trial analysis.

Pattern recognition techniques allow the investigator to identify segments of the EEG epoch that contain specific features (e.g., a particular peak pattern that is characteristic of a given ERP component). Examples of pattern recognition techniques are cross-correlation, Woody filter (Woody 1967), and stepwise discriminant analysis (Donchin & Herning 1975; Horst & Donchin 1980; Squires

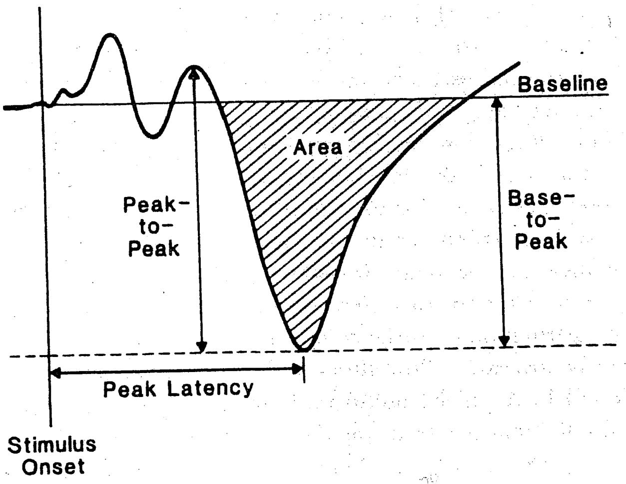


Figure 4. Schematic representation of an ERP waveform, indicating different procedures for component quantification. Three types of peak measures are indicated. The peak latency is obtained by measuring the interval (in msec) between the external triggering event and a positive or negative peak in the waveform. The base-to-peak amplitude measure is obtained by computing the voltage difference (in μV) between the voltage at the peak point and a baseline level (usually the average prestimulus level). The peak-to-peak amplitude measure is obtained by computing the voltage difference between the voltage at the peak point and the voltage at a previous peak of opposite polarity. The area measure is obtained by integrating the voltage between two timepoints.

& Donchin 1976). For more general discussions of pattern recognition techniques, see Fabiani et al. (1987), Glaser and Ruchkin (1976), and Chapter 33.

Peak Measurement

As we have indicated, ERP components can be defined in terms of peaks having characteristic polarities and latency ranges. Thus, a measurement operation that corresponds to this definition involves the assessment of peak amplitude (in microvolts) and/or peak latency (in milliseconds); see Figure 4. Amplitude is usually measured with reference either to the pre-event, or baseline, voltage level (base-to-peak amplitude) or to some other peak in the ERP waveform (peak-to-peak amplitude). Latency is measured with reference to the onset of the event. When the component under analysis does not have a definite peak, it is customary to measure the integrated activity (area measure) or the average activity (mean-amplitude measure) across a particular latency range.

Covariation Measures

Components can also be defined in terms of segments of the ERP waveform that exhibit covariation across subjects, conditions, and scalp locations. As a consequence, procedures are needed to identify and measure these segments. These procedures often entail measuring the extent to which a particular pattern of variation is represented in a waveform. This can be determined by measuring the covariation (or, sometimes, the correlation) of the waveform (or a segment of it) with an idealized wave representing the component of interest. The "ideal" wave can be identified using statistical methods, such as principal components analysis (PCA; Donchin & Heffley 1978) or discriminant analysis (Donchin & Herning 1975). Alternatively, the ideal wave can be selected using arbitrary models, such as a cosinusoidal function (Fabiani et al. 1987; Gratton et al. 1989b). These types of analyses are advantageous in the presence of noise or when there is substantial component overlap; however, Fabiani et al. (1987) and Gratton et al. (1989b) showed that component recognition using peak procedures may actually be both reliable and valid, provided that data are adequately filtered.

Source Activity Measures

A third way of defining components is in terms of underlying sources. According to this definition, we should quantify the activity of these sources to provide latency and amplitude measures of the different components. As noted previously, the relationship between scalp electrical activity and source activity is difficult to describe and requires a number of assumptions. Recently, large strides have been made in this area with the development of algorithms for dipole (e.g., BESA – Scherg & Von Cramon 1986; Scherg et al. 1989) and distributed (EMSE – Greenblatt et al. 1997; LORETA – Baillet & Garnero 1997; Pascual-Marqui, Michel, & Lehmann 1994) source analyses. Both of these approaches are based on modeling efforts. Spatiotemporal dipole models fit a small number of individual point dipoles to data that vary over space and time. The location and orientation of the dipoles may be fixed, whereas amplitude and polarity are left free to vary over time. In this way it is possible to represent variations in surface activity in terms of variations of the activity of a few underlying brain structures.

In contrast to dipole models, distributed source models assume that extended segments of the cortex (or even the entire cortex) can be active simultaneously. To express local variations (and hence explain variations in surface distribution), these algorithms allow the relative contribution of individual areas of the cortex to vary over time. These models, although perhaps more realistic, are usually underdetermined from a statistical point of view (i.e., they include more free parameters than data points). Therefore, external criteria are necessary to constrain the number of possible solutions (e.g., minimum norm, correlation between adjacent data points). Note that both dipole and distributed modeling efforts can be guided and constrained by anatomical and functional data obtained with other methods (e.g., MRI, fMRI, PET).

Problems in Component Measurement

In this section we discuss two specific problems that arise during component measurement. The first problem concerns the commensurability of the measurements of different waveforms. Is a particular component, recorded under a particular set of circumstances, the same as that recorded in another situation? This is especially a problem when we define components as a peak observed at a given latency. For example, if the latency of the peak differs between two experimental conditions, we would be led to conclude that different components are present in the two sets of data. How can we be sure that the same component varies in latency between the two conditions, rather than that two different components are present in the two different conditions? A solution to this problem could be derived from a careful examination of the pattern of results obtained and from a comparison of these results with what we already know about different ERP components. Of course, this means that we are including a large number of empirical and theoretical arguments in the definition of each ERP component – definitions that may differ from one component to another and from time to time. For example, the definition of a component may include not only polarity and latency but also distribution across the scalp and sensitivity to experimental manipulations (see e.g. Fabiani et al. 1987). Thus, it is clear that a correct interpretation of the component structure of an ERP waveform requires some background information about the components themselves. In turn, this indicates that the concept of component is likely to evolve over time (as more knowledge is accumulated) and that revisions of traditional component classifications may sometime be necessary.

A second problem in component measurement is that of component overlap. Usually, ERP components do not appear in isolation, but several of them may be active at the same moment in time. This reflects the parallel nature of brain processes. When this occurs, it is difficult to attribute a particular portion of scalp activity to a particular component. Peak and area measures are particularly susceptible to this problem. Principal component analysis has been proposed as a tool to separate the contribution of overlapping components (Donchin & Heffley 1978), but in some cases even PCA can misallocate variance across different components (Wood & McCarthy 1984). As a result, we may attribute a difference obtained between two particular experimental conditions to the wrong component.

Several procedures have been proposed to solve the problem of component overlap, but none of them seems to have universal validity. In some cases, it can be assumed that only one component varies between two experimental conditions. In this case, the variation of this component can be isolated by subtracting two sets of waveforms and performing the measurement on the resulting "difference waveform." Unfortunately, we can not always assume that the effect of an experimental variable is so selective. Furthermore, the subtraction procedure implies that only amplitude – and not latency – varies across experimental conditions. This may not always be true, which may result in a particularly serious problem when subtracted waveforms are used and latency varies across conditions.

Another approach is based on using scalp distribution data to decompose overlapping components (vector filter – Gratton, Coles, & Donchin 1989a; Gratton et al. 1989b). A prerequisite for this procedure is that hypotheses about the scalp distributions of the components contributing to the data can be made in advance. Furthermore, if the scalp distributions of different components are correlated, then attribution of variance to one or another component may be arbitrary. Procedures such as discriminant analysis and PCA can be useful in deriving orthogonal sets of scalp distributions from the data. Note that distributional filters perform the same kind of operations in the spatial domain that frequency filters perform in the frequency domain. Whereas frequency filters apply different weights to activity in different frequency bands, distributional filters apply different weights to activity from different spatial locations.

Inferential Context

In this section, we review the procedures through which we come to make inferences about psychological and physiological processes and states from the measurement of ERPs. Previous work by Cacioppo and Tassinary (1990) describes different types of relationships between psychological and physiological variables, relations that limit the extent and generalizability of inferences that can be drawn from psychophysiological data. More recent papers (Kutas & Federmeier 1998; Miller 1996; Sarter, Berntson, & Cacioppo 1996) also discuss existing limitations in making inferences about brain function on the basis of brain imaging data. The general framework described in these papers is assumed in the approach presented here, which is more limited in scope and is intended as a description of the experimental logic that is often employed in ERP research.

EXPERIMENTAL LOGIC

If the ERP waveform is interpreted as an aggregate of several components, then some theory about the functional significance of each component would be useful for understanding the meaning of changes that this component will exhibit as a function of specific contexts. We should emphasize that by "functional significance" we mean a specification not of the neurophysiological significance of the component but rather of the information processing transactions that are manifested by it. In this sense, then, neurophysiological knowledge may be useful – but not necessarily critical – to the psychophysiological enterprise. Of course, neurophysiological knowledge is very important if we wish to use ERPs as a tool to make statements about brain function.

In the case of all ERP components, the initial phase in the process of establishing functional significance begins with the "discovery" of a component. A theory about the functional significance of a component is then developed, a complex process that involves the following.

1. Studies of the component's antecedents. Antecedent conditions refer to those experimental manipulations that will produce consistent variations – in amplitude, latency, and (in some cases) scalp distribution – in an ERP component.
2. Establishing the consequences of variation in the latency or amplitude of the component. An examination of the consequences can be used to test statements relating to functional significance.
3. Speculations about the psychological and/or neurophysiological function it manifests (Donchin 1981).

Examples of this logic applied to the P300 are reviewed in a later section. Here we consider the ways in which ERP measures are used to make inferences about psychological processes and, in some cases, to make inferences about brain activity. We shall review a series of inferential steps that depend to an increasing extent on assumptions about the functional significance of the ERP. For the purposes of elucidating the inferential process, we shall consider an experiment in which subjects are run in two different conditions.

USING ERP MEASURES: PSYCHOPHYSIOLOGICAL INFERENCE

Inference 1: Conditions Are Different

At the most fundamental level, we can ask whether or not the two conditions are associated with different ERP responses. Note that both this inference and the next do not depend on the classification of the ERP into components. Rather, they are based on the evaluation of the waveforms obtained in different conditions. The analytic procedure necessary to answer this question would involve a univariate or multivariate analysis of variance (with condition and peak, or data point, within a specified time window as factors). Given that such an analysis yields a significant effect of condition or a condition-by-peak or data-point interaction, we can infer that the conditions are different. If we assume that the ERP is a sign of brain activity and/or that it reflects some psychological process, then we can infer that the brain activity and associated psychological processing are different in the two conditions.

