

1 Event-related brain potentials: an introduction

Michael G. H. Coles and Michael D. Rugg

1.1 INTRODUCTION

This book is concerned with the intersection of two research areas: event-related brain potentials (ERPs) and cognitive psychology. In particular, we will be considering what has been learned and what might be learned about human cognitive function by measuring the electrical activity of the brain through electrodes placed on the scalp. In this first chapter we focus on the methodology of ERP research and on the problem of isolating ERP components, while in Chapter 2 we review issues that arise in making inferences from ERPs about cognition.

We begin by considering how an ERP signal is obtained, as well as how such a signal is analysed. We consider at some length the issue of the definition of a component and we provide a brief review of some of the more well-known components. This latter review is intended to give a historical context for cognitive ERP research and the chapter as a whole should provide the reader with some understanding of the vocabulary of the ERP researcher and the 'lore' of the cognitive electrophysiologist.

1.2 ERP RECORDING AND ANALYSIS

In this section we review some of the basic facts and concepts germane to ERP recording and analysis. (Portions of this section are derived from Coles *et al.* (1990); see also Allison *et al.* (1986), Nunez (1981), and Picton (1985), for further information.)

1.2.1 Derivation

When a pair of electrodes are attached to the surface of the human scalp and connected to a differential amplifier, the output of the amplifier reveals a pattern of variation in voltage over time. This voltage variation is known as the 'electroencephalogram' (or EEG). The amplitude of the normal EEG can vary between approximately -100 and $+100$ μV , and its frequency ranges to 40 Hz or more.

Suppose that we present a stimulus to a human subject while recording the EEG. We can define an epoch of the EEG that is time-locked to the stimulus. For example, the epoch may begin 100 ms before the onset of the stimulus and end 1000 ms later. Within this epoch, there may be voltage changes that are

specifically related to the brain's response to the stimulus. It is these voltage changes that constitute the event-related potential, or ERP.

In early research involving these measures of brain potential, the term 'evoked potential', or EP, was used because it was believed that the potentials reflected brain activity that was strictly 'evoked' by the presentation of the stimulus, activity related to basic sensory processes. As we shall see, it is now proposed that at least some of these potentials are related to 'a variety of processes that are *invoked*' by the psychological demands of the situation' (Donchin *et al.* 1978, p. 350). The realization that the potentials reflected more than just evoked activity led to the use of the more neutral term 'event-related'.

1.2.2 The generation of the ERP

It is generally accepted that the ERP reflects activity originating within the brain (although see Section 1.2.5 on artefacts). However, the relationship between what is going on in the brain and what we observe at the scalp is not completely understood. Nevertheless, the following points appear to be clear (see Nunez (1981), Scherg and Picton (1991), and Wood (1987) for more detailed discussions of the physiological determinants of ERP waveforms). First, ERPs recorded from the scalp represent net electrical fields associated with the activity of sizeable populations of neurons. Second, and relatedly, the individual neurons that comprise such a population must be synchronously active, and have a certain geometric configuration, if they are to produce fields that can be measured at the scalp. In particular, the neurons must be configured in such a way that their individual electrical fields summate to yield a dipolar field (a field with positive and negative charges between which current flows). Such configurations are known as 'open fields' and usually involve the alignment of neurons in a parallel orientation. Finally, biophysical and neurophysiological considerations strongly suggest that scalp-recorded ERP waveforms are principally a reflection of post-synaptic (dendritic) potentials, rather than of axonal action potentials (Allison *et al.* 1986).

Consideration of the neural processes that we probably detect in the ERP has important consequences for their interpretation. First, there is undoubtedly much neural activity that is never apparent at the scalp. In many neuronal populations, even those with an 'open field' configuration, activity might be insufficiently synchronous to generate an electrical field that can be recorded at a distance. In some structures, such as the cerebral cortex, the geometric arrangement of neurons is conducive to the summation and propagation of their electrical activity because the neurons share the same orientation, perpendicular to the cortical surface. However, in other structures, such as the thalamus, the arrangement of neurons almost certainly guarantees their invisibility to distant recording electrodes. They are arranged in such a way as to produce no detectable field outside them.

The resultant selectivity of the ERP is both an advantage and a disadvantage. If we observed the totality of brain activity at the scalp, the resultant measures arguably would be so complex as to be difficult or impossible to analyse. However,

we need always to be aware that there are almost certainly numerous functionally important neural processes that cannot be detected using the ERP technique.

1.2.3 Recording issues

As we noted earlier, to obtain an ERP one needs to record the difference in voltage between two electrode sites; but where should the electrodes be placed? At present, the most common practice is to employ what is referred to as a 'common reference' recording procedure. This involves connecting each member of an array of scalp electrodes to a single 'reference', comprising either one other electrode or perhaps a pair of electrodes that have been linked together (as with the popular 'linked mastoid' reference, which consists of a linked pair of electrodes, one on each mastoid bone located behind each ear). The reference site is chosen so as to be relatively uninfluenced by the electrical activity of experimental interest. Recordings are based on the difference in voltage between each 'exploring' electrode and the same (common) reference electrode(s). More complex recording arrangements are also possible and are occasionally employed. These can involve computing voltage differences between subsets of adjacent electrodes (as in 'current-source density' analysis: Nunez 1990; Perrin *et al.* 1989), or subtracting the across-electrode mean voltage (as determined with respect to a common reference) from each electrode to yield recordings with respect to an 'average reference' (Lehmann 1987). Such procedures are used to accentuate or 'sharpen' regional differences in scalp fields, with the hope that this will allow greater insight into the likely locus of the generators of the fields.

Electrode locations are generally described with reference to the 10–20 system (Jasper 1958; and see Fig. 1.1). In this system, the location of an electrode is specified in terms of its proximity to particular regions of the brain (frontal, 'central', temporal, parietal, and occipital) and of its location in the lateral plane (odd number for left, the subscript *z* for midline, and even numbers for right). Thus, P_z defines a midline electrode location over the parietal lobe, while F3 defines a left frontal site. Although these electrode descriptors refer to particular brain areas, it is important to note that activity recorded at any particular scalp site is not necessarily attributable to activity in brain regions in close proximity to that site. This is because the brain acts as a volume conductor, meaning that electrical activity generated in one area can be detected at distant locations.

In recent years there has been an increased interest in the use of ERPs to make inferences about what is going on inside the brain (see Section 1.3.1.1). Because the techniques required to make these inferences require that the electrical fields on the scalp be sampled at a high spatial frequency, the 10–20 system has been enhanced by the use of both non-standard locations and a higher density of electrodes (e.g. Tucker 1993).

1.2.4 Conditioning the signal

The EEG includes frequencies that are often outside those that are of interest to the ERP researcher. For this reason, the amplifiers used to record the ERP usually

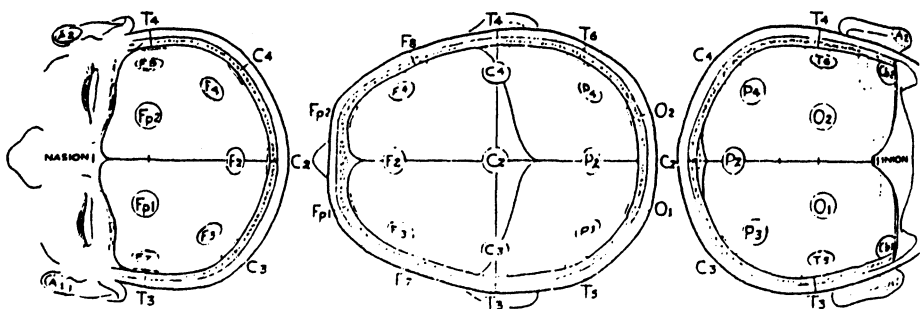


FIG. 5

Frontal superior and posterior views showing all the standard electrode positions as described in the text.