Inference 2: Conditions Differ at a Particular Time

The second level of inference concerns the time at which the two conditions differ. This inference could be made on the basis of post hoc tests of the significant condition-by-time interaction. It would take the form of "by at least msec X, processing of stimuli in condition A is different than processing of stimulus in condition B." This kind of inference is frequently made in studies of selective attention, where an important theoretical issue concerns the relative time at which an attended event receives preferential processing. As with the first, most primitive form of inference, we need only assume that the ERP is a reflection of some nonspecified aspect of psychological processing. Note that this same evidence can also be used to infer the time at which some (nonspecified) brain structure(s) shows differential processing for two events.

Inference 3: Conditions Differ with Respect to the Latency of Some Process

For this level of inference, additional assumptions and measurement operations must be made. Here we use ERPs to study the duration of processes preceding the occurrence of a particular physiological event (such as a component's peak). This requires that we can identify a particular physiological event (or component) across conditions and that this event varies in latency. Further, we usually assume that the ERP component can only occur *after* a particular psychological process is carried out. Note that, for this inferential level, we must first adopt a procedure to identify the component in question and measure its latency; we then use an analytic procedure (e.g., analysis of variance, *t*-test) to evaluate the difference between the conditions with respect to the component latency. As a result of this procedure, we make the inference that the conditions differ with respect to the timing of a given process.

Inference 4: Conditions Differ with Respect to the Degree to Which Some Process Occurs

The notion of component also allows us to use ERPs to infer that a particular process occurs to a greater extent under one condition than under another. In this case, we must assume that a particular ERP component is a manifestation of some process. We must further assume that changes in the magnitude of the component correspond directly to changes in the degree to which the process is invoked. Then, we must devise a suitable measurement procedure to identify and assess the magnitude of the component. Finally, we can proceed with the usual inferential test and determine whether or not the conditions differ with respect to the extent of the process. Of course, if precise knowledge were available about the underlying brain sources of a particular ERP activity, then statements made about the ERP could also apply to the brain structures in question.

Psychological Context: Selective Review of ERP Findings

In this section we review a number of findings in the ERP literature. We begin with a discussion of ERPs that are

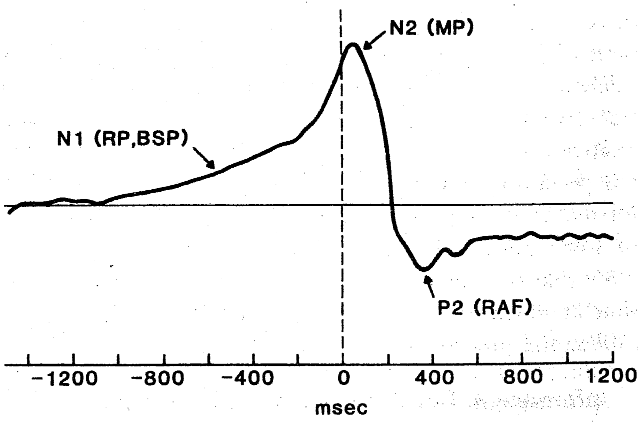


Figure 5. Typical movement-related potential (recorded from a central electrode, Cz) preceding a voluntary hand movement. Note that the potential begins about 1 sec before the movement (indicated by the dashed vertical line). The potential can be subdivided into different components as follows: N1 (RP = readiness potential, BSP = *Bereitschaftspotential*); N2 (MP = motor potential); P2 (RAF = reafferent potential). Adapted with permission from Kutas & Donchin, "Preparation to respond as manifested by movement-related brain potentials," *Brain Research*, vol. 202, pp. 95–115. Copyright 1980 Elsevier Science.

related to the preparation, execution, and evaluation of motor responses. This is followed by a brief overview of sensory and cognitive ERP components that occur after a marker event, with particular emphasis on ERP effects related to attention, memory, and language.

RESPONSE-RELATED POTENTIALS

In this section we review research on ERP activity that is typically observed in relationship to movement preparation and generation (readiness potential, lateralized readiness potential, contingent negative variation) or as a reaction to errors (error-related negativity).

Movement-Related Potentials

One class of event-preceding potentials includes those that are apparently related to the preparation for movement. These potentials were first described by Kornhuber and Deecke (1965), who found that – prior to voluntary movements – a negative potential develops slowly, beginning some 800 msec before initiation of the movement (see Figure 5). These "readiness potentials" (or *Bereitschaftspotentials*) were distinguished from those that followed the movement, the "reafferent" potentials. In similar conditions involving passive movement, only postmovement potentials were observed. Both readiness and reafferent potentials tend to be maximal at electrodes located over motor areas of the cortex. Furthermore, some components of the potentials are larger at electrode locations contralateral to the responding limb (at least for hand and finger movements). Indeed, this kind of lateralization has become an important criterion for movement-related potentials.

The investigation of movement-related potentials has developed along several different paths, including:

1. the discovery and classification of different components of the movement-related potential (for reviews see Brunia, Haagh, & Scheirs 1985; Deecke et al. 1984);
2. analysis of the neural origin using the scalp topography of ERPs (Vaughan, Costa, & Ritter 1972) or magnetic field recordings (Deecke, Weinberg, & Brickett 1982; Okada, Williamson, & Kaufman 1982);
3. analysis of the functional significance of different components (for reviews see Brunia et al. 1985; Deecke et al. 1984); and
4. recording of movement-related potentials in special populations (e.g., in mentally retarded children – Karrer & Ivins 1976; in Parkinson's patients – Deecke et al. 1977).

In general, these studies confirm that the potential described by Kornhuber and Deecke is generated, at least in part, by neuronal activity in motor areas of the cortex and is a reflection of processes related to the preparation and execution of movements.

The Lateralized Readiness Potential (LRP). Movement-related potentials have been applied to the investigation of human information processing. Studies reviewed in the previous section (Kornhuber & Deecke 1965) indicated that the readiness potential occurs prior to voluntary movements of the hand and is maximal at central sites, contralateral to the responding hand. In addition, the lateralized readiness potentials could also be observed in the foreperiods of warned reaction time tasks when subjects know in advance which hand to use in response to the imperative stimulus (Kutas & Donchin 1977).

Based on this evidence, researchers working independently at the Universities of Groningen (De Jong et al. 1988) and Illinois (Coles & Gratton 1986) concluded that one could exploit the lateralization of the readiness potential in choice reaction time tasks to infer whether and when subjects had preferentially prepared a response (see De Jong et al. 1988; Gehring et al. 1992; Gratton et al. 1988, 1990; Kutas & Donchin 1980).

The derivation of the LRP (Coles 1989) is based on the following steps, which are designed to ensure that any observed lateralization can be specifically attributed to motor-related asymmetries rather than to other kinds of asymmetrical brain activity. (1) Potentials recorded from electrodes placed over the left and right motor cortices are subtracted. This subtraction is performed separately for conditions where left-hand movements represent the correct response and for those where right-hand movements are correct. In each case, the potential ipsilateral to the side of the correct response is subtracted from the potential contralateral to the side of the correct response. (2) The asymmetry values for left- and right-hand movements are then averaged to yield a measure of the average lateralized activity as subjects prepare to move. This average measure is the LRP.

Measures of the LRP have been used to make three different kinds of inferences: (i) to infer whether a response has been preferentially activated or prepared (note that no LRP will be observed if both responses are equally activated); (ii) to infer the degree to which a response has been preferentially activated. This inference presupposes that the level of asymmetry as reflected by the LRP is related to the level of differential response activation. In fact, Gratton et al. (1988) observed that the level of the LRP at the time of an overt response was fixed: that is, there appeared to be a criterion level of the LRP which, when crossed, was associated with an overt response. Finally, LRP measures have also been used (iii) to infer when a response is preferentially activated. This inference has, perhaps, proved to be the most troublesome owing to the problems associated with the measurement of LRP onset (Smulders, Kenemans, & Kok 1996).

In order to use the LRP in the context of research in experimental and cognitive psychology, it is necessary to arrange the experimental design so that the question of interest can be phrased in terms of a question about the relative activation of the two responses, made with the left or right hands. To illustrate the LRP approach, we give two examples of work using the LRP.

The first experiment addressed a question about the nature of information transmission: Can partial information about a stimulus be transmitted to the response system before the stimulus is completely processed? (See e.g. Miller 1988; Sanders 1990.) The rationale is as follows. For a stimulus that contains two attributes, compare (a) conditions under which both attributes are mapped to the same (correct) response versus (b) conditions where the attributes are mapped to different (correct and incorrect) responses. If you observe incorrect response activation in the conflict condition, then partial information about the attribute must have been transmitted. Evidence in favor of partial transmission was reported by Gratton et al. (1988; see also Smid, Mulder, & Mulder 1990; Smid et al. 1991) using a noise compatibility paradigm (Eriksen & Eriksen 1974). They found that the incorrect response can be activated on the conflict trials even though the correct response is executed.

Similar findings were obtained in a Go–No-Go paradigm by Miller and Hackley (1992; see also Osman et al. 1992). In this case the trick is to map one stimulus attribute to response hand and the other attribute to response decision. If a response is activated when no response is required, then partial information about the attribute associated with response hand must have been transmitted.

In the experiment by Miller and Hackley, the stimuli were letters that had two attributes: size and identity, with size being deliberately made more difficult to determine than identity. Letter size was mapped to the Go–No-Go decision, while letter identity was mapped to response hand. Miller and Hackley found that, on Go trials, there was the expected development of an LRP associated with the subject's response on these trials. For No-Go trials, there was also a (smaller) LRP even though the subject showed no sign of any response-related muscular activity. These data indicate that, on No-Go trials, a response was activated even though that response was never executed. Partial information about letter identity was being transmitted to the response system.

These two examples are illustrative of the kinds of inferences that can be made using the LRP. The LRP has also helped to identify the processing locus of particular experimental effects and individual differences. Furthermore, measures of the LRP have provided insights into the question of the level in the processing system at which inhibitory mechanisms act to stop a response (De Jong et al. 1990). For further information about these and other issues, the interested reader should consult the reviews by Coles, Gratton, and Donchin (1988) and Coles et al. (1991, 1995).