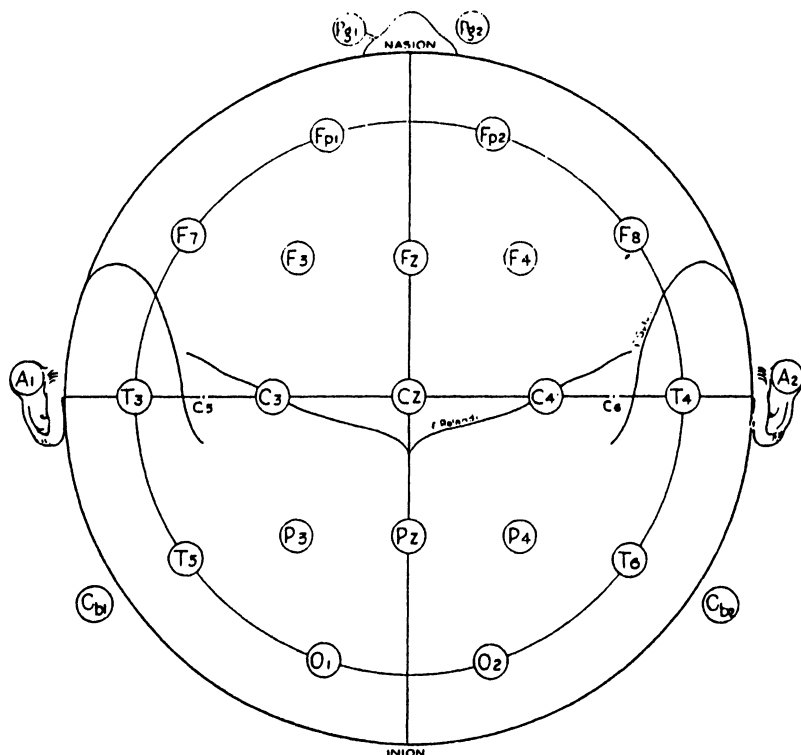


FIG. 6

A single plane projection of the head, showing all standard positions and the location of the Rolandic and Sylvian fissures. The outer circle was drawn at the level of the nasion and inion. The inner circle represents the temporal line of electrodes. This diagram provides a useful stamp for the indication of electrode placements in routine recording.

Fig. 1.1 The 10–20 system for electrode placement. The principal locations are defined in terms of the relative distances (in 10 or 20 percentile values) along two major axes: the anterior–posterior axis (from nasion to inion), and the coronal axis (from left to right post-auricular points). Other locations are defined in relation to these principal locations. The original legend for this figure reads as follows: ‘A single plane projection of the head,

include optional filter settings that allow the investigator to attenuate activity above and below selected frequencies. Of particular importance in this regard is high-frequency activity that is attributable to muscle (for example, of the jaws) rather than brain activity, and activity at the line (mains) frequency (60 or 50 Hz). Low-frequency activity can also be attenuated ('high-pass' filtering); however, care must be taken to ensure that low-frequency activity in the ERP waveform is not significantly distorted by such filtering.

1.2.5 Artefacts

The filtering procedures described in the previous section can sometimes be used to attenuate artefactual activity that arises from sources other than the brain. However, there are two major sources of artefact, movements of the eyes and eyelids, that cannot be dealt with in this way. This is because these movements occur at the same frequencies as important features of the ERP waveforms. Eye-movement and eye-blink artefacts arise because the eyeball functions like an electrical dipole, with positive and negative charge on either side. Movements of the eye therefore produce fluctuating electrical fields that are propagated back across the scalp. These fields are picked up by scalp electrodes and contaminate the recording of brain activity. To deal with these artefacts, investigators use one of several approaches. First, they may instruct subjects to maintain their gaze at a fixation point and to avoid blinking except at designated times when task events are not present. The problem with this approach is that it may impose a secondary task on the subject (the task of not moving their eyes), and this may interfere with the subject's performance on the primary task of interest. Second, investigators may discard all EEG epochs for which eye movements or blinks are detected. The problem here is that there may be an insufficient number of artefact-free trials for tasks that require eye movements for their successful performance or for some populations (for example the young and the aged) that have trouble keeping their eyes still. In the face of these difficulties, investigators have resorted to a third approach that involves estimation and removal of the contribution of the eye movements and blinks to the ERP signal (for example Gratton *et al.* 1983). The advantage of correcting the ERP signal in this way is that one can retain all the ERP data, even when substantial eye movements are present. Brunia *et al.* (1989) report the results of a comparison among six different correction procedures, and the reader who is interested in more information is referred to this article.

1.2.6 Extracting the signal

As we have noted, the ERP is set of voltage changes contained within an epoch of EEG that is time-locked to some event. In most cases, these changes are small

showing all standard positions and the location of the Rolandic and Sylvian fissures. The outer circle was drawn at the level of the nasion and inion. The inner circle represents the temporal line of electrodes. This diagram provides a useful stamp for the indication of electrode placements in routine recording.' (From Jasper (1958): Fig. 6, p. 374. Copyright © 1958 Elsevier Science Ireland Ltd., reprinted by permission.)

(on the order of microvolts) in relation to the EEG waveform (which is on the order of tens of microvolts) in which they are embedded. For this reason, it is necessary to employ signal processing techniques to extract the 'signal' (the time-locked ERP) from the 'noise' (the background EEG). By far the most commonly used signal extraction technique is averaging. This involves recording a number of EEG epochs, each of which is time-locked to repetitions of the same event (or event class). The digital EEG values for each time-point in the epoch are then averaged to yield a single vector of values representing the average activity at each time-point. This is the average event-related potential (see Fig. 1.2). Given the assumption that EEG activity not time-locked to the event will vary randomly across epochs, this 'background' EEG will tend to average to zero, and the residual waveform after averaging should therefore largely represent activity that bears a fixed temporal relationship to the event across epochs.