The Contingent Negative Variation (CNV). The CNV was first described by Walter and colleagues (1964) as a slow negative wave that occurs during the foreperiod of a reaction time task (see Figure 6). The wave tends to be largest over central (vertex) and frontal areas. Researchers investigating the functional significance of CNV have manipulated several aspects of the S1–S2 paradigm, including the subject's task, the discriminability of the imperative stimulus, foreperiod duration, stimulus probability, presence of distractors, and so forth. The component has been variously described as related to expectancy, mental priming,

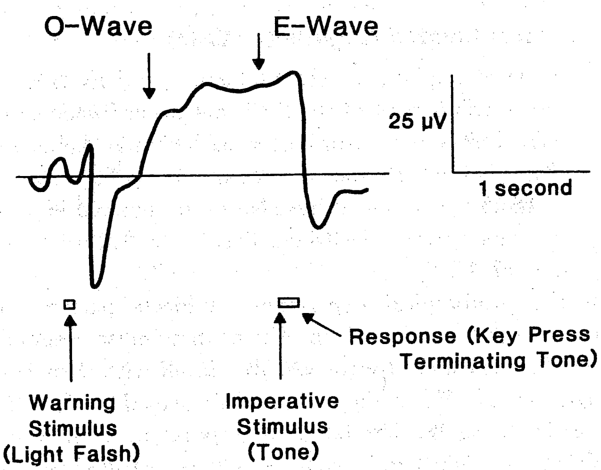


Figure 6. Schematic representation of a typical contingent negative variation (CNV) recorded from Cz. The CNV is the negative portion of the wave between the presentation of the warning and imperative stimuli. The early portion of the CNV is labeled "O-wave" (orienting wave); the late portion is labeled "E-wave" (expectancy wave). Adapted from Rohrbaugh & Gaillard (1983) with permission from the authors.

association, and attention (for a review see Donchin et al. 1978 or Rohrbaugh & Gaillard 1983).

A research controversy in this area concerns whether the CNV consists of one or rather several, functionally distinct, components. A further related question is whether the late portion of the CNV (just prior to the imperative stimulus) reflects more than the process of motor preparation as the subject anticipates making a response to the imperative stimulus. This controversy was raised by Loveless and his co-workers (e.g. Loveless & Sanford 1974; see also Connor & Lang 1969), who argued that the CNV consists of two components, an early orienting wave (the O-wave) and a later expectancy wave (the E-wave). Subsequent research by these investigators led them to argue that the E-wave is a readiness potential and reflects nothing more than motor preparation. Research by Rohrbaugh, Syndulko, and Lindsley (1976) and by Gaillard (1978; see also Rohrbaugh & Gaillard 1983) also supports this interpretation. However, the question of the functional significance of the latter component (the E-wave) remains controversial. Some investigators have claimed that, because a late E-wave is evident even in situations in which no overt motor response is required, the E-wave has a significance over and above that of motor preparation. However, it is clear that even though the overt motor response requirement may be removed from these situations, attention to a stimulus necessarily involves some motor activity associated with adjustment of the sensory apparatus. Perhaps the most persuasive arguments for a nonmotor role for the late CNV comes from a study of Damen and Brunia (1987), who found evidence for a motor-independent wave that precedes the delivery of feedback information in a time estimation task (see also van Boxtel & Brunia 1994).

The Error-Related Negativity (ERN)

As its name implies, the error-related negativity (ERN) is a negative component of the ERP that occurs when subjects make errors in sensorimotor and similar kinds of tasks. The component was first observed by Falkenstein and colleagues (1990), but it has also been observed in several other laboratories (Dehaene, Posner, & Tucker 1994; Gehring et al. 1993).

In the prototypical experiment, subjects perform a choice reaction time task in which they must respond to two different auditory (or visual) stimuli with their left or right hands. When they respond incorrectly – for example, by using the left hand to respond to a stimulus requiring the right-hand response – a negative potential is observed at the scalp. The negativity peaks at around 150 msec after response onset (defined in terms of EMG activity) and is maximal at fronto-central scalp sites. It is interesting that the negativity in the waveform for the incorrect trials begins to diverge from the waveform associated with correct trials at around the time of the response.

Several different studies have evaluated the functional significance of this component. For example, Gehring et al. (1993; see also Falkenstein et al. 1995) found that the amplitude of the ERN depends on the degree to which experimental instructions stress accuracy over speed (the amplitude is larger when accuracy is stressed). Bernstein, Scheffers, and Coles (1995) found that the amplitude also varies with the degree of error (defined in terms of movement parameters): it is larger when the incorrect response deviates from the correct response in terms of two rather than one parameter. Finally, although errors in these tasks are sometimes followed immediately by correct responses, error correction does not appear to be a necessary condition for the appearance of an ERN. An ERN is observed when subjects respond (incorrectly) to No-Go stimuli, a situation where the errors cannot be corrected by a second motor response (Scheffers et al. 1996).

The ERN is related to a variety of behaviors that together can be regarded as remedial actions taken to compensate for an error being made or having been made. These actions include attempts to inhibit the error, correct the error, or slow down so that the system does not make errors in the future (Gehring et al. 1993; Scheffers et al. 1996).

Evidence for the generality of the process manifested by the ERN was provided by Miltner, Braun, and Coles (1997). In this experiment, subjects were required to perform a time-interval production task. Shortly after subjects made a response indicating the end of a 1-sec interval, a feedback stimulus provided information about whether that interval was correct or incorrect. For incorrect feedback stimuli, an ERN-like negative potential was observed. These results suggest that the same error processing can be engaged by feedback stimuli as by incorrect actions themselves.

Finally, there is now evidence to suggest that the ERN is generated by frontal brain structures involving either the supplementary motor area or the anterior cingulate cortex. Equivalent dipole analyses for the ERN observed in choice reaction time tasks (Dehaene et al. 1994; Holroyd, Dien, & Coles 1998) and for the ERN-like negativity observed to feedback stimuli (Miltner et al. 1997) implicate activity in these neural structures as being responsible for the ERN signal recorded at the scalp.

Involvement of these structures is consistent with the picture that has begun to emerge from the functional studies of the ERN. That picture includes error monitoring and remedial action processes as essential aspects of the human cognitive system. Whenever humans perform tasks, they must set up not only their cognitive systems to execute the tasks but also a system to assure that performance on the tasks conforms to task goals. The ERN appears to be a manifestation of the activity of this system, although it is presently unclear whether it is more closely related to the error-detection process itself or to some consequence of error detection involving an aspect of remedial action (for reviews see Coles, Scheffers, & Holroyd 1998; Falkenstein et al. 1995; Gehring et al. 1995).

SENSORY COMPONENTS

The presentation of stimuli in the visual, auditory, or somatosensory modality elicits a series of voltage oscillations that can be recorded from scalp electrodes. In practice, sensory potentials can be elicited either by a train of relatively high-frequency stimuli or by transient stimuli. In the former case, the ERP responses to different stimuli overlap in time. The waveforms driven by the periodic stimulation have quite fixed periodic characteristics and are therefore referred to as "steady state" (Regan 1972). In the case of transient stimuli, the responses from different stimuli are separated in time.

Both steady-state and transient potentials appear to be obligatory responses of the nervous system to external stimulation. In fact, the earlier components of all sensory potentials (within, say, 100 msec) are invariably elicited whenever the sensory system of interest is intact. In this sense, they are described as exogenous potentials. They are thought to represent the activity of the sensory pathways that transmit the signal generated at peripheral receptors to central processing systems. Therefore, these components are "modality specific"; that is, they differ both in waveshape and scalp distribution as a function of the sensory modality in which the eliciting stimulus is presented. As would be expected of manifestations of primitive sensory processes, the sensory components are influenced primarily by such stimulus parameters as intensity and frequency. For a review of these components, see Hillyard, Picton, and Regan (1978).

For clinical purposes, sensory-evoked potentials are used in the diagnosis of neurological diseases (i.e., demyelinating diseases, cerebral tumors and infarctions, etc.). Of particular diagnostic importance are the auditory potentials (diseases involving the posterior fossa) and the steady-state visual potential (multiple sclerosis). Auditory potentials can also be used to diagnose hearing defects in uncooperative subjects (such as newborn infants). Because most sensory potentials appear to be insensitive to psychological factors, they have not been used extensively in the study of psychological processes.

THE EARLY NEGATIVITIES

Several negative components have been described in the period between 100 msec and 300 msec after the presentation of an external stimulus. In this section, we will examine two families of negative components that have been associated with selective attention, elementary feature analysis, and auditory sensory memory. Their scalp distribution and morphology vary as a function of the modality of the eliciting stimulus. These potentials may be considered as mesogenous, since they lie at the interface between purely exogenous and purely endogenous components.

ERPs and the Locus of Selective Attention

"Selective attention" refers to the ability of the human information processing system to analyze selectively some stimuli and ignore others. The locus at which selective attention occurs within the information processing flow has long been an issue of contention in psychology (see e.g. Johnston & Dark 1986). Two metaphors have been associated with selective attention: filtering (Broadbent 1957) and resources (Kahnemann 1973; Norman & Bobrow 1975). Filtering theories have focused on the debate about the locus of the filter. Does filtering occur at an early, perceptual level (early selection theories – Broadbent 1957) or at later stages of processing (late selection theories – Deutsch & Deutsch 1963)? According to the resource metaphor, selective attention is a mechanism by which the system allocates more resources to process information coming through a particular attended channel than through other, unattended channels. Thus, research questions concern how many processing activities can be performed simultaneously, as well as what factors limit the availability of processing resources. These issues have been addressed mostly in the context of research on the P300 (briefly reviewed in a subsequent section).

Psychophysiologists in general and ERP researchers in particular have rephrased the question of the locus of selective attention to ask where – in the sequence of electrophysiological responses that follow stimulation – the effect of selective attention begins to emerge. The "attention effect" is usually defined as a larger response to stimuli when the subject's attention is directed to some of the stimulus features than when the subject's attention is directed elsewhere.

The first indications that ERPs could be used to investigate attentional processes came from studies in which the ERP response to attended stimuli was compared to that to unattended stimuli (Eason et al. 1964; Hillyard et al. 1973). These kinds of studies suggested that attended stimuli are associated with a more negative ERP between 100 and 200 msec. Subsequent research has been concerned with three issues: (i) the use of ERPs to test theories of selective attention; (ii) the nature of the attentional effect on ERPs; and (iii) the neurophysiological basis of selective attention effects.