One of the disadvantages of the averaging procedure is that it cannot provide

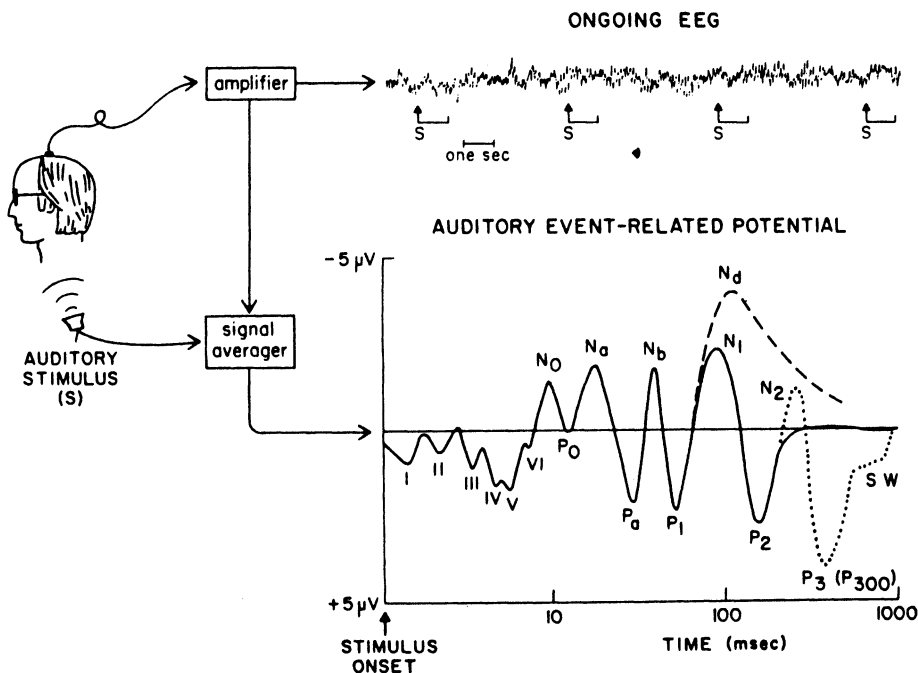


Fig. 1.2 'Idealized waveform of the computer-averaged auditory event-related potential (ERP) to brief sound. The ERP is generally too small to be detected in the ongoing EEG (top) and requires computer averaging over many stimulus presentations to achieve adequate signal/noise ratios. The logarithmic time display allows visualization of the early brainstem responses (Waves I–VI), the midlatency components (No, Po, Na, Pa, Nb), the "vertex potential" waves (P1, N1, P2), and task-related endogenous components (Nd, N2, P300, and slow wave).' (From Hillyard and Kutas (1983): Fig. 1, p. 35. Reproduced with permission from the *Annual Review of Psychology*, Volume 34, © 1983 by Annual Reviews.)

a direct estimate of the ERP elicited by individual events. For this reason, the resulting average ERP cannot be compared directly with other measures, such as reaction time, that can be derived from individual experimental trials. Furthermore, the average waveform may not, in fact, resemble the actual waveform that is recorded on an individual trial. For example, if the amplitude of a particular waveform feature on individual trials has a bimodal distribution, then the average amplitude will not correspond to the actual amplitude of any individual trial. Similar problems will occur if the latency of a particular waveform feature has a bimodal distribution. If this kind of situation obtains, then it is difficult to interpret an amplitude difference between two average waveforms. Such a difference could be due to a difference in latency variability or to a difference in the proportion of trials in the two modes of a bimodal amplitude distribution, rather than to a real change in amplitude on individual trials.

Because of these problems with signal averaging, there have been many attempts to devise other signal extraction procedures that can provide an estimate of the ERP for each event of interest. The most primitive of these involves the use of analogue or digital filters which attenuate frequencies in the EEG that are either higher or lower than those contained in the ERP signal of interest. More complex filters involve cross-correlation procedures that effectively search the epoch on each trial for regions of maximal correspondence with a predefined template. Thus, if one expects an epoch to contain an ERP of a particular kind (that is, a waveform with a characteristic shape), one can determine the portion of the epoch that corresponds best to this template (Glaser and Ruchkin 1976; Woody 1967). The template can be established on a priori grounds, or it can be derived empirically using a technique such as stepwise discriminant function analysis (Squires and Donchin 1976). The template might also take account of the expected distribution of the ERP across the scalp, in which case the filter responds to activity that has a particular topography (Gratton *et al.* 1989). While these techniques for generating measures of the ERP on individual trials show some promise, this promise has as yet only been realized for the largest ERP deflections.

1.3 ERP COMPONENTS AND THEIR MEASUREMENT

Probably no other issue in the methodology of ERP research has aroused more controversy than the question of 'what is an ERP component?'. On the face of it, an answer to the question would seem to be relatively straightforward. After extracting the signal using one of the procedures described in the previous section, one needs merely to focus on some feature of the resulting waveform (for example, a peak or trough), and this feature then becomes the component of interest. In this case, measurement of the feature can be accomplished in a relatively simple fashion merely by determining its amplitude (in μV) and latency (in ms). Amplitude can be measured in relation to some other feature of the waveform (in which case it is referred to as a 'peak-to-peak' measure) or in relation to a baseline (usually

defined as the mean voltage level for some period preceding the stimulus or event). Latency can then be measured in terms of the temporal relationship between the feature of the waveform and the stimulus or event of interest. Unfortunately, in at least some circumstances, there are problems with this simple approach to component definition and measurement, and in the next section we shall review these problems and attempts to solve them (see also Donchin *et al.* 1978; Picton and Stuss 1980; Rugg *in press*).

1.3.1 Defining and extracting ERP components

The greatest impediment to the simple approach mentioned above is 'component overlap'. Component overlap refers to the fact that the waveform we observe by measuring the voltage at the scalp results from the summation of electrical activity that may be generated by several different sources in the brain. As we noted earlier, the brain is a conducting medium. Thus, activity generated in one spatial location may be propagated through the brain tissue and be detectable at other locations. The single voltage we measure at a particular electrode at a particular time may well be attributable to the activity of a variety of different generators in different spatial locations.

One consequence of volume conduction is that there need be no direct correspondence between the timing of the distinctive features of an ERP waveform (that is, its peaks and troughs) and the temporal characteristics of the neural systems whose activity is reflected by the waveform. For example, an ERP peak with a latency of 200 ms, might reflect the activity not of a single neural generator maximally active at that time, but the combined activity of two (or more) generators, maximally active before and after 200 ms, but with fields that summate to a maximum at that time. The ambiguity surrounding the interpretation of peaks and troughs in ERP waveforms has led to the proposal that these features should be described by the theoretically neutral term 'deflection', the term 'component' being reserved for features of the waveform that can be attributed to the activity of specific neuronal populations (Näätänen and Picton 1987).

For researches such as Näätänen and Picton (1987), who adopt what might be called the 'physiological' approach to component definition, a defining characteristic of an ERP component is its anatomical source within the brain. According to this view, then, to measure a particular ERP component, we must have a method of making the contributing sources unambiguous. For other ERP researchers (e.g. Donchin 1979, 1981), who adopt what might be called the 'functional' approach to ERP definition, an ERP component is defined more in terms of the information processing operation with which it is correlated. Thus, components are defined in terms of the cognitive function thought to be performed by the brain systems whose activity is recorded at the scalp. The 'cognitive function' is specified by the nature of independent variables whose manipulation effects the component, and by the relationships observed between the component and other measures (e.g. overt behavioral measures like response speed and accuracy). According to this view, it is entirely possible for a component to be identified with a particular

feature of the waveform that reflects the activity of multiple generators within the brain, so long as these generators constitute a functionally homogeneous system.

Although it is easy to describe physiological and psychological approaches to component definition as if they are mutually exclusive, it should be noted that for many investigators both approaches play a role. For example, in what has become a classic approach to component definition, Donchin *et al.* (1978) argued that a component should be defined by a combination of its polarity, its characteristic latency, its distribution across the scalp, and its sensitivity to characteristic experimental manipulations. Note that polarity and distribution imply a consistency in physiological source, while latency and sensitivity imply a consistency in psychological function.

1.3.1.1 *Physiological approaches to component identification*

Recent years have seen increased interest in attempts to identify the intracranial sources of the electrical activity recorded at the scalp. A variety of different kinds of approaches have been used to inform source questions. These include: intracranial recording in humans (e.g. Halgren *et al.* 1980; McCarthy and Wood 1987), whereby electrical activity recorded from electrodes placed inside the brain is related to scalp activity; the use of PET and other functional neuroimaging techniques, to relate the scalp ERP to localized neural activity detected in analogous tasks (see Compton *et al.* 1991 and Chapter 2); the development of animal models (e.g. Pineda and Swick 1992) that permit one to apply the techniques of neuroscience (e.g. lesions, neurochemistry, and single- and multiple-unit recordings) to the study of neural systems in animals that may correspond to the systems responsible for ERP generation in humans; and studies of neurological cases, that allow one to identify relationships between brain lesions and distortions in scalp electrical activity (see Knight (1991) and Rugg (1992, in press) for reviews of this approach). Data from these different approaches can be used to constrain both the locus and number of sources for a given ERP effect, although the information they provide is somewhat indirect.

There has, however, been steady progress in the development of more direct techniques that allow ERP sources to be inferred directly from scalp fields themselves. Among the most advanced of these techniques is the Brain Electrical Source Analysis procedure (BESA: Scherg 1990). This procedure starts from the assumptions that the ERP waveform represents the summation of the activity of a number of different sources of fixed location within the brain, and that these sources can be appropriately modelled as 'equivalent dipoles'. A BESA 'solution' consists of the specification of these sources in terms of their number, location, orientation, and the time-courses and relative strengths of their activity. Such solutions can be assessed by computing the scalp fields that they would generate, and determining the 'goodness of fit' between these predicted fields and those observed empirically.

An important feature of the BESA procedure is that the location and other

parameters of putative sources can be constrained by the experimenter in the light of, for instance, anatomical knowledge, or of information obtained from a complementary technique such as PET scanning. A second important feature of the BESA procedure is that the contribution made by each source to the ERP can be regarded as an independent ERP component. Hence the technique provides, at least in principle, a means of reducing and describing ERP data in terms of the parameters of a relatively small number of underlying components, each associated with its own putative generator in the brain.

Because of the increasing availability of programs implementing 'source localization' procedures such as BESA, physiological approaches to the decomposition and quantification of ERP waveforms are likely to grow in popularity. Although these procedures undoubtedly provide a useful tool for the reduction and quantification of ERP data, it is as well to remember that such techniques are no panacea for some of the problems afflicting ERP research. First, when used in the hypothesis-generating mode, they do not solve the 'inverse problem'—that is, they do not provide a unique solution to account for the distribution of the scalp activity on the basis of the activity of a number of intracranial sources. Indeed, it is quite possible using, say, the BESA procedure to come up with more than one plausible, well-fitting configuration of sources for the same ERP data set. Second, the techniques are predicated on the assumption that it is physiologically meaningful to characterize ERP generators mathematically as 'equivalent dipoles'; ideal generators that, from a distance, behave as if they give rise to a classic dipolar electromagnetic field. While the approximation of active neural tissue to a single equivalent dipole is appropriate when the area of tissue is relatively small, this may not be so for larger areas. Note especially that, for mathematical reasons, the locus of the equivalent dipole for a large volume of active neural tissue (with a large number of neurons with parallel processes) will appear to be deeper within the brain than the neural tissue which it represents.

1.3.1.2 Psychological approaches to component identification

From a psychological perspective, the principal problem when decomposing ERP waveforms is posed by the need to select a specific feature of the waveform that is related to a specific psychological process. If one adopts any but the most simple view of the information processing system, then one would expect that different processing operations are likely to be occurring in parallel, and therefore that any particular 'surface' feature of the waveform, like a peak or trough, could reflect more than one process.

When conceptualized in this way, it can be seen that the one obvious approach to the problem of component overlap is to subtract waveforms obtained in different experimental conditions to 'isolate' the component whose presence differentiates between the conditions. Whatever is different between the two waveforms is the component of interest, and this component is then identified with whatever cognitive process is believed to differ between the conditions. Many different components have been identified in this way including the Nd or Processing

Negativity (see Hillyard and Hansen (1986); Näätänen (1992); and see Chapter 3), the Mismatch Negativity (see Näätänen 1992; and Chapter 3), and the Dm (see Paller *et al.* 1987; and see Chapter 5). Furthermore, this approach has also been adopted in PET studies to isolate patterns of brain metabolism that are associated with specific cognitive operations and processes (see Chapter 2).

To readers who are cognitive psychologists, this 'subtractive' approach will be reminiscent of the Donderian approach to the measurement of stage durations (e.g. Donders 1868/1969; and see Chapter 4). Of course, the assumptions that underlie this approach, particularly that of 'pure insertion', are also applicable to the subtraction procedure when applied to ERPs. In the ERP context, 'pure insertion' refers to the assumption that one can create two conditions such that the conditions differ only in the process of interest and are equivalent with respect to all other processes. It would clearly be inadvisable to use the subtraction procedure to extract components if the 'pure insertion' assumption cannot be demonstrably supported.

An additional problem for the use of the subtraction procedure in ERP research is that any difference in the latency of the same component in the two conditions will produce a deflection in the subtraction waveforms. This would suggest that there is a component when, in fact, the waveforms differ only with respect to the latency of the same component.

Other attempts to develop methods for component extraction have tried to exploit patterns of covariation in ERP data sets. The most popular such method is Principal Components Analysis (or PCA; see Donchin and Heffley (1978) for a thorough description of the procedure as applied to ERP data). The purpose of PCA is to identify common sources of variance in a set of data. For the ERP researcher, these data comprise values representing variation in the voltage over time during the recording epoch, variation in voltage across different electrode locations, and variation in voltage across different experimental manipulations. As we have noted, variation in ERP voltage across the scalp is attributed to the locus of the source(s) of the ERP in the brain, while variation in voltage as a function of experimental manipulation is attributed to variation in the psychological processes that are engaged in a situation. The purpose of PCA in this context is to identify aspects of the waveform that show covariation over both experimental conditions and scalp locations. Thus, PCA can be regarded as a hybrid approach that embodies features of both physiological and psychological approaches to component definition.

When PCA is applied to a set of ERP data, it yields a set of 'components', each of which is characterized by a vector of weights, one weight for each time-point in the waveform. These weights can be thought of as a linear filter that 'enhances' the waveform at some time-points and some scalp locations, while attenuating the waveform at other time-points and locations. When the values for a particular waveform are multiplied by the weights, and the resulting values are summed (to yield 'factor scores'), we have a measure of the degree to which the component is present in that waveform. These factor scores are then used as 'amplitude' measures of the component.

It is important to note that PCA is a procedure that merely identifies patterns of covariance in a set of waveforms. These patterns of covariance or components still need to be interpreted by the researcher. This is usually accomplished with reference to the polarity, latency, and distribution of the component, as well as to its sensitivity to experimental manipulations (Donchin *et al.* 1978).

From around the mid 1970s to mid 1980s PCA was perhaps the single most popular analytical method in cognitive ERP research. Since that time the technique has become less popular, at least in part because of two problems that limit its application. First, as with the subtraction procedure described earlier, PCA may yield spurious components if the latency of a component varies with experimental conditions. Second, a simulation study by Wood and McCarthy (1984) suggested that, when applied to ERP-like data, the PCA procedure tends to 'misallocate' variance between extracted components. Some of the variance that should have been attributed to one component (given the way the simulated data set was constructed) became associated with a second, supposedly orthogonal component. In the light of these findings, it would be unwise at present to use PCA as the sole means of component identification or quantification. Further work is required to determine the pervasiveness of the misallocation problem using a wider range of data sets, both simulated and real.