In a typical paradigm (Hillyard et al. 1973), four types of stimuli are presented. The stimuli (e.g., tones) differ along two dimensions (e.g., location and pitch), each having two levels (left vs. right ear and standard vs. deviant pitch). The subject is instructed to attend to stimuli at a particular location and to detect target tones of a deviant pitch (e.g., left-ear tones of high pitch). In order to investigate attention effects, ERPs to standard tones occurring

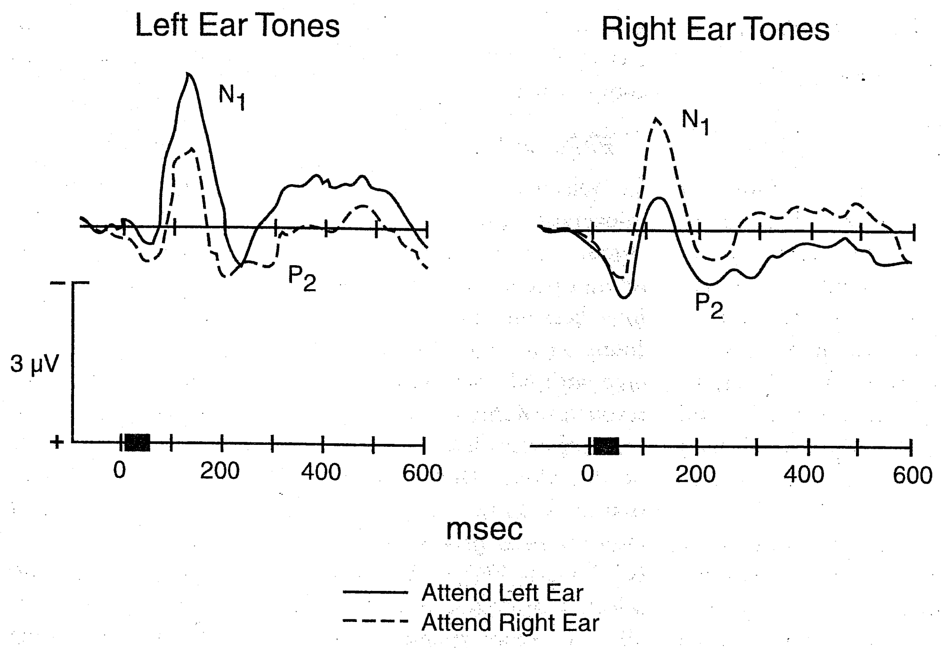


Figure 7. The effect of attention on early components of the auditory event-related potential recorded at the central electrode (Cz). The left panel shows ERPs for tones presented in the left ear. Note that the difference between the ERPs to attended tones (solid line) and those for unattended tones (dashed line) consists of a sustained negative potential. A similar difference can be seen for tones presented to the right ear (see right panel). Adapted with permission from Knight, Hillyard, Woods, & Neville, "The effects of frontal cortex lesions on event-related potentials during auditory selective attention," *Electroencephalography and Clinical Neurophysiology*, vol. 52, pp. 571–82. Copyright 1981 Elsevier Science.

in the attended location (channel) are compared to ERPs to standard tones in the unattended channel.

Using this paradigm, Hillyard and his colleagues have observed a larger negativity with a peak latency of about 100–150 msec for stimuli presented in the attended channel (see Figure 7, which shows data from a similar experiment by Knight et al. 1981). The moment in time at which the waveforms for attended and unattended stimuli diverge is considered as the time at which filtering begins to play a role.

Subsequent studies have shown that, by and large, ERP peaks are influenced by attention manipulations in one of three ways (see Hackley 1993).

1. They may be unaffected by the attention manipulation. In this case, the ERP activity is considered an automatic response to the stimulation. An ERP response with these properties is often referred to as an *exogenous* component.
2. They may be affected by the attention manipulation but occur even when attention is directed somewhere else. In this case, the ERP activity can be considered as a "semi-automatic" response in that it may occur even without attention, but it is larger (or smaller) when attention is deployed to the stimulus. An ERP response with these properties is often labeled a *mesogenous* component.
3. They may require attention to occur. In this case, the ERP activity is "optional" in that it occurs only when the subject is actively engaged in processing the information provided by the stimulus. An ERP response with these properties is often labeled an *endogenous* component.

With respect to the locus of selective attention, the issue then arises of which are the earliest ERP responses (after stimulation) to be influenced by attention manipulation. A theory advanced by Hernandez-Peon, Scherrer, and Jouvet (1956), called the peripheral gating hypothesis, proposes that attention influences responses at a very initial level within the sensory pathway. In favor of this theory are anatomical observations of centrifugal fibers from the central nervous system directed toward sensory organs (such as the cochlea and the retina). Indeed, Lukas (1980, 1981) reported that the earliest brainstem auditory-evoked potentials (BAEPs) – with a latency of just a few milliseconds from stimulation and presumably generated in the cochlea itself or in the early portions of the auditory pathway – were already influenced by attention manipulations. Similar results were reported by Eason and colleagues (1964) in the visual modality (in this case, using the electroretinogram). However, numerous subsequent attempts to replicate these findings failed, and methodological concerns were raised (for a review, see Hackley 1993). For this reason, it is now accepted that the earliest auditory-evoked potentials that are affected by attention have a latency of approximately 20–25 msec (McCallum et al. 1983). These potentials are likely to be generated in primary auditory cortex (Romani, Williamson, & Kaufman 1982a; Romani et al. 1982b;

Woldorff et al. 1993) – in which case, selective attention effects will appear when the signal arrives at the cortex. Findings leading to similar conclusions have been obtained for the somatosensory modality (Michie et al. 1987).

In the visual modality, a different pattern of results emerges. In this case, the earliest responses that are usually attributed to cortical involvement (latency of approximately 50–70 msec) appear to be unaffected by selective attention manipulations (provided, of course, that eye movements are not involved – Hansen & Hillyard 1980, 1984; Mangun, Hillyard, & Luck 1993). Attention effects occur only later, leading several investigators to speculate that attention effects emerge when the signal is transferred from the primary visual cortex to surrounding cortical areas (Mangun et al. 1993). Source modeling efforts (Clark & Hillyard 1996) and a combination of ERPs and other imaging methods (Heinze et al. 1994) provided support for this hypothesis. Further support was offered by optical imaging data showing that early attention effects (latency around 100 msec) are visible in extrastriate (area 19) but not in striate (area 17) cortex (Gratton 1997).

The Middle Latency Cognitive Components

So far we have discussed early ERP activity that is influenced by attention manipulations. However, another set of ERP activities are influenced by the "history" (or sequence) of stimuli that precede the current eliciting event. Some of these activities appear to occur in an automatic fashion – that is, they occur in response to both attended and unattended events. The most studied of these ERP activities is the mismatch negativity or MMN (Näätänen 1982). Because the MMN occurs even in the absence of attention, it has been associated with some form of preattentive (or sensory) memory. Other ERP activities – such as the N200s and the P300 – are sensitive to changes in the stimulus sequence, but they occur only in response to attended stimuli. These latter components can therefore be considered optional responses and are associated with postattentive forms of memory (short-term or working memory). In the next two sections we will describe research on the MMN and on the N200s; research on the frontal (novelty) P3, parietal P300 (or P3b), and slow waves will be reviewed in the section on late positivities.

The MMN. The MMN was first described by Näätänen, Gaillard, and Mäntysalo (1978; for extended reviews see Näätänen 1992 and Ritter et al. 1995). The MMN is typically studied using a passive auditory "oddball" paradigm. In this paradigm, subjects are presented with two auditory stimuli (or classes of stimuli) that occur in a Bernoulli sequence. The probability of one stimulus is generally less than that for the other, but the subject's attention is not devoted to the series of tones but instead to another task, such as reading a book. To derive the MMN, the average waveform elicited by the standard (frequent) stimuli is subtracted from that of the deviant (rare) stimuli. This subtraction yields a negative component with an onset latency as short as 50 msec and a peak latency of 100–200 msec (see Figure 8). This component is usually largest at frontal and central electrode sites, and it inverts in polarity at the mastoids (when the reference electrode is on the nose tip; see e.g. Alho et al. 1986). This evidence of polarity inversion, as well as intracranial recordings in animals (Csepe et al. 1987; Javitt et al. 1992, 1994) and dipole modeling in humans (Scherg et al. 1989), suggests that the primary auditory cortex and/or the immediately adjacent areas may be the brain generators of the MMN.

An MMN is elicited whenever the standard and deviant stimuli are discriminable on any of a number of features (such as pitch, intensity, and duration; see Näätänen 1992 for a review). Its onset latency and amplitude are both dependent on the ease of discriminating the stimuli from one another (i.e., the more discriminable the stimuli, the larger the amplitude of the MMN and the shorter its onset latency – see Figure 8). However, it is usually necessary to present two or three standards in order for a deviant stimulus to elicit an MMN (Cowan et al. 1993). In addition, an MMN is elicited with an interstimulus interval (ISI) of up to 10 sec between a standard and a deviant stimulus (Böttcher-Gandor & Ullsperger 1992). Finally, the amplitude of the MMN is larger for stimuli that differ along more than one dimension than for those that differ on only one dimension (see Ritter et al. 1995).

Taken together, these characteristics suggest that:

1. the MMN may reflect the operation of a "mismatch detector" (hence the label "mismatch negativity");
2. because the MMN is obtained even when the subject is not attending the stimuli, it is likely to be related to the automatic and preattentive processing of deviant features (cf. Treisman & Gelade 1980);
3. the MMN may be based on a type of memory that is transient in nature, as an MMN is not recorded after long ISIs; and
4. because the presence of more that one deviant feature affects the amplitude of the MMN, the MMN may reflect the outcome of a comparison in which multiple features can be processed in parallel.

Thus, it has been suggested that the MMN may be used as an index of the operation of an early, preattentive sensory (echoic) memory (Näätänen 1992; cf. Cowan 1995 and Ritter et al. 1995).

However, additional evidence suggests that the memory underlying the MMN may be of longer duration than previously thought (Cowan et al. 1993) and that the sensory memory underlying the MMN and the sensory memory investigated in behavioral tasks may be different (Cowan 1995; Ritter et al. 1995). One final problem in using the MMN as an index of sensory memory is that, contrary to behavioral evidence, a visual analog of the MMN has been