1.3.1.3. *Summary*

In this section we have considered two central issues in ERP methodology, the identification and the extraction of components. Whether a component is defined in terms of the brain system that generates it, or the psychological process it manifests, the problem of component overlap must be confronted. Particular brain systems and particular cognitive processes are unlikely to be activated in isolation, and we therefore need procedures that will allow us to make unambiguous (to 'disambiguate') the components whose activity contributes to the observed waveform. We have reviewed techniques that approach the problem from either the physiological or the psychological domain or both, and it is evident that the ultimate solution has not been reached. A promising approach would be to devise a technique that, like PCA, can incorporate both physiological and psychological definitions. However, unlike PCA, the technique would have to be able to handle the problems of latency variability and misallocation of variance. Although this perfect solution is not yet a reality, it is nevertheless the case that considerable progress has been made, and, in the next section, we review the more common of the ERP components that have been identified so far using the 'less-than-perfect' techniques currently available.

1.3.2 A compendium of ERP components

In this section we provide a brief review of some of the more commonly recorded components. The review provides some historical perspective. In most cases we reproduce the waveforms that were provided in the papers that contained the

initial reports of the components and we provide a brief narrative description of the paradigms. Following other reviews of this kind (for example, see Donchin *et al.* 1978), we find it convenient to categorize ERP components in terms of those that precede and those that follow events, whose occurrence can be defined in relation to external criteria, like the time of presentation of a particular stimulus or the time at which an overt behavioural response is executed. The need for an external criterion is occasioned by the fact that we must decide where in the ongoing EEG we should look for our ERPs. As we noted earlier, the ERPs are small in relation to the background EEG signal and we must therefore use averaging or some other technique to extract the ERP signal from the EEG noise. These signal extraction techniques require that the search for the ERP is confined to a particular epoch that is defined with reference to an external criterion. In the case of the event-preceding components, this means that one looks backward in time from the external criterion for the ERP that precedes the event in question. Of course, this should not imply that we believe in backward causation — rather, we just have no way of knowing when the antecedent causal event occurred. (For a discussion of this issue in the context of movement-related potentials, see Libet (1985) and associated commentary.)

1.3.2.1 Event-preceding components

Readiness potential (bereitschaftspotential) This component was first identified by Kornhuber and Deeke (1965) in their studies of voluntary movements. As can be seen in Fig. 1.3, there is a slow, ramp-like negative shift that precedes the actual production of a voluntary hand movement by as much as 1000 ms. The negativity is maximal at precentral electrode sites, and it peaks (about 10–15 μV) at about the time of overt movement. In Fig. 1.3 we see that, as the time of the impending

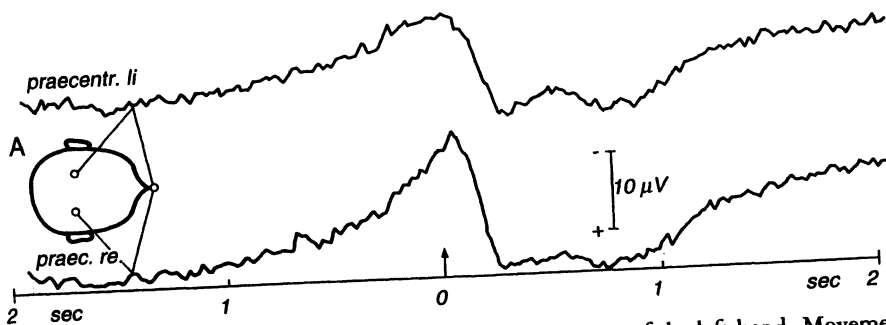


Fig. 1.3 'Brain potential changes during voluntary movement of the left hand. Movement onset . . . indicated by the arrow. Negative potential during preparation, positive potential after movement with larger amplitude over the contralateral (right) brain hemisphere. Unipolar derivation with the precentral regions referenced against the nose. Average of 512 movements. Negative is up. Left of 0 = time before movement onset in the electromyogram. Vp. G. F.' (From Kornhuber and Deeke (1965): Fig. 1, panel A, p. 4. Copyright © 1965 Springer-Verlag, reprinted by permission. Figure legend translated by Amy Adamson.)

movement approaches, the negativity becomes larger over the right scalp site, contralateral to the left-hand movement. Vaughan and his colleagues (for example Vaughan *et al.* 1968), who independently observed the same component, showed that this lateralized effect was evident for arm, hand, and finger movements. In fact, the precise scalp distribution of this component, has been linked to the somatotopic arrangement of motor cortex. This component, especially its lateralized aspect (referred to as the Lateralized Readiness Potentials LRP), has been related to motor preparation (see Coles 1989; and Chapter 4).

The Contingent Negative Variation (CNV) The CNV was first observed by Walter and his colleagues (Walter *et al.* 1964). Their paradigm involved the presentation of pairs of stimuli, separated by a time interval, and the establishment of a contingency between the stimuli. In the original experiments, the first stimulus was a click, the second, a flickering light, and the subject was required to make a button-press response to the light. The interval between click and flicker was one sec. As can be seen in Fig. 1.4 (panel D), during the interval between click and flicker, a slow negative wave occurs. The wave can be as large as 20 μV , and it is maximal over fronto-central regions. It has a ramp-like shape and tends to reach its maximum negativity at around the time of the second stimulus. This is the CNV. As can be seen by comparing panel D with the other panels in Fig. 1.4, the CNV is not evident when the click or light were presented alone or when they were paired without the response requirement. The CNV was originally described as an 'expectancy' wave, although more recently it has been linked to motoric and non-motoric preparatory processes (see O-wave and E-wave below).

The O-wave and the E-wave Several years after the discovery of the CNV, Loveless and Sanford (1974) conducted an experiment that suggested that the CNV was actually composed of at least two components. These two components 'emerged' when the interval between the two stimuli was extended beyond the 1 s originally used by Walter and his colleagues (Walter *et al.* 1964). As can be seen in Fig. 1.5, at intervals of 6 and 15 s there is evidently an initial negative-going response following the first stimulus and a later negative shift that precedes the second stimulus. Loveless and Sanford labelled the early response the 'O-wave', indicating their belief that the response was a sign of orienting, while they labelled the later wave the 'E-wave'. Loveless and Sanford noted the similarity between the E-wave and the readiness potential described by Kornhuber and Deeke. Indeed, some investigators have claimed that the E-wave is the readiness potential and that the requirement that the subject respond to the second stimulus is critical for the E-wave to occur. Others have argued for the existence of non-motoric E-waves that are associated with preparation for the processing of sensory information or performance feedback. For a discussion of these issues, see, for example, Brunia (1993), Harter and Anllo-Vento (1991), Rohrbaugh and Gaillard (1983), or Simons (1988).

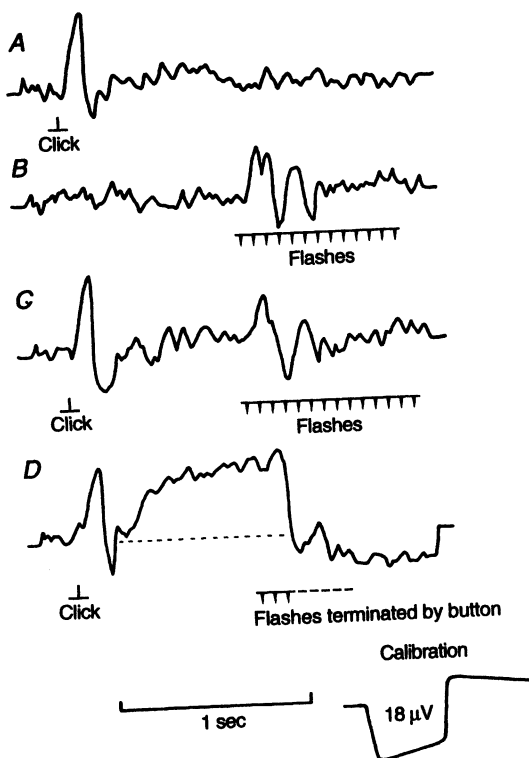


Fig. 1.4 'Averages of responses to 12 presentations. A, response in fronto-vertical region to clicks; B, flicker; C, clicks followed by flicker; D, clicks followed by flicker terminated by the subject pressing a button as instructed. The contingent negative variation (CNV) appears following the conditional response and submerges the negative component of the imperative response.' (From Walter *et al.* (1964): Fig. 1, p. 381. Reprinted with permission of *Nature*. Copyright © 1964 Macmillan Magazine Ltd.)

1.3.2.2 Event-following components

For the sake of classification, it has proved useful to distinguish between two classes of components that follow events. On the one hand there are a set of components whose characteristics (amplitude, latency, and distribution) seem to depend on the physical properties of sensory stimuli, such as their modality and intensity. These are *exogenous* components. It has been claimed that their characteristics are immune to variations in the subject's state and to the nature of the interaction between the subject and the stimulus—that is, that they are not influenced by 'cognitive' manipulations. On the other hand there is another set of components whose characteristics (and indeed whose very existence) depends on the nature of the subject's interaction with the stimulus. These components vary as a function of such factors as attention, task relevance, and the nature of

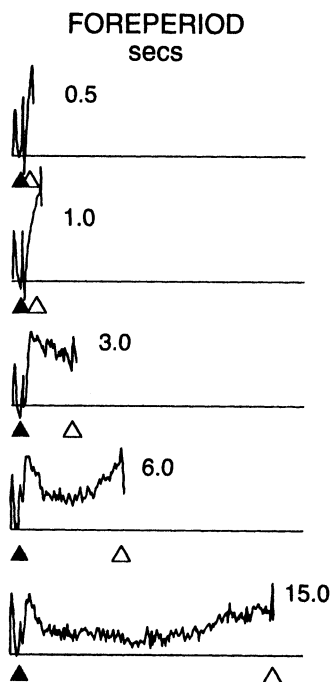


Fig. 1.5 'CNVs . . . at each of five intervals (0.5, 1.0, 3.0, 6.0, and 15.0 sec.) between warning signal (▲) and imperative signal (△) in a regular series. Each plot has been terminated after the major peak of the evoked response to the imperative signal. The baseline is the average level of the EEG during a period of 1 sec. preceding the warning signal. A calibration pulse of $-20 \mu\text{V}$ is shown at the beginning of each plot.' (From Loveless and Sanford (1974): Fig. 4, panel (a), p. 58. Copyright © 1974. Elsevier Science Publishers, reprinted by permission.)

the processing required by the stimulus, and some can be elicited even in the absence of an external event, as, for example, when an expected stimulus does not occur (e.g. Sutton *et al.* 1967). These are the *endogenous* components.

Like most dichotomies, the endogenous–exogenous distinction has proved to be an oversimplification of the real state of affairs. Almost all the early 'sensory' components have been shown to be modifiable by cognitive manipulations (e.g. attention) and many of the later 'cognitive' components have been shown to be influenced by the physical attributes of the eliciting conditions (e.g. modality of the stimulus). For this reason it appears to be more accurate to conceive of an exogenous–endogenous *dimension* that is roughly coextensive with time. Thus, those ERP components that occur within the first 100 ms of stimulus presentation tend to be more exogenous, while those occurring later tend to be more endogenous. In the following review, components are discussed in approximate order of their latencies and, thus, in order of increasing sensitivity to cognitive factors.

Sensory components Sensory stimuli in all modalities are associated with a series of deflections in the ERP that are related to the transmission of sensory information from the peripheral sensory system to the cortex and/or the arrival of that information in the cortex. For some modalities the latencies of the earliest of these deflections are extremely short (a few milliseconds) and, in this case, the deflections undoubtedly reflect the transmission of sensory information in the sensory pathways. For example, for auditory stimuli one can detect the so-called 'brainstem' responses that have a latency of less than 10 ms and, as their name implies, these deflections correspond to the activation of various nuclei in the brainstem that are associated with the transmission of auditory information. Later deflections (with latencies up to 100 ms) correspond to the arrival of this information in various regions of the cortex. A similar situation obtains with somatosensory stimuli. However, for visual stimuli only the later deflections seem to be evident, presumably because the neurons in the sensory relay nuclei (e.g. the lateral geniculate nucleus) are configured such that they constitute closed fields, and thus their activity is not observable at the scalp. Although, for all modalities, many of these sensory components are modifiable by, for example, attentional manipulations, the components are also 'obligatory' in the sense that they will be observed in every individual and on every occasion unless the sensory systems in question are compromised in some way.

Nd/processing negativity While the sensory components reviewed in the previous section are obligatory, the 'Nd' (or negative difference wave; see Hillyard and Hansen (1986) and Chapter 3) and the 'processing negativity' (Näätänen *et al.* 1978) provide a classic example of the optional, endogenous or more cognitive nature of some ERP components. The Nd and processing negativity are descriptors of the same component, although the claims about the functional significance of the component are somewhat different. 'Nd' emphasizes the polarity and operation used to identify the component, the Nd being isolated by taking the difference between two ERP waveforms that are elicited in response to the same physical stimulus. The critical comparison is between ERPs for the same stimulus when it is attended versus when it is unattended. 'Processing negativity' emphasizes the fact that the component is related to some form of extra processing accorded to attended events on the basis of a preceding selection process.

The typical paradigm involves the presentation of streams of stimuli at fast presentation rates, with the stimuli varying as a function of one or more critical attributes. For example, in the classic experiment by Hillyard and his colleagues (Hillyard *et al.* 1973), subjects heard a sequence of tone pips of 800 Hz in the left ear and a sequence of 1500 Hz tone pips in the right ear, in both cases with interstimulus intervals of between 250 and 1250 ms. About one-tenth of the tone pips in each ear were of a slightly higher frequency (840 Hz and 1560 Hz), and the subjects' task was to attend to one ear and count the number of these target higher-frequency tones. In some conditions, they attended to the right ear and in others to the left ear. In experiment 1, the two tone pip sequences were independent, while in experiment 2, a single sequence was used, with an interstimulus interval