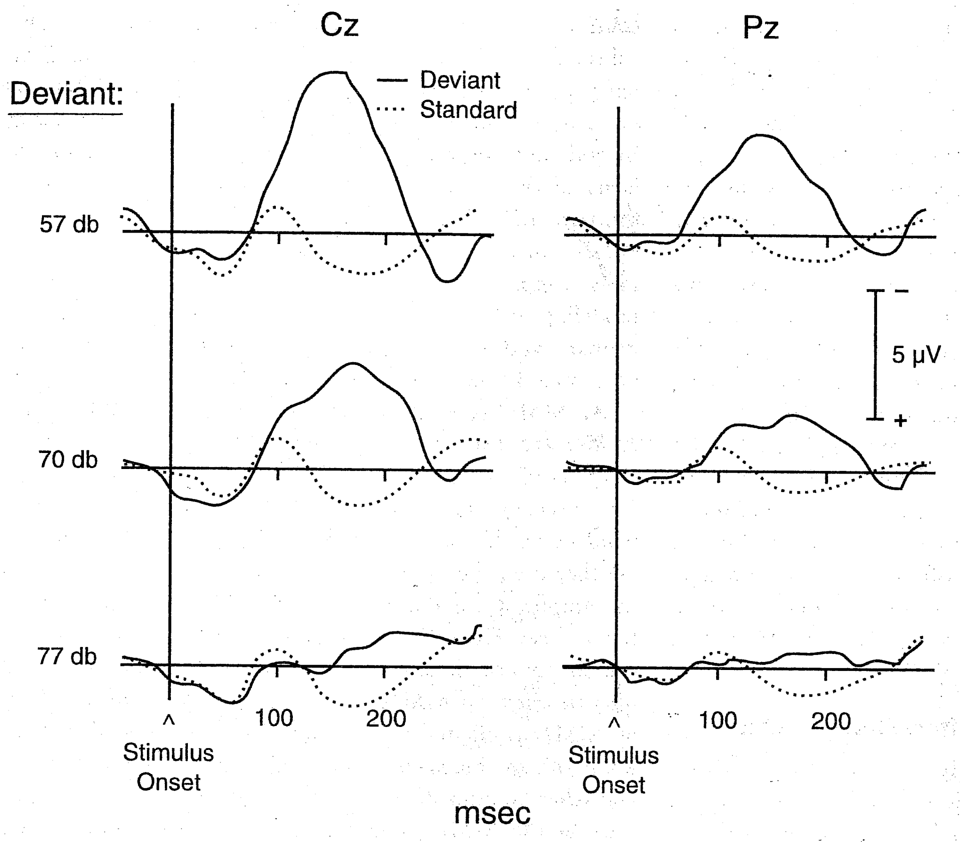


Figure 8. The effects of deviance on mismatch negativity (MMN). A standard (80-dB) tone was presented on 90% of the trials and a deviant tone (57, 70, or 77 dB, in different blocks) was presented on 10% of the trials. The ERP to the standard is indicated by the dotted line in each panel; the ERP to the deviant tone is indicated by the solid line. As the degree of mismatch between stimuli increases, the mismatch negativity also increases (i.e., the magnitude of the difference between standard and deviant ERPs increases). Redrawn from Näätänen & Picton (1987) with permission from the authors and The Society for Psychophysiological Research.

difficult to obtain. However, recent data obtained with optical imaging suggest that early memory effects (with a latency comparable to that of the MMN) can be observed in primary visual cortex and/or adjacent areas (Gratton 1997; Gratton et al. 1998).

The N200s. The label "N200" (or N2) is used to refer to a family of negative components that are similar in latency and whose scalp distribution and functional significance vary according to modality and experimental manipulations. For instance, different N200s can be observed for the visual modality (with maximum amplitude at occipital recording sites) and for the auditory modality (with maximum at the central or at frontal recording sites). In many experimental situations, the amplitude of the N200 appears to reflect the detection of some type of mismatch between stimulus features or between the stimulus and some previously formed template. The N200 differs from the MMN in that the subject's attention is usually engaged and the template for the comparison process may be actively generated by the subject.

Squires, Squires, and Hillyard (1975) first described the N200 using a paradigm in which they manipulated stimulus frequency and task relevance independently; they found that the N200 was larger for rare stimuli. Subsequent research has shown that several types of N200 can be described, even within the same modality. Specifically, Gehring et al. (1992) used a two-stimulus visual paradigm in which the first stimulus provided information about the most likely feature to be present in the second stimulus, thus creating expectations for specific stimulus features. They observed a larger N200 (with a frontal distribution) when the features in the second stimulus mismatched with the subject's expectancies (created by the first stimulus) than when the stimulus features were consistent with these expectancies. This paradigm differs from the typical MMN paradigm in that expectancy for particular features is dissociated from the physical presentation of the stimuli themselves. Therefore, the memory template to which the current stimulus is compared is generated internally and is not the result of previous presentations of the template itself. In the same paradigm, Gehring and colleagues also presented stimuli consisting of either homogenous or heterogenous features; they observed a larger N200 (with a central distribution) for the heterogenous than for the homogenous stimuli.

The N200 has also been used in the investigation of mental chronometry. In particular, Ritter et al. (1982) and Renault (1983) observed that the latency of this component covaries with reaction time. The high correlation between N200 latency and reaction time may reflect the importance of feature discrimination processes (signaled by the N200) in determining the latency of the overt response. However, the subtraction technique that Ritter et al. (1982) used to derive their measures of N200 must be interpreted with caution, because the latencies of components in the original waveforms differ. Furthermore, motor potentials, which are characterized by a large negativity, will also covary quite strictly with reaction times. Thus, it is important to disambiguate the N200 component from motor potentials when the former is used in the study of mental chronometry.

THE LATE COGNITIVE ERPs: MEMORY AND LANGUAGE EFFECTS

In this section we review a sample of the research dealing with two major families of endogenous components, the P300 (and similar late positivities) and the N400 (and other language-related components). For reasons of space we do not discuss in detail other late components, particularly a group of "slow waves." At the present time, the functional significance of these slow waves is largely unknown. However, for further information see Sutton and Ruchkin (1984) and the research on the O-wave (listed in earlier section on CNV).

The P300 and Other Late Positivities

In this section, we focus on studies of the relationship between memory and late positive components (including the P300, the frontal P3, and other positive components). These studies have focused on three types of effects: (1) effects that are associated with deviant, relevant items; (2) effects related to the memorability of items (in memory paradigms involving either direct or indirect memory tests); and (3) effects obtained during the retrieval of items (i.e., at the moment in which the direct or indirect memory test is administered).

Late Positivities Elicited by Deviant Stimuli: The "Classic" P300. As mentioned earlier, deviant items in an oddball paradigm elicit early and middle latency negative ERP activity. In addition, if the subject is attending the stimuli, deviant items also elicit various types of late positivities (with a typical latency exceeding 300 msec). The first of these positivities to be identified was the P300 (also labeled P3 or P3b; Sutton et al. 1965), which is elicited by task-relevant oddball stimuli and is maximum at posterior (parietal) scalp locations.

After more than 30 years of research on P300, there is still no conclusive indication of the brain sources underlying this scalp-recorded activity. The research conducted so far suggests that P300 may result from the summation of activity from multiple generators located in widespread cortical and possibly subcortical areas (Halgren et al. 1980; Johnson 1988, 1989, 1993; Knight et al. 1989; McCarthy et al. 1997). There has been some evidence that at least one of these sources may be located in the medial-temporal lobes (Halgren et al. 1980; Okada, Kaufman, & Williamson 1983). However, lesion data from animals (Paller et al. 1988b) and humans (Johnson 1988, 1989, 1993) indicate that it is unlikely that the scalp-recorded P300 is entirely generated in this area, as this component can still be recorded in the presence of medial-temporal lesions. In addition, Knight et al. (1989) reported that lesions of the temporo-parietal junction in certain conditions affected the amplitude of the scalp P300.

In contrast to the uncertainty about its neural origin, extensive information has been gathered on the factors that affect the amplitude and latency of the P300. For example, Duncan-Johnson and Donchin (1977) reported that P300 amplitude is sensitive to stimulus probability, provided that the stimuli are relevant to the subject's task. If the events occur while the subject is performing another task, then even rare events do not elicit the P300 (Figure 9; see also Gratton et al. 1990; Johnson & Donchin 1978). Further research has indicated that it is subjective, rather than objective, probability that controls the amplitude of P300 (Squires et al. 1976). In addition, P300 can be elicited by stimuli or stimulus classes in any modality, and the stimuli can be very diverse – as long as the subject is able to classify them unambiguously (Kutas, McCarthy, & Donchin 1977; Sutton et al. 1967; Towle, Heuer, & Donchin 1980). Finally, in another series of studies, Donchin, Kramer, and Wickens (1986; see also Sirevaag et al. 1989) demonstrated that the amplitude of P300 is related to the processing resources demanded by a particular task. In a dual-task situation, P300 amplitude to primary task events increases with the perceptual/cognitive resource demands while the P300 response to the concurrent secondary task decreases.

Research on P300 latency has focused on the identification of those processes that have elapsed prior to its elicitation. Donchin (1979) proposed that P300 latency may reflect stimulus evaluation or categorization time. This idea was supported by the observation that the correlation between P300 latency and reaction time is higher when subjects are given accuracy rather than speed instructions. Furthermore, as categorization becomes more difficult, P300 latency becomes longer (see Figure 10). Finally, it appears that the P300 latency is more dependent on the completion of processes of stimulus evaluation and categorization than on those related to the current overt response. Several studies (Magliero et al. 1984; McCarthy & Donchin 1981; Ragot 1984; Verleger 1997) demonstrate that manipulations that should affect the duration of response-related processes (i.e., stimulus–response compatibility) have relatively little effect on P300 latency (although a small effect is sometimes

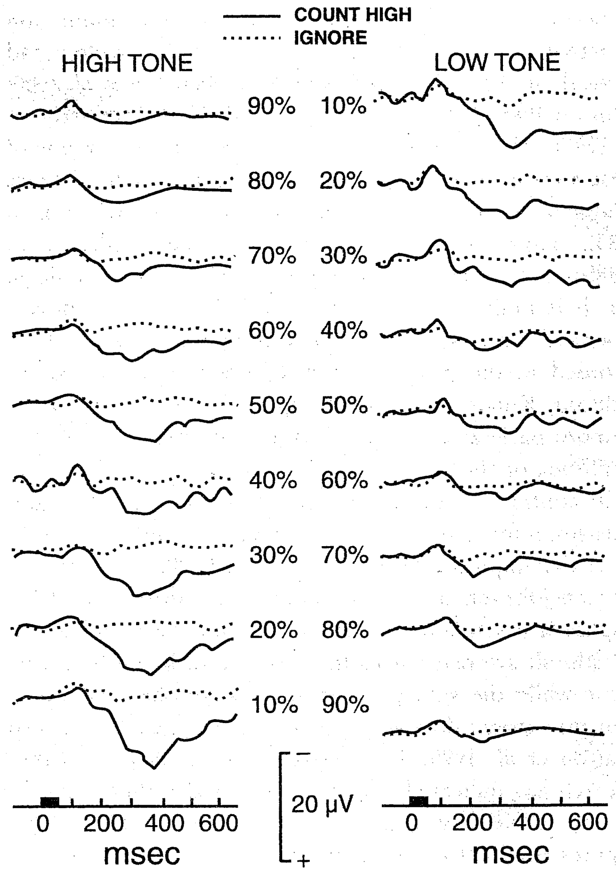


Figure 9. Grand-average ERP waveforms at Pz from 10 subjects for counted (high, left column) and uncounted (low, right column) stimuli (tones), with different a priori probabilities. The probability level is indicated by a percentage value beside each waveform. Waveforms from a condition in which the subjects were instructed to ignore the stimuli are also presented for a comparison. The occurrence of the stimulus is indicated by a black bar on the time scale. Positive voltages are indicated by downward deflections of the waveforms. Note that P300 amplitude is inversely proportional to the probability of the eliciting stimulus (probability effect) and, at the same probability level, P300 is larger for counted than uncounted stimuli (target effect). Redrawn from Duncan-Johnson & Donchin (1977) with permission from the authors and The Society for Psychophysiological Research.