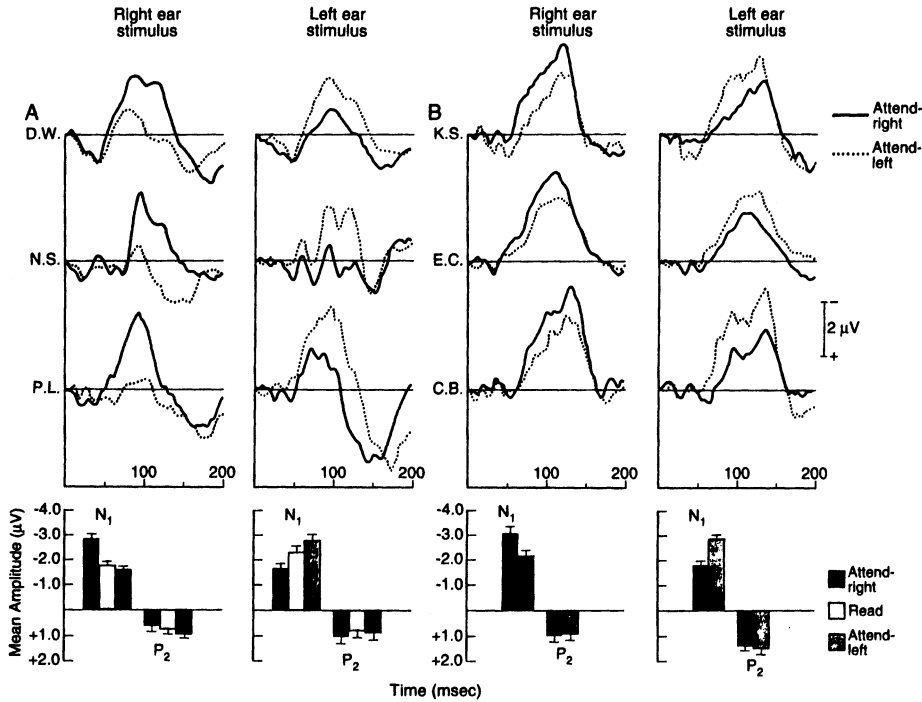


Fig. 1.6 (a) Vertex evoked potentials from three subjects in experiment 1. Each tracing is the averaged response to all 1024 stimuli that were presented to each ear under attend-right (solid lines) and attend-left (dotted lines) conditions. Stimulus onset is at beginning of tracing. Baselines were drawn through the mean voltage over 0 to 10 ms. Bar graphs give the mean and standard error (10 subjects) of the baseline to peak amplitudes of N_1 and P_2 evoked via each ear under all three experimental conditions. (b) Evoked potentials from three subjects in experiment 2, with bar graphs giving mean amplitudes from all ten subjects.' (From Hillyard *et al.* (1973): Fig. 1, p. 178. *Science*, Volume 182. Copyright © by the AAAS, reprinted by permission.)

of between 100 and 800 ms and each tone being delivered to either right or left ear. The critical comparison (shown in Fig. 1.6) is between the ERPs for attended and unattended stimuli presented in a particular ear. As can be seen in the figure, the attended ERPs were more negative than the unattended ERPs, and this difference was maximal at around 100 ms after stimulus presentation. Hillyard and his colleagues concluded that the effect of attention was to modulate the amplitude of the N_1 component, reflecting the fact that, when unattended, sensory input was excluded from further processing. This view can be contrasted with that of Näätänen and his colleagues (e.g. Näätänen *et al.*, 1978), who have argued that the effect of attention is to add a negative shift to the unattended ERP, a shift that is not specifically time-locked to the N_1 component. They have claimed that this negative shift was associated with the processing of the target stimulus dimension. Although variations in the paradigms used by Hillyard and

by Näätänen, with respect to the interstimulus interval, e.g., may be responsible in part for the differences in interpretation of 'the attention effect', disagreements still persist. These are considered in Chapter 3 and in Näätänen's recent synthesis (Näätänen 1992).

Mismatch negativity and the N2 At about 200 ms following the presentation of some classes of visual and auditory events, a negative component is evident in the ERP waveform. This negative component is referred to as the N200 or N2, although, as several investigators have argued, there may in fact be several different components that are present in the waveform at this time (see Pritchard *et al.* 1991 for a review). The critical condition for the elicitation of this component is that the event must deviate in some way from the prevailing context.

As with the P300 (see below), the typical paradigm involves the presentation of a series of events, with each event belonging to one or other of two or more classes. One class of events is improbable, and the presentation of these rare events elicits the N200. In a classic set of studies by Näätänen and his colleagues (Näätänen *et al.* 1978), probable and improbable events were distinguished first by their intensity (Experiment 1: 1000 Hz tone pips of either 70 or 80 dB) and then by their frequency (Experiment 2: 70 dB tone pips of either 1000 or 1140 Hz). As in the selective attention experiment described in the previous section, the tone pips could occur in either ear and, in different conditions, the subject was instructed to attend to one of the two ears and count the number of rare stimuli presented in the attended ear. To observe the mismatch negativity it is customary to subtract the ERP for the probable events (standards) from the ERP for the improbable events (signals). Of course, this can be done separately for events presented in the attended and in the unattended ear. Figure 1.7 shows the difference waveforms obtained by Näätänen and his colleagues (1978). As can be seen in this figure, the difference waveforms reveal a negativity that peaks at about 200 ms for both left- and right-ear stimuli. Importantly, this negativity is present for both Experiments 1 and 2 (that is for both intensity and pitch deviance) and for both attended and unattended conditions. In the attended condition, the negativity is followed by a positivity (the P300) which we shall discuss in the next section.

The fact that this mismatch negativity (also referred to as the N2a) is present even when the stimuli are unattended, led Näätänen and his colleagues to suggest that it reflects the automatic detection of physical deviance. Indeed, the mismatch negativity appears to be critically dependent on physical deviance of the current stimulus from the prevailing context, and several studies have illustrated that its amplitude is sensitive to the degree of deviance. However, the idea that the component reflects purely automatic processes has been challenged recently by Woldorff *et al.* (1991), who showed that its amplitude may be influenced by attention. Again, this is a controversial area and the interested reader should consult Chapter 3 for further information. Note that the mismatch negativity should not be confused with the second N200 component (the N2b), whose presence depends on the events being task relevant. In many circumstances, this component appears to covary with a later positive component, the P300, or P3b.

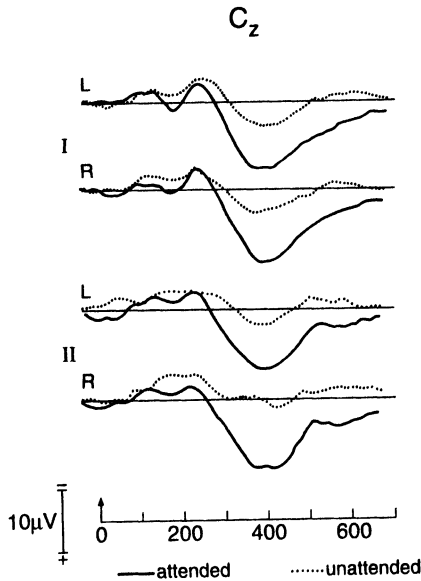


Fig. 1.7 'The difference between EPs to signals and standards (averaged across Ss) . . . for the left (L) and right (R) ear when attended and when unattended. These differences were obtained by subtracting the corresponding time points of the EP to standards from the EP to signals. I refs to Experiment 1, II to Experiment 2.' (From Näätänen *et al.* (1978): Fig. 4, left panel (C_z electrode). Copyright © 1978 Elsevier Science Publishers, reprinted with permission.)

P300, P3, P3a, and P3b Probably no other component has received as much attention as the P300 and related positive deflections. This is partly because of its size (5–20 μV) and because of the ease with which it can be elicited. In the classic original experiment by Sutton and his colleagues (Sutton *et al.* 1965), subjects were presented with a series of pairs of stimuli, a cueing stimulus and a test stimulus. The test stimuli could be clicks or light flashes. For some pairs, the cueing stimulus was always followed by the same test stimulus and the subject could thus be certain about the sensory quality of the stimulus before it occurred. For other pairs, the cueing stimulus could be followed by either visual or auditory test stimuli. After the presentation of each cueing stimulus, the subject had to guess the modality of the forthcoming test stimulus. The critical comparison concerned the ERPs following test stimuli in certain and uncertain conditions. As can be seen in Fig. 1.8, these ERPs differ in a number of ways. However, the most salient differentiating characteristic is the positivity that peaks at around 300 ms. This is the P300 or P3b.