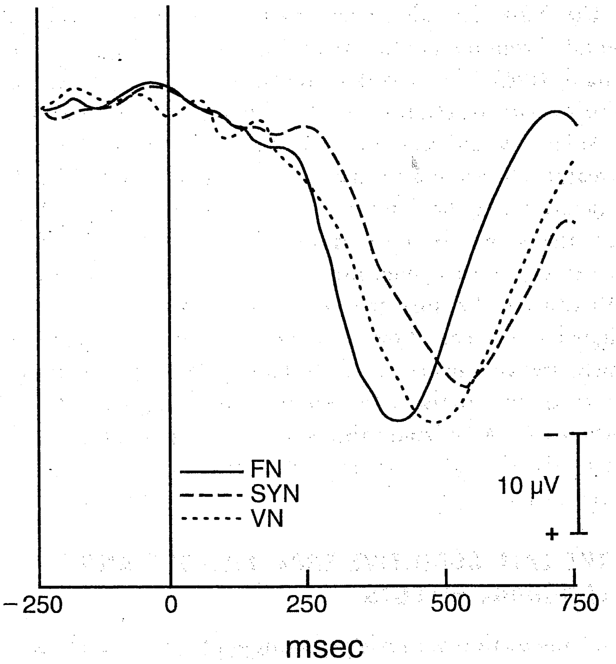


Figure 10. ERP waveforms at Pz averaged across subjects for three different semantic categorization tasks. The solid line indicates ERPs obtained during a task in which the subjects had to distinguish between the word DAVID and the word NANCY (the FN condition). The dotted line indicates ERPs obtained during a task in which the subjects had to decide whether a word presented was a male or a female name (the VN condition). The dashed line indicates ERPs obtained during a task in which the subjects had to decide whether a word was or was not a synonym of the word PROD (SYN condition). These three tasks were considered to involve progressively more difficult discriminations. Note that the latency of P300 peak is progressively longer as the discrimination is made more difficult. Adapted with permission from Kutas, McCarthy, & Donchin, "Augmenting mental chronometry: The P300 as a measure of stimulus evaluation time," *Science*, vol. 197, pp. 792–5. Copyright 1977 American Association for the Advancement of Science.

observed; see Ragot 1984 or Verleger 1997), whereas manipulations of stimulus complexity have a large effect.

These observations led Donchin (1981; Donchin & Coles 1988a,b) to propose that the P300 may be a manifestation of a process related to the updating of models of the environment or context in working memory. Such an updating would depend on the processing of the current event but would also have implications for the processing of and the response to future events (including the subsequent memory for the event itself). Other theories of the functional significance of P300 have been offered by Desmedt (1980), Rösler (1983), and Verleger (1988). Both Desmedt and Verleger proposed that the P300 may be related to the termination or "closure" of processing periods, while Rösler proposed that the P300 may reflect controlled processing. All of the theories provide a good account of the eliciting conditions for the parietal P300. Donchin's "context updating" hypothesis has also been used to generate predictions about the future consequences of the elicitation of a large (or small) P300 at a particular trial. Tests of these predictions have been taken as a validation benchmark for the context updating hypothesis. Because other theories did not generate competing hypotheses, it is difficult to determine whether or not they are confirmed by these data. One of the data sets used to validate the context updating hypothesis has been the research on the relationship between the amplitude of P300 elicited by an item and its subsequent memorability. This research will be reviewed in a subsequent section.

Statements relating to functional significance can be tested by an examination of the predicted consequences of variation in the latency or amplitude of the P300 for the outcome of the interaction between the subject and the

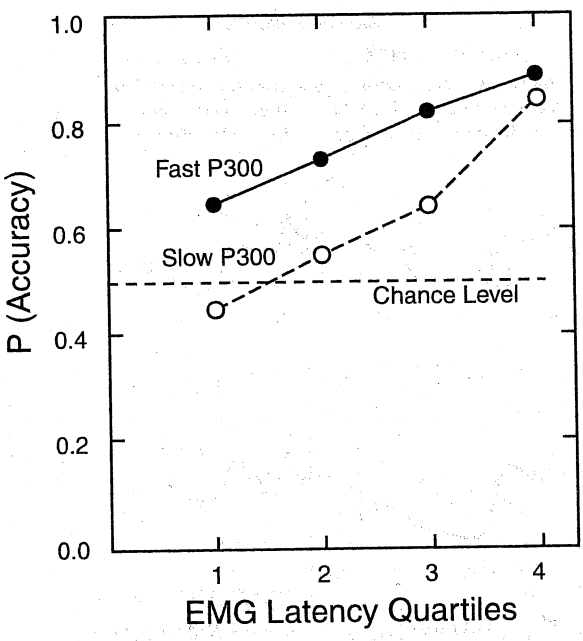


Figure 11. Accuracy of reaction time responses given at different latencies (speed–accuracy functions) for trials with fast and slow P300. Response latency (defined in terms of the onset of the EMG response) is plotted on the abscissa. The probability that a response would be correct is plotted on the ordinate. Note that the probability of giving a correct response increases as response latency increases. At very short response latencies, responses are at a chance level of accuracy (0.5). At long response latencies, responses are usually accurate. The speed–accuracy function for those trials with P300 latency shorter than the median latency ("fast P300" trials) are indicated by solid lines. The speed–accuracy function for those trials with P300 latency longer than the median latency ("slow P300" trials) are indicated by dashed lines. Note that, for each response latency, the probability of giving a correct response is higher when the P300 on that trial (reflecting the speed of stimulus processing on that trial) is fast than when it is slow. Redrawn with permission from Coles, Gratton, Bashore, Eriksen, & Donchin, "A psychophysiological investigation of the continuous flow model of human information processing," *Journal of Experimental Psychology: Human Perception and Performance,* vol. 11, pp. 529–53. Copyright © 1985 by The American Psychological Association.

environment. For example, if the P300 occurs after the stimulus has been evaluated, then the quality of the subject's response to that event should depend on the timing of that response relative to the occurrence of the P300. Thus, Coles and colleagues (1985; see also Donchin et al. 1988) showed that, for a given response latency, response accuracy is higher the shorter the P300 latency (see Figure 11).

The context updating hypothesis predicts further that, to the extent that the subject's future behavior depends on the degree to which an event leads to a change in their model of the environment, that behavior will be related to P300 amplitude. Several studies have demonstrated a relationship between the memorability of an event, assessed at some future time, and the amplitude of the P300 response to the event at the time of initial presentation (see three sections hence). As another example, it has been shown that the subject's future strategy as revealed in overt behavior can be predicted from the P300 response to current events (Donchin et al. 1988; Gratton, Coles, & Donchin 1992). In particular, in a speeded choice reaction time task, the amplitude of the P300 following an error was related to the latency and accuracy of overt responses on subsequent trials.

Late Positivities Elicited by Novel Stimuli: The "Frontal" P3. Courchesne, Hillyard, and Galambos (1975) used a modified oddball task in which unrecognizable complex stimuli were unexpectedly interspersed within the oddball sequence. They found that the unexpected novel stimuli elicited a positivity with a latency similar to that of the classic P300 but with a more frontally oriented scalp distribution. Since this initial experiment, a number of additional studies (Friedman, Simpson, & Hamberger 1993; Knight 1987; Yamaguchi & Knight 1991) have confirmed that a frontally oriented P300 is elicited by deviant stimuli that are exceedingly rare and unexpected within the context and for which there is no previously formed memory template (novel stimuli). As a consequence, the frontal P300 elicited by these stimuli has also been labeled "novelty P3."

The relationship between the frontal and parietal P300 has been subject to debate, with some researchers considering the two as completely different components (Donchin & Coles 1988a) and others considering them as variations of the same component (Pritchard 1981). More recently, Fabiani and Friedman (1995) have shown that *all* attended deviant items elicit frontal P3s when the stimuli are first presented (i.e., during a practice block). However, with subsequent repetitions of the same stimuli, the scalp distribution of the P3 reverts to a parietal maximum, which is typical for the "classic" P300 in young adult subjects. Interestingly, older adult subjects do not show this scalp distribution change over time; rather, they produce a frontally focused P3 in response to all deviant and novel stimuli (see also Friedman & Simpson 1994).

Fabiani and Friedman (1995) proposed that the frontal P3 may be elicited by items for which no memory template is available (and "orienting" may be required) and that it diminishes when a template is formed (i.e., with repeated presentations of the same stimuli). Older subjects or subjects with frontal lobe dysfunction may have problems forming and/or maintaining the stimulus template and therefore exhibit a frontal P3 even in response to deviant stimuli that are repeated a number of times. Knight (1984, 1997) found that the frontal portion of the novelty P3 is suppressed in patients with frontal lobe lesions. This, in turn, suggests that the presence of a frontal P3 to subsequent repetitions of deviant items may be associated with frontal lobe dysfunction, as measured by neuropsychological tests (e.g., the Wisconsin Card Sorting Test; see Fabiani, Friedman, & Cheng 1998).

ERP Effects Associated with Subsequent Memory. The relationship between P300 and memory has been tested in various paradigms. For example, Karis, Fabiani, and Donchin (1984b) recorded ERPs to words presented in a series that contained a distinctive word (an "isolate" – cf. von Restorff 1933). The isolation was achieved by changing the size of the characters in which the word was displayed. As is well documented (von Restorff 1933; Wallace 1965), isolated items are better recalled than are comparable nondeviant items (the von Restorff effect). The isolated items, being rare and task-relevant, can be expected to produce large P300s. Thus, it was predicted that the recall variance would be related to the very factors that are known to elicit and control P300 amplitude. Karis et al. (1984b) found that the magnitude of the von Restorff effect depends on the mnemonic strategy employed by the subjects. Rote memorizers (i.e., subjects who rehearse the words by repeating them over and over) showed a large von Restorff effect – and poor recall performance – relative to elaborators (i.e., subjects who combine words into complex stories or images in order to improve their recall). For all subjects, isolates elicited larger P300s than nonisolates. For rote memorizers, isolates subsequently recalled elicited larger P300s on their initial presentation than did isolates that were not recalled. This relationship between recall and P300 amplitude was not observed in elaborators (see Figure 12). It is noteworthy that the amplitude of a frontal positive slow wave was correlated with subsequent recall in the elaborators, suggesting that this component may be related to the degree of elaborative processing.

Karis and colleagues (1984b) interpreted these data as evidence that all subjects "noticed" the isolated words and reacted by updating their memory representations and producing large P300s. However, differences among the subjects emerged when they tried to memorize the stimuli by using different types of rehearsal strategies. When subjects used rote strategies, changes in the stimulus representation – induced by the isolation and manifested by P300 – made it easier to recall the word. For the elaborators, whose recall depended on the networks of associations formed as the series were presented, the effects of the initial memory activation and updating manifested by P300 were not noticeable because they were overshadowed by the more powerful elaborative processing that occurred after the time frame of P300.

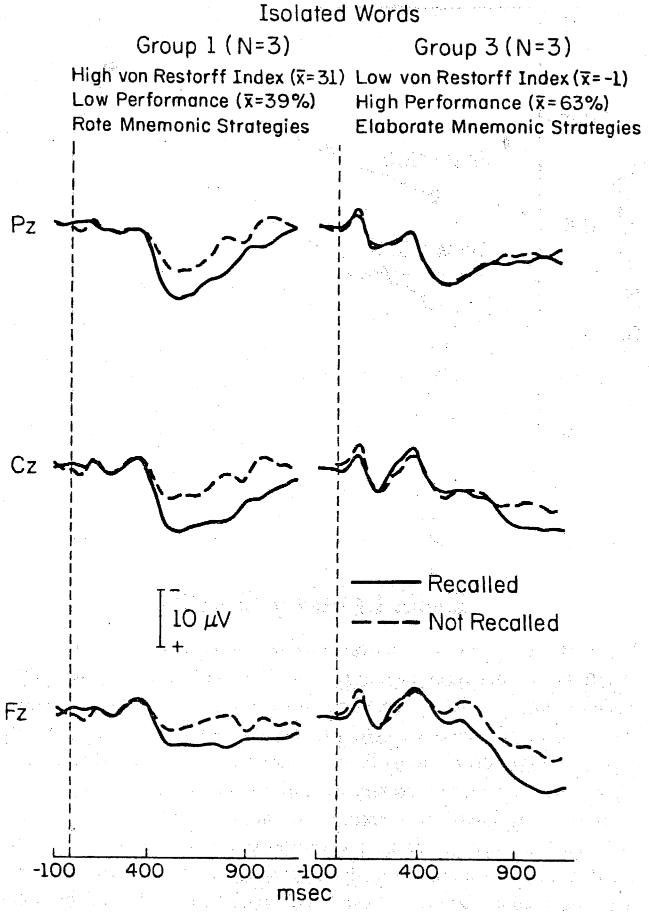


Figure 12. ERPs elicited by isolated words that were later recalled (solid line) or not recalled (dashed line). The left column shows ERPs for subjects who used rote mnemonic strategies; the right column shows ERPs for subjects who used elaborative strategies. Note that the amplitude of P300 is related to subsequent recall for the rote memorizers but not for elaborators. Reprinted with permission from Fabiani, Karis, & Donchin, "P300 and recall in an incidental memory paradigm," *Psychophysiology*, vol. 23, pp. 298–308. Copyright 1986 Elsevier Science.

The hypothesis that the relationship between P300 amplitude and subsequent recall does depend on the mnemonic strategy used by the subject was supported by subsequent studies in which the effects of strategies were investigated by: (a) manipulating instruction on a within-subject basis (Fabiani, Karis, & Donchin 1990b); (b) demonstrating that, in children who do not spontaneously use elaborative strategies, the P300–memory relationship is evident in all subjects in the absence of strategy instructions (Fabiani et al. 1990a); and (c) showing that the P300–memory relationship is clearer in adults in incidental memory paradigms (i.e., when the memory test is unexpected and mnemonic strategies are unlikely to be used; Fabiani et al. 1986). Finally, Fabiani and Donchin (1995) investigated the P300–memory relationship for the case in which words are semantically isolated; they also studied the effects of the type of orienting task given during the von Restorff paradigm. They found that both semantic and physically isolated words that were subsequently recalled elicited larger P300s than those that were not, and that the type of orienting task given to the subjects had an effect on whether or not an isolation effect was obtained.

The memory effects that can be observed in the ERP during study are not limited to isolated or rare items. In several recent studies, memory paradigms have been used that do not capitalize on stimuli for which the P300 is expected to be enhanced, that is, paradigms in which neither the distinctiveness nor the probability of occurrence of the stimuli to be memorized are manipulated. A seminal study in this respect (Sanquist et al. 1980) found that, in a same–different judgment task, larger-amplitude P300s (or late positive components) were elicited by stimuli that were correctly recognized in a subsequent recognition test. Johnson, Pfefferbaum, and Kopell (1985) recorded ERPs in a study–test memory paradigm. They reported that the P300 associated with subsequently recognized words was slightly, but not significantly, larger than that elicited by nonrecognized words.

Paller, Kutas, and Mayes (1987a) recorded ERPs in an incidental memory paradigm. Subjects were asked to make either a semantic or a nonsemantic decision and were subsequently, and unexpectedly, tested for their recognition or recall of the stimuli. They found that ERPs elicited during the decision task were predictive of subsequent memory performance, being more positive for words subsequently recalled or recognized than to words not recalled or recognized. Similarly, Paller, McCarthy, and Wood (1988a) recorded ERPs in two semantic judgment tasks, which were followed by a free recall and a recognition test. The ERPs to words later remembered were again more positive than those to words later not remembered, even though the memory effect was smaller for recognition than for recall. Neville and colleagues (1986) recorded ERPs to words that were either congruous or incongruous with a preceding sentence; subjects were asked to judge whether or not the word was congruent with the sentence. They found that the amplitude of a late positive component (P650) predicted subsequent recognition.

Paller and colleagues (1987b) defined the larger positivity for items later memorized than for items not memorized as "Dm" (difference based on subsequent memory). They used this terminology to stress the possibility that this difference may not be associated with a parietal P300, in part because the scalp distribution of the effect does not correspond exactly to that of the P300. In subsequent studies, Paller and colleagues (1987b; Paller 1990) attempted to determine whether the Dm can be observed in indirect (priming) memory tasks as well as direct memory tasks or whether it is specific to one form of memory. The results were ambiguous: in the first study (Paller et al. 1987b) the Dm effect was evident for direct tasks as well as for the indirect test (stem completion), but in a subsequent study (Paller 1990) the effect was evident only for the direct memory tasks. Rugg (1995) summarized a large body of research investigating the relationship between ERPs and subsequent memory and concluded that there is an undisputed relationship between a late positivity in the ERPs and the subsequent memory for these items. However, whether or not this subsequent memory effect is in fact entirely due to an increased P300 is still subject to debate. It is possible that more than one memory effect may be observable in the ERP, and its nature and scalp distribution may depend on whether or not the memory task emphasizes explicit memory instructions and/or the distinctiveness/probability aspects of items. It is important to emphasize that memory is a complex phenomenon that can be influenced by a multitude of variables and that can be probed with a number of different tests. Thus, it is unlikely that a single component of the ERP can be identified as "the" memory component. It is much more likely, and indeed more interesting, that a series of ERP components will prove to be significant in different memory tasks.

Several investigators have recently focused on differences in the scalp distribution of effects as a function of stimulus dimension. For instance, Mecklinger and Muller (1996) presented subjects with a visual recognition paradigm in which stimuli varied in both position and shape. In different blocks, subjects compared the study and test stimuli on the basis of one of the two dimensions. The interest was in the differences between the potentials elicited by the same stimuli in the two tasks. These changes in the ERP were interpreted as being due to differential use of brain structures for memorization of the shape and position dimensions. The shape task was associated with a posterior (occipital) P200 component, which was not observed for the spatial memory task. In addition, Mecklinger and Muller replicated the P300 and frontal slow-wave effects first reported by Karis et al. (1984a), although the P300 had a different scalp distribution in the two tasks.

ERP Effects Associated with Repeated Presentations of a Stimulus. Since the 1970s, ERPs have been recorded in paradigms testing the recognition of a previously presented item. Some of these early studies employed the Sternberg memory search paradigm, in which the subject is first presented with a short list of items to be memorized (the memory set) and is then presented with test items (one at a time) and asked to indicate (using a speeded response) whether or not each item belongs to the memory set. Whereas most of this research focused on variations in the latency of P300 as a function of the number of items in the memory set (Ford et al. 1982), it was generally observed that positive (Yes) responses were associated with larger P300s (or more positive waveforms) than negative (No) responses. This phenomenon was later replicated in studies using a more traditional recognition paradigm (e.g., Karis et al. 1984b).

Several investigators have attempted to determine if the ERPs elicited by test items can be used to validate the so-called two-process model of recognition. According to this model, successful recognition may occur either because subjects experience the conscious recollection of having previously seen the test item or because the item was "familiar" (although the subject could not recollect explicitly the previous encounter with the test item). The distinction between "recollection" and "familiarity" (see Tulving 1985) has now become a central issue in the investigation of conscious (or explicit) and unconscious (or implicit) processes. A popular paradigm for this research involves using a recognition test that requires subjects to indicate whether they experienced recollection or familiarity when confronted with the test items (i.e., distinguish between Know and Remember judgments). Using this paradigm, Smith (1993) observed that a larger P300 (or positivity) was observed for items for which the subjects indicated explicit recollection than for items for which they only experienced familiarity. Items for which a negative response was given elicited the smallest P300s. Smith (1993) interpreted these findings as indicating that the larger positivity is associated with the conscious recollection experience. However, alternative interpretations are possible, including one which assumes that the memory trace is stronger for items that are recollected than for items that are judged familiar. The P300 would then be related to the "strength" of the memory trace rather than to conscious experience. Another explanation was advanced by Spencer, Vila, and Donchin (1994), who suggested (a) that different patterns of results were obtained by different subjects who performed the task in different ways and (b) that some of the amplitude differences obtained by Smith (1993) may also have been due to latency differences in the averaged waveforms.

Another body of research has focused on the effect of repeating task-relevant items in tasks in which memory is not directly tested. As with the recognition paradigm, the repeated items are associated with increased positivity with respect to nonrepeated items (Besson, Kutas, & Van Petten 1991; Hamberger & Friedman 1992; Rugg 1990; see Rugg 1995 for a review). The interpretation of this finding is unclear. Rugg (1995), summarizing a large body of research, suggested that the increased positivity reflects a reduction of the N400 that is obtained after repeated presentations of a particular item (see next section) rather than an increase in the amplitude of a positive component. He interpreted this reduction in N400 as a manifestation of a context integration process: the first presentation of an out-of-context item requires processing, which is not required at its subsequent presentations. However, direct tests of this hypothesis have yielded ambiguous results (for a discussion, see Rugg 1995).

Note that whereas repetitions of verbalizable items are usually associated with increased positivities, this does not appear to be the case for visual material that cannot be verbally categorized. For instance, Gratton, Corballis, and Jain (1997) reported a more negative ERP at parietal locations for old than for new test items in a recognition task using novel line patterns (see also Rugg, Soardi, & Doyle 1995; Van Petten & Senkfor 1996). In one experiment, Gratton et al. (1997) used lateral presentations during the study phase and foveal presentations during test. They showed an increased temporal negativity during the test phase (when the stimuli were presented centrally) that was systematically contralateral to the side at which the stimuli were presented at study. They interpreted their findings as evidence of a hemispheric organization of visual memory.