In subsequent research, the standard paradigm evolved to one in which a series of events are presented to the subject, and the events comprise two classes. One class is generally rarer than the other—hence the name 'oddball task'—and the subject is required to respond in some way to the rarer of the two events. The

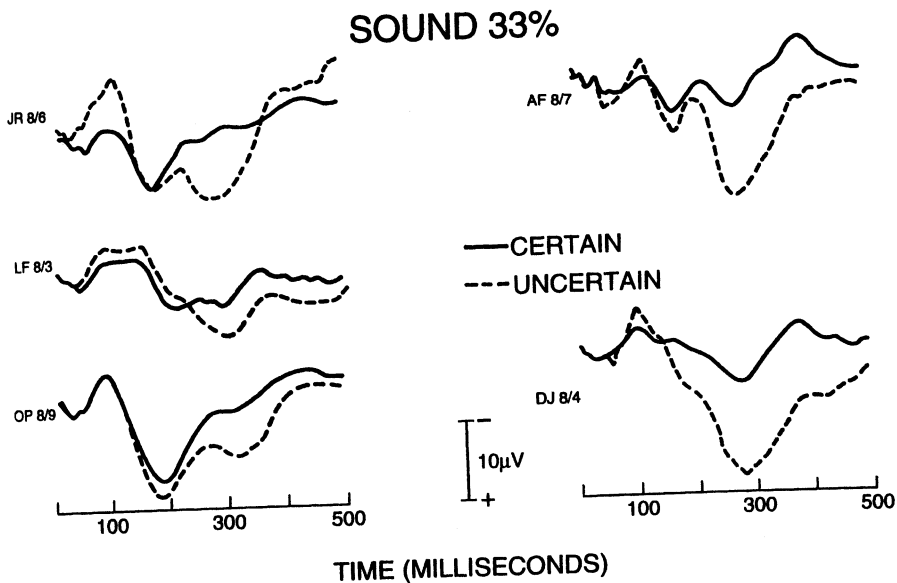


Fig. 1.8 'Average waveforms for certain and uncertain ($P=.33$) sounds for five subjects.' (From Sutton *et al.* (1965): Fig. 1, p. 1187. *Science*, Volume 150. Copyright © 1965 by the AAAS, reprinted by permission.)

ERP component consists of positive deflection, that is maximal over the parietal/central area, that has a latency of at least 300 ms and as much as 900 ms. This latency variability is controlled by the ease with which an event can be categorized as belonging to one of the two classes, the more difficult the categorization, the longer the latency. For this reason, it has been argued that the latency of the P300 can be used as a measure of 'stimulus evaluation time' (e.g. see Donchin and Coles 1988*a,b*, and Chapter 4 for a review). In tasks with a simple 'oddball' structure, the amplitude of the component depends on probability; the rarer the event, the larger the P300. It also depends on the amount of information extracted from the event. These and other considerations have given rise to the proposal that the P300 reflects a process of context or memory updating by which the current model of the environment is modified as a function of incoming information (e.g. see Donchin and Coles 1988*a,b*, and Chapter 4 for a review). Several investigators (e.g. Johnson 1986) have pointed out that the P300 does not appear to be a unitary component and, instead, may represent the activity of a widely distributed system whose constituent parts may be more or less coupled depending on the situation. More precise knowledge of the functional significance of this component or complex of components will have to wait until more information is available about the neural systems involved.

One part of this complex that has been distinguished is the so-called P3a. If a third 'novel' event is introduced into the oddball task, a positive component,

different from the classical P300, can be observed. Novelty is defined in the context of the other two events: e.g., a 'dog-bark' in the context of high and low tones. Such novel stimuli elicit a large positivity with a latency that is earlier than that of the target-evoked P300, and a scalp distribution that is more oriented towards the front of the scalp (e.g. see Knight *et al.*, 1989). This component is sometimes referred to as the 'frontal P3' or the 'P3a' to distinguish it from the classic, parietally distributed P300 described in the previous paragraph. The classic P300 is then referred to as the 'P3b' or 'parietal P3'. It is apparent that the P3a and P3b are dependent on the integrity of different brain regions, since Knight and his colleagues have shown that P3a (but not P3b) is influenced by lesions of the frontal cortex. The P3a has been linked to processes involved in the involuntary capture of attention by salient events (Knight 1991).

N400 While the N200 family of components are elicited in response to events that are physically deviant from the prevailing context, the N400 component is sensitive to deviance in relation to much more abstract attributes of the eliciting stimulus, such as meaning. The component was first observed by Kutas and Hillyard (1980) in their classic studies of sentence processing. Subjects were required to read sentences comprised of about seven words, with each word being presented individually at 1 s intervals. In some sentences, the final word was semantically inappropriate but syntactically correct, while in other sentences the final word was larger in letter size than the preceding words. Of course, there were also normal sentences that ended with normal sized, semantically appropriate words. As can be seen in Fig. 1.9, semantically deviant final words elicited a negative deflection with a latency of about 400 ms (the N400), while physically deviant words (in larger type) were associated with the classic P300 (with a latency of 560 ms).

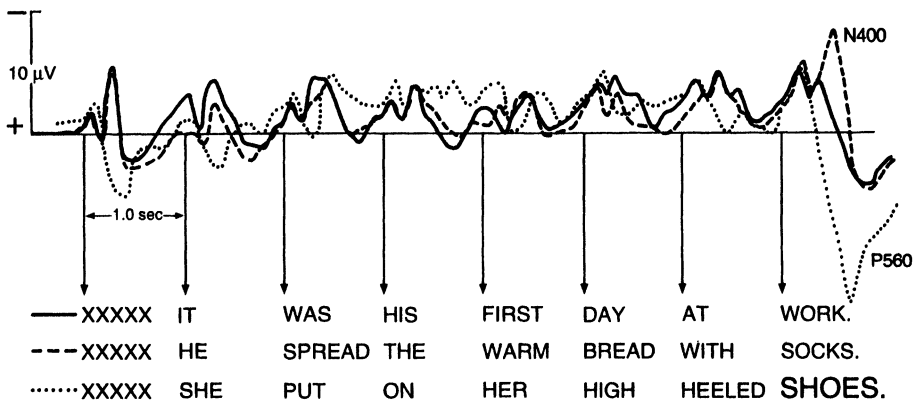


Fig. 1.9 'The timing of word presentations for three sample sentences and typical ERP waveforms recorded over the entire seven-word sentence, averaged over three subjects (in experiment 2 (dashed and solid lines) and three subjects in experiment 3 (dotted line).' (From Kutas and Hillyard (1980): Fig. 1, panel (A), p. 203. *Science*, Volume 207. Copyright © 1980 by the AAAS, reprinted by permission.)

Neither component was evident when the sentence terminated with a word that was both semantically and physically congruous with the preceding words.

Subsequent work has shown that the amplitude of the component is an inverse function of the semantic relatedness between a word and its sentence context, and that it can be elicited in semantic priming paradigms. Furthermore, large N400s are observed in response to isolated words (words with no context), when such words are processed to the level of their identity. Thus, the N400 appears to be a 'default' component, evoked by words whose meaning is unrelated to, or not predicted by, the prior context of the words. The effect of priming, whether contextual or semantic, is to attenuate the component. The dependence of the N400 on semantic relatedness has made it an important tool for the study of on-line semantic processing in written and spoken language (see Chapter 6). However, the N400 is also sensitive to a wide range of non-semantic relationships between words such as phonological or orthographic relatedness (e.g. Rugg and Barrett 1987). N400-like components have also been observed in response to non-verbal stimuli, such as pictures (Barrett and Rugg 1990). Current theories of the functional significance of N400 are discussed in Chapters 5 and 6.

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