Another example of negative activity (this time larger at right frontal locations) associated with recognition processes was reported by Friedman (1990). Although the significance of this activity is yet unclear, it is possible that it might be related to retrieval processes. Note that a negativity associated with retrieval processes was also described by Wijers and colleagues (1989) in a combined visual–memory search paradigm.

The N400 and Other Language-Related ERP Components

In this section we will review a number of ERP components that appear to index various linguistic processes (for a more extended review see Kutas 1997 or Chapter 21 of this volume). The first of these components to be described was the N400, originally recorded in a sentence reading task by Kutas and Hillyard (1980a). In this paradigm, words are presented serially and the subject is asked to read them silently in order to answer questions about the content of the sentence at the end of the experiment. In two studies reported by Kutas and Hillyard (1980a), 25% of the sentences ended with a semantically incongruous (but syntactically correct) word. These incongruous words elicited an N400 component that was larger than that elicited by words that were congruous with respect to the meaning of the sentence. Furthermore, the amplitude of the N400 appeared to be proportional to the degree of incongruity: moderately incongruous words ("he took a sip from the waterfall") had a smaller N400 than strongly incongruous words ("he took a sip from the transmitter"). Kutas and Hillyard (1982) reported that the N400 to incongruous endings was slightly larger and more prolonged over the right than the left hemisphere (see also Kutas, Van Petten, & Besson 1988b). More recent evidence from intracranial recordings suggests that the N400 may be generated in the parahippocampal anterior fusiform gyrus (McCarthy et al. 1995; Nobre, Allison, & McCarthy 1994; see also Kutas, Hillyard, & Gazzaniga 1988a for N400 in commissurotomy patients).

The basic incongruity effect reflected by the N400 has been replicated and extended repeatedly, using variations of the sentence reading paradigm just described. The aim of these studies has been to determine whether the N400 is a manifestation of a distinctively semantic process (i.e., a brain response to semantic violations) or whether it is elicited by other kinds of deviance. Kutas and Hillyard (1984) found that the amplitude of the N400 was inversely related to the subject's expectancy of the terminal word (cloze probability) but that it was insensitive to sentence constraints (i.e., to the number of possible alternative endings). Kutas and Hillyard (1980b) showed that an N400 followed semantic deviation, whereas a late positive complex (P300) followed physical deviation. In addition, Kutas

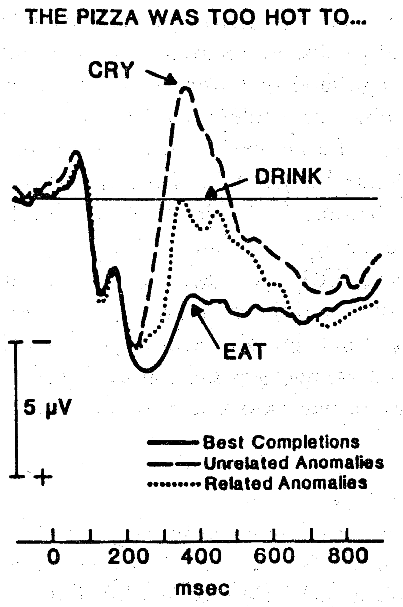


Figure 13. The effects of anomalous sentence endings on the N400. The ERPs (from Pz) depicted in the figure were recorded following visual presentation of words that varied in their relationship to the previous words in the sentence. For example, for sentences such as "The pizza was too hot to ...", three endings were possible: *best completion* – "eat"; *related anomaly* – "drink"; *unrelated anomaly* – "cry". Note that the N400 component is present only for anomalies and is larger for unrelated than for related anomalies. Reproduced with permission from Kutas & Van Petten, "Event-related brain potential studies of language," *Advances in Psychophysiology,* vol. 3, pp. 139–87. Copyright 1988 Jessica Kingsley Publishers.

and Hillyard (1983) inserted a number of semantic and grammatical anomalies in prose passages. They found that large N400s were associated with the semantic anomalies embedded in the text but not with the grammatical errors. Kutas, Lindamood, and Hillyard (1984) found that anomalous words that were semantically related to the sentence's "best completion" (e.g., "the pizza was too hot to drink") elicited smaller N400s than anomalous words unrelated to the best completion (e.g., "the pizza was too hot to cry"). This suggests that the degree of semantic relatedness is an important determinant of the N400 (see Figure 13).

Work by Van Petten and colleagues (see Van Petten 1995) indicated that the N400 elicited by semantically congruent words is influenced by the interaction of word characteristics (such as frequency in the language) and the sentence context. For example, low-frequency words usually elicit larger N400s than high-frequency words, but this effect is only apparent early in the sentence, before the sentence context is established (Van Petten & Kutas 1990; see also Van Petten & Kutas 1991).

A large N400 component is also evoked by semantic anomalies presented in the auditory modality (Connolly et al. 1992; McCallum, Farmer, & Pocock 1984) and in anomalies embedded in American Sign Language (ASL) gestures (Neville 1985). However, Besson and colleagues did not find N400 responses to anomalies embedded in music, finding instead that these anomalies are associated with positivities (Besson, Faïta, & Requin 1994; Besson & Macar 1986; Macar & Besson 1987). Finally, N400-like components have also been recorded in paradigms other than sentence reading, such as the sentence verification paradigm (e.g. Fischler et al. 1983). In this paradigm, sentences are presented in segments ("a robin / is / a bird"), and two dimensions are orthogonally manipulated: whether the sentences are positive or negative ("is," "is not") and whether they are true or false. The subject is required to indicate whether the sentence is true or false. A large negativity was elicited by false affirmative ("a robin / is / a tree") and true negative ("a robin / is not / a tree") sentences – that is, by sentences in which the first and last elements were semantically unrelated (see also Fischler et al. 1985; Kounios & Holcomb 1992).

In general, research on the N400 suggests that this component is specifically sensitive to the violation of semantic expectancies. Measures of the N400 have proven useful in testing theories and models relating to semantic priming (Van Petten & Kutas 1987) and in understanding the time course of language processing. For example, Pynte and colleagues (1996) found that N400s were elicited by the last word in metaphors (such as "John is a lion") but not in literal sentences (such as "John is a courageous"). This suggests that the literal meaning of sentences is accessed early on in processing, even if a metaphorical meaning is ultimately understood.

Several other ERP components are recorded in response to language processing. For example, a positivity – labeled P600 or syntactic positive shift (SPS) – is elicited by syntactic anomalies (e.g., lack of subject–verb agreement; Kutas & Hillyard 1983). In addition, some slowly developing sentencewide effects are visible when low-pass filtering is applied to the ERP encompassing an entire sentence; these effects are reviewed in detail by Kutas (1997; see also Chapter 21).

Social and Applied Context

So far, we have discussed a number of experimental manipulations that affect various ERP components and allow investigators to make inferences about the cognitive significance of the electrical brain activity observed at the scalp. However, our brain is also processing emotions and attitudes and also plays a fundamental role in maintaining vital bodily functions (see Kutas & Federmeier 1998 for an extended discussion of an integrated view of brain function). Thus, it is not surprising that emotional and social factors may also influence the latency and amplitude of ERP components. For example, experimental instructions are an important determinant of endogenous components. In fact, strategy instructions (Fabiani et al. 1986), speed–accuracy instructions (Kutas et al. 1977), bargaining (Karis et al. 1984a), and payoff manipulations (Karis, Chesney, & Donchin 1983) have all been shown to affect the ERP waveform.

As another example, Cacioppo and colleagues conducted a series of psychophysiological studies of social attitudes. They advocate the use of psychophysiological measures, especially for those cases in which subjects do not want (or are unable) to talk about their attitudes (Cacioppo et al. 1993, 1994a,b; Crites et al. 1995).

Several researchers have investigated the effects of emotional stimuli on the ERP. By and large, the data have been interpreted in terms of emotion effects on cognitive processing. For instance, Vanderploeg, Brown, and Marsh (1987) compared the ERP responses to faces and words that did or did not convey emotional meanings, finding that P3 was larger for neutral faces. Kestenbaum and Nelson (1992) compared the ERP elicited by angry and happy faces in 7-year-old children and adults, finding different effects of valence on P3 amplitude (see also Stormark, Nordby, & Hugdahl 1995). Naumann and colleagues (Diedrich et al. 1997; Naumann et al. 1992, 1997) have tried to identify ERP components specifically related to emotion rather than to cognitive processes. Their approach is based on an attempt to manipulate independently the emotional valence and the cognitive demands imposed by the stimuli. However, the results remain ambiguous, and the question of whether there are ERP components that are specifically related to emotional processes is still open.

There are now a considerable number of studies using ERPs in more applied areas. This includes work in human factors, for which we refer the reader to Chapter 29, as well as work on the use of ERPs in "lie detection" and on the effects of alcohol on the ERP. Studies of lie detection and ERP use a logic similar to that proposed by Cacioppo et al. (1994b) in that stimulus words or phrases relating to a crime may be categorized in one way if the information they represented were unknown to the individual but in another way if the information were known. The role of the ERPs, then, is to identify the categorization rule being used by the subject, who may otherwise be unwilling to reveal his or her "guilty knowledge." Both the P300 (Farwell & Donchin 1991) and the N400 (Boaz et al. 1991) have been used within this context.

As a final example of a more applied use of ERP research, investigators have been examining the effects of alcohol on P300 and other ERP components (such as the MMN and the O-wave) in the hope of identifying possible biological markers of high risk to developing alcoholism (Eckardt et al. 1996; Jaaskelainen et al. 1996b; see Jaaskelainen, Näätänen, & Sillanaukee 1996a and Porjesz & Begleiter 1996 for reviews).

Summary and Conclusions

Research conducted over the past four decades has established the ERP as one of the main tools available to cognitive neuroscientists. The advantages of ERPs include their exquisite temporal resolution, relatively low cost and portability, and their high level of sensitivity to cognitive processing. These qualities have allowed ERPs to be applied to the investigation of a number of theoretical issues that are relevant to cognitive psychology. Recently, several other neuroimaging techniques have joined ERPs as tools for investigating the function of the human brain. However, rather than replacing ERPs as a method of choice, it appears that a combination of different approaches (including not only imaging methods but also neuropsychological and neurophysiological data) may provide a more complete description than the use of one technique alone.

NOTES

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1. Note that this assumption may not always be valid – as, for example, in the case of variability in the latency and other characteristics of the ERP from sample to sample. Furthermore, the ERP derived by averaging may include potentials that do not originate in the brain but are time-locked to the event.

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